TESIS DOCTORAL

Minerva García Carmona

Role of biological soil crust and soil microbial communities in the recovery of burned soils exposed to post-fire management

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El papel de las costras biológicas y comunidades microbianas edáficas en la recuperación de suelos quemados sometidos a manejos post-incendio

Programa de Doctorado en Medio Ambiente y Sostenibilidad
Universidad Miguel Hernández de Elche
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La presente Tesis Doctoral, titulada "Role of biological soil crust and soil microbial communities in the recovery of burned soils exposed to post-fire management", se presenta bajo la modalidad de tesis por compendio de las siguientes publicaciones:

Chapter 3

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. Applied Soil Ecology, 168, 104130. doi:10.1016/J.APSOIL.2021.104130

Chapter 4

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. Journal of environmental management, 262, 110287. doi:10.1016/j.jenvman.2020.110287

Chapter 5

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. Science of the Total Environment, 846, 157467. doi:10.1016/J.SCITOTENV.2022.157467

Chapter 7

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La presente Tesis Doctoral, titulada "Role of biological soil crust and soil microbial communities in the recovery of burned soils exposed to post-fire management", incluye el siguiente trabajo:

Chapter 6

García-Carmona, M., Lepinay, C., Mataix-Solera, J., Baldrian, P., Arcenegui, V., Cajthaml, T., & García-Orenes, F. Post-fire wood mulch modulates the biocrust-forming mosses response and the soil fungal community composition (*submitted to Applied Soil Ecology).*

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El Dr. Jorge Mataix Solera, Catedrático de la Universidad Miguel Hernández de Elche, y Dra. Fuensanta García Orenes, Catedrática de la Universidad Miguel Hernández de Elche

INFORMAN:

Que Dña. Minerva García Carmona ha realizado bajo nuestra supervisión el trabajo titulado "Role of biological soil crust and soil microbial communities in the recovery of burned soils exposed to post-fire management" conforme a los términos y condiciones definidos en su Plan de Investigación y de acuerdo al Código de Buenas Prácticas de la Universidad Miguel Hernández de Elche, cumpliendo los objetivos previstos de forma satisfactoria para su defensa pública como tesis doctoral.

Lo que firmamos para los efectos oportunos, en Elche a 19 de diciembre de 2022.

Director de la tesis	Codirectora de la tesis
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El Dr. José Navarro Pedreño, Coordinador del Programa de Doctorado Medio Ambiente y Sostenibilidad de la Universidad Miguel Hernández de Elche

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A mi familia.

CONTENT

SUMMARY

Post-fire management is a critical step for ecosystem recovery, in combination with other factors such as fire history, ash properties, topography, post-fire weather conditions, or vegetation recovery. Although Mediterranean ecosystems are adapted to fire disturbances, soils are prone to degradation, thus, the forest management can either reduce soil degradation or add a new disturbance. Post-fire management in Mediterranean burnt forests includes interventions with contrasting approaches, including the management of burnt trees, the promotion of soil protection, or practices devoted to ecosystem restoration via the improvement of components or processes in the affected ecosystem. The consequences of forest management on soils are complex, thereby, in the context of the intensification of fire events and climate change, understanding the response of key soil components in managed ecosystems is critical for prioritizing soil conservation.

One interesting component in the early post-fire stages is moss biocrust. The rapid colonization of biocrust-forming mosses in early successional stages post-disturbance stabilizes soils in their most vulnerable period. However, it is completely unknown further implications as active agents in the recovery and resilience of soils, in the transient stage before vascular vegetation regrowth. In combination with the biocrust, the response of soil microbial communities to forest management is crucial for evaluating the soil recovery progress, given their active role in fundamental ecosystem functions. The additive consequences of fires and forest management on biocrust emergence or microbial composition and functionality are usually neglected in the investigation of post-fire systems, although of major relevance to support strategies to preserve soils against functionality loss.

This dissertation seeks a better understanding of the interactions of above and belowground soil components in order to guide post-fire forest managements toward accelerating recovery and resilience of semi-arid ecosystems prone to degradation. For this purpose, the main objective was to assess the effects of contrasting post-fire managements on soil recovery in fire-affected Mediterranean-type climate forests, by focusing on the effects of those managements on the promotion or disruption of the biocrust-forming mosses and the soil microbial communities, and their relationship with the post-fire environment. Specifically, the thesis aims: i) to determine the effects

on soils of forest management with contrasting approaches in relation to burnt wood extraction (salvage logging) (Chapters 3, 4, 5), soil protection (wood-mulching) (Chapter 6), and restoration practices (organic amendments application) (Chapter 7); ii) to elucidate the relevance of biocrust-forming mosses in the recovery and resilience of soils affected by wildfires and forest management (Chapters 4, 5, 6); and iii) to assess the response of microbial communities to different post-fire management and the presence of the moss biocrust, and to identify the soil properties that become dominant drivers of microbial community compositional shifts (Chapters 3-7).

Our results from chapters 3 and 4 confirm that forest management involving strong interventionism in highly erodible soils generates severe soil degradation with detrimental consequences for ecosystem functioning. Salvage logging performed seven months after the wildfire in vulnerable soils led to strong degradation, delayed the vegetation growth, and altered microbial community composition. In the short-term (22 months after the fire, Chapter 3), the degradation of soil structure, from the combining effects of the wildfire and the mechanical operations, profoundly impacted the soil microbial community and associated functions. Particularly, the loss in soil aggregate stability was the main driver of microbial community shifts, altering the resistance and resilience of soil microbial communities. Logging operations resulted in the creation of new niches related to anoxic habitats following soil compaction and promoting taxa capable of anaerobic respiration, surprisingly exhibiting a transient increase in microbial alpha diversity. On the opposite, the burnt wood maintenance ameliorated stressful soil surface conditions and served as a nutrient resource, promoting the microbial development such as the microbial populations sensitive to substrate availability (e.g., Actinomycetales).

Biocrust-forming mosses demonstrated to have an important role in the recovery of multiple soil functions in post-fire ecosystems. The early colonization of mosses after a wildfire mitigates the soil degradation threat, softening the logging legacies and enhancing the recovery of soil functionality in the short and mid-term (Chapters 4 and 5). However, the developmental stage or age of the moss biocrust is critical for controlling different functions performed in soils. Six years after the wildfire and salvage logging, the well-developed biocrust profoundly influenced soil fertility, critical biochemical processes, and microbial development (Chapter 4). Particularly, biocrust-forming mosses reach great relevance in fire-affected ecosystems thanks to their capacity to enhance soil fertility and nutrient fixation. Moss biocrust, colonizing soils rapidly after the wildfire, effectively stabilizes the soil surface and prevent soil loss by erosion, retaining nutrients and ashes. In addition, biocrust acts as dust trappers, incorporating fine particles into soils. But most importantly, mosses as primary producers fix carbon and nitrogen significantly contributing to nutrient cycling. In contrast to the effects at midterm, biocrust at early post-fire stages showed low impact, or even a slight decrease, on soil nutrients, but a minimal stimulation of critical biochemical processes (Chapter 5). Seven months after the wildfire and subsequent salvage logging, the emergence of moss biocrust was strategic for accelerating the recovery of the soil microbial communities. The biocrust that emerge in the post-fire environments improves the harsh conditions on the surface (e.g., desiccation, high temperature, and solar radiation), thereby facilitating microbial growth in biomass and diversity and thus accelerating key biochemical processes from nutrient cycling affected in the wildfire. Therefore, biocrust might play a critical role in the resilience of soil microbial communities affected by wildfires, an influence that persists and accentuates over time with biocrust development (Chapter 4).

Intensive salvage logging negatively affected the spreading of biocrust-forming mosses of fire-affected soils in the midterm (Chapter 4), which leads to negative cascade effects on ecosystem functioning given their role as ecosystem engineers. Similarly, the application of burnt wood mulch drastically suppressed biocrust development in one year (Chapter 6), which conflicts with the recovery of soils assisted by mosses (Chapters 4 and 5). The wood mulch had a limited effect on the physicochemical properties; however, an incipient acceleration of biochemical processes was remarkable at the lowest rate of mulch application, assisted by the presence of the biocrust. Nevertheless, microbial diversity was reduced under the mulch wood application as communities became transitorily highly homogeneous. It was particularly revealing the shifts observed in the fungal community, highly responsive to the wood mulch application. Consequently, mulch indiscriminately applied in soils can hamper microbial diversity recovery and, thus, ecosystem functionality in the short term. Therefore, there is a necessity of incorporating microbial diversity information into post-fire management planning to support practices that boost soil biodiversity conservation.

Results from chapter 7 showed contrasting effects in soils in response to the application of different organic amendments characterized by different origins and stability, demonstrating that restoration techniques trigger variable effects depending on the target component or process to strategically restore. All organic amendments improved soil fertility and stimulated soil microbial activity but with contrastable (transient or durable) implications on soils. Fresh amendments promoted immediate microbial growth and activity, but also greater mineralization rates and, thus, presumably shorter periods of carbon source consumption. On the opposite, soils treated with compost accumulated the most organic carbon and nitrogen, ensuring long-term nutrient release and soil fertility. Consequently, the amendment selection will depend on the goals of the soil restoration plan in terms of the immediacy of the soil response.

RESUMEN

El manejo post-incendio es un paso crítico para la recuperación del ecosistema, combinado con otros factores como el histórico de incendios, las propiedades de la ceniza, la topografía, las condiciones meteorológicas posteriores al incendio, o la recuperación de la vegetación. Aunque los ecosistemas mediterráneos están adaptados a las perturbaciones por incendios, los suelos son propensos a la degradación, así que la gestión forestal puede reducir la degradación del suelo o añadir una nueva perturbación. La gestión post-incendio en bosques mediterráneos quemados incluye intervenciones con enfoques contrastados, incluyendo la gestión de la madera quemada, la protección del suelo, o prácticas dedicadas a la restauración de ecosistemas a través de la mejora de componentes o procesos afectados. Las consecuencias de los manejos forestales en los suelos son complejas, por lo que, en un contexto de intensificación de los incendios y cambio climático, comprender la respuesta de componentes clave del suelo en los ecosistemas manejados es fundamental para priorizar la conservación del suelo.

Un componente interesante en los estadios tempranos post-incendio son las biocostras de musgo. La rápida colonización de los musgos formadores de biocostras en etapas tempranas de la sucesión después de perturbaciones estabilizan el suelo en su etapa más vulnerable. Sin embargo, se desconoce por completo más implicaciones de los musgos como agentes activos en la recuperación y resiliencia del suelo, en la etapa transitoria previa a la recuperación de la vegetación vascular. En combinación con la biocostra, la respuesta de las comunidades microbianas del suelo al manejo forestal es crucial para evaluar el progreso de la recuperación del suelo, dado su papel activo en funciones ecosistémicas fundamentales. Las consecuencias aditivas de los incendios y el manejo forestal sobre la aparición de la biocostra, o la composición y funcionalidad microbiana, generalmente se descuidan en la investigación de los ecosistemas post-incendio, aunque son de gran relevancia para respaldar estrategias que preserven los suelos contra la pérdida de funcionalidad.

Esta tesis busca una mejor comprensión de las interacciones de los componentes que están por encima y debajo del suelo con el fin de guiar la gestión forestal posterior a los incendios para acelerar la recuperación y la resiliencia de los ecosistemas semiáridos propensos a la degradación. Para ello, el objetivo principal fue evaluar los efectos de

manejos contrastados sobre la recuperación de suelos en bosques de clima tipo mediterráneo afectados por incendios, centrándose en los efectos de dichos manejos sobre la promoción o disrupción de los musgos formadores de biocostras y las comunidades microbianas del suelo, y su relación con el ambiente post-incendio. Específicamente, la tesis tiene como objetivo: i) determinar los efectos en los suelos del manejo forestal con enfoques contrastados, relacionados con la extracción de madera quemada (tala y saca de madera) (Capítulos 3, 4, 5), la protección del suelo (mulch de madera) (Capítulo 6) y las prácticas de restauración (aplicación de enmiendas orgánicas) (Capítulo 7); ii) dilucidar la relevancia de los musgos formadores de biocostras en la recuperación y resiliencia de los suelos afectados por incendios y manejos forestales (Capítulos 4, 5, 6); y iii) evaluar la respuesta de las comunidades microbianas a diferentes manejos posteriores al incendio y a la presencia de la biocostra de musgo, e identificar las propiedades del suelo que se convierten en impulsores de los cambios en la composición de la comunidad microbiana (Capítulos 3-7).

Los resultados de los capítulos 3 y 4 confirman que el manejo forestal que suponen un fuerte intervencionismo en suelos altamente erosionables genera una severa degradación del suelo con consecuencias perjudiciales para el funcionamiento del ecosistema. La tala y saca de madera realizada siete meses después del incendio forestal en suelos vulnerables provocó una fuerte degradación, retrasó el crecimiento de la vegetación y alteró la composición de la comunidad microbiana. A corto plazo (22 meses después del incendio, Capítulo 3), la degradación de la estructura del suelo, debido a los efectos combinados del incendio forestal y las operaciones mecánicas, impactó profundamente las comunidades microbianas del suelo y sus funciones asociadas. En particular, la pérdida de estabilidad de agregados del suelo fue el principal impulsor de los cambios en la estructura, alterando la resistencia y resiliencia de las comunidades microbianas del suelo. Las operaciones de tala dio como resultado la creación de nuevos nichos relacionados con hábitats anóxicos, debido a la compactación del suelo, y la promoción de taxones capaces de respiración anaeróbica, mostrando de manera sorprendente un aumento transitorio en la alfa diversidad microbiana. Por el contrario, el mantenimiento de la madera quemada mejoró las condiciones estresantes de la superficie del suelo y sirvió como fuente de nutrientes, promoviendo el desarrollo microbiano, como el de las poblaciones microbianas sensibles a la disponibilidad de sustrato (ej., Actinomycetales).

Los musgos formadores de biocostras demostraron tener un papel importante en la recuperación de múltiples funciones del suelo en los ecosistemas post-incendio. La colonización temprana de musgos después de un incendio forestal mitiga la amenaza de degradación del suelo, amortiguando el legado de tala y mejorando la recuperación de la funcionalidad del suelo a corto y medio plazo (Capítulos 4 y 5). Sin embargo, la etapa de desarrollo o edad de la biocostra de musgo es fundamental, ya que controla las diferentes funciones que se proporcionan a los suelos. Seis años después del incendio forestal y la tala y saca de madera, la biocostra bien desarrollada influyó profundamente la fertilidad del suelo, procesos bioquímicos críticos y el desarrollo microbiano (Capítulo 4). En particular, los musgos formadores de biocostras alcanzan una gran relevancia en los ecosistemas afectados por incendios gracias a su capacidad para mejorar la fertilidad del suelo y la fijación de nutrientes. La biocostra de musgo, colonizando el suelo rápidamente después del incendio, estabiliza eficazmente la superficie del suelo y previene la pérdida de suelo por erosión, reteniendo nutrientes y cenizas. Además, la biocostra actúa como captador de polvo incorporando partículas finas al suelo. Pero lo más importante es que los musgos, como productores primarios, fijan carbono y nitrógeno, contribuyendo de forma significativa al ciclo de nutrientes en los suelos. En contraste a los efectos a medio plazo, la biocostra en las primeras etapas posteriores al incendio mostró un impacto bajo, e incluso una ligera disminución en los nutrientes del suelo, pero una ligera estimulación de procesos bioquímicos críticos (Capítulo 5). Siete meses después del incendio y la posterior tala y saca de madera, la aparición de la biocostra fue estratégica para acelerar la recuperación de las comunidades microbianas del suelo. La biocostra emergida en los entornos posteriores al incendio mejora las duras condiciones en superficie (p. ej., desecación, alta temperatura y radiación solar), facilitando el crecimiento microbiano en biomasa y diversidad y, por lo tanto, acelerando procesos bioquímicos clave del ciclo de nutrientes afectados en el incendio forestal. Por lo tanto, la biocostra podría desempeñar un papel fundamental en la resiliencia de las comunidades microbianas del suelo afectadas por incendios, una influencia que persiste y se acentúa con el tiempo con el desarrollo de la biocostra (Capítulo 4).

La tala y saca de madera aplicada de forma intensiva afectó negativamente la propagación de los musgos formadores de biocostra en suelos afectados por incendios a medio plazo (Capítulo 4), lo que lleva a efectos negativos en cascada en el funcionamiento de los ecosistemas dado su papel como ingenieros de ecosistemas. De manera similar, la aplicación de mulch de madera quemada suprimió drásticamente el desarrollo de la biocostra en un año (Capítulo 6), generando un conflicto con la recuperación de los suelos asistida por los musgos (Capítulos 4 y 5). El mulch de madera tuvo un efecto limitado sobre las propiedades fisicoquímicas; sin embargo, una incipiente aceleración de los procesos bioquímicos fue notable en la tasa más baja de aplicación de mulch, asistida por la presencia de la biocostra. Sin embargo, la diversidad microbiana se redujo bajo la aplicación de mulch de madera, las comunidades se volvieron de forma transitoria altamente homogéneas. Fue particularmente revelador los cambios observados en la comunidad fúngica, altamente sensible a la aplicación de mulch de madera. En consecuencia, la aplicación indiscriminada de mulch en los suelos puede dificultar la recuperación de la diversidad microbiana y, por lo tanto, la funcionalidad del ecosistema a corto plazo. Existe la necesidad de incorporar información sobre diversidad microbiana en la planificación de la gestión posterior a los incendios, para apoyar prácticas que impulsen la conservación de la biodiversidad del suelo.

Los resultados del capítulo 7 mostraron efectos contrastados en los suelos en respuesta a la aplicación de diferentes enmiendas orgánicas, caracterizadas por diferentes orígenes y estabilidad, lo que demuestra que las técnicas de restauración desencadenan efectos variables según el componente o proceso estratégicamente a restaurar. Todas las enmiendas orgánicas mejoraron la fertilidad del suelo y estimularon la actividad microbiana, pero con implicaciones contrastables (transitorias o duraderas) en los suelos. Las enmiendas frescas promovieron el inmediato crecimiento y actividad microbiana, pero también mayores tasas de mineralización y, por lo tanto, presumiblemente períodos más cortos de consumo de fuentes de carbono. Por el contrario, los suelos tratados con compost acumularon la mayor cantidad de carbono orgánico y nitrógeno, asegurando la liberación de nutrientes y fertilidad del suelo a largo plazo. En consecuencia, la selección de la enmienda dependerá de los objetivos del plan de restauración del suelo en términos de la inmediatez de la respuesta del suelo.

CHAPTER 1

General introduction

1. Fire: the driving force

Fire is an ecological and evolutionary force in most terrestrial ecosystems on Earth (Pausas and Bond, 2019). As a recurrent process, fire regimens have direct ecological effects on species traits, species interactions, community composition, carbon and nutrient cycling, and ecosystem functions (McLauchlan et al., 2020). The Mediterranean-type climate is an example of a fire-adapted ecosystem; the climatic seasonality, with precipitation in winter under mild temperatures and drought in the summer with high temperatures, enables plants to grow during the rainy season and become highly flammable during the dry summer season. Some plant species have developed adaptive strategies to resist, promote, or recover from recurrent fires, such as the resprouter and germinator species (Pausas and Keeley, 2009; Keeley et al., 2011). Despite often being perceived as destructive disturbances nowadays, fires provide important ecosystem services to humankind, including the provision of open spaces for pastures, agriculture, and hunting, the regulation of catastrophic wildfires, and the provision of scientific knowledge about the origin of biodiversity (Pausas and Keeley, 2019). However, human influence on fire activity has intensified during the last few centuries due to the effects of industrialization and climate change (Bowman et al., 2020). In the European Mediterranean, the strong suppression policies to protect ecosystems and human properties, coupled with rural exodus, led to an increase in fuel accumulation, increasing the fire risk, which was exacerbated by the investment in monospecific plantations of extremely flammable species (Pinus and Eucalyptus) (Mataix-Solera and Cerdà, 2009; Moreira et al., 2020). The combination of these factors with climate predictions, which point to intensification in the frequency and severity of drought events and warmer conditions, has the potential to magnify the wildfire impacts (Pausas, 2004; IPCC, 2018), threatening the resilience of ecosystems (Flannigan et al., 2009).

Fire alters multiple physical, chemical, and biological properties of soils (Doerr et al., 2022), with the magnitude of effects being highly variable. Intensification of fire events, in both frequency and severity, is expected to result in detrimental effects on soils (Guénon et al., 2013; Pellegrini et al., 2018), with severe consequences for the hydrological response and erosion dynamics, the loss of soil structure, modification of soil organic matter and soil biochemistry, and substantial shifts in overall soil biodiversity with a special impact on microbial communities (Neary et al., 1999; DeBano, 2000; González-Pérez et al., 2004; Certini, 2005; Muñoz-Rojas et al., 2016; Doerr et al., 2022). Fire effects on soils are coupled with changes aboveground. The rapid vegetation recovery after fires is of primordial importance for soils since it guarantees soil protection against erosive forces, the main threat to Mediterranean post-fire soils (Cerdà and Robichaud, 2009; Vallejo et al., 2012). However, post-fire interactions above-belowground may suffer alterations under changing fire regimes, for example, by the change in soil nutrient pools over time (Caon et al., 2014; Pellegrini et al., 2018; Dove et al., 2020). Understanding how vegetation regenerates after fires is essential for mitigating the escalating fire effects in ecosystems (Fernández-García et al., 2019).

Aboveground and belowground soil components are strongly linked; therefore, apart from the direct effect of heating, fire may modify the microbial communities by altering plant-induced changes in the soil environment (Hart et al., 2005; Knelman et al., 2015; Dove et al., 2021). Soil microbial communities facilitate the recovery of fire-affected soils by participating in critical ecosystem processes, including nutrient cycling, physical stability, carbon sequestration, and support for plant growth (Fultz et al., 2016; Keesstra et al., 2016). However, changes in fire regimen and increases in fire severity could profoundly alter the microbial communities over time (Ferrenberg et al., 2013; Dove and Hart, 2017; Whitman et al., 2019; Sáenz De Miera et al., 2020). Vegetation and microbial communities in post-fire systems act as indicators of changes in disturbed soil processes, while at the same time, they act as active agents driving ecosystem functions recovery (Kardol and Wardle, 2010; Delgado-Baquerizo et al., 2017). Given global change projections indicate increased frequency and severity of fires, additional work is necessary to better disentangle ecosystem resilience exposed to additional disturbances, such as human intervention through forest management, of magnitude relevance for soil recovery and resilience (Pereira et al., 2018; Tomao et al., 2020; Lucas-Borja et al., 2021; Averill et al., 2022).

2. Biocrust-forming mosses

2.1. What is a biocrust?

Biological soil crust, hereafter "biocrust", is defined by Weber et al. (2022), a refinement of the definition proposed in the first review volume on biocrust by Belnap and Lange (2003), as the "result from an intimate association between soil particles and differing proportions of photoautotrophic (e.g., cyanobacteria, algae, lichens, bryophytes) and heterotrophic (e.g., bacteria, fungi, archaea) organisms, which live within, or immediately on top of, the uppermost millimeters of soil. Soil particles are aggregated through the presence and activity of these often extremotolerant biota that desiccate regularly, and the resultant living crust covers the surface of the ground as a coherent layer." Therefore, biocrusts are defined by elements related to habitat, function, physical structure, and taxonomy

Biocrust communities cover around 12% of Earth´s terrestrial surface (Rodriguez-Caballero et al., 2018), dominating the plant interspace in many drylands thanks to specific adaptations to survive in unfavorable and often extreme environments (Belnap et al., 2016). Mosses are typically found creating carpets in habitats where water is not a limiting factor, dominating ecosystems like tundra and taiga, or in temperate regions where vascular plants are limited, like in low light conditions inside forests. These groups of organisms are excluded from being considered biocrust since biomass occurs above the mineral soil surface with no contact with the soil (Weber et al., 2022). However, a group of moss species develops in drylands forming moss biocrust, in habitats where they must cope with high insolation, low rainfall, and drought. These communities are poikilohydric, i.e., when water is not available, mosses desiccate, equilibrating their cellular water content with water levels in ambient air, and are rapidly rehydrated and reactivated once water is available (Slate et al., 2019). Their physiological and morphological characteristics determine their distribution patterns globally, with the semiarid Mediterranean region dominated by lichens and bryophytes biocrust (Maestre et al., 2021; Ladrón De Guevara and Maestre, 2022). The dependency on water availability makes biocrust-forming mosses particularly sensitive to climate change (Delgado-Baquerizo et al., 2016; Ferrenberg et al., 2017), a factor to consider as climate projections suggest that drylands will experience higher temperatures and more severe droughts (IPCC, 2018).

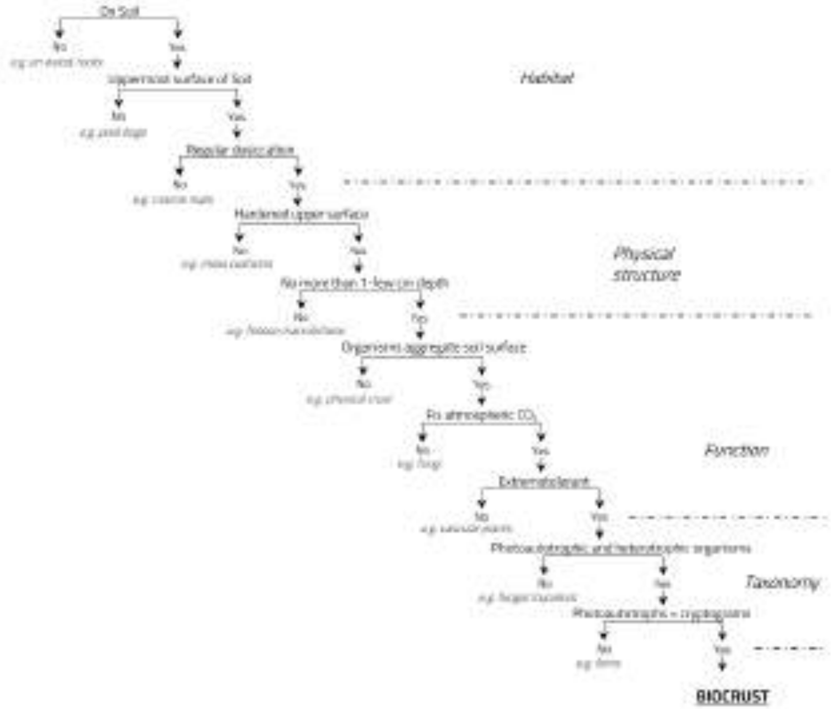

Fig. 1. Definition of biocrust based on elements related to habitat, function, physical structure, and taxonomy, adapted from Weber et al. (2022).

2.2. Ecology of moss biocrust

Biocrust-forming mosses are considered ecosystem engineers; they regulate soil properties, alter microbial communities, and intervene in key ecosystem processes such as water infiltration, nutrient cycling, or carbon sequestration (Ferrenberg et al., 2017; Ladrón De Guevara and Maestre, 2022). Above all, biocrusts are recognized as major soil stabilizers in drylands (Belnap and Büdel, 2016). The morphology of mosses through growing fine rhizoids and protonema mats allows strong cohesion of surface particles, resulting in high soil stability (Seppelt et al., 2016). This high resistance enables effective mitigation of soil erosion, directly, by creating a physical barrier and roughening the surface, but also indirectly by affecting soil properties, mainly by increasing the organic matter content (Gao et al., 2020; Zhang et al., 2022). Nevertheless, the efficiency of biocrust in erosion control is subordinated to its development stage, which is influenced as well by the extent, intensity, and time since disturbances (Belnap and Büdel, 2016). Biocrust controls local hydrological cycles in drylands, distributing surface flows between infiltration and runoff, and regulating soil moisture and water holding capacity (Belnap, 2006; Eldridge et al., 2020). The positive effects of moss biocrust on water infiltration present some inconsistencies in the literature, as the water storage in upper soil layers sometimes is related to decreases in water infiltration to deeper soil horizons (Xiao et al., 2019b), as well as infiltration reductions related to the creation of hydrophobic surfaces when the biocrust cover is substantial (Rodríguez-Caballero et al., 2013; Kidron et al., 2022).

Biocrust also promotes soil formation by accelerating the chemical and physical weathering of soil and, at the same time, acting as dust particle trappers, contributing indirectly to soil fertility (Reynolds et al., 2001). Therefore, biocrusts represent islands of fertility (Ferrenberg et al., 2018) for plants and microorganisms through the concentration of essential elements in soils, promoting essential biochemical processes. Moss biocrust contributes directly to soil fertility by fixing carbon and nitrogen, increasing the organic matter in soils beneath the crust (Cheng et al., 2021). The nutrient status in the soil biocrust facilitates the development of microbial communities, playing fundamental roles in ecosystem multifunctionality and acting as hotspots of soil biodiversity (Delgado-Baquerizo et al., 2016; Maier et al., 2016; Zhang et al., 2022).

2.3. Natural recovery after fire disturbances

Natural recovery rates of biocrust after disturbances are known to be slow, as observed after wildfire events with long-lasting consequences for biocrust community structure and diversity (Johansen, 2001; Root et al., 2017). The meta-analysis by Palmer et al. (2020) documented approximately a 50% reduction in biocrust cover after fires, especially cyanobacteria biocrust, although the authors claim more global surveys are needed since studies are predominantly from the United States. Above all, there is not a general consensus on how biocrusts respond to fire disturbances because it depends on the biocrust type, the ecosystem, and variables related to the fire, such as severity, frequency, and disturbance history (Zaady et al., 2016; Palmer et al., 2020). Weber et al. (2016), after reviewing biocrust succession patterns under the influence of soil conditions, climate, and the severity and timing of disturbance, concluded biocrust recovery rates are not linear. Under favorable, stable soil conditions, the initial soil-stabilizing cyanobacteria-dominated succession stages may be omitted, and moss-dominated biocrusts develop instead in the initial phases of biocrust development. This succession pattern is highly observed in fire-affected systems under suitable climate conditions (Bowker et al., 2004; Grover et al., 2020; Weber et al., 2022). Fire disturbances provide an opportunity for biocrust to develop in areas that are commonly covered with vascular plants and plant litter. With time biocrust will be diminished in abundance or replaced by vascular plant vegetation with natural recovery succession; however, persistent stressful conditions for vascular plants, e.g., soil compaction provided by heavy machinery in post-fire management, might create conditions that support long-term persistence of biocrust in those environments (Gall et al., 2022b).

Vascular plant communities following wildfire disturbances have been extensively investigated (Bond and Keeley, 2005), in contrast to the dynamics of non-vascular plants like bryophytes, which has been less studied although partially explored in different biomes (Eldridge et al., 2000; Hilty et al., 2004; Ryömä and Laaka-Lindberg, 2005; Pharo et al., 2013; Hylander et al., 2021). In Mediterranean forests, where large numbers of species are adapted to fire events (Keeley et al., 2011), bryophytes are highlighted as recurrent elements in the post-fire vegetation succession (During, 1979; De las Heras et al., 1994; Esposito et al., 1999; Castoldi, 2013; Stinca et al., 2020). After wildfires, ruderal mosses rapidly colonize bare soils in a transient succession stage before vascular plant colonization. This is especially documented in forests affected by high-intensity fires, in which ecosystems are largely dominated by ruderal moss biocrust during the first 2–3 years after the disturbance (De las Heras et al., 1994; Esposito et al., 1999), revealing the high resilience of mosses to the post-fire environment (Reed et al., 2016; Condon and Pyke, 2018). The reason for their quick response may be related to the wide dispersal of diaspores, the possible regeneration from dormant propagules in sub-surface soil banks, and rapid protonema and gametophyte growth facilitated by their ability to develop on unstable substrates like charred surfaces and ashes (Esposito et al., 1999; Smith et al., 2014). The colonization stage is characterized by the dominant presence of a few pioneers colonizing species, where *Funaria hygrometrica* is the most representative of this group showing a very fast development and protonema able to survive the desiccation, typically occurring in open recently burnt soils (During, 1979; De las Heras et al., 1994; Esposito et al., 1999).

Biocrust-forming mosses emerging after fires have received attention lately due to their efficiency in stabilizing the soil surface and controlling soil water erosion (Silva et al., 2019; Gall et al., 2022a). Fire-affected areas are particularly vulnerable to soil erosion because of the low levels of vascular vegetation, soil moisture, and organic matter (Shakesby, 2011). The emergence of biocrust may form a valuable ecosystem component in post-fire environments beyond soil stabilization. Despite the growing body of knowledge demonstrating their role as ecosystem engineers, pioneer moss biocrusts are often neglected in studies assessing their effect on fire-affected ecosystems.

Fig. 2. Detail of ashes trapped under moss biocrust emerged after the wildfire.

The use of biocrust in restoration strategies to rehabilitate degraded soils have emerged lately as a novel tool. Effective biocrust establishment has the potential to improve restoration practices, given its effects on biodiversity increases and the improvement in ecosystem resilience (Bowker, 2007; Antoninka et al., 2020). The new strategies offer solutions to stabilizing soils with biocrust colonization, which is a crucial step for post-fire restoration success (Muñoz-Rojas et al., 2021). Promising techniques to rehabilitate fire-affected soils are based either on inoculating cyanobacteria (Chamizo et al., 2020) or cultivating mosses (Grover et al., 2020). Beyond the stabilization effects, understanding the soil biochemistry and microbiome response to the biocrust emergence is required to provide valuable information to apply in post-fire management strategies toward accelerating recovery, especially relevant for ecosystems prone to degradation like the Mediterranean.

3. Soil microbiology in fire disturbances

3.1. Ecosystem functionality after wildfires

Soil harbors up to a quarter of all living species on Earth, representing the main repository of terrestrial biodiversity (FAO et al., 2020). Soil biodiversity drives a wide variety of ecosystem processes and functions, including nutrient cycling, primary production, litter decomposition, climate regulation, and soil formation (Bardgett and Van Der Putten, 2014; Delgado-Baquerizo et al., 2020). Fire disturbances generate complex effects on ecosystem functioning, in which alterations can last months to years depending on the interactive plant and microbial communities' responses to fires (Kardol and Wardle, 2010; Pérez-Valera et al., 2019). Microbial communities exposed to fire disturbances can be resistant (i.e., without changes), resilient (i.e., return to their pre-fire structure), or remain altered, exhibiting high sensitivity to the disturbance (Allison and Martiny, 2008). In Mediterranean soils, microbial communities generally show high resilience to fire disturbances, and ecosystem functioning related to microbial performance recovers relatively quickly (Ferrenberg et al., 2013; Pérez-Valera et al., 2020). However, increasing disturbance pressure on soil microorganisms may hamper the recovery ability of the ecosystem (Villnäs et al., 2013; Mendes et al., 2015). Microbial functionality is linked to the soil post-fire status (Nelson et al., 2022) since the environment strongly filters the abundance and composition of microbial communities (e.g., pH, soil nutrients, climatic variables) (Bahram et al., 2018). Given its essential role in maintaining multiple ecosystem processes, the study of microbial communities and their relationship with soils is particularly strategic to evaluate the recovery process in fire-affected systems and predict the ecosystem's resilience to further disturbances (Adkins et al., 2020; Dove et al., 2020).

3.2. The microbial response to wildfires

The direct effect of fire on soil microorganisms results in cell death; the magnitude of the impact depends on the soil water content and thus the heat transmission (Barreiro et al., 2020). The temperatures reached in the soil filter the microbial populations that will recolonize the post-fire environment, thus differentiating the heat-sensitive versus heat-resistant microbes (Neary et al., 1999). Indeed, some microorganisms have developed several mechanisms to cope with high temperatures and take advantage of post-fire environments, exhibiting strategies such as fast-growth or the formation of heat-resistant structures (Smith et al., 2008; Ferrenberg et al., 2013; Whitman et al., 2019). This is the case of spore-formers bacteria Firmicutes and Actinobacteria, highly dominant immediately after fire events. The response to fire depends on the type of microorganism, and in general, soil bacteria are considered less sensitive than fungi to wildfires in terms of biomass, richness, and diversity (Mataix-Solera et al., 2009; Pressler et al., 2019).

Immediately after fires, stochastic processes structure the microbial community (Ferrenberg et al., 2013), but subsequent evolution of soil properties in response to the fire disturbance acts as an intense filter determining the community assembly, thus environmental characteristics becoming dominant drivers of microbial community composition (Prendergast-Miller et al., 2017; Li et al., 2019). Therefore, indirect impacts on soil microbial communities are mediated by modifications in the physical and chemical soil properties, including changes in soil organic matter quality (González-Pérez et al., 2004), loss of soil structure (Mataix-Solera et al., 2011), soil moisture retention, soil pH, changes in nutrient availability, etc. (Certini, 2005; Fuentes-Ramirez et al., 2018). Changes in soils can persist over time depending on the fire severity, a factor that controls, directly and indirectly, the microbial communities (Holden et al., 2016; Lucas-Borja et al., 2019b; Adkins et al., 2020). In fact, wildfires create a mosaic of diverse severity patches in soils, composed of unburned vegetation or less severely affected soils (Keeley, 2009), creating islands of inoculum sources from which start the recolonization (López-Poma and Bautista, 2014; Glassman et al., 2016; Ammitzboll et al., 2022).

3.3. What to measure

Soil microbial communities are highly responsive to fires. Given their essential role in ecosystem functionality, they act as precise indicators of soil processes and ecosystem restoration after disturbances (Muñoz-Rojas and Bárcenas-Moreno, 2019). Multiple international efforts have defined essential biodiversity variables to effectively monitor soil biodiversity conservation (e.g.: The Soil Biodiversity Observation Network, (SoilBON, 2021)): variables defining different dimensions of the soil system (physics, chemistry, biodiversity, and ecosystem functions) that serve as indicators of soil health, nutrient cycling, and soil carbon stock (i.e., soil biomass, nutrient cycling, soil aggregation, enzymatic activities, soil respiration), or soil biodiversity conservation (i.e., taxonomic diversity, functional diversity, population abundance) (see in Guerra et al., 2021). Focus on those essential variables allows predicting the recovery state in fire-affected ecosystems.

3.3.1. Soil microbial abundance and activity

Immediately after a fire, reductions in microbial biomass are frequently observed, determined by the fire intensity and severity (Holden and Treseder, 2013; Pressler et al., 2019), and subsequently affected through changes in the soil environment, such as those in the organic carbon composition (González-Pérez et al., 2004). Bacteria and fungi differ in their sensitivity to fire, with fungi generally exhibiting more drastic reductions due to their lower thermal tolerance, and the mortality of host plants during fires (Neary et al., 1999). Therefore, fire impacts on fungal biomass can persist for over a decade (Dooley and Treseder, 2012). Increasing abundances immediately after fires can also be found. Heating consumes soil organic matter, but ephemerally increases the content of some nutrients (soluble organic compounds, ammonium, phosphorous) that allows the rapid growth of microbial populations, mainly heterotrophic bacteria. Once the easily mineralizable compounds are consumed or rapidly mineralized, the remaining carbon and nitrogen become more recalcitrant to microbial attack (González-Pérez et al., 2004), and a decrease in microbial abundance and their activity is usually observed (Bárcenas-Moreno et al., 2011; Goberna et al., 2012).

Microbial indicators of ecosystem functioning that are widely used to assess post-fire disturbances traditionally include microbial activity, carbon use efficiency, and enzymatic activities related to carbon, phosphorous, and nitrogen compounds (Muñoz-Rojas et al., 2016; Pérez-Valera et al., 2019). Increases in basal respiration rates after the pulse of nutrients are also reported right after the fires, subsequently modulated by vegetation recovery (Bárcenas-Moreno et al., 2011; Marañón-Jiménez et al., 2011). The study of enzymatic activities reveals critical information thanks to their implication in soil nutrient cycling (Allison and Vitousek, 2005). Multiple extracellular enzymes are interesting in post-fire systems, which measure the potential use of labile carbon (β-glucosidase), different forms of nitrogen (urease or protease), or the mineralizing of phosphorous (phosphatases), together with intracellular enzymes related to active microorganisms (dehydrogenase). Enzymes are negatively affected by fires both directly, with immediate reductions (Lucas-Borja et al., 2018), and indirectly, by changes in physicochemical soil properties (Sardans and Peñuelas, 2005). Additionally, vegetation recovery also modulates enzyme activities (López-Poma and Bautista, 2014). The activities are ultimately mediated by the microbial community structure since those activities result from the response to a specific environment (Pérez-Valera et al., 2020).

3.3.2. Soil microbial diversity: bacteria and fungi

Bacteria and fungi communities dominate terrestrial soil habitats in terms of biodiversity and biomass, both playing a central role in the turnover of carbon and nitrogen as the predominant decomposers in soils (Baldrian, 2017; Lladó et al., 2017). After wildfires, dramatic changes are documented in the microbial communities. The diversity estimators indicate bacteria richness tends to recover faster after wildfires, benefiting from fast division and colonization during the growing season (Li et al., 2019; Pressler et al., 2019), compared to fungi. Several meta-analyses report a reduced fungal richness after fires (Dooley and Treseder, 2012; Pressler et al., 2019), and according to Dove and Hart (2017), without subsequent disturbance and favorable growing conditions, communities recover in less than ten years. If microbial communities are not resilient to fire within a decade, the predicted increase in fire frequency can hinder the recovery of microbial communities and the important ecosystem processes they regulate, as warned by Pressler et al. (2019).

The structure of the microbial communities is profoundly altered after a fire, with communities becoming more dissimilar with increasing fire severity (Lucas-Borja et al., 2019a; Whitman et al., 2019), with long-lasting effects on the community complexity both in bacteria and fungi (Treseder et al., 2004; Holden et al., 2016; Muñoz-Rojas et al., 2016; Cutler et al., 2017; Su et al., 2022). The assembly of the microbial communities strongly determined over time by soil factors altered by the fire, e.g., changes in pH, one of the major drivers of bacterial assembly (Rousk et al., 2010; Ferrenberg et al., 2013).

The study of the microbial community composition after a wildfire reveals interesting changes in the taxonomical structure, in which it is observed that some groups dominate as a response to the ecological strategy associated (Pérez-Valera et al., 2018). In bacteria, there are commonly reported increments in soil Firmicutes, especially *Bacillus*, due to the capacity to form endospores and possibly withstand fire (Smith et al., 2008). Actinobacteria usually decrease (Rodríguez et al., 2018), with a few exceptions, such as the genus *Arthrobacter* that plays an important role in the nitrogen cycle and plant growth (Cobo-Díaz et al., 2015; Fernández-González et al., 2017). Alphaproteobacteria generally decrease since they are found in richer environments, contrary to Betaproteobacteria in the Oxalobacteraceae family (predominantly *Massilia*), which are largely found after fires (Prendergast-Miller et al., 2017; Sáenz De Miera et al., 2020). In fungal communities, Basidiomycota usually declines in favor of saprophytes from Ascomycota, and plant host mortality declines the arbuscular mycorrhiza, represented in the Glomeromycota phyla (Treseder et al., 2004; Holden et al., 2016; Smith et al., 2017).

The identification of taxa that are responsive to disturbances provides valuable information in order to predict microbial structure and functionality. One of the most best-known indicator taxa after fires is the pyrophilous fungi, or "loving fungi" (Bruns et al., 2020; Fox et al., 2022). The group, mainly composed of *Morchella, Pyronema, Anthracobia*, and *Geopyxis* species, are fungi (Ascomycota) that fruit abundantly after fires due to heat stimulation, lack of competition and tolerance to post-fire conditions (Reazin et al., 2016; Bruns et al., 2020; Raudabaugh et al., 2020). Recently, the functional roles that play in post-fire systems are starting to be disentangled, related to soil stabilization. The pyrophilous fungi are responsible for aggregating soil particles, with important consequences for soil erosion reductions and improvements in soil moisture (Filialuna and Cripps, 2021), contributing to the overall rapid ecosystem recovery following a fire.

3.4. Microbial communities associated with moss biocrust

Biocrust in drylands facilitates the development of microbial communities, promoting soil biodiversity (Delgado-Baquerizo et al., 2016; Zhang et al., 2022). The main component of the biocrust, either cyanobacteria, lichen, or bryophyte, determines the soil microbiome, most times reflecting successional stages (Maier et al., 2016). According to Maier et al. (2018), fungi become more predominant with succession progression, and bacterial communities shift from more generalized to specialized organisms along succession. Therefore, moss biocrust is known for harboring a high diversity of bacteria and fungi beneath it, but those communities are highly sensitive to disturbances (Xiao and Veste, 2017; Bao et al., 2019; Cheng et al., 2021). Nonetheless, despite the growing body of knowledge regarding biocrust, biocrust-forming mosses are often neglected in post-fire studies, and thus the microbial communities living in soils under the influence of the pioneer ruderal mosses. Therefore, it is completely unknown the relevance of the biocrust emergence for microbial diversity resilience and conservation in fire-affected ecosystems.

4. Post-fire management in Mediterranean forests: restoring or adding a new disturbance

The management of fire-affected areas represents a crucial step for the fate of soils after fires. The decision will determine the ecosystem's capacity to recover from the fire disturbance, combined with factors such as the fire history, ash properties, topography, post-fire weather, and vegetation recuperation (Pereira et al., 2018). Post-fire management involves complex decisions, often taken under strong political and social pressure to act immediately after fires, which can lead to adopting measures not based on ecological arguments, e.g., the traditional reforestation based on planting pines in areas where their regeneration is expected to be high or where the specie is outside its natural distribution (Pausas, 2004; Vallejo et al., 2012; Castro, 2021). Immediately after wildfires, soils are unprotected and exposed to erosion events (Shakesby, 2011). Under this circumstance of high vulnerability, some post-fire management place additional pressure on soils already disturbed, increasing the impact on the ecosystem by triggering soil erosion processes. Erosion is the major threat soils face in dry regions, where soil formation rates are very low, inducing irreversible soil degradation. In essence, ecosystem resilience is bound to its disturbance history, increasing disturbance stress can threaten the ecosystem's tolerance to further perturbations (Villnäs et al., 2013; Ammitzboll et al., 2021).

4.1. Management of burnt trees: salvage logging

A common first management action performed after a wildfire in Mediterranean ecosystems, particularly in coniferous forests, is salvage logging (Chapters 3, 4, 5). Salvage logging consists of the removal of burnt trees, most often in combination with the removal of the remaining woody debris by chopping, mastication, or burning. The purpose is primarily economic: the harvesting of commercially valuable timber as soon as possible to maximize economic benefit since value decreases with time due to wood decay. Another argument that supports the practice is that it reduces the risk of insect outbreaks and fire hazards (Vallejo et al., 2012; Lucas-Borja et al., 2019a).

Increasing evidence of the negative impacts of logging operations on ecosystem recovery has been widely reported lately. The direct consequence of logging operations is soil compaction, which modifies the hydrological response of soils and triggers erosion processes (Morgan et al., 2015; Slesak et al., 2015; Malvar et al., 2017). Performing salvage logging on vulnerable soils may cause more erosion than the fire itself. The soil degradation results in the delay of vegetation recovery (Wagenbrenner et al., 2016; García-Orenes et al., 2017), disturbance of nutrient cycling (Pereg et al., 2018), alteration in carbon fluxes (Serrano-Ortiz et al., 2011; Hartmann et al., 2014), and disruption in soil biodiversity directly or indirectly, e.g., disturbing the deadwood-dependent species (Thorn et al., 2020), as bryophytes (Bradbury, 2006; Pharo et al., 2013). Soils can suffer persistent alterations, ultimately reducing forest productivity and ecosystem functionality (Hartmann et al., 2014; Chen et al., 2015). Nevertheless, the effects on soils are highly dependent on the context, the site characteristics, the soil erodibility, and the way to perform the management (Fernández and Vega, 2016; García-Orenes et al., 2017; Francos et al., 2018).

After a wildfire, burnt wood is a biological legacy of key relevance in forests; it constitutes a stock of nutrients that slowly fertilize soil through decomposition (Juan-Ovejero et al., 2021; Marañón-Jiménez & Castro, 2013; Thorn et al., 2018). In addition, the permanence of wood over the soil ameliorates the stress conditions by increasing soil moisture, enabling vegetation and microbial development, and acting as a barrier for sediments against water erosion (Baldrian et al., 2016; Marañón-Jiménez et al., 2013). The deadwood forms part of a complex food chain (Baldrian, 2017; Lladó et al., 2017), with fungi and bacteria being the main decomposers and the basis of a complex community, sustaining biodiversity and ecosystem services (Thorn et al., 2018, 2020). Therefore, leaving burnt wood spread over the ground avoids the logging machinery impacts and represents an influx of soil nutrients and a biological legacy for soils. However, this practice (non-interventionism) is highly controversial, first for forest owners that pursue timber benefits and then for forest managers since it can hinder the movement of machinery and people and represent pest and new fire risks (Castro, 2021).

4.2. Emergency stabilization treatments: mulching

Emergency treatments are commonly implemented in burnt areas to stabilize soils where there is a high risk of soil erosion and runoff, including barrier treatments or mulching techniques. Mulching is considered the most cost-effective intervention to mitigate soil erosion (Robichaud et al., 2013; Girona-García et al., 2021), with materials forming the protective soil covers can be composed of in situ materials (wood-residues) or other foreign materials, usually straw (Chapter 6). Straw mulches from agricultural residues are the most commonly applied and, although highly effective (Lucas-Borja et al., 2019), present some drawbacks, like the introduction of non-native or invasive species and low wind resistance (Beyers, 2004; Kruse et al., 2004). In contrast, wood-based mulches exhibit great resistance to wind displacement and long longevity due to their decay resistance (Bautista et al., 2009; Jonas et al., 2019). The major drawback of wood mulches is the possible hindering of vegetation recovery due to the thick layer of mulch (Bautista et al., 2009), a regrowth that is ultimately crucial for soil protection. More importantly, wood residues generated in the framework of logging operations via the mastication of non-commercial debris are often applied where intensive logging operations may have created the necessity of the mulch application after triggering erosion processes (Castro, 2021). The machinery compacts the soil and delays vegetation recovery, and the application of burnt wood again requires the use of heavy machinery with its associated impact. The feasibility of broad-scale mulching with local material is a complication in management planning (Fernández et al., 2019; Castro, 2021). Nonetheless, after salvage logging operations, burnt wood application in soils is expected to produce positive effects in soils related to microclimatic improvement and nutrient supply, although the biological soil response is still rather unexplored.

4.3. Restoration practices: organic amendments

Other types of post-fire management focus on restoring components or processes of the ecosystem in order to recover ecosystem functionality (Hueso-González et al., 2018; Muñoz-Rojas, 2018), and the application of organic amendments is an example of these practices (Chapter 7). After the consumption of elevated levels of organic carbon in high-severity fires, the additional source of organic matter in soils induces a cascade of effects in multiple components of the perturbed ecosystem (Heneghan et al., 2008; Costantini et al., 2016). The organic application promotes the belowground functions by increasing biological productivity, nutrient cycling, physical stability, and carbon sequestration, thus supporting plant growth and productivity (Ros et al., 2003; Tejada et al., 2009; Larney and Angers, 2012; Luna et al., 2016). However, the feasibility of large-scale applications in extensively damaged areas faces multiple problems. In this sense, the most viable approach to proceed might be the creation of patches of soils organically amended, and strategically distributed in the most endangered soils on a landscape scale, generating fertility islands from which the recovery of the affected vegetation is accelerated and expanded to the non-amended soils.

Regardless of the origin of the organic material (compost, manures, crop residues, or sewage sludge), the decisive step relies on the selection of the stability of the organic material, referred to as the rate of organic matter decomposition (Hueso-González et al., 2018), related to the transient or durable effects on soils (Diacono and Montemurro, 2011; González-Ubierna et al., 2012). The application of fresh materials (e.g., manures) implies a significant amount of labile C fraction that easily decomposes, which boosts microbial activity and favors the rapid establishment of plants (Haynes, 2005). Some of the adverse effects of their use include increasing the mineralization rate of native soil organic carbon, alteration of salinity and acidity, microbial immobilization of available nitrogen, and addition of potential pollutants or pathogens into soils (Kowaljow and Mazzarino, 2007; Bernal et al., 2009). On the contrary, stable materials (e.g., compost), provide durable organic carbon substances contributing to long-term fertility, improving soil structure and water holding capacity at the same time reduceing the erosion risk (Ojeda et al., 2003; Larchevêque et al., 2005; Bernal et al., 2009; Larney and Angers, 2012). Consequently, the amendment selection will depend on the goals of the soil restoration plan.

5. AIM AND OUTLINE THESIS

Post-fire management is a critical factor for ecosystem recovery, a decision that can trigger or reduce soil degradation. Mediterranean ecosystems are resilient to fire events but prone to degradation. Post-fire management planning in a Mediterranean burnt forest includes interventions with contrasting approaches related to the management of burnt trees, the promotion of soil protection, or practices devoted to ecosystem restoration via the improvement of components or processes in the affected ecosystem. The consequences of forest management on soils, and especially soil biology, are particularly complex and conditioned by multiple factors. They are, however, often neglected in the investigation of post-fire systems and in the decision-making process. In the context of intensified of fire events and climate change, understanding the response of key soil components in managed ecosystems is critical to prioritizing soil conservation.

One overlooked component in post-fire environments is biocrust-forming mosses. The rapid colonization of pioneer mosses in early post-fire successional stages stabilizes soils in their most vulnerable period. However, further implications as active agents in the recovery and resilience of soils, in the transient stage before vascular revegetation, are completely unknown. In combination with the biocrust component, the response of soil microbial communities to forest management is crucial to evaluating the recovery progress, given their active role in fundamental ecosystem functions. Literature covering the additive consequences of post-fire management and biocrust emergence or microbial composition and functionality is scarce, which we believe is of main relevance and pivotal to support strategies that preserve soils against biodiversity loss.

This dissertation contributes to a better understanding of the collective interactions of above and belowground components in post-fire systems, providing new insights into the field of forest management to guide forest strategies toward accelerating recovery and resilience in semi-arid ecosystems prone to degradation. To summarize, the thesis includes a compilation of five studies. In Chapter 3, the short-term consequences (22 months) of aggressive salvage logging on the resilience of soil microbial communities disturbed by the fire and the management was investigated. Chapter 4 was focused on the mid-term legacies of biocrust emergence on soil functionality after the salvage logging disturbance. In Chapter 5, the role of moss biocrust emergence on soils and on the assembly of soil microbial communities after seven months since the wildfire and subsequent salvage logging was studied. In Chapter 6, it was assessed the recovery and resilience of soil microbial communities under wood-based mulch application in soils dominated by an emergent moss biocrust. In Chapter 7, contrasting organic amendments as a restoration strategy to promote the recovery of biotic and abiotic edaphic conditions were evaluated in the Chilean Mediterranean affected by megafires.

The general objective of the thesis was to assess the effects of contrasting post-fire managements on soil recovery in fire-affected Mediterranean-type climate forests, by focusing on the effects of those managements on the promotion or disruption of soil components biocrust-forming mosses and the soil microbial communities, and their relationship with the post-fire environment. Specifically, the objectives were:

1. To determine the effects on soils of forest management with contrasting approaches in relation to burnt wood extraction (salvage logging) (Chapters 3, 4, 5), soil protection (wood-mulching) (Chapter 6), and restoration practices (organic amendments application) (Chapter 7).

2. To elucidate the relevance of biocrust-forming mosses in the recovery and resilience of soils affected by wildfires and subsequent forest management, in the transient stage before vascular vegetation dominance (Chapters 4, 5, 6).

3. To assess the response of microbial communities to different post-fire management and the presence of biocrust, and determine the soil properties that become dominant drivers for the microbial community compositional shifts (Chapters 3-7).

CHAPTER 2

Materials and methods

1. Study sites and experimental design

This doctoral thesis covers three different study sites in Mediterranean ecosystems affected by wildfires, two of them in the semi-arid Alicante province (Spain), and the other one in Chilean Mediterranean ecosystems.

Site 1 (Chapters 3 and 4) is located in "Sierra de Mariola Natural Park" in Alicante, where mean annual precipitations is 490 mm and mean temperatures is 15.2 °C. The soil is classified as Typic Xerorthent developed over marls with low depth, highly vulnerable to erosion and degradation processes. The landscape is characterized by terraced hillslopes, and forest composed of mainly 40 years old *Pinus halepensis* Mill. trees from afforestation.

A wildfire in July 2012 of moderate severity burned 546 ha. Seven months after the wildfire, salvage logging was carried out, consisting of a complete extraction of the burnt wood using heavy machinery. The burnt trees were cut down with a chainsaw and dragged with chains at the top of the slope. After an extreme rainy event in September 2013 (50 mm in less than 3 h), soil erosion rates were high and gullies were formed in areas where the trunks were dragged

Fig.1. Gullies formed in Sierra de Mariola as a consequence of the soil erosion where the trunks were dragged.

In **Chapter 3**, we assessed the impacts of salvage logging on soils and on the composition and functionality of soil bacteria and fungi communities. For that purpose, we sampled soils 22 months after the wildfire, where salvage logging was performed 7 months after the fire. Six sampling plots (3 m × 3 m) were randomly established in a burnt affected area of 2500 m^2 where salvage logging was carried out, and another six sampling plots in a nearby-burnt area, comprising the same area and aspect where burnt wood remained as the untreated control. Within each plot, one composite sample comprised of five subsamples were randomly collected from the A horizon mineral (5 cm depth).

In **Chapter 4**, we investigated the role of moss biocrust emergence in soil recovery affected by a wildfire and subsequent salvage logging at the medium term (six years after fire). For this purpose, a vegetation cover study was conducted using the quadrat methodology, randomly distributed in the managed area (n = 25) and control area (n = 25). For the soil sampling and field measurements, we compared the soils covered by moss biocrust to bare soils (expressing evidence of remaining soil degradation), i.e., 100 points were randomly distributed, 50 points for each management, logging and control, 25 replicates over mosses and 25 over bare soils for both management. Soil samples were collected from the A horizon mineral (2.5 cm depth).

Site 2 (Chapter 5 and 6) is located in "Sierra de la Replana" in Beneixama, Alicante, where mean annual precipitation is 456 mm and mean temperature is 14.9 °C. Soil is classified as Typic Xerorthent with low depth and clay loam texture. The vegetation is mainly composed of 50 years old *Pinus halepensis* Mill. trees from afforestation.

A wildfire in July 2019 of moderate to high severity burned 862 ha. In early September, salvage logging operations were carried out in the area, consisting of a complete extraction of the burned wood using heavy machinery. Soils experienced erosion processes triggered by events of strong precipitations (40 mm in an hour in October). Seven months after the wildfire, slopes facing south showed evidence of surface runoff and soil erosion, and harsher conditions for plant regrowing.

In **Chapter 5**, we studied the effects of the burgeoning moss biocrust on soil physicochemical and biochemical properties and on the diversity and composition of microbial communities. The study was performed seven months after the wildfire, and subsequent salvage logging, in slopes facing south representing the most degraded area. Nine experimental plots (2 m × 2 m) were placed in the fire-affected area, and three plots in a nearby-unburned area used as control. Salvage logging effects on soils could not be evaluated separately from the wildfire effects due to the lack of a non-intervention area, thus the effects of fire disturbance and logging operations were studied together on biocrust and microbial communities. Within each experimental plot in the burned area, four soil samples were collected, two of them soils under the moss biocrust and the other two in bare soils (top 2.5 cm depth). At the unburned area, two soil samples were collected per plot at 2.5 cm after the removal of organic debris. In total, 15 samples were selected representing bare soils, 15 samples under mosses, and 5 samples from the unburned soils (n = 35).

Fig. 2. Patches of moss biocrust stabilizing soils surrounded by bare soils exhibiting erosion symptoms.

In **Chapter 6**, after evidences in Chapter 5 of the positive effects of the biocrust on soil microbial communities, we studied the additional effects of the application of wood mulch during one year (material from logging operations). In specific, we investigated the interactive effects of wood-mulch with the moss biocrust presence on soil physicochemical and biochemical properties and the diversity and composition of microbial communities. Three treatments were evaluated, i.e., mulch application at two rates, "Rate 1" covering 65% of soil, "Rate 2" covering 100% of soil, and "Control" as non-application. Within the twelve experimental plots (from Chapter 3), three plots per treatment were established in the fire-affected area, and another three experimental plots in a nearby-unburned area. Two sampling campaigns were conducted, the first one right before the mulch application, and the second, one year after the application. At each sampling period, four soil samples were collected from the top 2.5 cm of soil 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 soils). In total, 70 samples were selected for the present study: 35 samples per sampling year, from which 15 of them are from uncrusted soils, 15 samples under mosses, and 5 samples from the unburned soils. The moss biocrust cover monitoring was performed at each experimental plot using four random replicates of a 25 cm × 25 cm quadrat at both sampling times.

Fig. 3. Experimental plot of application of wood mulch at a rate of 65% of soil covered.

Site 3 (Chapter 7) is located in the Pumanque commune, the Chilean Mediterranean zone of the O'Higgins Region, one of the most affected regions during the 2016–2017 summer megafire events. The average annual precipitation is 451 mm, with an average temperature of 15.4 °C. Forests are composed by native sclerophyllous species. Soil is classified as Aquic Dystroxerepts with low depth and sandy loam texture.

In **Chapter 7**, we explored the response of soil physicochemical and microbial parameters to the application of contrasting organic amendments. Treatments were applied six months after the wildfire, amendments consisting on fresh (poultry and swine manure) and stabilized (compost of agricultural waste origin) organic amendments, applied together with straw mulch. In total, six treatments were evaluated: T0, reference (unburned area); T1, control; T2, mulch; T3, compost; T4, poultry manure; and T5, swine manure. Treatments were each distributed in four parcels (3 m × 1.5 m) within a burned area of 50 m × 50 m (T1–T5), and nearby to the unburned reference area of 20 m × 20 m.

2. Vegetation monitoring

Vegetation cover studies were conducted using a 50 cm × 50 cm quadrat divided into 100 cells (Chapter 4). When the survey was exclusively for mosses (Chapters 5 and 6), a 25 cm × 25 cm quadrat divided into 100 cells was used.

3. Soil Analyses

Several soil physicochemical, biological, and biochemical parameters were analyzed in order to examine the impact of fires, post-fire managements and the presence of biocrust in soils, and their role in the microbial community structure. In this section, we present a summary of the methods, further details about the procedures can be found in Chapters 3-7.

3.1. Physicochemical soil analyses

Three physical measurements were performed in the field (Chapter 4). The unsaturated hydraulic conductivity was measured with a Mini-Disk Infiltrometer (Decagon Devices, 2018), as the volume of water infiltrated every 30 s. Soil penetration resistance, representing the pressure applied to the soil surface before it breaks, was analyzed using a field penetrometer (Geotester Pocket Penetrometer, Italy) (Zaady & Bouskila, 2002). Water repellency was measured in the field, over mosses and bare soils, and under controlled conditions in the laboratory, using the water drop penetration time test (Wessel, 1988).

Variables analyzed related to the physical stability of soils were the aggregate stability, measured as the proportion of macroaggregates (4-0.25 mm) that remain stable after the soil sample is subjected to an artificial rainfall of known energy (279 J min^{-1} m^{-1}) (Roldán et al., 1994), and water-soluble carbohydrates, determined in a 1:5 (w/v) aqueous extract using the anthrone method as reported by Brink et al. (1960). Soil moisture was determined by gravimetry from field wet soils after drying for 24 h at 105 °C.

Soil pH and electrical conductivity were measured in a 1:2.5 and a 1:5 (w/v) aqueous extract, respectively. Soil organic carbon was determined by the Walkley-Black method (Nelson and Sommers, 1983); total nitrogen by the Kjeldahl method (Bremner and Mulvaney, 1982); and available phosphorus by the Burriel-Hernando method (Díez, 1982). Available micronutrients (Fe, Zn, Cu, and Mn) and potential pollutants (Ni, Cr, Pb, and Cd) were extracted by EDTA (1:10 w/v) or DTPA (1:2 w/v) (Quevauviller et al., 1998) and determined by an atomic absorption spectrophotometer.

Fig. 4. Mini-disk infiltrometer.

3.2. Biological and biochemical soil analyses

Biological and biochemical parameters were measured as indicators of microbially-mediated ecosystem functions. Microbial biomass was determined by the fumigation-extraction method (Vance et al., 1987), or by the substrate-induced respiration (SIR) method using an automated impedance-meter (BacTrac 4200 Microbiological Analyser, Sylab, Austria). In the same analyzer the basal soil respiration was measured as the CO_2 emissions by soil microorganisms incubated at 30 °C for 24 h (Anderson, 1983).

To estimate the microbial community biomass, phospholipid fatty acid analysis (PLFA) and neutral lipid fatty acid analysis (NLFA) were performed. Lipids extracted were methylated to estimate the arbuscular mycorrhiza biomass (NLFA), and the total fungal and bacterial biomass (PLFA) (Bossio et al., 1998; Bååth, 2003).

Enzymatic activities were used as indicators of functions related to C, P and N cycling. β-glucosidase catalyzes the breakdown of cellulose compounds releasing simpler compounds of glucose, alkaline phosphatase the catalyzes the hydrolysis of ester–phosphate bonds and release inorganic phosphorous, urease catalyzes the hydrolysis of urea and protease peptides releasing ammonia (Nannipieri et al., 1981; Tabatabai, 1983; Naseby and Lynch, 1997; Kandeler et al., 1999). Dehydrogenase activity is determined by the reaction product INTF (iodonitrotetrazolium formazan) formed by reduction of the substrate (García et al., 1997).

3.3. Microbial diversity

Microbial communities were studied by next-generation sequencing methodologies, specifically through amplicon sequence analyses of target genes. In the metabarcoding analyses, the V3–V4 region of bacterial 16S rRNA gen was amplified for bacterial with selected primers, and the internal transcribed spacer (ITS) region for fungi. Further details about library preparation and procedures, as well as bioinformatics performed, are elaborated and explained in the material and methods section for each corresponding chapter (Chapter 3 different from 5 and 6). In general, sequences were clustered into operational taxonomic units (OTUs) at a 97 % similarity level using UPARSE implemented within USEARCH (Edgar, 2013). The identification of bacterial and fungal sequences was performed using BLASTn at the Ribosomal Database Project (Cole et al., 2014) and UNITE (Nilsson et al., 2019), respectively (Chapters 3 and 4). The assignment of putative ecophysiological categories for fungi was performed based on the published literature using the FungalTraits (Põlme et al., 2020).

Bacteria and fungi in soils were studied at the community level and different phylogenic ranks, and the relationship of their community structure with the environmental factors, previously altered as a consequence of the wildfires and the different post-fire management. Microbial patterns were studied through diverse alpha and beta diversity indicators, and the study of responsive taxa as indicators of soil conditions.

CHAPTER 3

Salvage logging alters microbial community structure and functioning after a wildfire in a Mediterranean forest

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This chapter corresponds to the article:
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. Applied Soil Ecology, 168, 104130. doi:10.1016/J.APSOIL.2021.104130

Abstract

Salvage logging is one of the most common post-fire management strategies, known for trigger soil degradation processes. Soil compaction, the major disturbance associated with logging operations, could seriously hamper the resilience of soil microorganisms after the perturbation produced by fire. The main objective of this work was to assess the impact of post-fire salvage logging on the composition and structure of soil bacterial and fungi communities, as well as to correlate these findings with the changes in soil physicochemical properties. The management severely affected the soil physicochemical and microbial properties. Whereas an increase of alpha diversity was detected in the treated soils for the microbial community, the microbial functionality registered was lower when compared to control soils. Salvage logging profoundly altered the structure and composition of the microbial communities, being modifications in soil structure the main driver in the microbial community shifts. Soil degradation induced by logging operations resulted in new niches related to anoxic habitats, being Proteobacteria and Firmicutes families, capable of anaerobic respiration, families with high abundance in the affected soils. In addition, the depletion in C and N nutrients as a consequence of the soil erosion reduced the microbial populations sensitive to substrates availability, e.g. Actinomycetales. Ascomycota increased proportionally in managed soils, which might be due to the removal of host plants dependent on ectomycorrhizal fungi. This study demonstrated that physical soil disturbance performed by the post-fire salvage logging profoundly impacted the soil microbial community and associated functions. A deeper understanding of the relationship between disturbances caused by forest management and resilience of soil biodiversity is required.

1. Introduction

Fire is a common environmental perturbation in Mediterranean ecosystems. Many soil physical, chemical, and biological properties can be altered by wildfires, being fire severity, climate, topography, vegetation type, and soil type, the main factors that control the impacts on the soil system (Certini, 2005; Fernández-González et al., 2017; Whitman et al., 2019). Fire can lead to major shifts in highly heat-sensitive soil microorganisms; direct effects of fire provoke cell death, reduction in microbial biomass, and changes in microbial community composition and diversity (Dooley and Treseder, 2012; Weber et al., 2014). While bacteria have developed several mechanisms to deal with heating, the fungi kingdom has been found to be less resistant to fire disturbance (Ferrenberg et al., 2013; Pressler et al., 2019). Despite the protective mechanisms expressed in fire-adapted systems, post-fire soil conditions ultimately mediate the soil microbial community composition shifts (Prendergast-Miller et al., 2017; Li et al., 2019). Soil pH, which usually increases due to ash incorporation to the soil, as well as soil nutrient state, have been described as major drivers in soil microbial populations (Pérez-Valera et al., 2019; Adkins et al., 2020). Indeed, the post-fire vegetation recolonization indirectly affects microbial communities by influencing soil properties, which is of special relevance in the Mediterranean ecosystem in which numerous plant species exhibit adaptive mechanisms to persist the fire and regenerate after it (Pausas et al., 2009; Moya et al., 2021). Moreover, ecosystem functions performed by microbial communities are tied to the soil status after the fire (Pérez-Valera et al., 2020), and tend to recover quickly thanks to resistance and resilience of soil biota to abiotic disturbances and the functional redundancy of microbial taxa (D'Ascoli et al., 2005; Mendes et al., 2015). However, further disturbances such as post-fire management practices may place additional pressure on the recovery ability of the ecosystem.

Salvage logging (SL), one of the most common management strategies after wildfire, and primarily used to recover timber values, has numerous benefits as the economics, the reduction to fire recurrence, or the reduction in safety hazards (Lucas-Borja et al., 2020). However, by increasing soil compaction and modifying the hydrological response during the logging operations, negative impacts affecting vegetation structure and soil degradation have been often reported (Morgan et al., 2015; Slesak et al., 2015). Alterations in the microbial properties have been also registered after post-fire logging operations, e.g., lesser microbial activity and biomass (García-Orenes et al., 2017), impact on CO_2 emission (Hartmann et al., 2014) and adverse consequences for microorganisms involved in N cycling according to Pereg et al. (2018). Soil compaction, the major disturbance associated to salvage logging, implies the collapse of soil structure reducing water and air conductivity, and ultimately the loss of multiple microenvironments that ensure long-term microorganism proliferation and diversity (Rabbi et al., 2016). Consequently, the soil system can suffer substantial and persistent alterations, which ultimately reduce forest productivity and ecosystem functionality via modifications in the microbial community composition and diversity (Hartmann et al., 2014; Chen et al., 2015). However, the effects of post-fire management on microbial community composition and structure, and its consequences for ecosystem recovery, remain partially unknown, being especially important in Mediterranean forests where soils are prone to degradation.

Ecosystem resilience is tied to its disturbance history. Increasing disturbance stress could lead ecosystems to lose the adaptive capacity and threaten their toleration to further perturbations (Villnäs et al., 2013). Therefore, a combination of wildfire and an aggressive post-fire management might shift the ecosystem to another state, exceeding the capacity for the ecosystem recovery (Ammitzboll et al., 2021). In a context of increasing frequency and severity of forest fires and climate change (Moreira et al., 2020), understanding how shifts in soil microbial communities contribute to the ecosystem functioning could help to evaluate the capacity to recover of a system after a disturbance and also guide the post-fire restoration strategies.

The use of high-throughput sequencing approaches can be suitable to assess the effects of the forest management on soil microbial communities in soils previously affected by a wildfire. It was hypothesized that the salvage logging management, additional pressure to fire disturbance, will cause a shift in soil microbial community resulting in a less diverse community. In addition, the microbial functionality in the post-fire managed soils will diminish in comparison to those of non-intervention where all burnt trees were left standing. Therefore, the objectives were: (1) to ascertain the effects of SL post-fire management on the composition and structure of soil bacterial and fungal communities and their associated functions, and (2) to identify the soil factors related to shifts in soil microbial communities and their functionality.

2. Material and Methods

2.1. Study site

The study area is located in "Sierra de Mariola Natural Park" in Alcoy, Alicante, in E Spain (38°43′59″ N, 0°29′16″ W). Climate in the area is Mediterranean, 3–4 months of summer droughts, dry-hot summer, and wet-warm spring, autumn and winter. The precipitation concentrates in October–November with an annual average of 490 mm, and mean temperature is 15.2 °C. The soil is classified as a Typic Xerorthent (Soil Survey Staff, 2014) developed over marls with low depth, very vulnerable to erosion and degradation processes, characterized by clay loam texture with 40, 25 and, 35% of sand, silt and clay respectively, and 40% of carbonates. The landscape is characterized by terraced hillslopes. The forest is composed mainly of *Pinus halepensis* Mill. trees, around 40 years of age, together with an understory of typical Mediterranean shrubs species such as *Quercus coccifera* L., *Rosmarinus officinalis* L., *Thymus vulgaris* L., and *Brachypodium retusum* (Pers.) Beauv.

The forest fire occurred in July 2012 affected a total of 546 ha. Fire severity was moderate according to Keeley (2009); as all understory plants were charred or consumed, fine dead twigs on soil surface were consumed and log charred, also the pre-fire soil organic layer was largely consumed. The forest lacked any pre-fire management. Seven months after the wildfire, in February 2013, salvage logging (SL) was carried out, consisting of a complete extraction of the burned wood using heavy machinery. The burnt trees were cut down with a chainsaw and dragged with chains at the top of the slope where a processor removed limbs and treetops. After an extreme rainy event in September 2013 (50 mm in less than 3 h), some gullies were formed as a consequence of the vulnerability of soils to erosion where the trunks were dragged.

2.2. Experimental design and soil analysis

Soil sampling was conducted in May 2014, just after 22 months had passed since the fire and 15 months since the implementation of the salvage logging management (SL). Sampling plots were established the same day of SL implementation as a part of a previous study to monitor plant and soil recovery after the wildfire and post-fire management (García-Orenes et al., 2017). Six sampling plots (3 m × 3 m), with a minimum distance of 15 m between them, were randomly established in a burnt affected area of 2500 m^2 where SL was carried out. Another six sampling plots in a nearby-burnt area comprising the same area and aspect where burned wood remained for investigation purpose were established as the untreated control (C). Within each plot, one composite sample comprised of five subsamples were randomly collected from the A horizon mineral (5 cm depth). The selection of the sampling depth was decided after estimations of the averaged mineral soil depth directly affected by the SL treatments (García-Orenes et al., 2017). According to the vegetation survey carried out in the same area, a significantly higher recovery of plants in terms of evenness in control plots was reported after 15 months since the SL operations (for further details see García-Orenes et al., 2017).

For each soil sample, a first portion was frozen at –20 °C for DNA extraction and a second one was kept at 4 °C for biochemical analysis. The remainder was dried at room temperature and sieved a part between 4 and 0.25 mm for aggregate stability tests and the remaining at 2 mm for the rest of the physicochemical analyses. Soil pH and electrical conductivity were measured in a 1:2.5 and a 1:5 (w/v) aqueous extract, respectively. Soil organic carbon was determined by the potassium dichromate oxidation method (Nelson and Sommers, 1983); total nitrogen was analysed by the Kjeldahl method (Bremner and Mulvaney, 1982); and available phosphorus was determined by the Burriel-Hernando method (Burriel and Hernando, 1950; Díez, 1982). Aggregate stability was measured using the method of Roldán et al. (1994) based on the method of Benito and Díaz-Fierros (1989). This method examines the proportion of aggregates that remain stable after a soil sample is subjected to an artificial rainfall of known energy (279 $J\ min^{-1}\ m^{-1}$). In a 1:5 (w/v) aqueous extract, water soluble carbohydrates were determined in using the anthrone method as reported by Brink et al. (1960). Soil moisture was analysed from field wet soils by gravimetry after heating for 24 h at 105 °C.

Soil microbial biomass carbon was estimated by the substrate-induced respiration (SIR) method using glucose (3 mg per gram of soil) as the available substrate (Anderson and Domsch, 1978). Soil basal respiration was measured by incubating soil moistened to 60% of its water holding capacity. The amount of CO_2 emitted during both incubations was determined by an automated impedance meter (BacTrac 4200 Microbiological Analyser, Sylab, Austria) based on the changes in the impedance of a KOH solution (2%).

Urease and protease activities were determined as described by Kandeler et al. (1999) using as substrates urea or N-α-benzoyl-l-arginine amid, respectively (Nannipieri et al., 1981). β-Glucosidase and alkaline phosphomonoesterase activities were quantified colorimetrically as the p-nitrophenol produced during the incubation of soil with the substrates p-nitrophenyl-β-d-glucopyranoside (Tabatabai, 1983) and p-nitrophenyl phosphate disodium, respectively (Naseby and Lynch, 1997). Dehydrogenase activity was determined by colorimetric estimation of the reaction product INTF (iodonitrotetrazolium formazan) formed by reduction of the substrate INT (2-p-iodophenyl-3-p-nitrophenyl-5-phenyltetrazolium chloride), following the procedure described by García et al. (1997).

2.3. DNA extraction, amplification, and sequencing

DNA was extracted from 0.25 g of each soil sample using the DNA PowerSoil kit (Mo Bio, Carlsbad, USA), with the following modifications to the manufacturer's instructions: initial vortexing was at 300 rpm for 20 min (STD 3500 Shaker VWR) and DNA was eluted with 65 μL elution buffer. The selected primers for DNA metabarcoding library preparation were 341F and 806R to amplify a bacterial 16S rRNA fragment from the V3–V4 region; and ITS1F and ITS2 to amplify the complete fungal ITS1 region. The Illumina sequencing primers were attached to their 5′ ends. A mixture of 2.5 μL of the DNA template, 0.5 μL of the corresponding primers and 12.5 μL of Supreme NZYTaq 2× Green Master Mix (NZYTech) were contained for each PCR, and were diluted with ultrapure water to a total volume of 25 μL. For the PCR incubation program, an initial denaturation was fixed at 95 °C for 5 min, followed by 35 cycles of 95 °C for 30 s, 55 °C for 30 s, 72 °C for 30 s and a final extension step at 72 °C for 10 min. To multiplex different libraries in the same sequencing pool, the barcodes identifiers were attached in a second PCR round with identical conditions but only five cycles and 60 °C as the annealing temperature. The amplified DNA in equimolar amounts from each library was pooled according to the Qubit dsDNA BR Assay (Thermo Fisher Scientific, Waltham, MA, USA) results. Previously, each library was purified using the Mag-Bind RXNPure Plus magnetics beads (Omega Biotek Inc., Norcross, GA, USA) following the manufacturer indications. Finally, the equimolar pool was sequenced using an Illumina MiSeq sequencing platform (Illumina Inc., San Diego, CA, USA) with 2 × 300 base pair paired-end chemistry at the Australian Genome Research Facility (Brisbane, Australia).

Paired-ends reads were assembled by aligning the forward and reverse reads using PEAR (version 0.9.5) (Zhang et al., 2014). Primers were trimmed using Seqtk (version

1.0). Trimmed sequences were processed using Quantitative Insights into Microbial Ecology (QIIME 1.8) (Caporaso et al., 2010) USEARCH (version 8.0.1623) (Edgar, 2010; Edgar et al., 2011) and UPARSE software. Using USEARCH, tools sequences were quality filtered, full length duplicate sequences were removed and sorted by abundance. Singletons or unique reads in the data set were discarded. Bacterial and fungal sequences were clustered followed by chimera filtered using "rdp_gold" database and "Unite" database as reference, respectively. To obtain number of reads in each OTU, reads were mapped back to OTUs with a minimum identity of 97%. Taxonomy was assigned using Greengenes database (Version 13_8, Aug 2013) (DeSantis et al., 2006) for bacterial sequences and using Unite database (Unite Version7 Dated: 02.03.2015) (Kõljalg et al., 2005) for fungal sequences by QIIME.

2.4. Statistical analysis

The adjustment of data to a normal distribution was checked by Shapiro-Wilk's test and variables were transformed when necessary in order to assume statistical parametric assumptions. Analyses were performed using the RStudio (RStudio Team, 2020). The effect of the post-fire management (SL and C) in the variables was tested by t-test ($p < 0.05$), and Pearson's correlation coefficients were calculated to quantify the linear relationship between the physic-chemical and biological and biochemical soil properties using the RStudio function "cor".

Concerning microbial communities' datasets, the number of sequences per sample was rarefied to the lowest one and rarefaction curves were calculated (Fig. A1, Appendix A). The α-diversity estimators, including Shannon and Inverse Simpson, were calculated using the resultants OTUs after rarefying the number of sequences per sample, and t-test was used to assess significant differences between managements, both for bacteria and fungi (Fig. A2, Appendix A).

To analyse the β-diversity, non-metric multidimensional scaling (NMDS) was performed for bacterial and fungal communities in order to obtain the spatial distribution of their communities. With this aim, the "metaMDS" function implemented in "vegan" package for R was used. The effect of the management factor on the microbial communities' composition and structure were confirmed by permutational multivariate analysis (perMANOVA) with the "adonis" function using 9999 permutations.

To assess the relationships between the structural variability of bacterial or fungal communities and soil physicochemical and biochemical properties, canonical correspondence analyses (CCA) were carried out. In order to avoid multicollinearity, the variance inflation factor (VIF) was calculated and variables with a VIF > 10 were sequentially removed, and the remaining variables were then subjected to a forward selection procedure to select the subset of constraining variables that better explain the communities' variation in the CCA final model. The significance of the CCA final models was tested by Monte-Carlo permutational test (999 permutations).

An indicator species analysis (ISA) was conducted with the "indicspecies" package for R in order to identify indicator taxa characteristic of the bacterial and fungal communities (Rodríguez-Caballero et al., 2017b; Pérez-Izquierdo et al., 2020). The relative abundances of microbial families and OTUs in each sample were used to calculate the Indicator Value (IndVal) and its significance.

3. Results

3.1. Soil physic-chemical, biochemical, and biological properties

The results showed a significant effect of the SL management on all the soil parameters (Table 1). The SL management provoked a decrease in the soil nutrients, a reduction of 60% of organic matter and nitrogen, around 80% for the available phosphorus, and in the soil structure with lower aggregate stability. Additionally, the microbial biomass carbon and basal respiration showed the negative impacts of SL management with lesser values for both parameters. The same pattern was found for all the enzymatic activities measured in this study, dehydrogenase, urease, protease, alkaline phosphomonoesterase, and β-glucosidase. Most of the biological and biochemical soil properties were highly influenced by the soil physic-chemical properties, positively correlated with the soil nutrients and the aggregate stability of soils, and negatively correlated with the pH (Table 2).

Table 1. Physical-chemical, biological and biochemical properties of control (C) and salvage logging (SL) soils.

	Control	**Salvage logging**
pH (H_2O, 1:5)	8.12 ± 0.07b*	8.35 ± 0.09a
Electrical conductivity (S/cm)	216 ± 53b	151 ± 10a
Organic Matter content (%)	7.25 ± 1.36b	2.80 ± 0.87a
Total Nitrogen (%)	0.29 ± 0.05b	0.12 ± 0.02a
Available phosphorus (mg kg^{-1})	37 ± 14b	6 ± 3a
Aggregate stability (%)	85.9 ± 2.0b	70.8 ± 4.5a
Water soluble carbohydrates (mg kg^{-1})	62 ± 26b	37 ± 12a
Basal soil respiration (µg C-CO_2 h^{-1} g^{-1} soil)	2.37 ± 0.54b	1.52 ± 0.38a
Microbial biomass carbon (mg C kg^{-1} soil)	1160 ± 162b	568 ± 85a
Dehydrogenase (µg INTF g^{-1})	30.0 ± 4.4b	16.7 ± 1.6a
Urease (µmol N-NH_4^+ g^{-1} h^{-1})	1.12 ± 0.38b	0.57 ± 0.21a
Protease (µmol N- NH_4^+ g^{-1} h^{-1})	0.74 ± 0.22b	0.38 ± 0.12a
β-glucosidase (µmol PNP g^{-1} h^{-1})	2.12 ± 0.44b	0.73 ± 0.23a
Alkaline phosphomonoesterease (µmol PNP g^{-1} h^{-1})	5.64 ± 1.43b	2.32 ± 0.41a

*Mean ± standard deviation. Values in rows sharing the same letter do not differ significantly ($p < 0.05$) as determined by the t-test.

Table 2. Correlation coefficients (r values) for relationships between the physical-chemical soil properties and the biological and biochemical properties.

	pH	Electrical conductivity	Water soluble carbohydrates	Aggregate stability	Available phosphorus	Organic Matter	Total Nitrogen
Basal soil respiration	-0.64*	ns	ns	ns	0.69*	0.78**	0.70*
Microbial biomass	-0.81**	0.72**	ns	0.92**	0.81**	0.79**	0.85**
Dehydrogenase	-0.71**	0.77**	0.74**	0.86**	0.77**	0.85**	0.90**
Urease	ns	0.66*	0.69*	0.70*	ns	ns	ns
Protease	-0.64*	0.82**	ns	0.79**	0.64*	0.62*	0.72**
β-glucosidase	-0.90**	ns	ns	0.82**	0.80**	0.81**	0.83**
Alkaline phosphomonoesterease	-0.86**	ns	ns	0.78**	0.73**	0.74**	0.78**

ns: not significant; * Significant at $p < 0.05$; ** Significant at $p < 0.01$

3.2. Bacteria diversity and community composition

Bacterial α-diversity was significantly different between managements (p-value < 0.05 in Shannon and Inverse Simpson indices, Fig. A2), with higher values for SL soils. In addition, the perMANOVA test on β-diversity confirmed that the soil bacterial community composition and structure were significantly different between the SL and C managements ($F = 3.98$, p-value = 0.006). The spatial ordination of the bacteria communities (stress value of 0.046) showed that the communities of SL and C soils clustered separately along the X axis (Fig. 1).

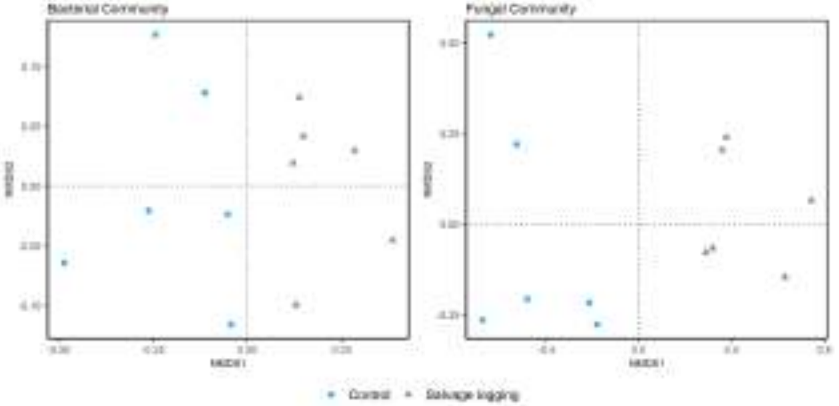

Fig. 1. Two-dimensional non-metric multidimensional scaling (NMDS) ordination based on Bray-Curtis dissimilarities at OTU level for bacterial and fungal communities of control (C) and salvage logging (SL) soils.

The taxonomic profile at the phylum level (Fig. 2) showed Actinobacteria and Proteobacteria as predominant phyla, altogether representing around 70% of the total abundance. At the order level, Actinomycetales (Actinobacteria) was the most abundant followed by the abundance of Solirubrobacterales (Actinobacteria), Sphingomonadales and Rhizobiales (Alphaproteobacteria). At the family level, Sphingomonadaceae and Streptosporangiaceae were the most abundant (Fig. A3, Appendix A). The relative abundance of the main phyla shifted after SL application. A significant decrease in Actinobacteria (44.94% in C, 37.62% in SL), Firmicutes (9.47% in C, 4.96% in SL), Bacteroidetes (4.31% in C, 3.10% in SL), and Verrucomicrobia phyla (1.62% in C, 1.11% in SL) were observed in SL soils with respect to C soils, whereas an increase of relative abundance was detected for Acidobacteria (4.02% in C, 8.06% in SL), Chloroflexi (4.45% in C, 7.34% in SL), and Gemmatimonadetes (3.75% in C, 4.79% in SL).

The indicator species analysis (ISA) showed higher number of indicator taxa in SL soils, at OTU level with 235 for C and 589 for SL, and at the family level, 40 and 154 for C and SL of bacterial indicator families (Table A1). The most abundant indicator families for the bacterial community of C soils were Streptosporongiaceae (12.6%), Bacillaceae (5.2%), Oxalobacteraceae (2.7%), Cytophagaceae (3%), Conexibacteraceae (1.3%), and Bifidocteruaceae (1%). Among the indicator families for the bacterial community of SL soils, those with the most relative abundance were Gaiellaceae (3%), Hyphomicrobiaceae (1.4%), Rhodospirillaceae (1.4%), and C111 (1%).

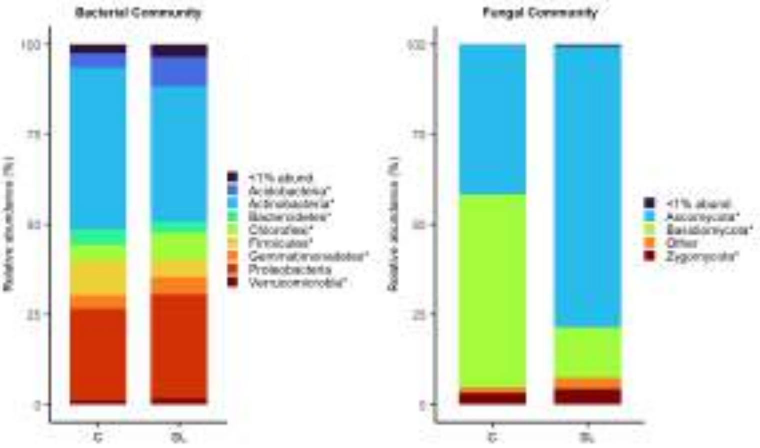

Fig. 2. Relative abundances of the dominant bacterial and fungal phyla of control (C) and salvage logging (SL) soils. For each phylum, significant differences were assessed by the t-test calculated at $p < 0.05$ and indicated by an asterisk

3.3. Fungal diversity and community composition

The α-diversity analyses for the fungal communities showed significant differences for the Shannon and Inverse Simpson indices between the managements, reaching the highest values in SL soils (p-value < 0.05, Fig. A2). The β-diversity was also significantly different between the managements according to the perMANOVA test (F = 9.83, p-value = 0.002). In the NMDS analysis (stress value of 0.060), the fungal communities cluster differently by the management along the X axis (Fig. 1).

At phylum level, the fungal taxonomic profile dominance was reduced in both soils to two phyla, Ascomycota and Basidiomycota, representing together more than 90% of the relative abundance (Fig. 2). The dominance of the main phyla was shifted due to the SL management; whereas the Ascomycota increased after the SL management (41.53% in C, 78.08% in SL), a strong decrease was registered for the Basidiomycota (53.58% in C compared to 14% in SL).

According to the indicator species analysis (ISA) performed (Table A2) higher number of indicator taxa were found at the family level for SL soils. Two fungal indicator families were found in C soils, being Thelephoraceae (2%) the most representative, while 31 indicator families were statistically relevant in SL. The most abundant families included Trichocomaceae (27%), Chaetomiaceae (7.6%), followed with less abundance by Lasiosphaeriaceae (1.1%), Pezizaceae (1%), and Inocybaceae (1%).

3.4. Influence of soil properties in microbial communities

After a forward selection of the constraining variables, the CCA final model for the bacterial communities included the aggregate stability (AS) as the most explanatory environmental variable in the model (Fig. 3). The CCA final model explained 40.9% of the total inertia and the first two axes accumulated 57.7% of the variance in the bacterial communities, being the first CCA axis highly related to aggregate stability. The bacterial community from the C management clustered on the left-hand side of the plot, exhibiting higher values of AS than the SL management.

Concerning the fungal communities, the forward selection procedure reduced the constraining variables to aggregate stability (AS) and water soluble carbohydrates content (WSCH) (Fig. 3). The CCA final model explained 42.2% of total inertia, and the first two axis explained 64.7 and 35.3% of the constrained inertia, respectively. The constraining variables showing the most important relationship with the fungal community distribution along the first CCA axis were aggregate stability and water soluble carbohydrates. The fungal community of C soils was clustered on the left-hand side of the plot, some samples significantly influenced by higher AS and other samples with higher WSCH.

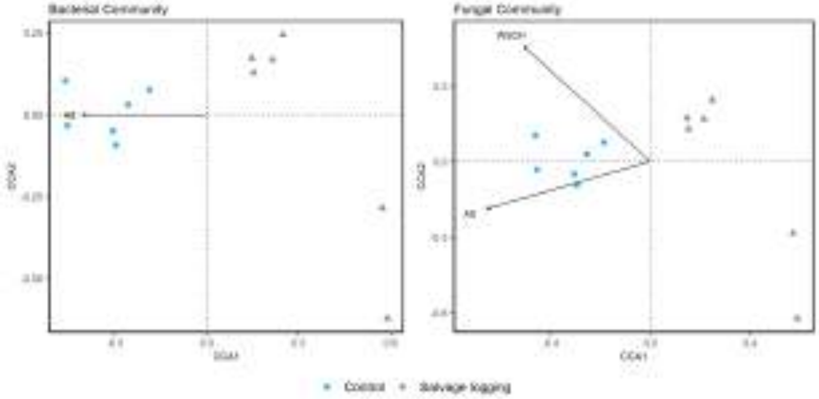

Fig. 3. Canonical correspondence analysis (CCA) at OTU level for bacterial and fungal communities of control (C) and salvage logging (SL) soils. The explanatory variables (arrows) are AS, aggregate stability, and WSCH, water soluble carbohydrates.

4. Discussion

The post-fire management based on salvage logging (SL), conducted seven months after the wildfire in a coniferous forest ecosystem, profoundly affected the structure and composition of the microbial communities placing additional pressure on the recently disturbed microbial communities. After a fire, the recolonization is pioneered by spore-formers or fast-growth strategies microorganisms adapted to the high release of nutrients of a post-fire environment, principally oxidizable carbon and inorganic nitrogen (Choromanska and DeLuca, 2002; Bárcenas-Moreno et al., 2011; Goberna et al., 2012). This fact might be related to the high dominance of Actinobacteria and Firmicutes bacteria phyla and Ascomycota and Basidiomycota fungi phyla in the soils unaltered by SL (C), all described as positively influenced by fire disturbances

(Ferrenberg et al., 2013; Prendergast-Miller et al., 2017; Pérez-Izquierdo et al., 2020). Moreover, the mosaic of soil patches, that offer the burned wood distribution, provides a variety of carbon substrates that promote specialization strategies (Miller and Chesson, 2009; Goldfarb et al., 2011), and simultaneously softens microclimatic conditions facilitating microbial development (Marañón-Jiménez et al., 2013). Thus, the patchiness (heterogeneity) of C soils was revealed by the higher dispersion of the bacterial community among their replication samples, as shown in the NMDS ordination plot. The high presence of Actinomycetales (Actinobacteria) in C soils, known as highly specialized in organic matter degradation, supports the idea of a profound specialization in response to a higher resource availability induced by the burned wood retention. It has been registered that microbial diversity tends to increase after a fire disturbance due to the alteration in resource supply and new habitat creation (Ferrenberg et al., 2013; Shen et al., 2016). After 22 months since the fire, the control soils registered lower α-diversity compared to soils where the salvage logging carried out. This practice, conducted seven months after the fire, might be increased the pressure in the affected-soil and lead to the microbial communities to a stage dominated by species more tolerant to disturbance (Tanentzap et al., 2013).

The implementation of salvage logging management triggered severe soil physic-chemical degradation with a critical decrease in the nutrient content and soil structure deterioration, favoured by the high vulnerability of soils developed over marls. García-Orenes et al. (2017), who studied the soil evolution affected by SL management in the same study area, registered an increase in bulk density and a decrease in aggregate stability, pointing out the low resistance and resilience of soil structure to mechanical stresses. The degradation of soil structure - promoted by the decrease in organic matter content and reduced plant development (Mataix-Solera et al., 2011) - resulted in the main driver in microbial community composition and structure shifts. Our findings are in accordance with Hartmann et al. (2014), who found soil compaction induced by logging operations provoked lower microbial abundances but increasing bacterial and fungal diversity associated with new niches related to anoxic habitats. In this sense, families with anaerobiosis characteristics Hyphomicrobiaceae, Hyphomonadaceae (Middleton et al., 2020), Syntrophobacteraceae (Liu and Conrad, 2017), or Kouleothrixaceae (Astorga-Elő et al., 2020) were more abundant in soils under SL management than in soils under C management. In addition to the soil physical deterioration, the depletion in C and N compounds as a consequence of the erosion triggered by the SL reduced the microbial populations sensitive to substrates availability (e.g., lower abundance of Actinomycetales in SL) and promoted instead certain phylotypes highly competitive in oligotrophic systems (e.g., Saprobic fungi, especially the Trichocomaceae family) (Fultz et al., 2016; Bastida et al., 2017). Studying the microorganisms involved in N cycling in the same study area, Pereg et al. (2018) found that the lower abundance in soils affected by SL was strongly related to the microaggregate fraction, described as a hotspot for nitrogen cyclers and bacterial biodiversity (Rabbi et al., 2016). The better vegetation development in C soils (García-Orenes et al., 2017) might have enhanced the soil structure recovery, influenced as well by the microbial biomass growth (De Gryze et al., 2005; Hart et al., 2005). The removal of host plants dependent on ectomycorrhizal fungi (mainly Basidiomycota) by SL management altered the fungal community composition (Kennedy and Egger, 2010). On the contrary, Ascomycota increased proportionally in SL soils, possibly as a result of plant detritus and woody debris supply to the soil after logging operations (Fraterrigo et al., 2006; Chen et al., 2017; Rasmussen et al., 2018).

Whereas an increase of the alpha diversity was detected for the soil microbial community affected by SL, lesser microbial functionality was registered compared to soils with burned wood maintenance (C). Values for the parameters that act as indicators of general microbial activity, as microbial biomass carbon and basal respiration, as well as the specific parameters of microbial performance, the enzymatic activities, suggest a loss in the ecosystem functions performed by the soil microorganisms. In fire-adapted Mediterranean ecosystems, short-time recovery of soil microbial community, and the ecosystem functions they deliver, are usually reported (Prendergast-Miller et al., 2017; Rodríguez et al., 2018; Pérez-Valera et al., 2019). However, subsequent disturbances are susceptible to alter profoundly the soil microbial community and then the ecosystem functioning (Hooper et al., 2005; Allison and Martiny, 2008). It is well known that the biodiversity is key to maintain ecosystems functioning (Mendes et al., 2015), however ecosystems are valued for multiple ecological functions (i.e., multifunctionality) and other major microbial drivers of soil biodiversity are responsible as well for ecosystem functioning, e.g., species abundance or species composition (Maestre et al., 2012; Delgado-Baquerizo et al., 2017). According to that, Villnäs et al. (2013) argued the effects on ecosystem functioning after multiple disturbances depends on the specific species lost and the functional traits they express in the environment. In this regard, a greater number of microbial indicator taxa associated with SL soils were largely unidentified or unclassified taxa, and thus not known functions are associated to them. Although their functions are yet to explore, rare taxa could be driving the functional response in SL disturbed soils, acting as a reservoir that can rapidly respond to environmental changes (Lynch and Neufeld, 2015).

The fire-affected soils with burned wood maintenance presented higher contents of nutrients and a more stable structure than the soil under SL management, which was associated with a greater abundance of microorganisms with the ability to degrading the organic matter compounds. In this sense, the presence of Actinomycetales (Actinobacteria) in C soils was highly representative thanks to their important role in decomposition of labile (Goldfarb et al., 2011) and recalcitrant organic substances (Mokni-Tlili et al., 2020). Families found as relevant were Streptosporangiaceae as cellulose destructor (Wei et al., 2020), the Microbacteriaeae as lignocellulose decomposer (Argiroff et al., 2019); and the Coriobacteriaceae both labile carbon and cellulose decomposer (Goldfarb et al., 2011). Other Actinobacteria taxa, reported as pioneers in extreme environments, were representative in C soils, e.g., Geodermatophilaceae (Xing et al., 2020) and Cellulomonadaceae after wildfires (Aanderud et al., 2019). Firmicutes phyla reached high relevancy in C soils with special dominancy of family Bacillaceae, whose species have reported the ability to degrade hydrocarbons accumulated during fires (Xiang et al., 2014) and fix nitrogen (Yeager et al., 2005). The families of Bacteroidetes Cytophagaceae and Sphingobacteriacea, both indicators taxa in C soils, are related to organic matter enrichment in soils (Fierer et al., 2012; Hellequin et al., 2018). Among indicator taxa of Proteobacteria in C soils, Burholderiales and Oxalobacteraceae (Betaproteobacteria) are families positively affected by fires with the ability to degrade labile and recalcitrant carbon substances (Aanderud et al., 2019; Puentes-Téllez and Salles, 2020; Stinca et al., 2020), and Desulfovibrionales (Deltaproteobacteria) as lignin degrader.

Bacterial taxa positively associated with the SL management were assigned mainly to families of Acidobacteria, Chloroflexi, and Alpha-, Delta- and Gamma-proteobacteria. Among the families with recognized functions, bacteria associated with anaerobic respiration significantly increased in SL soils, highly represented by Gram-negative bacteria (Fraterrigo et al., 2006). Bacteria families with these characteristics in SL soils were the nitrate reducers and denitrifiers Hyphomicrobiaceae and Hyphomonadaceae (Alphaproteobacteria) (Middleton et al., 2020); the sulfate reducers in anoxic environments Syntrophobacteraceae (Deltaproteobacteria) (Liu and Conrad, 2017); the anoxygenic but potential N fixer Chloroflexaceae (Chloroflexi) (Xun et al., 2018); and Kouleothrixaceae (Chloroflexi), carbon degrader in anoxygenic environments (Astorga-Eló et al., 2020). Induced by the stressful conditions after SL performance, the families radiation-resistant Deinococcaceae and Trueperaceae (Thermo) prospered (Maier et al., 2018). Gaiellaceaem (Actinobacteria) was previously reported as an indicator of specific anthropogenic activities in Hermans et al. (2017), and the predators Myxococcales members (Haliangium) survive in oligotrophic and anaerobic environments (Li et al., 2017; Wang et al., 2020).

After the wildfire, Ascomycota and Basidiomycota were dominant phyla in soils, but SL significantly shifted the community composition favouring the Ascomycota dominance. Similar results have been previously reported after different forest management (Fraterrigo et al., 2006; Hartmann et al., 2014; Smith et al., 2017). Ascomycetes express high tolerance to environmental stress, playing a dominant role under scarce resource availability (Bastida et al., 2017; Huang et al., 2021). In SL soils, almost all the indicator taxa were saprophytes fungi, except the Pezizezae family that is an ectomycorrhizal group associated with post-fire environments (Pérez-Izquierdo et al., 2020). Saprophytes play an important role in organic matter decomposition making nutrient available, and some of the indicator taxa associated to low nutrient content and stressful conditions were the family Verrucariaceae (Prieto et al., 2012); the Herpotrichiellaceae and Chaetothyriales families, and Sordiales and Hypocreales orders (Ma et al., 2018; Praeg et al., 2020; Huang et al., 2021). Trichocomaceae, saprobic fungi with a ruderal lifestyle (Houbraken and Samson, 2011), was the most abundant family among all the indicators taxa, together with Chaetomiaceae, cellulotic fungi that degrade plant material (Habtewold et al., 2020). On the other hand, Thelephoraceae was the only indicator family in C soils, found as favoured in fire Mediterranean forests (Buscardo et al., 2014; Pérez-Izquierdo et al., 2020), but negatively related to thinning and frequently after prescribed burning (Rasmussen et al., 2018).

5. Conclusions

Salvage logging as post-fire management is a major problem for vulnerable soils to erosion. Performed seven months after the wildfire, the forest management placed additional pressure on soils recently disturbed, compromising the capacity of the fire-adapted ecosystem recovery. The deterioration of soil structure profoundly and persistently altered the soil microbial community composition and structure. Despite the higher diversity found in soils affected by salvage logging, the indicator species reveal that new habitats related with transient environmental conditions were created due to the logging operations. Indeed, the aggregate stability of soils, better conserved in non-intervention soils, resulted in the best soil variable to predict the microbial communities shifts. Increasing intensity and severity of wildfires in the fire-adapted Mediterranean ecosystem, in a global change scenario, demand a better understanding of the relationship between disturbances caused by forest management and soil biodiversity, thus better predicting the resilience of the soil microbial response to future disturbances.

CHAPTER 4

The role of mosses in soil stability, fertility and microbiology six years after a post-fire salvage logging management

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This chapter corresponds to the article:

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. Journal of environmental management, 262, 110287. doi:10.1016/j.jenvman.2020.110287

Abstract

After a wildfire, moss crust develops in early post-fire stages revealing important roles related to soil erosion prevention and increase of soil fertility. However, the post-fire management selected could determine the capacity of soil to recover and the active role of mosses in the ecosystem recovery. Salvage logging (SL) was performed in the wildfire that occurred in July 2012 in "Sierra de Mariola Natural Park" (E Spain), with detrimental consequences to soils in the short-term. The aim of the study is to assess if the presence of a biocrust dominated by mosses six years after the wildfire improved the soil quality and functions, and if the salvage logging management influenced the process. Our results showed that the SL management affected in a medium-term to the percentage of soil covered by mosses, reaching 78.4% in control soils compared to 56% in SL soils. Regarding the influence of mosses in soils, our results did not show greater differences in the physical parameters measured, hydraulic conductivity, water repellency and soil penetration resistance, possibly related to the lower developmental stages of the biocrust. However, it was observed that the presence of mosses played a significant role in both the soil fertility and the microbial activity. The improvement in soil fertility was registered mainly in the organic carbon, nitrogen, and phosphorous contents, and for the microbial parameters, for which higher values for the microbial biomass carbon and basal soil respiration were reached in soils under mosses. In conclusion, we can suggest that mosses had an important role in the functional recovery of degraded ecosystems after wildfires, and therefore we encourage considering the presence of mosses in the post-fire managements.

1. Introduction

Biological soil crusts (BSCs) are a community of organisms composed mainly by cyanobacteria, lichens, and mosses, which inhabit the soil surface (Belnap and Lange, 2003). Although they are particularly important in drylands, BSCs are present in most environments. BSCs have key roles for the health and functionality of the ecosystems, improving soil structure and stability, influencing the local hydrologic cycles (Belnap, 2006), enhancing fertility and nutrient fixation (Belnap et al., 2001), increasing the biodiversity of soil microbial community (Xiao and Veste, 2017) and enabling plant establishment and growth (Muñoz-Rojas et al., 2018).

Biocrust are sensitive to disturbances, and wildfire induces severe impacts on them; biomass, cover and diversity use to decline dramatically (Johansen, 2001). Low-intensity fires were observed to have much less drastic effects (Bowker et al., 2004), although repeated burning by changes in fire regimes may destroy structures of soil organisms and threaten biocrust recovery (Greene et al., 1990; Hilty et al., 2004; Root et al., 2017). The recovery rates after a wildfire, in particular, will depend on fire severity and frequency, climatic conditions, topographical conditions, the availability of inoculant material and the adaptation of the biocrust community to fires (Weber et al., 2016). Mosses have been described as faster colonizers after wildfires creating a dense layer that precedes the establishment of vascular vegetation, also in the temperate Mediterranean forest (De las Heras et al., 1994; Castoldi, 2013; Silva et al., 2019). This could suggest a relative role of mosses in early post-fire stages.

After a wildfire, the soil surface is exposed due to the absence or low vegetation cover (Bowker et al., 2008), very vulnerable to rainfall events, runoff and erosion processes (Chamizo et al., 2015). The presence of mosses in the first stages after wildfire provides high protection against the raindrop impacts and contributes to the roughening of the soil surface, which increases the water retention time hence leading to an improvement of the infiltration rates (Rodríguez-Caballero et al., 2015). Moreover, soils covered by mosses register fertility increases (Guo et al., 2008). However, additional disturbances associated with the restoration methods could negatively affect the development of the biocrust and, ultimately, hinder ecosystem recovery (Hilty et al., 2004). Reductions in cover, richness, and diversity have been reported in mosses under different forest management in few studies: clear cutting (Paquette et al., 2016); harvesting (Caners et al., 2013), or salvage logging (Bradbury, 2006; Pharo et al., 2013).

Post-fire management is an important factor that will determine the capacity of soil to recover from degradation, together with fire history, ash properties, topography, post-fire weather, and vegetation recuperation (Pereira et al., 2018). Mediterranean ecosystems are resilient to fire disturbance. Hence, only when high severity fires could cause strong soil degradation, post-fire interventions should be planned to decrease the negative impacts, based on sustainable practices aimed at the maintenance and improvement of soil ecosystems services and to increase the resilience of forest to fire.

Salvage logging (SL) is common management after a wildfire worldwide. However, multiple studies in the recent decades have reported negative impacts on plant regeneration and diversity (Beschta et al., 2004), soil erosion (Slesak et al., 2015), detrimental effects on microbial biomass and activity (Marañón-Jiménez et al., 2011), and impacts on nutrient cycling (Serrano-Ortiz et al., 2011; Pereg et al., 2018). SL can be very aggressive if soils are vulnerable to erosion and depending on the way to perform it. Whereas Francos et al. (2018) reported non-detrimental effects on the soil by manual log, the use of heavy machinery has reported adverse effects in several studies (Wagenbrenner et al., 2016; García-Orenes et al., 2017).

Little is known about the effects of the presence of a biocrust and their active role in the recovery of a soil affected by wildfire and post-fire management disturbances. Considering their highly relevant ecological functions, we hypothesize that the presence of a biocrust may improve the functional recovery of degraded soils, and thus, the ecosystem. For this purpose, we studied the role of a biocrust dominated by mosses in a soil affected by an aggressive post-fire salvage logging management six years after the disturbances (fire and SL). We assessed their influence in the soil attending to their role in soil stability studying relevant physical properties, their impact on soil fertility and the effects on the microbial activity. The aim of the research is to provide greater information to support the understanding of the function of mosses in the ecosystem recovery in order to improve post-fire management knowledge.

2. Material and methods

2.1. Site description

The study area is located in "Sierra de Mariola Natural Park" in Alcoy, Alicante, in E Spain (38°43′59″ N, 0°29′16″ W). Climate in the area is Mediterranean, 3–4 months of summer droughts, dry-hot summer, and wet-warm spring, autumn and winter. The precipitation concentrates in October–November with an annual average of 490 mm, and mean temperature is 15.2 °C. *Pinus halepensis* Mill. trees around 40 years old are the main components of the forest, together with an understory of typical Mediterranean shrubs species such as *Quercus coccifera* L., *Rosmarinus officinalis* L., *Thymus vulgaris* L., and, *Brachypodium retusum* (Pers.) Beauv. The landscape is characterized by terraced hillslopes. The soil is classified as a Typic Xerorthent (Soil Survey Staff, 2014) developed over marls with low depth, very vulnerable to erosion and degradation processes, characterized by clay loam texture with 40, 25 and, 35% of sand, silt and clay respectively, and 40% of carbonates.

A wildfire occurred in July 2012 affecting a total of 546 ha. Fire severity was moderate according to Keeley (2009). All understory plants were charred or consumed, fine dead twigs on soil surface were consumed and log charred, also the pre-fire soil organic layer was largely consumed. Six months after the wildfire, in February 2013, SL management consisting of a complete extraction of the burned wood using heavy machinery was applied in a part of the affected forest. Due to the vulnerability of soils, the management resulted in rills formation. At present, six years after, the affected soils are mostly covered by vegetation, but bare soils remain in the burned area as a symptom of degradation.

2.2. Experimental design and sampling

Two adjacent study areas of 2500 m^2 each were established, one of them where SL management, consisting of complete extraction of the burned wood using heavy machinery, was carried out, and the other in a similar nearby area where no intervention took place (all trees left standing), referred as control (C).

Previous to the soil sampling, a vegetation cover study was conducted in both areas using a 50 cm × 50 cm quadrat divided into 100 cells. The quadrat was distributed randomly in the area managed by SL ($n = 25$) and control area ($n = 25$) to sampling total and moss covers.

For the study, we compared the soils covered by a dense layer of mosses to bare soils, or barely covered by vegetation, considered a symptom of remaining soil degradation (Fig. 1). For field measurements and soil sampling, 100 points were randomly distributed, 50 points for each management, SL and C, 25 replicates over mosses and 25 over bare soils for both management. Soil samples were taken from the upper soil layer (0–2.5 cm) since the influence of the mosses in soils is concentrated in the first centimeters of topsoil.

Fig. 1. Detail of the spatial distribution of mosses and bare soils in the field.

2.3. Field measurements

A Mini-Disk Infiltrometer (MDI) (Decagon Devices, 2018) was used to measure hydraulic conductivity (K) due to its small size and easy handling (Robichaud et al., 2008), and according to its technical manual and equations proposed by Zhang (1997). The volume of water infiltrated was recorded every 30s and at least 10 min. Water repellency (WR) in soils and mosses was assessed in the field by the Water Drop Penetration Time (WDPT) test (Wessel, 1988), taking the average time for 5 drops as the WDPT value of a sample. Soil penetration resistance (PR), representing the pressure applied to the soil surface before it breaks, was measured in each point in 2 cm intervals by 5 pseudoreplicates, using a field penetrometer (Geotester Pocket Penetrometer, Italy) (Zaady and Bouskila, 2002).

2.4. Laboratory analysis

Samples were divided into two subsamples, one subsample was stored at 4 °C and used for microbial analysis, and the other was air-dried at room temperature (20 °C), during 1–2 weeks until constant weight. A part was sieved between 4 and 0.25 mm to measure the aggregate stability (AS), and at < 2 mm for the chemical analysis.

Soil organic carbon (OC) was determined by the potassium dichromate oxidation method (Nelson and Sommers, 1983); total nitrogen was determined by the Kjeldahl method (Bremner and Mulvaney, 1982); and available phosphorus was determined by the Burriel-Hernando method (Díez, 1982). The aggregate stability (AS) was measured by the method of Roldán et al. (1994), based on the method of Benito and Díaz-Fierros (1989). This method examines the proportion of aggregates that remain stable after a soil sample is subjected to an artificial rainfall of know energy (279 J/min/m). Available micronutrients Fe, Zn, Cu, and Mn were extracted by DTPA in a soil:solution ratio 1:2 and 2 h shaking at room temperature, determined by atomic absorption spectrophotometry (AAS). The basal respiration (BR) of soil was measured in an automated impedance-meter (BacTrac 4200 Microbiological Analyser, Sylab, Austria), based on CO_2 emission by soil microorganisms at 30 °C for 24 h detected by indirect impedance measurement. Microbial biomass carbon (Cmic) was measured, also in the impedance-meter, as substrate-induced respiration with glucose (3 mg per gram of soil) as carbon substrate according to the Anderson and Domsch (1978).

2.5. Statistical analysis

For the study of vegetation cover, non-parametric Mann-Whitney U test was performed due to the lack of normality and homoscedasticity requirements. In the case of soil parameters, normal distribution was checked by Shapiro-Wilks test and variables were transformed when necessary in order to assume statistical parametric assumptions. In order to study the effect of factors in soil parameters, a two-way ANOVA test was performed considering two factors, management that include the levels SL and C, and the presence of not of a biocrust, with two levels, mosses (M) or bare soils (BS). Multiple comparisons were performed with Tukey's test ($p < 0.05$). A Principal Component Analysis (PCA) was performed to determine the effects of the management in the parameters analyzed. The physical parameters K, WR, PR, and AS were removed to simplify the overall analysis due to the low contribution with any principal components. The variables finally included in PCA were the chemical N, OC, P, Mn, Fe, Zn, Cu, and microbial Cmic and BR.

All these analyses were performed with a confidence level of 95% by Rstudio (2015) (Rstudio Team, Boston, USA), with "agricolae" package (De Mendiburu, 2019), and the PCA with "FactoMineR" (Lê et al., 2008) and "factoextra" (Kassambara and Mundt, 2017) packages.

3. Results

3.1. Vegetation and moss cover dynamics

The study of vegetation in the area showed a high percentage of total cover, with significant differences between managements, 93.8% in SL and 99.8% in C soils ($p < 0.05$). Differences between moss cover were more noticeable ($p < 0.05$), 56% (± 30.7) for SL in contrast to 78.4% (± 29.7) of cover in the no intervention area. The elevate variance was due to the high spatial variability of mosses in the field for both areas (for more details see Table B1, Appendix B).

3.2. Physical properties

The parameters measured showed low differences between the managements and the presence or absence of mosses covering the soil (Fig. 2). The hydraulic conductivity (K) results did not show significant differences, however, there is a slightly increasing trend of this parameter appreciated over mosses. In addition, mosses developed WR (mean values 10 s), while bare soils hardly ever showed repellency. Nevertheless, the maximum value for WR was 60 s, reveling that drop penetration was relatively rapid on both, over mosses and bare soils.

The resistance to penetration (PR) did not show differences for the managements and soil cover (moss or bare soil), with very low values (1.2–1.5 kg/cm^2). The same happened for the percentage of aggregate stability (AS), but in this case with high levels of aggregation (around 75%).

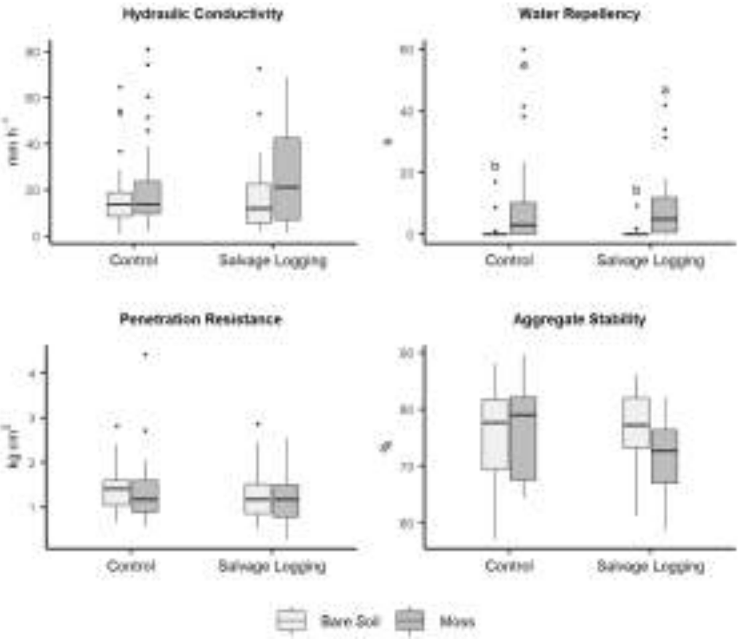

Fig. 2. Box-plots of hydraulic conductivity, K (mm/h); water repellency, WR (s); penetration resistance, PR (kg/cm^2); and aggregate stability, AS (%), measured in soils managed by salvage logging (SL) and control (C), on bare soils and on mosses. Points represent outliers, lowercase letters represent significant differences among mean groups (Tukey test, $p < 0.05$).

3.3. Soil fertility

The organic carbon, nitrogen and phosphorous contents concentrated in soils under mosses at depth 0–2.5 cm. The three parameters were significantly influenced by the presence of mosses covering the soil surface as we can see in Table 1. In addition, for OC and N, soils under mosses and without SL showed significantly higher concentration in relation to the managed: 3.16% in control soils in contrast to 2.36% in SL soils for the OC, and for N 2.26% in control soils and 1.99% for SL. In contrast, although higher values were recorded for P under mosses, values in SL were significantly higher than in C. An interaction between the two factors, management and presence of biocrust, was detected for the element.

Table 1. Mean and standard deviation values measured in soils managed by salvage logging (SL) and control (C) (factor management), on bare soils and on mosses (factor biocrust), two-way ANOVA results and significant differences at p <0.05*, p <0.01** and p <0.001***. n.s. not significant at a p <0.05. Lowercase letters represent significant differences among mean groups (Tukey test, p <0.05). (OC: organic carbon; N: total nitrogen; P: available phosphorous; Fe: iron; Zn: zinc; Cu: copper; Mn: manganese).

	Management	Biocrust	Mean	*sd*	Factors	p-value
OC	C	Bare Soil	2.44a	*0.87*	Management	***
(%)		Mosses	3.16b	*0.83*	Biocrust	***
	SL	Bare Soil	1.90a	*0.61*	Manag:Biocrust	n.s.
		Mosses	2.36a	*0.79*		
N	C	Bare Soil	1.79ab	*0.56*	Management	*
(%)		Mosses	2.26c	*0.55*	Biocrust	***
	SL	Bare Soil	1.56a	*0.41*	Manag:Biocrust	n.s.
		Mosses	1.99bc	*0.55*		
P	C	Bare Soil	6.15a	*4.37*	Management	n.s.
(mg/kg)		Mosses	7.99ab	*4.24*	Biocrust	***
	SL	Bare Soil	5.67a	*1.29*	Manag:Biocrust	*
		Mosses	11.36b	*7.03*		
Fe	C	Bare Soil	1.09a	*0.33*	Management	n.s.
(mg/kg)		Mosses	1.46ab	*0.62*	Biocrust	***
	SL	Bare Soil	1.25a	*0.43*	Manag:Biocrust	n.s.
		Mosses	1.75b	*0.92*		
Zn	C	Bare Soil	0.33a	*0.22*	Management	**
(mg/kg)		Mosses	0.32a	*0.16*	Biocrust	n.s.
	SL	Bare Soil	0.38ab	*0.11*	Manag:Biocrust	n.s.
		Mosses	0.53b	*0.30*		
Cu	C	Bare Soil	0.19b	*0.09*	Management	**
(mg/kg)		Mosses	0.11a	*0.06*	Biocrust	***
	SL	Bare Soil	0.26c	*0.08*	Manag:Biocrust	n.s.
		Mosses	0.12c	*0.07*		
Mn	C	Bare Soil	0.42ab	*0.55*	Management	***
(mg/kg)		Mosses	0.16a	*0.13*	Biocrust	n.s.
	SL	Bare Soil	0.90b	*0.44*	Manag:Biocrust	*
		Mosses	0.97b	*0.39*		

Micronutrients showed different behavior among them (Table 1). Fe showed the same pattern as P, influenced by the presence of the biocrust, with higher values under mosses, significant in SL soils. Zn was also accumulated under mosses but only in SL soils, showing significant influence by the management applied. In contrast to Fe and Zn, Cu values were two-fold significantly lower in soils under mosses. On the other hand, Mn contents were highly influenced by the management applied, showing significantly higher values regardless of the presence of mosses or not, but an interaction between management and mosses was detected.

3.4. Microbial parameters

Both microbial parameters measured showed the same pattern as can be observed in Fig. 3. Values for Cmic were significantly higher in soils under mosses, without differences between managements, 612 mg/kg in SL soils under mosses, two-fold higher than in bare soils (292 mg/kg), and 703 mg/kg in soils under mosses in C, more than 2.5-fold higher than in bare soils (267 mg/kg).

The microbial activity, reflected in the soil basal respiration (BR), showed significantly higher values in soils under mosses. No significant differences between managements were showed, 7.14 µg/h/g dry soil in control and 7.99 µg/h/g dry soil in SL, but with shorter differences with the bare soils in both cases.

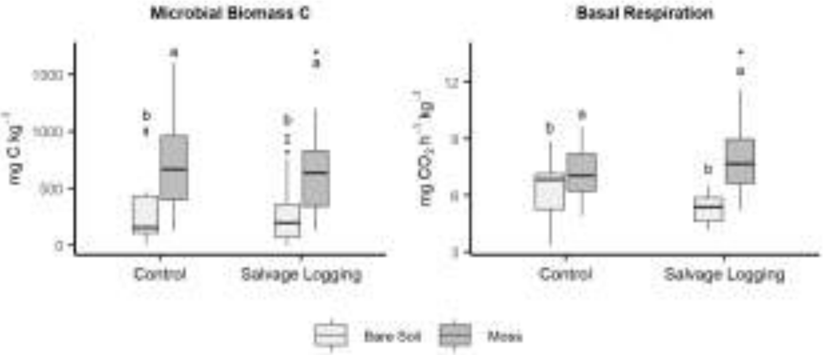

Fig. 3. Box-plots of microbial biomass carbon, Cmic (mg/kg), and soil basal respiration, BR (µg/h/g dry soil), measured in soils managed by salvage logging (SL) and control (C), on bare soils and on mosses. Points represent outliers, lowercase letters represent significant differences among mean groups (Tukey test, $p < 0.05$).

3.5. Multivariable analysis

The PCA showed chemical and microbiological properties explaining the relationships between the managements studied (Fig. 4). The model explained 70.2% of the total variation. In the first component, positively grouped with high loadings were N, OC, Cmic, highly influenced by the C management, and BR. Negatively correlated to them was Cu. In this first component, high loadings were also reached for Fe and P, mainly explained for the SL management. This also occurred for Mn and Zn variables grouped together in the second component, with the highest loading for the Mn element.

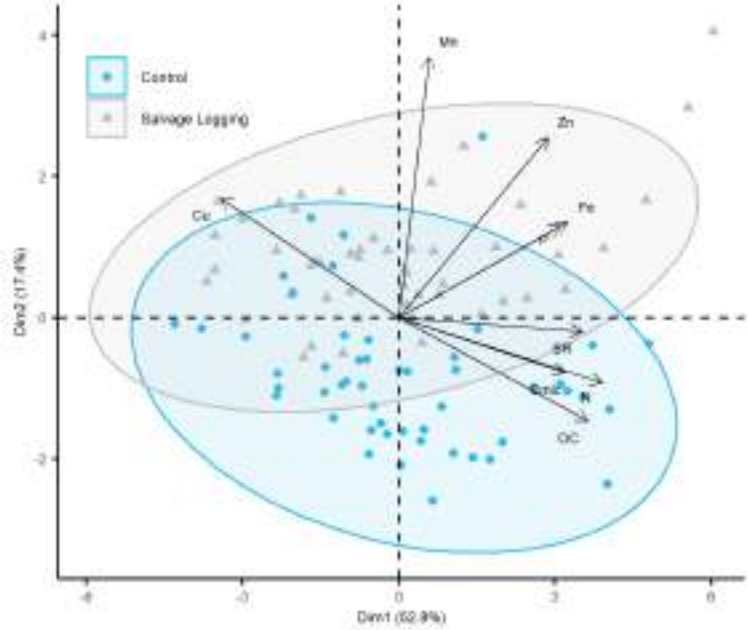

Fig. 4. Scores and loadings for PCA performed for control soils and salvage logging soils. (OC: organic carbon; N: total nitrogen; P: available phosphorous; Fe: iron; Zn: zinc; Cu: copper; Mn: manganese; Cmic: microbial biomass carbon; BR: soil basal respiration).

4. Discussion

Post-fire management selection will be crucial in how the ecosystem functionality will recover after a fire disturbance. Salvage logging practice has reported in several works detrimental effects that hamper the ecosystem recovery (Lindenmayer and Noss, 2006; Leverkus et al., 2014). In a study carried out in the same area by García-Orenes et al. (2017), after two years of monitoring since the management, the affected area registered adverse effects on the vegetation recovery, together with general soil degradation. Six years after the wildfire, our findings suggest that both areas, SL and C, are mostly recovered showing high levels of soils cover by vegetation (see also in Table B1). However, a high percentage of soils in SL were barely covered by dense vegetation, which is a symptom of degradation compared to C soils, a consequence of a very aggressive management. In addition, the post-fire SL was found to have a medium-term impact on the moss recovery. The percentage of cover could be decisive to reduce runoff since recent studies (Silva et al., 2019; Gao et al., 2020) suggest threshold values from which the presence of mosses could significantly reduce the sediment losses after the rain season. The negative effects on the recovery rate of bryophytes (liverworts, hornworts, and mosses) by SL management have been reported in other studies (Bradbury, 2006; Caners et al., 2013), highlighting the importance of maintaining the burned structures on topsoil since these acts as substrates that provide abundant resources to allow rapid dissemination.

Attending the physical parameters measured in soils and mosses, no greater differences were found six years after the disturbance. Immediately after the fire, the hydraulic properties of soils suffered important changes that can trigger erosion processes, due to the removal of protective vegetation, burning of organic matter that aggregates the soil and water repellency development (Shakesby, 2011). However, in medium-term hydraulic conductivity values did not show marked differences, which is in accordance with Robichaud et al. (2013) who using the MDI found that infiltration rates tend to recover in a short time after the wildfire. Nevertheless, the effects on the physical properties of SL are high depending on the type of soil and the equipment used (Fernández and Vega, 2016; Lucas-Borja et al., 2019a).

Disturbances in BSCs caused by logging and fire have demonstrated to increase soil erosion (Wilson, 1999). The main reason is BSCs play critical roles in soil stabilization and erosion prevention, especially by influencing in different aspects the hydrological cycles: modifications in soil porosity, absorptivity, roughness, aggregate stability, texture, and water retention (Belnap, 2006). The pass of the time affects how BSCs influence hydrological processes (Chamizo et al., 2016), therefore the early presence of mosses after the fire presumably helped to control the erosion by covering the soil. But 6 years after the disturbance may not be enough time to develop higher biomass and a complex structure that could significantly affect the hydraulic conductivity (Faist et al., 2017), although a tendency is marked.

Our soils rarely showed water repellency, in contrast to mosses with slight WR times, also reported in other studies (Kidron et al., 2010; Moore et al., 2017). The hydrophobicity expressed by mosses, combined with pore clogging, could generate important runoff responses depending on the rainfall intensity (Xiao et al., 2011). However, the slight hydrophobic characters shown in the study could have a positive effect and help to trap water near the soil surface enhancing infiltration (Faist et al., 2017), reducing losses by evaporation.

In the case of surface penetrability, our soils did not present soil sealing and physical crusting, showing low PR values. For BSCs, higher developmental stages are related to higher penetration resistance (Zaady et al., 2014; Chamizo et al., 2015). Therefore, six years after a perturbation may not be enough time to develop a complex state of the biocrust that could reach higher levels of compaction comparing to bare soils. Similar happened with the AS parameter. In a previous work (García-Orenes et al., 2017), a decrease of nearly 15% in AS was registered two years after the fire in soils affected by SL. A decrease in the aggregate stability of soil due to the combustion of organic matter after a fire can significantly trigger runoff processes (Mataix-Solera et al., 2011; Shakesby, 2011). At present, AS values have recovered due to the high content of organic carbon (2–4%) in the forest soils, reaching similar values to unburned soils in this area (Chrenková et al., 2014; Jiménez-Pinilla et al., 2016).

Severe events of wind and water erosion after a wildfire usually involve important soil losses with high quantities of nutrients. In our soils, the fast colonization of mosses covering the soil helped to retain ashes into the soil in multiple samples (personal observations), which is an essential process to boost the short and long-term ecosystem recovery after a wildfire (Caon et al., 2014). BSCs have reported increasing soil nutrients, considered patches of fertility in drylands (Belnap and Lange, 2003). In our results, soils under mosses showed a significant increase of nutrients compared to bare soils. Together with the retention of ashes into the soil, their ability to transform organic matter is related to the increase of nutrients in soils. In this sense, higher OC and N content linked to a higher developmental of mosses showed a significant correlation in the PCA in soils. The increase of fertility in soils, due to the presence and development of BSCs, has been also corroborated by multiple studies, especially for total nitrogen (DeFalco et al., 2001; Barger et al., 2016), available phosphorous (Jafari et al., 2004; Guo et al., 2008) and organic carbon content (Kidron et al., 2010; Yang et al., 2019)).

Results for micronutrients were variable. While Fe and Zn concentration could be explained by the presence of mosses, Mn and Cu showed different behavior. Apart from trapping ashes into the soil in early post-fire stages, other mechanisms of BSCs to increase micronutrient fertility is via dust trap, fine particles, clay, silt, and possibly ash particles (Belnap et al., 2001). The roughness of mosses in the soil surface helps to incorporate the dust, whose nutrients positively charged remain bonding to negatively charged clay particles (Belnap and Harper, 1995). Indeed, recent publications highlighted the considerable ability of mosses to accumulated trace elements in different ambient, including Fe, Mn, Cu and Zn (Bidwell et al., 2019; Wang et al., 2019). Higher values for Zn, Fe, and Mn (also for P) in SL soils, correlations showed in the PCA, could be due to the higher area of bare soils exposed, thereby more dust particles in the air and finally trapped over the mosses for some of the elements. In contrast, Cu values were lower under mosses, reported in Beraldi-Campesi et al. (2009) as leaching effects for many metals and metalloids (also Cu) promoted by the activity of the microorganisms, hypothesis that will need direct testing in the future. Nevertheless, concentrations for all micronutrients were low in our soils (Kabata-Pendias, 2011).

Mosses covering the soil showed a clear effect on the microbial parameters measured. Biologic parameters are expected to increase under BSCs, influenced by the improvement of soil parameters like the organic matter content, the activity, and abundance of microorganism activity will be boost (Belnap and Harper, 1995). However, the improvement is related to the age since the disturbance, progressively increasing with time (Liu et al., 2017b). In our results, a significant improvement of the microbial parameters under mosses was found, being this related to the increase in OC and N in soils observed in the PCA analysis, a correlation that is stronger for Cmic in C soils. In

García-Orenes et al. (2017), short-term results showed low microbial biomass and activity after the fire, since microbiological parameters respond very quickly to perturbations in soil (Mataix-Solera et al., 2009), nonetheless recovery of soils affected by SL was much slower compared to soils with no intervention. Presumably, Cmic will significantly increase with time together with the improvement of the chemical parameters related to the fertility of soils. Multiple studies recommend the maintenance of the burn wood (total or partially) on the topsoil to create microclimatic conditions enhancing soil moisture; thereby promote microorganisms development (Marañón-Jiménez et al., 2011). Future research should examine soil microbial functions under mosses to better understand their role in microbial improvement.

Given their relevant role in soils after a wildfire, mosses should be considered in the post-fire management plans. Ensure their development and dispersal is a restoration strategy to take into account, assisted by the preservation of woody substrates as provisions and controlling the managements like salvage logging. However, in agreement with Silva et al. (2019), the feasibility as a practical post-fire measure still needs to be proved, partly since mosses respond to different ambient conditions. Nevertheless, the interest in using BSCs as biotools in restoration is becoming increasingly relevant and a reality (Maestre et al., 2017; Bethany et al., 2019).

5. Conclusions

Salvage logging, a practice that has been demonstrated to be aggressive with soils in the short-term, has affected in a medium-term to the percentage of soil covered by mosses. In this study, we observed that the soils covered by a biocrust dominated by mosses showed better conditions since protected from erosion the soils showed better soil quality, hence creating better conditions for soil functions. The presence of mosses promotes soil recovery after a severe disturbance like a wildfire continued by aggressive post-fire management such as salvage logging. The improvement has been registered mainly in the fertility characteristics and microbial parameters. The physical parameters have not registered greater differences, and we hypothesize that mosses have key roles in early post-fire stages but more developmental stages of the biocrust and time will be necessary to register more differences in those parameters.

Considering their relevant ecological functions, such as increasing the stability of surface soils, improving soil fertility, and microbial activity, mosses could be key in the functional recovery of degraded ecosystems after wildfires. For this reason, mosses should be considered in the post-fire management. Therefore, we recommend to forest managers to take into account the natural recovery of mosses in order to do not affect them if any post-fire management is planned, thereby develop a sustainable forest that increases biodiversity and resilience. Moreover, the maintenance of the burnt wood could have long-term consequences for the conservation of biocrust and mosses.

CHAPTER 5

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

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This chapter corresponds to the article:
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. Science of the Total Environment, 846, 157467.
doi:10.1016/J.SCITOTENV.2022.157467

Abstract

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

1. Introduction

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

Biocrusts are complex assemblages of cyanobacteria, lichen, and/or bryophyte that support a huge diversity of microorganisms (Warren et al., 2019), which provide key ecosystem functions such as stabilization of soil surface, increase soil fertility, control of local hydrological dynamics, facilitate plant germination and establishment, and promote microbial abundance (Belnap and Lange, 2003). Considering their functional roles in ecosystems, the pioneer moss biocrust may accelerate the recovery of the ecosystem functioning in the early stages after the fire disturbance, through the mitigation of the detrimental consequences of fires in soils. Nevertheless, growing biocrust to rehabilitate fire-affected soils has been recently studied as a promising stabilizing technique, either inoculating cyanobacteria (Muñoz-Rojas et al., 2021) or cultivating mosses (Grover et al., 2020). Apart from soil stabilization, the repercussion for soil microbial biodiversity is far to be understood and still needs to be elucidated. Understanding the soil biochemistry and microbiome response to the early biocrust emergence is required to provide valuable information to apply in management strategies toward accelerating recovery in semi-arid ecosystems prone to degradation.

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

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

2. Materials and methods

2.1. Site description

The study area is located in "Sierra de la Replana" in Beneixama, Alicante, Spain (38°44'15" N, 0°44'56" W, 940 m). The area has a warm Mediterranean climate, 3–4 months of summer droughts, dry-hot summer, and wet-warm spring, autumn and winter. The average temperature is 14.9 °C and the average annual precipitation is 456 mm. The vegetation is mainly composed of 50 years old *Pinus halepensis* Mill. trees from afforestation, and *Quercus ilex* L., and typical Mediterranean shrubs species such as *Quercus coccifera* L., *Rosmarinus officinalis* L., *Juniperus phoenicea* L., *Juniperus oxycedrus* L., *Ulex parviflorus* Pourr., *Erica multiflora* L., *Stipa tenacissima* L., and *Stipa offneri* Breistr. The steep slopes are terraced facing south, where soil was classified as a Typic Xerorthent (Soil Survey Staff, 2014) with low depth and clay loam texture (29 % clay, 49 % silt, 22 % sand).

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

2.2. Experimental design, biocrust monitoring, and soil sampling

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

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

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

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

2.3. Laboratory analysis

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

The soil microbial biomass carbon was determined by the fumigation- extraction method (Vance et al., 1987). Soil basal respiration was measured in an automated impedance-meter (BacTrac 4200 Microbiological Analyser, Sylab, Austria), based on the changes in the impedance of a KOH solution (2 %) due to the CO_2 emissions by soil microorganisms incubated at 30 °C for 24 h. The estimation of urease activity was based on the release of NH_4^+ from hydrolytic reactions where soil samples were exposed to the substrate urea (Nannipieri et al., 1981). β-Glucosidase and alkaline phosphomonoesterase activities were quantified colorimetrically as the p-nitrophenol produced during the incubation of soil with the substrates p-nitrophenyl-β-D-glucopyranoside (Tabatabai, 1983) and p-nitrophenyl phosphate disodium salt, respectively (Naseby and Lynch, 1997).

To estimate the biomass of the microbial community, phospholipid fatty acid analysis (PLFA) and neutral lipid fatty acid analysis (NLFA) were used. Lipids were extracted with a chloroform–methanol–phosphate buffer mixture (1:2:0.8), and then fractionated using solid-phase extraction cartridges (LiChrolut Si 60, Merck), eluted in three fractions containing neutral lipids, glycolipids and phospholipids with 2 mL of chloroform, 6 mL of acetone and 2 mL of methanol, respectively. The first fraction and the third fractions were subjected to mild alkaline methanolysis. The free methyl esters of NLFA and PLFAs were analysed by gas chromatography–mass spectrometry (450-GC, 240-MS ion trap detector, Varian, Walnut Creek, CA, USA), the instrument and program settings described in Frouz et al. (2016). Methylated fatty acids were identified according to their mass spectra and by using a mixture of chemical standards from Sigma–Aldrich

(Prague, Czech Republic) and Matreya LLC (Pleasant Gap, PA, USA). Fungal biomass was quantified based on the 18:2ω6,9 content, and bacterial biomass was quantified as the sum of the contents of the fatty acids i14:0, i15:0, a15:0, 16:1ω7t, 16:1ω9, 16:1ω7, 10Me-16:0, i17:0, a17:0, cy17:0, 17:0, 10Me-17:0, 10Me-18:0, and cy19:0 (Stella et al., 2015). The content of arbuscular mycorrhiza biomass was estimated using 16:1ω5 concentration in the NLFA fraction (Bååth, 2003). The total PLFA was calculated as the sum of all the fatty acids.

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

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

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

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

2.5. Statistical analysis

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

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

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

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

3. Results

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

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

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

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

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

The total PLFAs, significantly reduced in the fire-affected soils in all cases (Fig. 1), did not significantly respond to the moss biocrust, although a trend to higher biomass was found for bacterial and total biomass in soils under mosses (Fig. 1). In comparison with bare soils, moss biocrust soils concentrated higher bacteria biomass and thus higher extracellular enzyme activities associated (Appendix C, Fig. C1). With lesser effect, soils under moss biocrust also concentrated higher fungi biomass, correlated to the higher moisture in those soils. Contrary, the arbuscular mycorrhizal biomass was highly correlated to the slight increase in organic carbon and nitrogen content and basal respiration found in bare soils (Fig. C1).

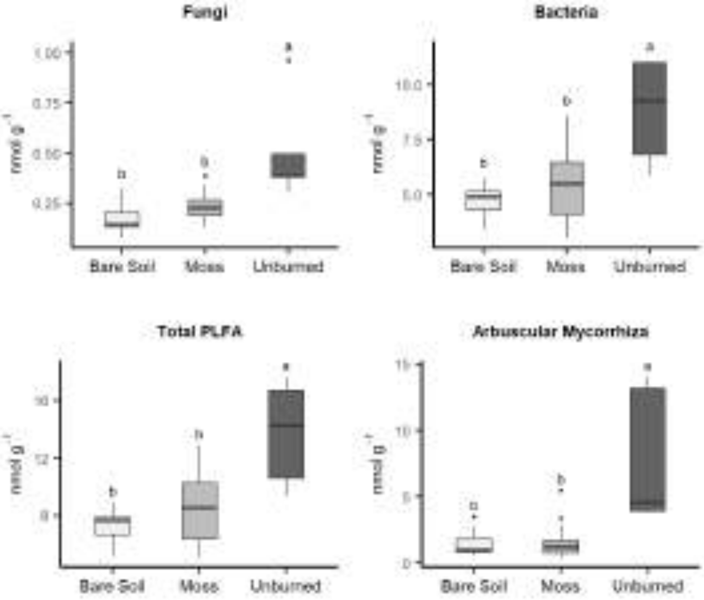

Fig. 1. Box-plot of bacterial, fungal, arbuscular mycorrhiza biomass and total PLFAs, measured in of burned soils, with mosses and without mosses bare soils, and unburned soils. Lowercase letters indicate statistical differences at $p < 0.05$ (post-hoc Tukey test).

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

Alpha diversity values for soil bacterial community were higher under the moss biocrust (Fig. C2), reaching the same levels as in unburned soils, while bare soils were identified to have significantly lower bacterial richness (i.e., number of phylotypes) and diversity indices (Shannon and Chao1). In contrast, the fire strongly impacted the fungal community, significantly decreasing values for richness and diversity indices, without registering any effect due to the moss biocrust (Fig. C2).

Regarding the structure of the microbial communities, both bacterial and fungal communities were drastically altered by the fire, and then reshaped after the biocrust emergence. Fig. 2 shows bacterial communities in unburned soils and burned soils to cluster separately, and moss communities and bare soil in burned soils to cluster separately as well. The effect of a biocrust in burned soils was confirmed by the PERMANOVA analysis, which showed bacterial communities under mosses statistically differ from those in bare soils (F = 3.273, p-value < 0.001). The effect of burning on fungal community structure was even more marked than for bacteria, separating the unburned and burned communities along the X-axis (Fig. 2). Communities of fungi under mosses clustered separately along the Y-axis from those in bare soils, a difference that was confirmed after the PERMANOVA analysis (F = 2.343, p-value < 0.001).

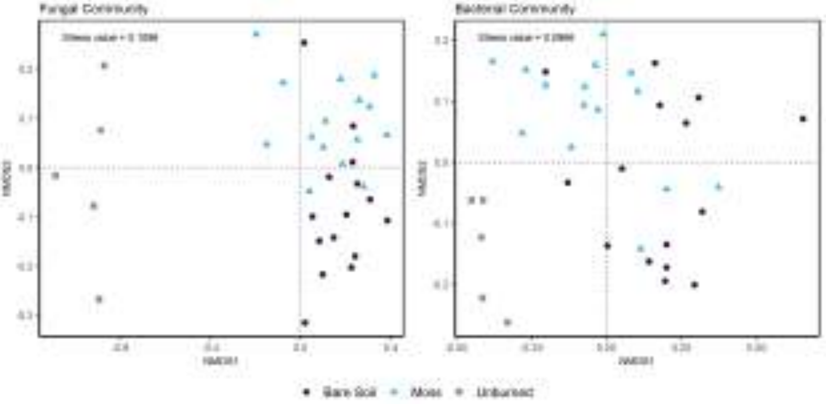

Fig. 2. Two-dimensional non-metric multidimensional scaling (NMDS) ordination based on Bray-Curties dissimilarities at OUT level for bacterial and fungal communities.

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

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

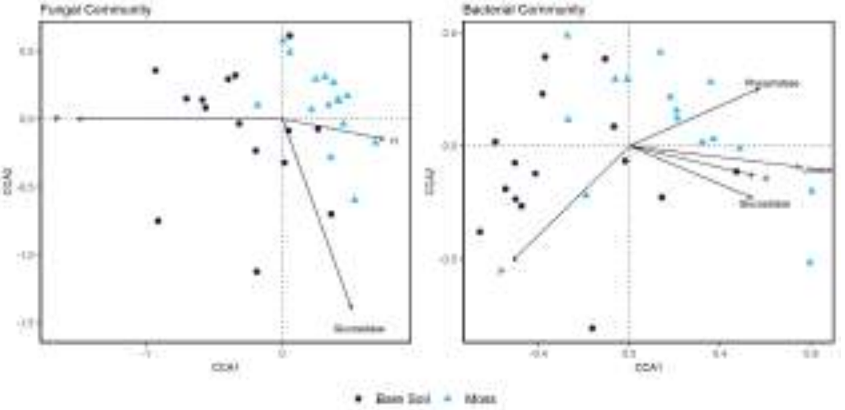

Fig. 3. Canonical correspondence analysis (CCA) at OTU level for bacterial and fungal communities of burned bare soils and moss biocrust. The explanatory variables are expressed with arrows (H: soil moisture; P: available phosphorous).

3.3. Bacterial community composition

The study of the bacterial community showed a drastic shift in burned soils. However, the biocrust buffered the effect of fire on the bacterial community, for which the relative abundances of most of the dominant phyla showed values intermediate between the values for unburned soils and those for bare soils. The dominant phylum, Actinobacteria, significantly decreased after burning, shifting the dominance to Proteobacteria in bare soils (see Appendix C, Fig. C3). Fire promoted Firmicutes and Bacteroidetes, in this case with lower values in soils under mosses than in bare soils. Similarly, higher abundances compared to bare soils were found under mosses for phylum Planctomycetes and Chloroflexi, which decreased with burning.

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

A high number of responsive OTUs were found for bare soils (441), mosses (318), and unburned soils (2152) (Appendix C, Tables C1 and C2), the majority corresponding to taxa with low abundance in soils. At the genus level, *Arthrobacter* highlighted as the most abundant indicator for soils under mosses (8 % versus 3.2 % in bare soils and 0.12 % in unburned soils), whereas indicator genera at bare soils reported were *Blastococcus*, *Bacillus*, *Massilia*, *Comamonas*, *Shingomonas*, *Paenisporosarcina*, *Adhaeribacter*, and others.

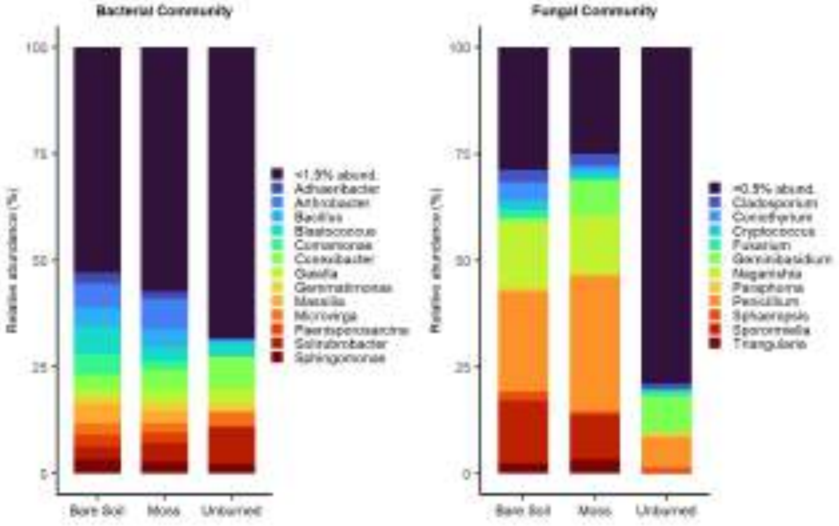

Fig. 4. Relative abundances of the dominant bacterial and fungal genera of burned soils, with mosses and without mosses bare soils, and unburned soils.

3.4. Fungal community composition

The fire disturbance strongly changed the composition of the dominant groups of the fungal community; additionally, the moss biocrust influenced some fungal taxa that expressed intermediate abundances between the unburned soils and bare soils (Fig. C3, Fig. 4). An increment in the dominance of Ascomycota after fire was revealed (60–70 %) in detriment of the Basidiomycota (from 34.1 % in unburned soils to 23.6 % in bare soils values in soils under mosses in between). In fire-affected soils, a significant increment in phyla Chytridiomycota was found (genera *Phlyctochytrium* and *Spizellomyces*), and a significant decrease in Glomeromycota with values almost negligible in bare soils. The increase in Ascomycota in burned soils was highly represented by the dominant *Penicillum*, followed by the increase in *Naganishia* (Basidiomycota) and *Sporormiella* (order Pleosoporales), among others. Contrary, genera that were negatively affected by fire were represented by the common yeast *Solicoccozyma* or *Paraphoma* (Pleosoporales). Fungal genera in moss biocrust that showed the same abundance than in unburned soils were *Geminibasidium* (Basidiomycota) and *Rhizopogon* (Boletales). Contrary, soils under mosses registered a significant decrease (2-fold) of *Fusarium* (Hypocreales).

The indicator species analysis, performed at both genus and OTUs level (Tables C3, C4), highlighted the saprotroph *Coniothyrium* as the major indicator of bare soils, followed by *Pyronema*, *Filobasidium,* and *Papilotrema*, with fungal parasite decomposer function, or the yeasts *Naganishia* and a *Saitoella*. For soils under mosses, the most representative and abundant indicator was the saprotroph *Penicillium*, followed by the other saprotrophs as *Clonostachys* or *Geminibasidium*.

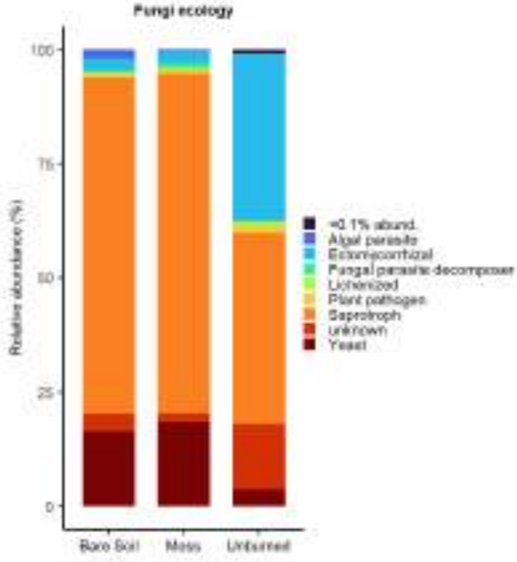

Fig. 5. Relative abundances of the dominant fungal ecological roles of burned soils, with mosses and without mosses bare soils, and unburned soils.

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

4. Discussion

Seven months after the fire disturbance, the reduction of organic carbon and nitrogen content and the unfavourable response of the biological properties, with the microbial activity and biomass severely affected, reflected the legacies of a medium to high severity fire. The posterior emergence of the moss biocrust in the affected soils, creating a mosaic of heterogeneous soil microenvironments, greatly influenced the physicochemical soil properties and, consequently, the microbial composition and activity. Knowing that biocrusts help to stabilize the soil surface (Silva et al., 2019; Cania et al., 2020), together with the fact that mosses as primary producers with significant contributions to nutrient cycling (Cheng et al., 2021; Xu et al., 2022), an increment in soil fertility compared to their neighbouring bare soils was expected. However, contrary to expected, bare soils registered the highest aggregate stability, which is presumably related to a selection of the most stables aggregates after the erosion processes occurred post-fire in those soils (Mataix-Solera et al., 2021). In addition, soils beneath moss biocrust registered a slight lower OC content, either due to the exhaustion of labile forms released after the wildfire by the burgeoning microbial community, or the preference of mosses to establish where lower recalcitrant organic matter concentrates after the fire (González-Pérez et al., 2004). The strong impact observed in the soil properties is commonly found after high severity fires, nutrients cycling is profoundly altered and the microbial activity immediately reduced, which is expected to takes time to recover to pre-fire levels under semi-arid conditions (Pérez-Valera et al., 2020).

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

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

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

The fire-associated Firmicutes, Bacteroidetes and Betaproteobacteria were favoured in the severely burned soils (Prendergast-Miller et al., 2017; Rodríguez et al., 2018). *Arthrobacter* (Microccocaceae), the major indicator found for moss biocrust soils, is known to play an important role in the nitrogen cycle and plant growth in Mediterranean burned forests (Cobo-Díaz et al., 2015; Fernández-González et al., 2017), while *Blastococcus*, the indicator of bare soils, is commonly described as pioneers in extreme environments (Miralles et al., 2020; Xing et al., 2020). Whereas Proteobacteria dominate in bare soils, Actinobacteria dominate in moss biocrust soils, suggesting key roles in initial crust development (Belnap and Lange, 2003). Copiotrophic Proteobacteria presumably increased with the release after fire of labile carbon (Goldfarb et al., 2011), then decreasing in abundance once consumed by the higher bacterial biomass growth under moss biocrust soils. Lower abundance in moss biocrust was detected for *Massilia* and *Comamonas* (Burkholderiales), usually found in burned soils due to their ability to degrade labile and recalcitrant carbon compounds (Puentes-Téllez and Salles, 2020; Stinca et al., 2020) and in biocrust in drylands (Moquin et al., 2012; Li and Hu, 2021), and Sphingomonadaceae, especially associated with bryophyte crusts (Cutler et al., 2017; Maier et al., 2018). Bacillales family (mainly *Bacillus*), increased after fire and indicator, is described as desiccation-tolerant copiotrophs with the ability to degrade hydrocarbons accumulated after fires (Ferrenberg et al., 2013), and families of Bacteroidetes Cytophagaceae (genus *Adhaeribacter*) and Sphingobacteriacea were already described as indicators of Mediterranean burned soils (Stinca et al., 2020; García-Carmona et al., 2021a) and moss biocrust in drylands (Moquin et al., 2012).

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

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

5. Conclusions

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

CHAPTER 6

Post-fire wood mulch modulates the biocrust-forming mosses response and the soil fungal community composition

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This chapter corresponds to the work:
García-Carmona, M., Lepinay, C., Mataix-Solera, J., Baldrian, P., Arcenegui, V., Cajthaml, T., & García-Orenes, F. Post-fire wood mulch modulates the biocrust-forming mosses response and the soil fungal community composition.

Abstract

Post-fire mulches are highly effective in mitigating erosion; however, the implications of adding wood mulches on ecosystem recovery, and in particular on the biological soil response, remain unexplored. This study aimed to assess the recovery and resilience of soil microbial communities under wood-based mulch application in soils where an emergent biocrust dominated by mosses accelerates the ecosystem response in early post-fire stages. For this purpose, wood mulch was applied at two rates, "Rate 1" (65% of cover), and "Rate 2" (100% of cover), both compared to "Control" soils without application. One year after the application, the moss biocrust was drastically inhibited, and the positive effects of biocrust on microbial diversity were reduced, communities became highly stochastic and less diverse under the mulch influence. Variations in soil properties in response to different application rates were transferred to the microbial communities driving the community structure, with fungi being particularly sensitive. The study of the dominant microbial taxa revealed different legacies in the fungi and bacteria regarding the fire, the moss biocrust presence, and the mulch application. The fungal community reported contrasting differences between moss biocrust and uncrusted soils, while soils under mulch were less heterogeneous in composition. In contrast, bacterial community composition revealed a slight response to the mulch application, and negligible effects due to the soil crust presence. Therefore, wood mulch addition did not positively affect microbial diversity and ecosystem functionality. Studying the additive effects of forest management and the aboveground 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 in the Mediterranean ecosystem has been a historical key component shaping the structure and distribution of aboveground and belowground communities (Pausas and Keeley, 2009; McLauchlan et al., 2020). Intensification in fire events, in both frequency and severity, is expected in the near future due to land-use changes and climate-change induced scenarios (Moreira et al., 2020), threatening the capability of ecosystem to recovery following extreme wildfire. Understanding the recovery of soil microbial communities, involved in critical ecosystem services related to nutrient cycling and soil formation (Bardgett and Van Der Putten, 2014), is essential for the sustainable management of fire-affected ecosystems in a context of increasing fire disturbances (Pellegrini et al., 2018; Adkins et al., 2020). High severity fires reduce soil microbial biomass, decrease microbiome diversity, and profoundly reshape the microbial community composition (Pressler et al., 2019; Nelson et al., 2022), 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). During the first years after high-intensity fires, the dominance of biocrust-forming mosses in semi-arid areas reveals their important role as ecosystem engineers (Esposito et al., 1999; Ladrón De Guevara and Maestre, 2022; Weber et al., 2022), stabilizing the soil surface and accelerating the recovery of soil functioning (Muñoz-Rojas et al., 2021; García-Carmona et al., 2022). Active restoration, human-induced, may be required if sites have suffered intense disturbance. However, the combined effects of these operations with the passive effects of the emergent moss biocrust on the soil microbial recovery after a fire remain unexplored.

Many Mediterranean forests affected by wildfires are subjected to salvage logging, a management performed primarily to recover timber value, also to reduce the risk of insect outbreaks and fire hazards (Lucas-Borja et al., 2019a). Adverse consequences are often reported since logging operations can compact the soil and delay the recovery of vegetation (Wagenbrenner et al., 2016; García-Orenes et al., 2017), affecting the soil biodiversity directly or indirectly e.g., disturbing the deadwood-dependent species (Thorn et al., 2020). As a result of the logging operations, the hydrological response can be modified forcing the implementation of soil stabilization treatments to mitigate the increases in runoff (Robichaud et al., 2013). Among the emergency stabilization actions, mulching is highlighted as the most cost-effective treatment (Girona-García et al., 2021). Compared to straw-based mulches, wood residues generated in the framework of logging operations (mastication of non-merchantable debris) comprise materials with greater resistance to wind displacement and longevity due to their decay resistance (Jonas et al., 2019), but together with the feasibility of broad-scale mulching with local material, a major drawback is the possible hamper of the vegetation recovery following the wood mulch application (Bautista et al., 2009; Castro, 2021). The effects on moss biocrust development are unclear since differences in the preference for microhabitats provided by litter coverage among moss species are reported, some of them take advantage of high light intensity, temperature, and soil nutrient status in open sites (Ladrón De Guevara and Maestre, 2022). Despite being a common practice, relatively little is known about the effects of adding wood mulches on ecosystem recovery, and in particular on the biological soil response, which is especially important for the post-fire management in semi-arid areas where ecosystems are water and nutrient-limited and prone to degradation (Sardans and Peñuelas, 2005; García-Orenes and García-Carmona, 2022).

Deadwood comprises a primary source of nutrients for forest soils, which largely contributes to the carbon stock, and participates in soil formation and nutrient cycling at the ecosystem level (Tláskal et al., 2021). Through decomposition, nutrients are progressively released into the soil, a process that depends on climatic conditions (i.e., temperature and moisture), tree species (i.e., physical and chemical properties), and microbial communities (Fukami, 2015; Baldrian et al., 2016; Lepinay et al., 2021). After the strong perturbation that a wildfire represents to nutrient cycling, the burnt wood constitutes a nutrient stock that fertilizes the soil, at long-term, supporting soil biodiversity (Marañón-Jiménez and Castro, 2013; Thorn et al., 2018; Juan-Ovejero et al., 2021). Wood-based mulches spread on the soil surface change the soil microclimatic conditions, increase soil moisture, and thereby promote microbial activity and abundance, with subsequent shifts in the microbial community composition (Goodell et al., 2020; Ammitzboll et al., 2022). The physical and chemical properties of deadwood (high lignin and low N content) make it impermeable and resistant to colonization by bacteria (Baldrian, 2017), thus, being mainly decomposed, though not exclusively, by saprotrophic fungi (Arnstadt et al., 2016; Tláskal et al., 2021), favoured by their filamentous growth, lower demand of N and their ability to translocate nutrients (Baldrian et al., 2016). Wood-inhabiting bacteria and fungi change in composition and abundance during the decay process (Baldrian et al., 2016; Lepinay et al., 2021), influenced by the direct contact of deadwood with soil microbiome which intensifies over decomposition (Baldrian et al., 2012; Urbanová et al., 2015). The soil microbial community alterations under wood mulch application remain unknown, as well as potential implications for the recovery and resilience of ecosystems affected by fires in semi-arid ecosystems.

Bearing in mind those considerations, 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 biocrust dominated by mosses demonstrated to accelerate the ecosystem response in early post-fire stages. We hypothesized that the wood-based mulch positively impacts the physicochemical and biological soil properties, and through the alterations of microhabitats and nutrient introduction, it favours the abundance and diversity of microbial soil communities and their performance. However, we expect that the effects depend on the rate of mulch applied and the interactive effects with the presence of moss biocrust cover. Our aims were (i) to determine the effects of wood mulch on the physicochemical and biological soil properties after one year of application, (ii) to detect the dominant fungal and bacterial taxa and changes in microbial community composition after one year of mulch cover at different application rates 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 among treatments and crust presence. Understanding the soil microbiome response to the mulch application, and the interaction with the post-fire biocrust mosses, could provide valuable information for optimal post-fire management strategies toward accelerating recovery of semi-arid Mediterranean ecosystems affected by wildfires.

2. Materials and methods

2.1. Study site

The area of study was located in "Sierra de la Replana" in Beneixama, Alicante (E Spain), characterized by a warm Mediterranean climate, 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 low depth 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 log charred, and soils were mainly covered by grey colour ash. In early September 2019, salvage logging was carried out in the area consisting of a complete extraction of the burnt wood using heavy machinery that, after strong precipitation events, exposed soils to important erosion processes. Slopes facing south evidenced the higher impact of soil erosion seven months after the wildfire with harsher conditions for vegetation regrowing. Biocrust-forming mosses dominate 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, the protective intervention based on wood mulch application was applied, prior to the spring rainfalls, in a representative affected area of slopes facing south characterized by lesser vegetation regrowing after the impact of the wildfire and salvage logging. Mulch was composed of the chopped pine residues (*Pinus halepensis* Mill.), wood chips around 5 cm wide and 0.5 cm thick, 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. Three plots per treatment were established in the fire-affected area, and another three experimental plots in a nearby-unburned area, located at approximately 500 m and at least 100 m away from the fire edge, were used as reference. 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 presence of moss biocrust was identified at each experimental plot in the burned area. At each sampling, four soil samples were collected from the top 2.5 cm of soil 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 representing the homogeneous area. From the total number of samples collected (84 in total), for operative purposes 70 samples in total were selected for the present study: 35 samples randomly selected by sampling year, from which 15 of them in uncrusted soils, 15 samples under mosses, and 5 samples from the unburned soils.

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

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 and biochemical parameters, 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. The potassium dichromate oxidation by the Walkley-Black method (Nelson and Sommers, 1983) was used to determine the soil organic carbon, the

Kjeldahl method for the total nitrogen (Bremner and Mulvaney, 1982), and the Burriel-Hernando method for the available phosphorous (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 (Tabatabai, 1983; Naseby and Lynch, 1997).

The microbial community biomass in soils was estimated by the phospholipid fatty acid analysis (PLFA) and neutral lipid fatty acid analysis (NLFA). A chloroform-methanol-phosphate buffer mixture (1:2:0.8) was used for lipid extraction, then fractionated using solid-phase extraction cartridges (LiChrolut Si 60, Merck), and eluted in three fractions containing neutral lipids, glycolipids and phospholipids with 2 mL of chloroform, 6 mL of acetone and 2 mL of methanol, respectively. The neutral lipids and the phospholipids were subjected to mild alkaline methanolysis. The free methyl esters of NLFA and PLFAs were analysed by gas chromatography-mass spectrometry (450-GC, 240-MS ion trap detector, Varian, Walnut Creek, CA, USA) as described in Frouz et al. (2016), and identified according to their mass spectra by using a mixture of chemical standards from Sigma–Aldrich (Prague, Czech Republic) and Matreya LLC (Pleasant Gap, PA, USA). Fungal biomass was quantified based on 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 following the manufacturer's instructions. DNA was resuspended in a final volume of 100 μL and quantified using the Qubit High Sensitivity dsDNA Assay (Thermo Fisher Scientific).

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

The 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 first step was to identify the effects of the wood mulch application on the moss biocrust dynamics, exploring the differences in the biocrust cover at the end of the experiment with ANOVA test, after testing the statistical parametric assumptions. The response of soil properties and PLFAs and NLFA content to the treatments applied and the presence of a biocrust over time was explored using linear mixed models using the "lme" function from the "nlme" package. Fixed factors for models were "Time" (T0, starting point of the experiment, and T1, one year after the treatments application), "Treatment" (Rate1, Rate2 and Control), "Mulch" (agglutination of both mulch application rates versus control), and "Crust" (uncrusted soils and moss biocrust soils). Unburned soils were introduced as a level when their study was appropriated. Location of samples along the experimental plots was included as a random effect. Statistical differences among treatments and crust types were explored at the end of the experiment (T1). The relationship among all soil parameters in the context of the treatments applied was explored at T1 using principal component analysis (PCA) with the "FactoMineR" package (Lê et al., 2008).

α-Diversity parameters were estimated from OTU tables in which all samples were resampled to equal the smallest library size to reduce the effect of variation in sequencing depth using the "rarefy_even_depth" function in "phyloseq" package. From the rarefied matrices, we calculated OTU richness (function "specnumber") for both fungi and bacteria, exploring the differences regarding the factors “Time”, “Treatment” and “Crust” after linear mixed models were fitted. To reveal the impact of factors “Time”, “Crust”, “Treatment” and “Mulch” in the microbial (fungal and bacterial) community structure in burned soils, permutational multivariate analysis (PERMANOVA) was tested with the “adonis2” function using 9999 permutations. Shifts in the spatial distribution of the community´s structures were visualized after non-metric multidimensional scaling (NMDS) ordination analysis based on Bray-Curtis distances of OTU relative abundances using the “metaMDS” function, and by including the unburned soils to visualize the effect of wildfire on microbial communities.

In order to assess the potential drivers for the microbial communities in the fire-affected soils, variation partitioning analyses of the microbial composition variation were performed to explore the effects of the different factors plus all the soil parameters together. The identification of the soil parameters related to the bacterial and fungal community composition in soils under mulch treatments and crust presence at the end of the experiment (excluding unburned soils) was tested with redundance analyses (RDA) performed with the “rda” function. First, multicollinearity was avoided with the calculation of the variance inflation factor, and variables with values > 10 were sequentially removed. The remaining variables were subjected to a forward selection procedure to select the subset of constraining variables that better explain the communities' variation in the final model with the “ordistep” function. The compositional matrices were transformed using Hellinger transformation before the statistical analysis.

Shifts in the composition of dominant fungal and bacterial taxa at the end of the experiment were explored after the treatment application and the crust presence. The microbial communities were analysed for significant differences systematically at different phylogenetic ranks (phylum to genus-level) using relative abundances with the non-parametric “kruskal” function, with p-values correction based on Benjamini–Hochberg false-discovery rate with 95% confidence interval. It was also performed for the ecological categories in the fungal community.

3. Results

3.1. Mulch effects on moss biocrust dynamics

The moss biocrust cover survey revealed noticeable differences regarding the mulch application. With a starting point of 30% of moss cover seven months post-fire, after one year the moss 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, reporting a 2-fold lower cover under Rate 1 (42%) compared to control soils, and strongly inhibited at Rate 2 (18% of moss cover) (Fig. D1, Appendix D).

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

One year and a half after the wildfire, the contents of organic C and N in burned soils increased and did not statistically differ from the unburned soils. The soil crust significantly influenced the aggregate stability and soil moisture after being slightly reduced by the fire (Table 1). Fire legacies were noticeable in the available P content, significantly higher in burned soils. Moreover, all the biochemical parameters were negatively impacted by the wildfire (Table 1). The moss biocrust emergence influenced the recovery of some of them, especially relevant for the microbial biomass carbon, with higher values reached under mosses in control soils and in soils under mulch at Rate 1, an increase not observed in Rate 2 where mosses were inhibited.

Microbial biomass (PLFA and NLFA biomarkers) was impacted by the time elapsed in the experiment and the mulch application, but none statistically responded to the soil crust (Table D1). While the total microbial biomass increased in the period of study, similarly to the bacterial biomass response (p-value = 0.03), the fungal biomass remained low. The biomass of arbuscular mycorrhiza strongly decreased in burned soils compared to unburned soils. Fungi were impacted by the mulch application, adversely affected in some treatments (p-value = 0.04).

Table 1. Physicochemical and biochemical soil properties after one year of 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. Different lowercase letters indicate significant differences among soils (post-hoc Tukey test, p-value <0.05). Significance results for factors in linear mixed models fitted are shown, including factors "Crust" (moss biocrust vs. uncrusted soils), "Mulch" (control vs. soils under mulch), and the interaction between factors (n.s. not significant at p-value >0.05).

Treatment	Crust	Organic Carbon (%)	Nitrogen (%)	Phosphorous (mg kg^{-1})	Aggregate stability (%)	Soil moisture (%)
Unburned		5.5 ± 0.55	0.38 ± 0.06	4.1a ± 0.9	83 ± 3	15.4 ± 3.1
Control	Uncrusted	5.01 ± 1.09	0.33 ± 0.06	29ab ± 25.1	83.2 ± 10.3	13 ± 1.8
	Mosses	4.19 ± 0.58	0.29 ± 0.05	40.7ab ± 29.2	77.9 ± 3.5	11.2 ± 1.4
Rate1	Uncrusted	5.12 ± 1.60	0.35 ± 0.11	20ab ± 5.7	79.7 ± 6.0	13.5 ± 2.8
	Mosses	4.89 ± 1.33	0.32 ± 0.07	27.2ab ± 18.8	79.6 ± 6.1	13 ± 3
Rate2	Uncrusted	4.46 ± 2.28	0.29 ± 0.12	52.4b ± 34.7	77.4 ± 6.5	12.8 ± 2.6
	Mosses	3.96 ± 1.17	0.25 ± 0.06	37.9ab ± 29.8	74.9 ± 5.2	12.7 ± 3
Factors						
	Crust	n.s.	n.s.	n.s.	0.004	0.005
	Mulch	n.s.	n.s.	n.s.	n.s.	n.s.
	Crust:Mulch	n.s.	n.s.	n.s.	n.s.	n.s.

		Basal respiration (mg CO_2 kg^{-1})	Microbial biomass (mgCO_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})
Unburned		15.4 ± 3.1	614bc ± 85	2.14b ± 0.30	2.39b ± 0.32	1.82b ± 0.55
Control	Uncrusted	13 ± 1.8	320ac ± 100	1.05a ± 0.31	1.07a ± 0.37	0.45a ± 0.22
	Mosses	11.2 ± 1.4	590c ± 289	1.04a ± 0.54	0.92a ± 0.26	0.38a ± 0.19
Rate1	Uncrusted	13.5 ± 2.8	257ab ± 195	1.46ab ± 0.36	1.11a ± 0.38	0.84a ± 0.59
	Mosses	13 ± 3.0	497ac ± 195	1.34ab ± 0.70	1.35a ± 0.77	0.68a ± 0.43
Rate2	Uncrusted	12.8 ± 2.6	203a ± 120	1.17a ± 0.33	0.92a ± 0.23	0.51a ± 0.16
	Mosses	12.7 ± 3.0	182a ± 117	1.04a ± 0.43	0.98a ± 0.21	0.76a ± 0.39
Factors						
	Crust	n.s.	0.003	n.s.	0.043	n.s.
	Mulch	n.s.	n.s.	n.s.	n.s.	n.s.
	Crust:Mulch	n.s.	n.s.	n.s.	n.s.	n.s.

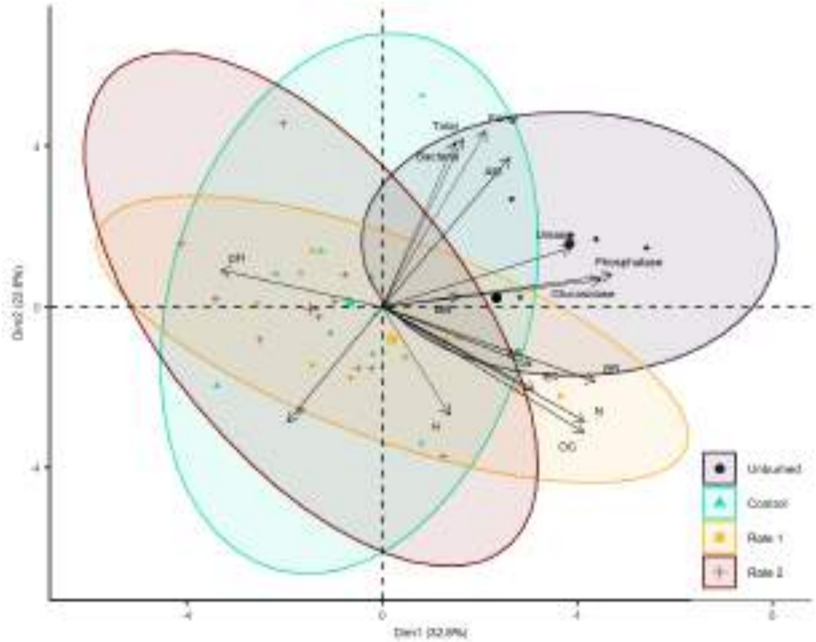

Fig. 1. Relationship among the physicochemical and biochemical soil properties after one year of mulch application for soils under treatment and unburned soils. Mean points for each group of treatment are represented in the PCA. (OC: organic carbon; N: kjheldal nitrogen; P: available phosphorous; H; 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).

The study of the physicochemical and biochemical properties relationship in the treated soils showed how the abundance of all biomarkers clustered together between the unburned soils and the burned control soils (Fig. 1), opposite to the P content and the bacteria to fungi ratio, higher under the Rate 2 treatment. The fire impact was observed in the response of the enzymatic activities, which clustered together in the unburned soils, contrary to the pH increase representative in the burned soils. The slight increase in organic carbon, N, and electrical conductivity grouped the variables representing the mulch treatment Rate1, and this Rate 1 treatment shared with the unburned the higher basal respiration and aggregate stability. From a global perspective, whereas Rate 2 treatment soils grouped apart from the other treatments, control and Rate 1 soils shared more similarities regarding the soil characteristics measured.

3.3. Richness and diversity of microbial communities

The evolution in time of microbial richness, represented by the OTUs number, differed between fungi and bacteria. Fungal richness significantly increased during the year of the experiment, although values were still below the ones in unburned soils 19 months since fire. The increase was more noticeable in soils under mulch application, especially under Rate 1, and under Rate 2 in moss biocrust (Fig. 2). In contrast, seven months after the wildfire (T0), bacterial richness was already comparable to the richness of unburned soils. However, the bacterial community under mosses in control soils experienced a significant decrease in OTU richness (Fig. 2).

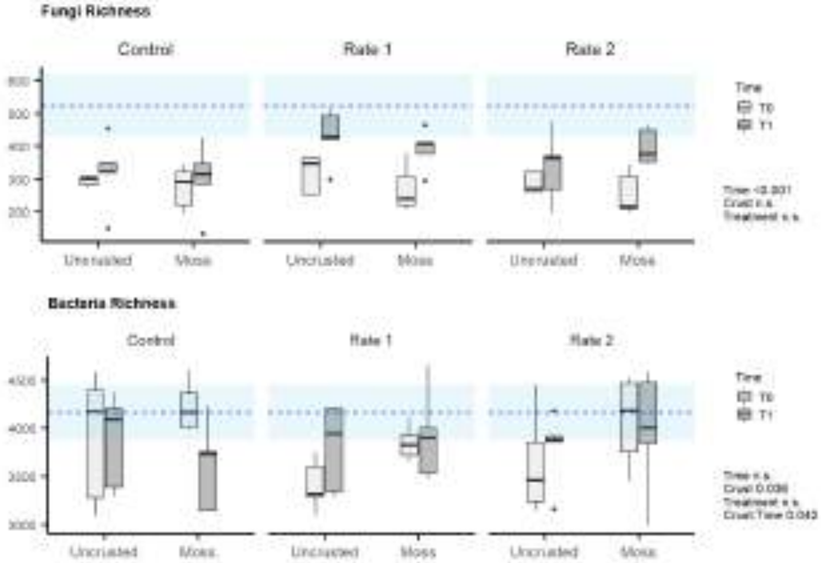

Fig. 2. Fungal and bacterial richness evolution of treatments application (controls and soils under mulch at Rate1 and 2) over time (T0 and one year after, T1), with the presence of crust (moss) and without (uncrusted soils). Dashed line represents the mean value for the unburned soils, shade area the confidence interval. Significance of factors in the models are included ("Time", "Crust", and "Treatment"), and interactions among factors when significant (n.s. = no significant).

According to the PERMANOVA analysis (unburned soils excluded), the composition of the microbial communities showed interesting differences, greatly influenced by the time elapsed (p-value =0.0001***) (Table D2). The fungal community was strongly shaped by the mulch application (p-value = 0.0055**), and to a lesser degree by the crust presence (p-value = 0.036*), both parameters interactive with the time elapsed. In contrast, for the bacterial community the soil crust had the strongest effect on its structure (p-value = 0.004**), and in less degree the mulch application (p-value = 0.011*). Interestingly, despite mulch addition being a significant factor for both communities, when differentiated by application rates the factor was not significant, suggesting that only the global effects of mulch application impacted the communities.

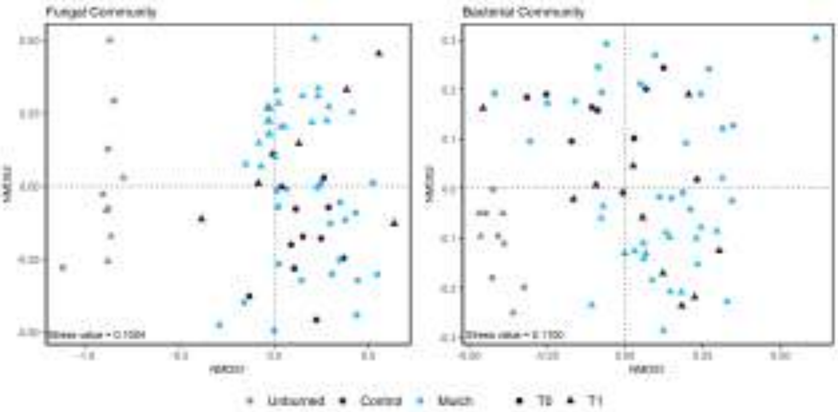

Fig. 3. Impact of mulch application over time in the composition of the microbial communities. Ordination plots represent two-dimensional non-metric multidimensional scaling (NMDS) ordination based on Bray-Curtis dissimilarities at OTU level for fungal and bacterial communities, representing differences at "Time" (T0 and T1) and "Mulch" application (unburned, controls and mulch soils).

The strong legacies of the fire event in the fungal community were represented in the division along the X- axis between the unburned and burned soils in the ordination plot (Fig. 3). At the beginning of the experiment (T0), microbial communities in burned soils clustered separately regarding the presence or not of the moss biocrust soils; however, this dissimilarity was not appreciable after one year of mulch application (Fig. D2). Thus, fungi in soils treated with mulch clustered closer (T1, upper part) in comparison to the control soils, which showed major dispersion (Fig. 3). Similar patterns were found in the bacterial community (Fig. 3). At the beginning of the experiment, higher dissimilarity was observed among samples, clustered differently soils under mosses and uncrusted soils (Fig. D2). One year after the mulch application, soils under treatment tended to the similarity (right bottom of the figure), while control soils were more dispersed (Fig. 3).

3.4. Relationship between the environmental variables under mulch and microbial communities

The variation partitioning of the fungal and bacterial community exposed the relative low explanation of the experimental variables and factors of study in its composition, revealing high stochasticity of the microbial community. Nevertheless, among the explainable variation, most variation in the communities was attributable to the influence of the measured soil properties (Table D3).

The soil parameters that significantly explained the fungal community variation after one year of mulch application were soil moisture, aggregate stability, nitrogen, and available phosphorous (Fig. 4). The higher soil moisture under moss biocrust strongly influenced the fungal community. Fungal communities at different treatments were driven by different soil properties. Part of the community of control soils and under mulch application in Rate 1 was influenced by the higher aggregate stability and nitrogen, in opposite to soils with Rate 2. Similarly, some fungi in control and Rate 1 were influenced by the P content in those soils.

The bacterial community structure was statistically influenced by the available P, the organic carbon, and soil moisture (Fig. 4). Bacteria under mosses were influenced by the phosphorous content, regardless of the treatment applied. The soil moisture and organic carbon content were the most important parameters influencing the community under mulch application, both at Rate 1 and Rate 2.

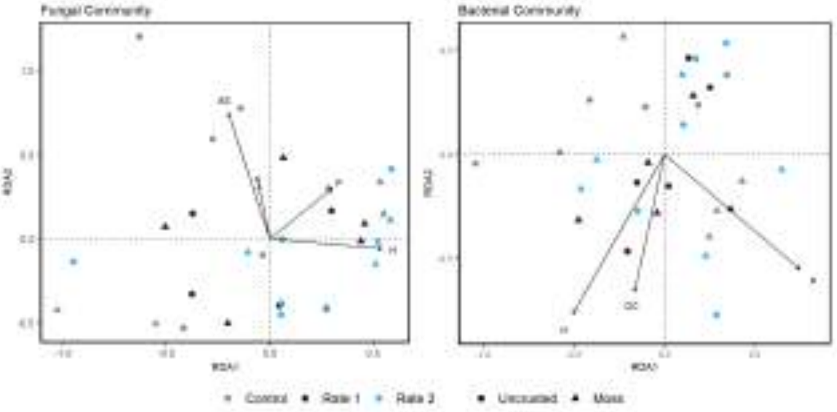

Fig. 4. Soil parameters related to the bacterial and fungal community composition in soils under mulch treatments and crust presence at the end of the experiment. Plots represent redundancy analyses (RDA) at OTU level for fungal and bacterial communities, representing differences at “Treatment” application (controls and soils under mulch application at Rate1 and 2) and “Crust” presence (uncrusted and moss soils). The explanatory variables are expressed with arrows (AS: aggregate stability; H: soil moisture; OC: organic carbon; P: available phosphorous).

3.5. Mulch effects on the fungal community composition in moss biocrust and uncrusted soils

The study of the dominant taxa in the fungal community revealed the legacies of the fire, the moss biocrust presence, and the mulch application in soils (Fig. 5). Burned soils without mulch application revealed contrasting dominance in fungal taxa between moss biocrust and uncrusted soils, whereas soils under mulch were less heterogeneous in the composition of the dominant taxa, especially regardless the soil crust, only soils under moss in Rate 2 differ in the relative abundance of some genera.

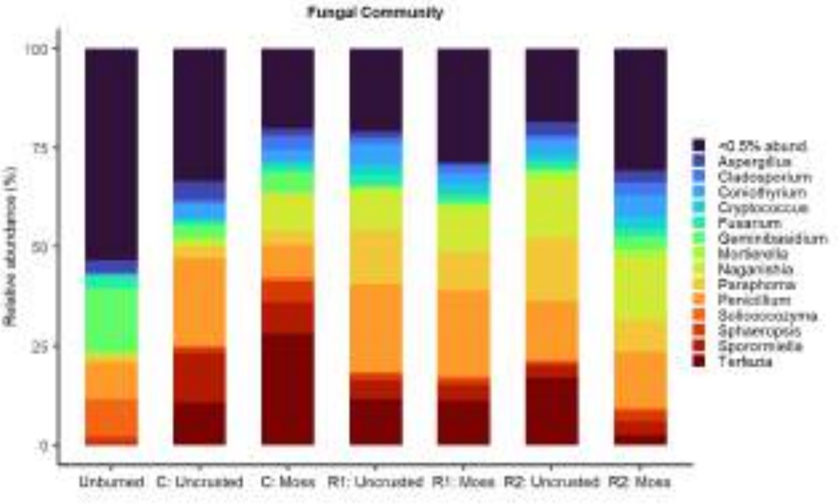

Fig. 5. Effects of mulch treatments and crust presence on the dominant fungal genera at the end of the experiment. Data represent the relative abundance for soils under "Treatment" application (unburned soils, controls and soils under mulch application at Rate1 and 2), and differentiated by "Crust" presence (uncrusted and moss soils).

The dominance of Ascomycota after the fire diminished after the mulch application by increasing the abundance of the fire-reduced Basidiomycota (Fig. D3). In wood mulch soils, the Chytridiomycota phylum significantly increased (genera *Rhizophlyctis*, *Spizellomyces*, and *Powellomyces*, especially under mosses), as well as the Zygomycota, exclusively due to the genus *Mortierella*. The relevant post-fire increase in Ascomycota *Terfezia* (Pezizales) and *Sporormiella* (Pleosoporales) was reduced after mulch application mainly in favour of genera *Paraphoma* (Pleosoporales) and the Basidiomycota *Naganishia* (Tremellaes). Both genera, *Naganishia* and *Paraphoma*, were also promoted under moss biocrust soils. In addition, *Cryptococcus*, and in less 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 fungal functional roles were registered due to the wood mulch. A tendency to lower ectomycorrhizal fungi was reported under mulch, while significant increases in yeast were observed, especially higher under mosses in application Rate 2.

The fire effect was noticeable in the significant reduction of fungi lichenized and parasites of lichen (Fig. 6).

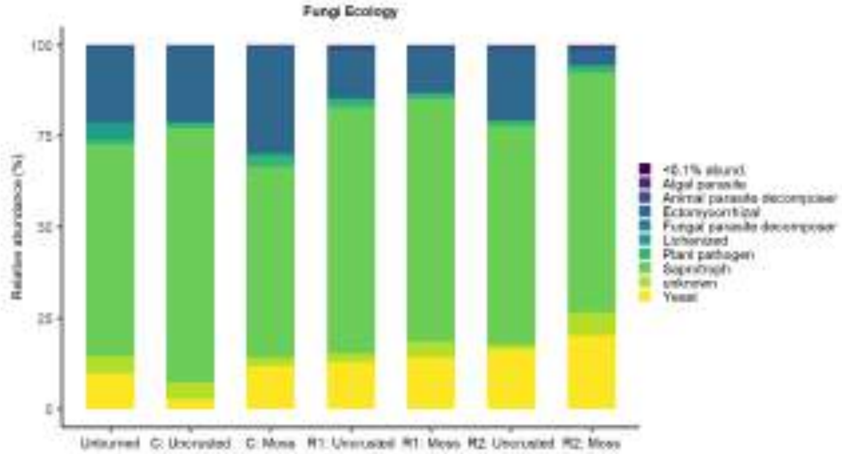

Fig. 6. Effects of mulch treatments and crust presence on the dominant fungal ecological roles at the end of the experiment. Data represent the relative abundance for soils under "Treatment" application (unburned soils, controls and soils under mulch application at Rate1 and 2), and differentiated by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

3.6. Mulch effects on the bacterial community composition

After one year from the wood mulch application in soils, the study of the dominant taxa in the bacterial community revealed slight response of the bacteria composition to the mulch (Fig. D3, Fig. 7), and negligible effects due to the soil crust presence (excluded in the figure). At phylum and genus level, Proteobacteria was the most reactive to the wood mulch presence, with increases in Betaproteobacteria *Massilia* and *Comamonas* (Burkholderiales), and in lower degree *Ramlibacter* (Burholdeeriales), and the Alphaproteobacteria *Devosia* (Rhizobiales). The Alphaproteobacterial genus *Sphingomonas* was negatively affected. In addition, some Actinobacteria were responsive to the mulch, and increases were found for Arthrobacter (Actinomycetales) and decreases in Solirubrobacteraes (*Conexibacter* and *Solirubobacter*).

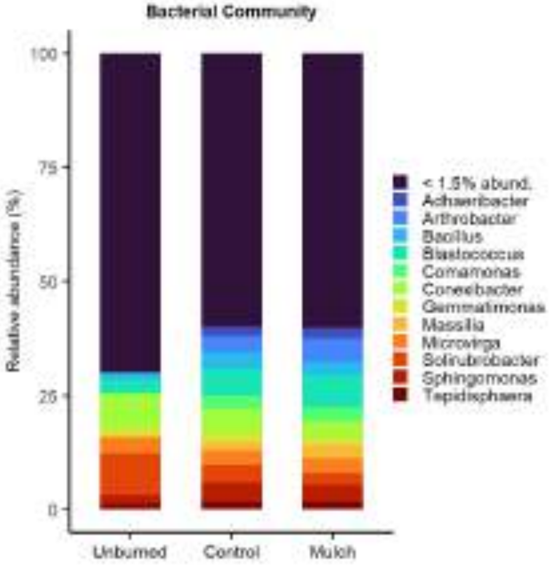

Fig. 7. Effects of mulch treatments on the dominant bacterial genera at the end of the experiment. Data represent the relative abundance for soils under "Mulch" application (unburned soils, controls and soils under mulch).

4. Discussion

After one year of application of a protective cover based on wood mulch in soils recently affected by a wildfire and subsequent salvage logging, the study revealed contrasting responses from different components of the studied soils. Firstly, the moss biocrust exposed high sensitivity to the wood mulch, drastically inhibited below the sudden wood cover, with the strongest reduction under the thicker layer of wood, similarly reported in other studies where mulching controls the vegetation recovery after fires (Bautista et al., 2009). This response corroborates biocrust-forming moss species that emerge after fires present adaptive traits to high radiation and temperatures (Ladrón De Guevara and Maestre, 2022), with preference to open spaces characteristic in the early post-fire stages (Esposito et al., 1999). Proven the ability of mosses to effectively stabilize soil surface in fire-affected areas (Silva et al., 2019; Gao et al., 2020; Gall et al., 2022b), percentages of 82% of biocrust cover 19 months after the fire suggest its development may be fast enough to counteract erosion processes, thus additional mitigation treatments would be unnecessary, even more considering the long persistence of wood mulch on the forest floor (Robichaud et al., 2020). In this case, the mulch application for restoration purposes would conflict with the passive soil restoration performed by the moss biocrust, which in early post-fire stages demonstrated to accelerate the recovery of soils, thus the ecosystem functioning (García-Carmona et al., 2022).

The limited effect on the soil physicochemical properties after one year of mulch application was expectable in a Mediterranean climate, where low precipitations combined with high temperatures slowdown the decomposition rates, adding to the low degradability of wood in early decomposition stages (Goodell et al., 2020; Bonanomi et al., 2021). However, as reported by Marañón-Jiménez and Castro (2013), in the first years after a wildfire in a Mediterranean forest a progressive N and P leaching from wood to soils is expected, as well as increases in organic carbon in a medium-term (Juan-Ovejero et al., 2021). The small changes in the biochemical soil properties (microbial biomass carbon, β-glucosidase, and phosphatase) were revealing, possibly promoted by the effectiveness of mulches and biocrust-forming mosses in water retention and infiltration in soils (Xiao et al., 2016; Luna et al., 2018). The combination of the biocrust development with the initial wood decay boosts the microbial biomass carbon and the microbial activity, which indicates an initial cascading effect on the soil nutrient cycling (Kahl et al., 2017; Cheng et al., 2021). Nonetheless, the microbial biomass carbon was adversely affected under the higher rate of mulch. A homogeneous and total wood cover provides low microhabitat heterogeneity, but also recalcitrant carbon low in N, which could lead to a transitory N microbial immobilization limiting their growth (Jonas et al., 2019). The recalcitrant wood substrate did not highly stimulate the hydrolase activities in bulk soils as it known lignin of coniferous species is known to be recalcitrant and difficult to degrade (Blanchette, 1991; Kahl et al., 2017). Nevertheless, β-glucosidase was responsive to Rate 1 of mulch, characterized by a more heterogeneous microhabitat that is favourable to host a diversity of microbes having diverse functions that allow the degradation of a larger range of wood compounds (Larrieu et al., 2014). The similarities between Rate 1 mulch with unburned soils, with increasing organic carbon, N, microbial biomass, and respiration, suggest an improvement in soil conditions toward the recovery of soil functionality.

The contrasting response in the fungal and bacterial biomass corroborates their different sensitivities to disturbances (Muñoz-Rojas et al., 2016; Bastida et al., 2017). Under natural wood decay, an increment of fungal abundance is not expected until late stages of wood decomposition (Baldrian et al., 2016), thus not surprisingly fungal soil biomass remained low after being severely affected by a wildfire (Dooley and Treseder, 2012). In contrast, a quick response of bacteria is generally observed under favourable conditions as the nutrients are released after the fire (Pressler et al., 2019), and is expected to gradually increase during decomposition (Urbanová et al., 2015). The microbial growth patterns did not correlate with the microbial richness, fungi increasing in richness with mulch application, especially under Rate 1. The explanation for this increment could be related to the higher microenvironment heterogeneity created, supporting more diversity combined with an increment in saprobes variability after the fresh wood incorporation on the forest floor (Arnstadt et al., 2016; Song et al., 2017; Lepinay et al., 2021). Contrary to expected, bacteria richness in moss biocrust soils (without treatment) decreased compared to uncrusted soils after one year, despite the initial boost in the early post-fire stages and the improvement in soil stability over time (Garcia-Pichel et al., 2003; García-Carmona et al., 2022). The reason remains speculative, may be related to variations in the soil chemical composition, i.e., the transitory exhaustion of labile nutrients released by the fire invested in fast growth bacteria (Aanderud et al., 2019).

The alterations observed in the microbial community structure evidence how management practices profoundly change soil microbial composition, sometimes with consequences for the forest ecosystem functioning (Kohout et al., 2018; Pereg et al., 2018). Both fungi and bacteria showed short-term alterations after the wildfire, as demonstrated in previous studies (Prendergast-Miller et al., 2017; Li et al., 2019), combined with the additional effects of the wood mulch application. The fungal community was the most sensitive to the wood mulch presence, which is understandable due to their ability to colonize fresh wood and lead the degradation in the early stages (Lepinay et al., 2021). Nevertheless, a trend of increasing similarities in composition for both fungi and bacteria was documented in soils subjected to wood mulch application, being the high microbial diversity described seven months after the wildfire between the moss biocrust soils and the uncrusted soils (García-Carmona et al., 2022) diluted after one year of mulch treatment. This may be attributable to the sensitivity of soil microorganisms to induced disturbances (Tomao et al., 2020). In soils affected by a wildfire and logging, subsequent forest practices such as mulch application limited the short-term diversity of soils increasing similarities among microbial communities. As many fungal and bacterial taxa colonize fresh wood, the assembly of communities seem to respond to stochastic processes (Baldrian et al., 2016; Lladó et al., 2017), but it is expected to boost the microbial specialization over time during the wood decay process (López-Mondéjar et al., 2018; Lepinay et al., 2021).

Stochastic assembly processes for microbial communities are inherent in soils recently disturbed, such as following wildfires (Nelson et al., 2022). In fire-affected soils, the emergence of biocrust slowly alters the underlying soils and filters over time the soil microbial composition (Ferrenberg et al., 2013; Li and Hu, 2021). The slight moisture improvement in moss biocrust soils under the stressful semi-arid conditions strongly impacted the fungal community composition, which was also probably influenced by the higher soil stability, shade, and enrichment in soil nutrients provided by mosses (Weber et al., 2016; Bao et al., 2019). In accordance with this, the higher P content accounted in moss biocrust soils was highlighted as a driver for both fungal and bacterial communities. After a wildfire, the release of available phosphorous is of high relevance in nutrient restrictive soils since it ensures the plant community development in the first post-fire successions (Certini, 2005; Fultz et al., 2016) and controls the microbial community composition after the disturbances when nutrient cycling is profoundly altered (Pérez-Valera et al., 2019). Despite the homogeneity described in mulch soils, the slight differences developed in soils under different application rates were transferred to the microbial communities driving part of the community structure, fundamentally observed in fungi. Fungi were sensitive to the N content in soils under mulch, showing a contrasting behaviour between soils under Rate 1, with the higher content in N, in contrast to soils under the highest rate of wood mulch. The high C/N ratio of wood could create N limitation in the microbial community, strongly immobilized under high doses of wood mulch (Laiho and Prescott, 2004; Jonas et al., 2019), an effect also described for wood-inhabiting fungi in which N influences the community composition and the enzymatic activity (Baldrian et al., 2016; Bonanomi et al., 2021).

The study of the dominant taxa revealed differences in the fungal community in response to the mulch application and the biocrust presence. After the detriment in burned soils in favour of Ascomycota (Reazin et al., 2016; Smith et al., 2017), Basidiomycota increased in mulch soils presumably due to their important role in wood decay. Ascomycota are generally dominant compared to Basidiomycota, especially at the early stages of decomposition (Baldrian et al., 2016; Purahong et al., 2018). However, Basidiomycota are fully involved in the decomposition process due to their ability to degrade lignin and other complex wood components (Eichlerová et al., 2015). Although Ascomycota play a lesser role in wood decomposition (Eichlerová et al., 2015; Tláskal et al., 2021), they constitute an important part of the wood fungal community and are known to regulate the plant-microbes interactions (Challacombe et al., 2019). Positively related to the mulch application, Chytridiomycota have been described by its ability to degrade recalcitrant materials in forest soils (Smith et al., 2017), but also found associated with mosses (García-Carmona et al., 2022), as well as the Zygomizota genus *Mortierella*, frequently found in coarse wood debris associated to decomposing fungal biomass (Baldrian et al., 2016; Brabcová et al., 2016). The substantial differences in the genera dominance between uncrusted soils and moss biocrust soils were diluted under the two rates of mulch. This effect was observed in the fire-responsive fungi or pyrophilous, usually dominated by species from Pezizales order which are known to produce resistant propagules and sclerotia (Pulido-Chavez et al., 2021). Apart from the strong response of *Terfezia*, it was noticeable the maintenance under mulch soils of genus *Pyronema*, *Pustularia,* and *Geopyxis* (Pyronemataceae) (Reazin et al., 2016; Bruns et al., 2020). Wood saprotrophs Pleosporales showed different behaviour; the increase in *Sporormiella* after the fire decreased one year later in mulch soils, and *Paraphoma*, which was negatively affected by the fire 7 months later, increased under mulch application (García-Carmona et al., 2022). However, the highest shift under mulch corresponds to the increase in Basidiomycota yeasts (Tremellomycetes). In addition to the responsive to C enrichment *Cryptococcus* (López-Mondéjar et al., 2018), *Naganishia* was highlighted as the most abundant under mulch, yeast described as able to utilize a wide spectrum of C sources materials (Mašínová et al., 2017), which would suggest the initial degradation of wood mulch in soils.

Shifts in the fungal community composition were translated into fungal functional shifts in soils. The removal of vegetation after fire makes harsh ecosystems, and the uncrusted soils without mulch deal with the highest solar radiation and low soil moisture, the reason for expressing the most different functional community. By comparison, moss biocrust soils expressed a higher concentration of ectomycorrhiza, which may be benefited by the presence of fire-responsive mosses since in ecosystems adapted to fires the spore bank can remain intact even after high severity fires (Glassman et al., 2016). In addition, it has been demonstrated that several pyrophilous taxa are endophytes of bryophytes (Raudabaugh et al., 2020). Soils under mulch compared to moss biocrust increased in yeast, presumably *Naganishia*, added to a high proportion of saprotrophs are found. After fires, saprophytes, as the pyrophilous fungi, restore nutrients to the soil and promote the conditions for plant succession to begin, and also stabilize burned soils reducing risks of soil erosion and increasing soil humidity (Filialuna and Cripps, 2021). Nevertheless, in contrast to the rapid colonization of some post-fire fungi, the recovery of fungal communities is known to be a slow process after a wildfire, especially for those fungi dependent on host plants recovery, and after the shifts in plant dominance and litter structure (Owen et al., 2019; Pérez-Izquierdo et al., 2020).

Bacterial dominant taxa undergo less drastic changes than fungal communities following mulching, thus changes found in the community structure must be related to less abundant or rare taxa. The dominant bacteria slightly responded to the wood mulch, and barely expressed differences in soil crust. The wildfire imposed important shifts in the community, Firmicutes and Bacteroidetes increase in detriment of Actinobacteria, as observed in many studies (Prendergast-Miller et al., 2017; García-Carmona et al., 2022; Nelson et al., 2022). Proteobacteria was almost the exclusive phylum to respond to the wood mulch application after one year. The Proteobacteria increment was led by Betaproteobacteria Burkholderiales, specifically *Massilia*, *Comamonas*, and *Ramlibacter*, and Alphaproteobacteria Rhizobiales (*Devosia*). In contrast, a decrease in *Sphingomonas* was observed. In addition, some Actinobacteria were mulch responsive, positively *Arthrobacter* (Actinomycetales), and negatively Solirubrobacterales (*Conexibacter*, *Solirubacter*). Proteobacteria are generally considered copiotrophs that preferentially consume the labile pool of organic C (Fierer et al., 2007), so are typically found in freshly fallen litter, not in fresh wood that represents a source of organic matter yet recalcitrant and impermeably thanks to the high lignin content (López-Mondéjar et al., 2016). Burkholderiales bacteria have been described as associated to wood due to their ability to the breakdown of phenolic compounds, including lignin (Lladó et al., 2017), also associated with wood-decay fungi (Tláskal et al., 2017). Rhizobiales is responsive to cellulose (Eichlerová et al., 2015), commonly found at late stages of wood decomposition thanks to their N-fixation ability (Lladó et al., 2017).

5. Conclusions

After one year of wood mulch application in fire-affected soils, mulch adversely affected the biocrust development interfering with the passive restoration of soils assisted by mosses, which are known to have great impact on the ecological processes. The presence of mulch barely impacted the physicochemical soil properties, but it did the biochemical ones. When compared rates, mulch at rate 1 (65% of soil cover) boosts the recovery of some properties, at the same time that partially simulates the natural heterogeneity of forest cover. However, the positive effects of biocrust on microbial diversity were reduced after the mulch application, i.e., the microbial communities become transitorily highly stochastic and less diverse. In particular, fungi acted as a good indicator of shifts induced by wood mulch application since the community responded with alterations in richness and structure, especially responding to the slight modification in soils between application rates. Consequently, despite preventing soil erosion after a wildfire, wood mulch may not be the best management practice to restore microbial community and preserve ecosystem functionality. Therefore, this practice should be applied only in high potential erosion risk areas but avoiding patches of emerging biocrusts. Nevertheless, wood-base mulching needs to be tested at larger scales to include the assessment of soil disturbance from the transit of heavy machinery, a factor that largely contributes to soil microbial community alteration.

CHAPTER 7

Contrasting Organic Amendments Induce Different Short-Term Responses in Soil Abiotic and Biotic Properties in a Fire-Affected Native Mediterranean Forest in Chile

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This chapter corresponds to the article:
Garcia-Carmona, M., Marin, C., García-Orenes, F., & Rojas, C. (2021). Contrasting organic amendments induce different short-term responses in soil abiotic and biotic properties in a fire-affected native Mediterranean forest in Chile. Journal of Soil Science and Plant Nutrition, 21(3), 2105-2114.
doi:10.1007/S42729-021-00506-Z/TABLES/2

Abstract

This study aimed to evaluate contrasting organic amendments as a strategy to promote the recovery of biotic and abiotic edaphic conditions central to the reestablishment of soil ecosystem functions at a site in south-central Chile affected by megafires in the 2016–2017 summer season. We analyzed the effects of the application of fresh (poultry and swine manure) and stabilized (compost of agricultural waste origin) organic amendments on microbial parameters, including basal respiration, microbial biomass, the carbon mineralization coefficient, and the microbial metabolic quotient, along with soil physicochemical properties related to soil fertility and stability. All organic amendments improved soil fertility and stimulated soil microbial activity. Fresh amendments, particularly swine manure, promoted the immediate recovery of the microbial conditions evaluated. However, greater mineralization rates and thus presumably shorter periods of carbon (C) source consumption were related to the application of such organic amendments. Soils treated with compost accumulated the most organic carbon and nitrogen, ensuring long-term nutrient release and thus long-term soil function recovery. Choosing the type of organic amendment to use to sustain ecosystem resilience will highly depend on the restoration goals over time.

1. Introduction

Fires in Chilean Mediterranean ecosystems have increased over the last two decades, coinciding in the last 10 years with a period deemed as “megadrought” due to consecutive dry years, causing major socioeconomic and environmental impacts (Garreaud et al., 2020). The latest fire of vast magnitude, the so-called extreme fire event or megafire, occurred in the 2016–2017 summer season in central and south-central areas of Chile (32–40° S latitude) and reached a historical maximum affected area of approximately 600,000 ha (De la Barrera et al., 2018).

Although Mediterranean landscapes are prone to fires (Pausas et al., 2009), the intensity and severity of wildfires increase dramatically in megafire events, endangering the resilience of forest ecosystems (Moreira et al., 2020). In this context, where the natural recovery of native vegetation is hampered, restoration efforts towards post-fire recovery of ecosystem services become crucial (Muñoz-Rojas, 2018). Thus, restoration of belowground functions, such as biological productivity, nutrient cycling, physical stability, carbon sequestration, and support for plant growth (Keesstra et al., 2016), is essential to sustain aboveground ecosystem conditions. These efforts not only should take into account the characteristics of the landscape to be restored, but also the processes or components aimed to recover in the short and long term (Costantini et al., 2016).

The effects of fires on soil properties depend primarily on pre-fire edaphic conditions, the type of ecosystem affected, the severity and intensity of fires, and post-fire meteorological conditions (Neary et al., 2005). Microbial dynamics and growth can be strongly affected by frequent fires and droughts (Guénon and Gros, 2016), hindering the recovery of microbially driven ecosystem functions, including nitrogen and carbon cycling (Pérez-Valera et al., 2019). Moreover, high-severity fires damage soils mainly due to the combustion of organic matter, a critical component of terrestrial ecosystems, since it plays key roles in nutrient cycling, microbial activity, and soil structure formation (González-Pérez et al., 2004). Thus, considering a key component in the restoration process as soil organic matter has cascading effect implications in multiple components in a perturbed ecosystem (Heneghan et al., 2008). The reestablishment of organic matter levels in post-fire restoration efforts, for example, by applying organic amendments, is an effective strategy to promote vegetation reestablishment and the recovery of soil health, thus restoring its ecosystem functions and services (Larney and Angers, 2012; Hueso-González et al., 2018). In the short term, an increase in organic matter through the addition of organic amendments boosts soil fertility and nutrient cycling, stimulates soil microbial growth and activity, and favors a rapid plant establishment, whereas in the long term, soil structure and stability and water holding capacity improve, hence reducing the risks of erosion and nutrient loss (Ojeda et al., 2003; Larchevêque et al., 2005).

In soil restoration plans, choosing the type of organic amendment to use is an important step, as this decision dictates decomposition rates and has transient and durable implications on soil conditions (González-Ubierna et al., 2012). The application of fresh organic amendments adds a high amount of labile, easy-to-degrade organic carbon to soils with short turnover times, which promotes the rapid growth of microorganisms and vegetation (Haynes, 2005). However, fresh organic amendments can have potential adverse effects, including increases in autochthonous soil organic carbon mineralization, short-term CO_2 emissions, salinity or acidity, nitrogen immobilization, and/or the addition of potential pollutants and pathogens into soil and bodies of water (Bernal et al., 2009). In contrast, stabilized materials, such as compost, provide a high proportion of stable organic substances contributing to enduring soil fertility (Larney and Angers, 2012). Consequently, the amendment selection will depend on the goals of the soil restoration plan. While fresh amendments with high contents of labile organic matter might enhance biological activity by acting as a fast release of C in recently burned soils, the more stabilized organic amendments would ensure carbon and nutrient storage with slow mineralization rates over time (Kowaljow and Mazzarino, 2007).

This study aimed to evaluate the effect of contrasting organic amendments in the restoration of biotic and abiotic edaphic conditions, which are key to the recovery of ecosystem functions, in a fire-affected sclerophyllous forest in the Mediterranean zone of central Chile. For this purpose, microbial parameters, including basal respiration, microbial biomass, the carbon mineralization coefficient, and the microbial metabolic quotient, along with soil physicochemical properties, such as organic carbon, nutrient, and metal contents, were studied after the application of fresh (poultry or swine manure) and stabilized (compost of agricultural waste origin) organic amendments. We hypothesize that fresh amendments, poultry and swine manure, would promote immediate, but transient, microbial conditions recovery, enhancing microbial biomass and activity in a short term. On the contrary, the compost amendment, characterized by stabilized organic matter, would impact long-term soil function recovery by increasing organic matter and nutrient contents in soils.

2. Materials and Methods

2.1. Research site

The study was conducted in the Chilean Mediterranean zone of the O'Higgins Region, one of the most affected regions during the 2016–2017 summer megafire (CONAF, 2017). The study site is located in the Pumanque commune (34° 36.502' S, 71° 42.281' W; altitude: 130 m.a.s.l.), in the region's dryland coastal zone. According to information provided by local residents, within the last 30 years, the site was mainly used by small farmers for livestock pasture and wood charcoal production and had not experienced fire events until January 2017. The average annual precipitation is 451 mm, with an average temperature of 15.4 °C (summer: 29.9 °C, winter: 5.3 °C). The site is mainly covered by native sclerophyllous forest species, dominated by *Quillaja saponaria* Molina, *Lithraea caustica* Hook. & Arn., and *Peumus boldus* Molina in the canopy, and *Trevoa trinervis* Miers, *Azara serrata* Ruiz & Pav., and *Colliguaja odorifera* Molina in the understory. Soils are classified as Aquic Dystroxerepts (Soil Survey Staff, 2014) with low depth (40 cm on average) and sandy loam texture (58% sand, 34% silt, and 8% clay) located on a 10% slope facing south.

2.2. Experimental design

The application of organic amendments and different vegetation establishment methods were implemented in early June of 2018, as part of a previous study, to evaluate the effect of them on early soil biological conditions (Marín and Rojas, 2020). Poultry and swine manure were organic materials easily available at the site location, while compost consisted of a commercial product originating from agricultural wastes. Chemical analyses of organic amendments have been previously reported (Marín and Rojas, 2020). Briefly, organic carbon and total nitrogen contents were 10.38% and 0.83% in compost, 23.47% and 1.92% in poultry manure, and 12.89% and 0.75% in swine manure (further information on the amount of OM, OC, and N added by each organic amendment is provided in Table S1). The pH (1:5 w/v water extract) values varied from 6.77 (in poultry manure) to 8.8 (in swine manure), while electrical conductivity (1:5 w/v water extract) fluctuated from 1.12 (in compost) to 3.56 mS cm^{-1} (in poultry manure). These amendments were incorporated over the upper 30 cm of soil, with a 1-cm mulch layer consisting of a wheat and oat straw mix (except for the reference and control treatments), following rototilling at the same depth (Marín and Rojas, 2020).

For the present work, soils receiving organic amendments and plants were revisited in January of 2019. Six treatments were evaluated, these consisted of T0, reference (unburned area); T1, control (burned); T2, mulch (burned + mulch); T3, compost (burned with 200 m3 ha^{-1} or 78.77 t dry weight ha^{-1} + mulch); T4, poultry manure (burned with

200 m3 ha^{-1} or 150 t dry weight ha^{-1} + mulch); and T5, swine manure (burned with 200 m3 ha^{-1} or 95.67 t dry weight ha^{-1}+ mulch). Treatments were each distributed in four parcels (3 m × 1.5 m) within (1) a burned area of 50 m × 50 m (T1–T5) and (2) an unburned area of 20 m × 20 m (T0), located within the research site at a distance of approximately 500 m from the burned area.

2.3. Soil sampling and analyses

Soil sampling was conducted 8 months after organic amendment application in January 2019, which coincided with the summer season in the Southern Hemisphere. Four composite soil samples (1 kg each sample approx.) were taken per experimental parcel (3 m × 1.5 m). These samples were collected at a 6-cm depth in the A horizon following the removal of organic debris (including mulch when applied). In total, 96 composite soil samples were analyzed (six treatments × four parcels per treatment × four technical replicates per parcel). Each technical replicate consisted of five subsamples taken at the corners and center of each parcel. For each composite soil sample, an aliquot was used to measure microbiological parameters (using samples kept at 4 °C) and to perform the aggregate stability test (using samples dried at room temperature and sieved apart between 4 and 0.25 mm). The remaining aliquot was sieved at 2 mm for the rest of the physicochemical analyses.

Soil organic carbon (OC) was determined by the potassium dichromate oxidation method by the Walkley-Black procedure (Nelson and Sommers, 1983); total nitrogen was determined by the Kjeldahl method (Bremner and Mulvaney, 1982); and available phosphorus was determined by the Burriel-Hernando method (Burriel and Hernando, 1950; Díez, 1982). Soil pH and electrical conductivity (EC) were determined in a 1:2.5 and a 1:5 (w/v) water extract, respectively. Aggregate stability was measured using the method of Roldán et al. (1994) based on the method of Benito and Díaz-Fierros (1989). This method examines the proportion of aggregates that remain stable after a soil sample is subjected to an artificial rainfall of known energy (279 J min^{-1} m^{-1}). Water-soluble carbohydrates were determined in a 1:5 (w/v) aqueous extract, using the anthrone method as reported by Brink et al. (1960). EDTA-extractable trace elements (Fe, Zn, Cu, and Mn as available micronutrients and Ni, Cr, Pb, and Cd as potential pollutants) were obtained from a 1:10 (w/v) extract with 0.05 M EDTA (pH 7), following shaking for 1 h at room temperature (Quevauviller et al., 1998), determined by an atomic absorption spectrophotometer.

Regarding the microbial parameters used in this study, the basal respiration was measured based on the CO_2 emission from 4 g of fresh soil adjusted to 60% water holding capacity and incubated for 24 h at 30 °C. The microbial biomass was estimated by the substrate-induced respiration (SIR) method using glucose (3 mg per gram of soil, the optimum rate of glucose determined after calibration as the available substrate (Anderson and Domsch, 1978), based on the CO_2 emission from 4 g of fresh soil adjusted to 60% water holding capacity and incubated for 6 h at 30 °C). The amount of CO_2 emitted during both incubations was detected by indirect impedance measurement in an automated impedance meter (BacTrac 4200 Microbiological Analyzer, Sylab, Austria) based on the changes in the impedance of a KOH solution (2%) after potassium carbonate formation (Mengual et al., 2014; Rodríguez et al., 2018; García-Carmona et al., 2020). In addition, two biological indices were calculated with these values: the coefficient of carbon mineralization, determined as the basal respiration divided by total organic carbon, to assess the mineralizing capacity of soil in the presence of the amendments (Fernández et al. 2007), and the metabolic quotient (qCO_2) determined as the basal respiration divided by microbial biomass carbon, to estimate the efficiency of C decomposition by the microorganisms (Anderson and Domsch, 1978).

2.4. Statistical analysis

To test whether soil characteristics differed among treatments, we fitted generalized linear models (GLMs) using the soil properties analyzed as response, followed by multiple comparisons performed with the Tukey test ($p < 0.05$). The relationship between the soils parameters measured regarding the treatments applied was analyzed using principal component analysis (PCA). These statistical analyses were performed in RStudio v.3.6.2 (RStudio Team, 2020) using the RStudio base function glm and the FactoMineR package (Lê et al., 2008).

In order to test the effects of soil physicochemical parameters on microbial parameters, and then the effect of organic amendments (T1–T5) on these same parameters, linear regressions were performed. First, stepwise regressions independent of treatment with all physicochemical parameters were performed in both directions in order to identify those abiotic parameters that better explained microbial parameters. Then, in a new model (that included physicochemical parameters selected in the first model), the effect of treatments with organic amendments was included as a predictor. Analyses were performed using the RStudio base function lme.

3. Results

The soils under study showed variable responses in physicochemical conditions following fire occurrence and the incorporation of treatments (Table 1). Eight months after the treatment establishment, amended soils showed the highest OC contents (Table 1): those receiving compost showed significantly higher values (5.19%), followed by poultry manure (4.73%), and swine manure (4.14%) amended soils. The same pattern was observed for N contents, where soils amended with compost had significantly higher values (0.54%) than those receiving fresh amendments in the form of poultry manure (0.47%) and swine manure (0.36%). Thus, a more stable material as compost, although providing fewer initial amounts of OC and N than manures (Table E1, Appendix E), resulted in greater amounts of these elements in amended soils. In addition, phosphorus contents registered a noticeable increase due to the addition of compost and manures, especially in soils treated with poultry manure, which showed approximately one to two orders of magnitude greater values than in mulch (burned + mulch) and control (burned) soils, respectively. Carbohydrate contents increased significantly in soils receiving not only compost and manure but also mulch, while high aggregate stability levels were observed for all soils. Increases in salinity and metal contents were registered in all amended soils; nevertheless, they were still under toxic levels for most plants (Kabata-Pendias, 2011) (Table 1).

Table 1. Means ± standard deviation of the main physicochemical properties analysed in the soil treatments. T0, reference (unburned); T1, control (burned); T2, mulch (burned +mulch); T3, compost (burned + compost + mulch); T4, poultry manure (burned + p.manure + mulch); and T5, swine manure (burned + s.manure + mulch). Lowercase letters represent significant differences among mean groups after GLMs models (Tukey test, p <0.05). (AS, aggregate stability; Ch, carbohydrates).

	T0	**T1**	**T2**	**T3**	**T4**	**T5**
OC (%)	3.99 ± *0.58* bc	3.27 ± *0.52* a	3.66 ± *0.38* ab	5.19 ± *1.22* d	4.73 ± *0.57* cd	4.14 ± *0.51* bc
N (%)	0.31 ± *0.03* ab	0.27 ± *0.04* a	0.26 ± *0.03* a	0.54 ± *0.12* d	0.47 ± *0.07* c	0.36 ± *0.04* b
P (mg kg^{-1})	22.03 ± *8.08* a	8.08 ± *3.88* a	20.78 ± *10.19* a	169.1 ± *38.9* b	625.8 ± *151.7* d	302.4 ± *138.8* c
Ch (mg kg^{-1})	16.67 ± *3.58* a	31.48 ± *7.60* a	66.56 ± *29.53* b	58.32 ± *12.47* b	57.17 ± *8.53* b	64.39 ± *19.85* b
AS (%)	75.32 ± *6.12* b	74.41 ± *7.16* b	71.48 ± *7.86* ab	65.81 ± *5.44* a	73.27 ± *6.79* b	73.13 ± *6.95* b
pH	6.94 ± *0.10* cd	6.49 ± *0.19* a	7.12 ± *0.33* d	7.43 ± *0.10* e	6.89 ± *0.11* ab	6.69 ± *0.22* bc
EC (µS cm^{-1})	56.6 ± *6.7* a	54.9 ± *5.7* a	115.8 ± *59.9* b	164.7 ± *25.4* c	286.6 ± *52.4* d	199.0 ± *49.4* c
Zn (mg kg^{-1})	4.52 ± *1.93* a	3.51 ± *1.11* a	4.56 ± *1.01* a	28.91 ± *6.74* c	31.59 ± *6.73* c	18.64 ± *5.99* b
Cu (mg kg^{-1})	1.16 ± *0.22* a	2.15 ± *0.76* ab	3.55 ± *0.67* bc	11.76 ± *2.45* e	7.29 ± *1.08* d	5.48 ± *2.51* c
Mn (mg kg^{-1})	0.23 ± *0.06* ab	0.27 ± *0.03* ac	0.29 ± *0.06* c	0.23 ± *0.05* a	0.27 ± *0.04* bc	0.27 ± *0.04* ac
Fe (mg kg^{-1})	0.21 ± *0.04* a	0.21 ± *0.03* a	0.18 ± *0.02* a	0.45 ± *0.10* c	0.31 ± *0.05* b	0.32 ± *0.05* b
Ni (mg kg^{-1})	0.11 ± *0.09* a	0.27 ± *0.08* bc	0.31 ± *0.10* c	0.22 ± *0.10* ac	0.12 ± *0.05* bc	0.26 ± *0.16* ab
Cr (mg kg^{-1})	3.90 ± *2.38* b	2.54 ± *1.13* a	1.41 ± *0.73* a	2.05 ± *0.47* a	3.21 ± *0.74* a	2.02 ± *0.75* a
Pb (mg kg^{-1})	0.49 ± *0.53* a	0.56 ± *0.33* a	1.08 ± *1.14* a	1.72 ± *0.95* a	7.37 ± *2.72* b	3.16 ± *2.61* a
Cd (mg kg^{-1})	0.05 ± *0.04* ab	0.02 ± *0.02* a	0.13 ± *0.04* b	0.26 ± *0.09* c	0.34 ± *0.02* c	0.21 ± *0.13* c

Soil microbial processes responded differently to the effect of land burning and established treatments (Fig. 1). Basal respiration particularly responded to organic amendments, showing higher values in soils receiving swine manure and poultry manure than in soils amended with compost (Fig. 1). Although soil covered with mulch showed significantly lower respiration rates than soils receiving compost or manure, it had significantly greater values than control and reference soils. In contrast to basal respiration, microbial biomass showed few differences among treatments; however, the greatest values were observed in soils receiving fresh amendments in the form of swine manure and poultry manure, although the latter did not show a significant increase when compared to the rest of the treatments (Fig. 1). Regarding the microbial indices, the coefficient of carbon mineralization showed an increase in all fire-affected soils, including the control (Fig. 1). Similarly, the metabolic quotient (qCO_2) also increased in all fire-affected treated soils and the control, with significantly higher values in compost- and manure-amended soils (Fig. 1).

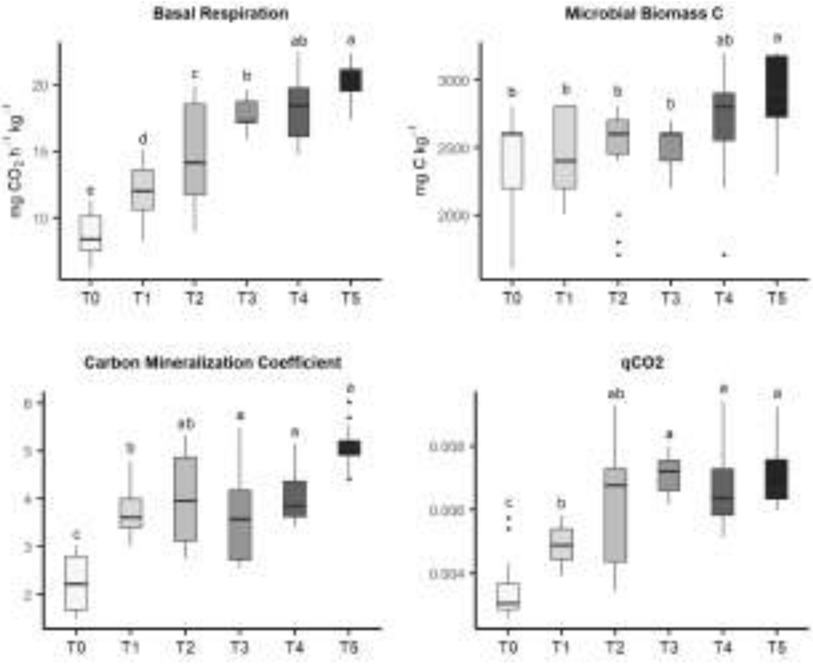

Fig. 1. Box-plot of basal respiration (mg h−1 kg−1), microbial biomass (mg kg−1), coefficient of carbon mineralization, and microbial metabolic quotient, qCO2, measured in soils treatments: T0, reference (unburned); T1, control (burned); T2, mulch (burned + mulch); T3, compost (burned + compost + mulch); T4, poultry manure (burned + p.manure +mulch); and T5, swine manure (burned + s.manure +mulch). Points represent outliers, lowercase letters represent significant differences among mean groups after GLM models (Tukey test, $p < 0.05$).

According to the PCA, soils receiving organic amendment were grouped apart from those at the reference (unburned) forest, control (burned), and mulch (burned + mulch) parcels (Fig. 2), with the first two components explaining 56% of the variation. All soil parameters grouped towards the first PCA component were positively correlated and highly influenced by the treatments tested in this study. The ordination of soils amended with compost was highly influenced by N and OC contents and Fe, Cu, and Zn micronutrients. These micronutrients, along with the basal respiration, qCO_2, EC, and P, highly influenced the ordination of poultry manure-amended soils, while microbial parameters, especially the coefficient of carbon mineralization, also highly influenced poultry manure-amended soils (Fig. 2).

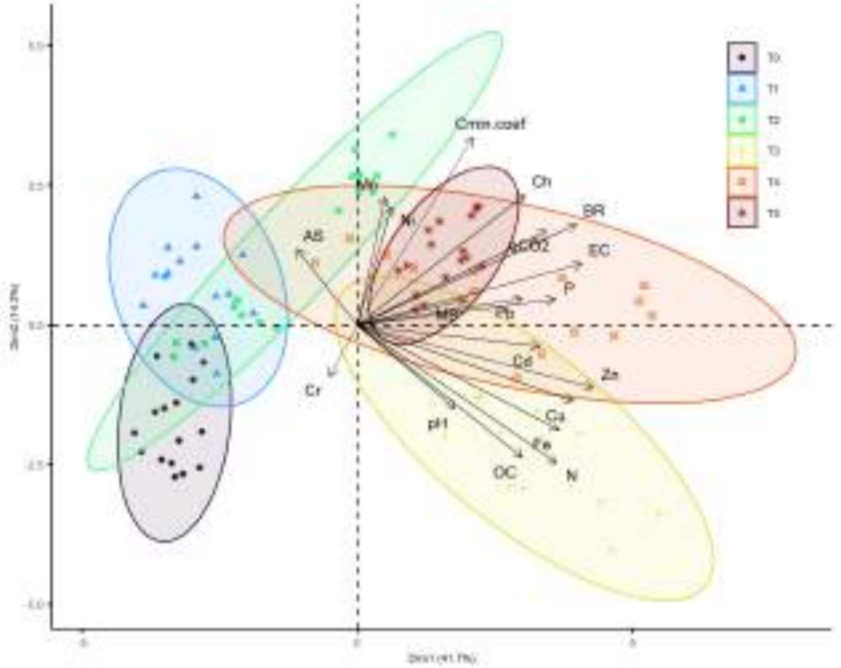

Fig. 2. Scores and loadings for PCA performed for soil treatments: T0, reference (unburned); T1, control (burned); T2, mulch (burned +mulch); T3, compost (burned + compost +mulch); T4, poultry manure (burned + p.manure + mulch); and T5, swine manure (burned + s.manure +mulch). (OC, organic carbon; N, total nitrogen; P, available phosphorous; AS, aggregate stability; Ch, carbohydrates; BR, basal respiration; MB, microbial biomass; qCO2, microbial metabolic quotient; Cmin.coef., coefficient of carbon mineralization; EC, electrical conductivity).

Table 2. a.) ANOVA of linear models for microbial parameters (basal respiration, microbial biomass, coefficient of carbon mineralization, and qCO2, microbial metabolic quotient) that included treatments as a predictor, in addition to those abiotic parameters that better explained microbial parameters (Table E2), and b.) specific effects of each treatment (T1, control (burned); T2, mulch (burned +mulch); T3, compost (burned + compost + mulch); T4, poultry manure (burned + p.manure + mulch); and T5, swine manure (burned + s.manure + mulch)).

	Basal respiration	Microbial biomass	Mineralization C coefficient	qCO_2
a. ANOVA of the models				
Model AIC	1615.496	1940.612	286.888	478.328
Treatments	129.019***	48.380***	51.187***	8.733***
EC	74.460***	44.624***	25.756***	0.486ns
Cu	0.639ns			0.214ns
Mn	9.823**	1.174ns	1.322ns	0.053ns
Fe	0.171ns	0.292ns	11.781***	0.247*
Cr	10.530**	0.168ns	2.018ns	
Pb	<0.001ns	0.140ns	11.711***	9.213**
Cd	0.959ns		7.537**	
pH		8.734**		2.151ns
N		1.714ns		
OC			2.582ns	
Ni				3.272ns
b. Specific treatments effects				
T1	6.628***	1.476^{ns}	8.012***	2.614*
T2	6.403***	5.973***	5.039***	3.096**
T3	4.794***	2.801**	2.416*	0.862^{ns}
T4	1.813^{ns}	-2.287*	1.535^{ns}	1.572^{ns}
T5	8.063***	2.156*	5.860***	1.146^{ns}

a. F-values$^{p\text{-values}}$ are indicated; empty cells indicate that the variable was not included in the model (Table S2).

b. t-values$^{p\text{-values}}$ are indicated. *P*-values: ***=<0.001; **=<0.01; *=<0.05; ^{ns}=non-significant.

After performing stepwise regressions (Table E2), models including the treatments and soil physicochemical parameters were run to test their effects on the indicators of microbial activity used in this study (Table 2). The organic treatment had a significantly higher effect than the soil physicochemical parameters on these four microbial parameters (Table 2). Among soil physicochemical parameters, EC had an effect on all measurements except for qCO_2; in addition, all treatments (except T2) had a strong effect on EC (F value: 73.195: p value: >0.001). Some micronutrients (Fe and Mn) and potential pollutants (Pb and Cd) also slightly affected some of the microbial parameters (Table 2). Among treatments, T1 (burned control) also had effects on microbial parameters except for microbial biomass, thus showing that while lower, the effects of the aforementioned chemical parameters were still important.

4. Discussion

4.1. Responses of Biotic Soil Conditions Following Organic Amendments

Soil microbial conditions showed different responses following fire and the application of the treatments evaluated. Similar microbial biomass observed between unburned and burned soils (with no amendments) could be due to soil heating, which increases easily mineralizable compounds that can promote microbial activity and biomass growth immediately after land burning (Goberna et al., 2012). Indeed, our findings are consistent with those by Fuentes-Ramirez et al. (2018), who reported an increase in soil microbial activity 1 year after wildfires in mixed temperate rainforests of Araucaria araucana and Nothofagus pumilio ((Poepp. & Endl.) Krasser) in southern Chile due to changes in organic matter mineralization rates and the contribution of nutrients from ashes. Although wildfires usually result in a reduction in soil microbial biomass (Holden and Treseder, 2013), our findings suggest that the fire severity occurred at the studied site was likely of low to moderate. Nevertheless, the application of organic amendments significantly influenced soil microbial conditions, especially those related to basal respiration, reflecting its importance as an indicator of soil recovery, along with other soil parameters (Bastida et al., 2008). This finding was particularly significant for soils receiving swine manure, where the values obtained were significantly higher than those registered from reference unburned ecosystems, suggesting great short-term effects on the microbial population due to the high release of labile C compounds. Although less marked than basal respiration, microbial biomass also showed short-term responses to fresh organic amendments, which is consistent with results obtained in previous comparable studies (Ros et al., 2003). These observations were supported by previous findings within the same study system, where colony-forming unit (CFU) counts showed higher values in both fresh material-amended soils, reaching levels closer to the reference unburned ecosystem after 6 months of organic treatment establishment (Marín and Rojas, 2020).

4.2. Influence of Organic Amendment Type on Soil Organic Carbon

As opposed to microbial conditions, OC evidenced a decrease following land burning, which could reflect a symptom of soil degradation and potential loss of ecosystem resilience (Keeley, 2009). The fire-affected soils behaved differently depending on the type of organic matter used, which supports the idea that restoration success greatly depends on the characteristics of the organic amendment applied to soils (Hueso-González et al., 2018). The organic matter contents in animal manures were originally greater than in compost, but soils treated with the latter material showed the highest OC content at the end of this study. This fact relates to the coefficient of carbon mineralization values observed, where rates from soils amended with animal manures, particularly those with swine manure, evidenced greater mineralization rates and thus presumably shorter periods of C source consumption. Along with short-term activation in soil biological parameters following the addition of fresh materials, it is important to consider the priming effect, i.e., the mineralization of autochthonous soil organic matter driven by the input of fresh organic matter. Fresh materials could induce this phenomenon as a consequence of increased microbial activity (Kuzyakov, 2006), which could be a problem in soils impoverished in organic matter (Bastida et al., 2013), such as those affected by high-severity wildfires. Therefore, the use of more stabilized organic amendments such as compost in fire-affected soils could ensure greater long-term positive impacts on edaphic conditions due to greater turnover times (Haynes, 2005), for example, strongly influencing nutrient cycling and storage over time, soil structure stability, or water holding capacity, thus improving soil health and productivity. Despite the organic matter mineralization rates observed in all treatments, OC remained above the control burned soil at the end of the study.

4.3. Soil Nutrient Conditions After Treatment Application

Despite the greatest amount of total N in the poultry manure, when compared to compost and swine manure, all of the organic amendments added significant N contents into soils compared to reference (unburned) soils. However, considerable N loss was detected for soils receiving fresh materials, notably poultry manure, presumably via volatilization or leaching (Cellier et al., 2014). Usually, the use of fresh materials stimulates N immobilization in soils due to the high concentrations of easily degradable C compounds (Paul, 2014), but the nutritional balance of all organic amendments was adequate, as the C/N ratios were < 30; therefore, mineralization could have prevailed over immobilization (Bernal et al., 2009). Greater available P levels were also detected in soils amended with poultry manure, but these levels do not represent environmental risks over time, as P tends to accumulate in the topsoil layer without mobilization into the subsoil following long-term poultry manure application (Hoover et al., 2019). In addition, different responses to organic amendments between the microbial biomass and the basal respiration highlight the variable sensitivity of these biological parameters to these additions, which could be attributed in part to the toxicity produced by elements supplied with the organic amendments, which some studies have registered to affect soil microbial biomass (Tejada and Gonzalez, 2006). However, despite potential inhibitory effects in microbial biomass caused by the increase in salinity and Pb content, particularly those observed in the poultry manure amendment and soils treated with it, the levels of potentially toxic elements (Cu, Zn, Cr, Cd, Pb) in our study were very low and far from any problem of toxicity (Kabata-Pendias, 2011).

4.4. Recovery of the Soil Ecosystem Following Fires

In the context of global change and an increase in the severity and frequency of wildfires, it is crucial to understand how soil functions are recovered following fires so that the resilience potential of ecosystems vulnerable to land degradation is better understood. In this study, we observed different responses in soil properties with different types of organic amendments; our findings suggest that the addition of fresh materials has rapid and noticeable effects in soil microbial properties. Nevertheless, compost addition may provide the maintenance of the soil biogeochemical cycles over time, which would later result in higher microbial biomass and in the establishment of a plant cover indispensable for the long-term recovery of Mediterranean soils (Kowaljow and Mazzarino, 2007; Guénon and Gros, 2016). The consequences of restoration efforts in Chilean sclerophyllous forests affected by the increasing occurrence of wildfires need to be further investigated due to the importance of soil recovery to ecosystem functioning and to provide a better understanding of post-fire management plans.

5. Conclusions

The results obtained in our study suggest that swine manure had the most noticeable microbial response in the short term, reaching values above the reference unburned ecosystem. However, greater mineralization rates and thus presumably shorter periods of C source consumption related to such organic amendments might condition the recovery of ecosystem functions over time. Soils amended with compost accumulated the most OC, ensuring long-term nutrient release. Nevertheless, monitoring the evolution of microbial responses to contrasting organic amendments would be necessary to elucidate the implications of C as an energy source to sustain soil recovery in the long term. Wildfire increases in intensity and severity, as predicted for Mediterranean ecosystems under a global change scenario, demand a better understanding of the short- and long-term implications of restoration efforts. Thus, a good comprehension of contrasting organic amendment effects in soil functions and their implications on overall ecosystem recovery is central to sustaining the resilience of sclerophyllous forests following fires.

CHAPTER 8

General discussion

The general aim of the dissertation was to investigate the effects of contrasting types of post-fire management via the study of different key soil indicators of ecosystem recovery, i.e., the investigation of collective interactions among the response of soil properties, the alterations of microbial communities, and the functional roles of moss biocrust-forming mosses. Overall, the findings presented in this dissertation contribute to increasing the global understanding of post-fire ecosystems, especially the relevance of two active agents in soil recovery: the biocrust-forming mosses in early post-fire stages and the response of the soil microbial communities to fire and post-fire disturbances. The study of post-fire management allowed us to evaluate the involvement of each one in the protection or promotion of soil biodiversity and ecosystem functionality.

Our results agree with previous evidence suggesting that forest management involving strong interventionism generates severe soil degradation with detrimental consequences for ecosystem functioning (Hartmann et al., 2014; Mayer et al., 2020; Praeg et al., 2020; Thorn et al., 2020; Tomao et al., 2020). The damage is particularly accentuated when the management is conducted intensively in highly erodible soils, a situation in which the post-fire salvage logging triggers soil erosion processes with critical consequences for ecosystem recovery (García-Orenes et al., 2017; Pereg et al., 2018). A common recommendation when soils are vulnerable is postponing the operations (if not previously excluded) until a protective vegetation cover is developed, usually after the first spring (Vallejo et al., 2012). In the study area from Chapters 3 and 4, logging was performed seven months after the wildfire; however, the vulnerability of soils led to severe soil degradation, delaying vegetation regrowth, and profoundly altering the microbial composition, detected at short- and mid-term after the wildfire (García-Carmona et al., 2020, 2021a). Our findings reveal that the degradation of soil structure from the combining wildfire and mechanical operations disturbances seriously hinders ecosystem recovery in the short-term (García-Carmona et al., 2021a; Chapter 3). In particular, the loss in soil aggregate stability was the main driver of microbial community shifts, altering the resistance and resilience of soil microbial communities already disturbed by the wildfire. Surprisingly, higher bacterial and fungal richness was registered in disturbed soils compared to non-intervention. The results contrast with what was expected, as soil compaction implies the collapse of soil structure and thus the reduction of microenvironments suitable for soil biodiversity proliferation (Rabbi et al., 2016). The study of responsive taxa was revealing in this work, indicating the creation of new niches related to anoxic habitats following soil compaction, with taxa capable of anaerobic respiration from the Proteobacteria and Firmicutes families (Hartmann et al., 2014; García-Carmona et al., 2021a; Longepierre et al., 2021).

On the opposite, the relevance of burnt wood for soil microorganisms was exposed in non-intervened soils, where the wood distributed on the ground ameliorates the stressful soil surface conditions and serves as a nutrient resource (Marañón-Jiménez and Castro, 2013; Thorn et al., 2018; Juan-Ovejero et al., 2021). Non-interventionism promotes microbial development, in special taxa responsive to higher resource availability, mainly Actinomycetales (Actinobacteria), known for their specialization in organic matter degradation (Goldfarb et al., 2011; Goberna et al., 2012).

Our main finding reveals that biocrust-forming mosses have a key role in the recovery of multiple soil functions in post-fire ecosystems. The early colonization of mosses after a wildfire mitigates the soil degradation threat, i.e., softens the logging legacies in highly vulnerable soils, enhancing their functionality recovery in the short and mid-term (García-Carmona et al., 2020, 2022; Chapters 4, 5). The main functional role of biocrust in soils is to provide stability (Weber et al., 2022), which after wildfires is primordial to protect soils from erosion processes (Silva et al., 2019; Gao et al., 2020). Our field observations corroborate the fact that moss biocrust, both at seven months and six years after a wildfire (Chapters 5, 4), effectively retains soil against the runoff forces (i.e., evidence of soil erosion surrounding biocrust patches). Nevertheless, the developmental stage or age of the moss biocrust is critical for controlling the functions performed in soils (Faist et al., 2017; Drahorad et al., 2020; Tucker et al., 2020). Six years after the wildfire, the biocrust in an advanced developmental stage profoundly impacted soil fertility, critical biochemical processes, and microbial development (García-Carmona et al., 2020; Chapter 4). Despite the strong influence generally attributed to biocrust in local hydrological cycles via modifications in soil porosity, absorptivity, roughness, aggregate stability, texture, water retention, etc. (Belnap, 2006; Eldridge et al., 2020), our results did not expose a robust influence on water infiltration. The slight water repellency expressed in the field by mosses could contribute to trapping water near the soil surface (Faist et al., 2017; Xiao et al., 2019b), representing a mechanism for increasing moisture in soils as observed in Chapter 5 (García-Carmona et al., 2022).

Biocrust-forming mosses reach great relevance in fire-affected ecosystems thanks to their capacity to enhance soil fertility and nutrient fixation (Belnap et al., 2001; Ferrenberg et al., 2018). Several mechanisms contributed to this role. First, moss biocrust effectively stabilizes the soil surface, preventing soil loss after fires (Silva et al., 2019; Cania et al., 2020), and more importantly, it retains ashes thanks to their rapid colonization (field observation) (Caon et al., 2014). Second, moss biocrust acts as dust trappers, incorporating fine particles into soils (Belnap et al., 2001). This was particularly observed in Chapter 4, in which a high percentage of exposed soils after the severe salvage logging produced fine soil particles that eventually became trapped in the moss roughness, resulting in higher micronutrient content in soils (García-Carmona et al., 2020). Finally, and most importantly, mosses are primary producers that significantly contribute to nutrient cycling by fixing carbon and nitrogen, while at the same time promote phosphorous desorption from parent rock (Delgado-Baquerizo et al., 2018). Bryophytes, among other components of biocrusts, have the highest capacity for carbon fixation (Weber et al., 2015; Tian et al., 2022), but contrasting results were reported in our studies regarding the time since the fire disturbance. Contrary to the high increase in nutrient content found at mid-term (García-Carmona et al., 2020), biocrust at early post-fire stages showed no impact, or even a slight decrease, in the organic carbon and nitrogen contents in soils under the biocrust (García-Carmona et al., 2022). Different explanations are plausible for the lower content, either the transitory exhaustion of labile forms fire-released and utilized by the biocrust and microbial growth, or the preference of mosses to establish where lower recalcitrant organic matter concentrates after high-severity fires (González-Pérez et al., 2004; Slate et al., 2020). In addition, the fast-growing mosses demand N in order to colonize new areas, thus mobilizing N from soils (Ladrón De Guevara and Maestre, 2022), which is highly available following wildfires (Certini, 2005; Fultz et al., 2016). Nevertheless, the minimal contribution to accelerating critical biochemical processes in early successional stages represents a huge impact on soils in comparison to the effects of late successional stages of biocrust (Ferrenberg et al., 2022).

Despite the short time that elapsed after the wildfire and subsequent salvage logging (seven months), the emergence of the moss biocrust was strategic for accelerating the recovery of the soil microbial communities recently disturbed (García-Carmona et al., 2022; Chapter 5). The biocrust emergence softens the severe post-fire scenario, improving the harsh conditions on the soil surface (e.g., desiccation, high temperature, and solar radiation), thereby facilitating microbial growth and thus accelerating key biochemical processes from nutrient cycling affected in the wildfire (Garcia-Pichel et al., 2003; Maier et al., 2016). Therefore, the diversity and composition of soil microbial communities are profoundly affected by moss biocrust colonization. In particular, the abundant presence of copiotrophic Proteobacteria in uncrusted soils, characteristic of nutrient-rich post-fire systems (Goberna et al., 2012; Prendergast-Miller et al., 2017; Whitman et al., 2019), was rapidly substituted in moss biocrust soils, in which a rapid successional transition toward the unburned soil community was exhibited. The acceleration in the successional stage indicates that biocrust might play a critical role in the resilience of soil microbial communities affected by fires. The effect was more evident in bacterial diversity, whereas long-lasting fire legacies are expected in the fungal community. The strong influence of moss biocrust on soil microbiology persists over time with biocrust development. Biocrust soils six years after the fire and subsequent salvage logging reported significant increments in microbial abundance and activity. Our findings are in accordance with other observations, in which microbial performance intensifies with the successional stage or the age of the biocrust, reaching the highest levels in well-developed moss biocrust (Maier et al., 2016, 2018; Liu et al., 2017b). Without post-fire intervention, Palmer et al. (2022) recently concluded that biocrust microbiome composition and functionality recover after six years since the wildfire. The role of mosses in the resistance and resilience of microbial communities allows the development and succession of ecosystems (Maestre et al., 2012; Weber et al., 2015), which has special relevance after severe disturbances.

One concerning finding of this dissertation is that intensive salvage logging adversely affects the spreading over soils of the biocrust-forming mosses that emerged after the wildfire. The removal of burnt wood deprives bryophytes of resources for their dissemination (Bradbury, 2006; Caners et al., 2013; Paquette et al., 2016), while at the same time severely degrading soils and delaying vegetation regrowth (García-Orenes et al., 2017). Six years after the aggressive salvage logging, soils still exhibit symptoms of degradation with a high percentage of bare soil exposed, highlighting the reduction of more than 20% of moss biocrust cover (García-Carmona et al., 2020; Chapter 4). Given their role as ecosystem engineers, the reduction of moss biocrust leads to negative cascade effects on ecosystem functionality in the midterm. Likewise, degradation of soils after salvage logging at the early post-fire stages would hinder the soil biodiversity recovery, affecting the ecosystem succession in sensitive to disturbance semi-arid areas (Maestre et al., 2012; Rodríguez-Caballero et al., 2017a). Therefore, protecting biocrust-forming mosses in recently fire-affected areas from disruptive management can be strategic to accelerate the recovery of multiple components and processes after wildfires.

In the same way as aggressive salvage logging, the application of burnt wood mulch drastically suppresses biocrust development (Chapter 6) since mosses that emerge after fires present adaptive traits to high radiation, preferring the open spaces created after a wildfire (Esposito et al., 1999; Ladrón De Guevara and Maestre, 2022). Therefore, the stabilization technique conflicts with the passive restoration of soils assisted by mosses (Chapters 4 and 5). The wood mulch has a limited effect on the physicochemical properties in the short term, expectable in a Mediterranean climate where low precipitations combined with high temperatures slow down the decomposition rates, added to the low degradability of wood composed of recalcitrant carbon and low N (Jonas et al., 2019; Goodell et al., 2020; Bonanomi et al., 2021). An incipient acceleration of biochemical processes, remarkable in the lower rate of mulch application, was thanks to the combination of biocrust emergence and initial wood decay, boosting microbial activity and initiating cascading effects on soil nutrient cycling (Kahl et al., 2017; Cheng et al., 2021). Nevertheless, microbial diversity was reduced under the mulch application, i.e., microbial communities became transitorily highly homogeneous and less diverse. It was particularly revealing the shifts observed in the fungal community, highly responsive to the wood mulch application. Consequently, despite being conceived as a soil stabilization technique after a wildfire, mulch indiscriminately applied in soils can hamper microbial diversity recovery and, thus, ecosystem functionality recovery.

The findings regarding the management based on wood mulch warn about the necessity of incorporating microbial diversity information into post-fire management planning. To support management practices that boost soil biodiversity and preserve ecosystem functionality (Guerra et al., 2021; Averill et al., 2022), threats must be identified in order to establish priorities and formulate strategies. Clearly, intensive salvage logging represents an important threat to soil biodiversity, affecting microbial diversity in the short- and mid-term and the development of mosses (Chapters 3, 4, 5). Timber activities in Mediterranean forests are important from a social perspective; thus, the management should be included in the post-fire goals, but the economic aspects should never surpass the ecological benefits (Castro, 2021). The inclusion of land diversification approaches through patches of different intensities of wood extraction could increase the resilience to future disturbances (FAO et al., 2020). On the other hand, preventing soil loss in Mediterranean forests must be a major goal in post-fire planning. However, mulching based on wood application can constitute a potential threat to microbial diversity when performed incorrectly. Multiple studies express recommendations or guidelines in this aspect (Vallejo et al., 2012; Robichaud et al., 2013; Pereira et al., 2018; Lucas-Borja et al., 2019b; Castro, 2021): interventions focused on soil protection that involve machinery should be limited to very specific situations, i.e., high risk of erosion, slow vascular plant recovery rate, risk downslope, etc. Our findings contribute to gaining a better insight into the management of fire-affected ecosystems committed to nature conservation through the investigation of two key components for soil recovery: microbial diversity and biocrust-forming mosses. Post-fire management should seek the restoration of ecosystem functionality, with special attention to the active agents of soil processes restoration. As pointed out by multiple studies recently, considering the natural distribution and functions of biocrust can ensure the success of restoration management (Corbin and Thiet, 2020; Gall et al., 2022b). We highly recommend preserving large patches or emergent biocrust since they can effectively counteract water erosion (beyond a determined threshold) and actively recover soil processes in early post-fire stages.

Although forest management aimed at the restoration of ecosystem functioning is the goal that must be pursued, restoration practices still demand better understanding since the effects on the ecosystem are highly variable depending on the target component or process to strategically restore. A clear example was demonstrated in Chapter 7 (García-Carmona et al., 2021b), in which contrasting effects in soils were expressed as a response to the application of organic amendments characterized by different origins and stability. All organic amendments improved soil fertility and stimulated soil microbial activity; however, contrastable (transient or durable) implications on soils are expected in response to their different decomposition rates (Tejada et al., 2009; González-Ubierna et al., 2012; Larney and Angers, 2012). Fresh amendments promote immediate microbial growth and activity, but greater mineralization rates and, thus, presumably shorter periods of carbon source consumption are expected, as clearly observed in swine and poultry manures, being poultry manure more rapidly consumed. Soils treated with compost accumulated the most organic carbon and nitrogen, ensuring long-term nutrient release and long-term soil fertility (García-Carmona et al., 2021b). The addition of highly stabilized organic matter avoids the potential adverse effects of manures (Bernal et al., 2009), but no strong and immediate effects are expected in microbial populations since it does not represent a quick release of labile carbon components. Consequently, the amendment selection will depend on the goals of the soil restoration plan in terms of the immediacy of the soil response. In any case, the creation of more diverse and functioning ecosystems promotes the protection of global biodiversity (Averill et al., 2022).

Limitations and caveats

In this dissertation, some limitations and caveats were identified, some of which being part of the nature of works related to wildfires and others that can be addressed in future works.

First, working with fire implies working with unpredictability. In addition, research projects in post-fire management represent working with what forest managers, or timber companies, leave behind without previous (research) design. This directly translates into the lack of true or proper controls of the management performed. In this regard, the study area from Chapters 3 and 4 (site 1, see Chapter 2) lacked an unburned soil control that would represent the baseline for the recovery process after the fire. The wildfire and site characteristics impeded the establishment of a control area in close proximity since soil type (parent material) and slope aspect and orientation abruptly change in a short distance. Luckily, forest managers in this case designed an area of non-intervention for investigation purposes. Otherwise, the most common situation is that salvage logging is extensively performed in the whole area. This is the situation for Chapters 5 and 6 (site 2), where control soils representing the non-intervention were lacking, unfortunately. An area of non-intervention would allow the study of two contrasting scenarios of wood fate after wildfires: leaving the burnt wood in situ after the wildfire versus applying mulch based on burnt wood as post-fire management. Short- and long-term implications would provide further insights for post-fire management planning.

Second, working at small scales (in space and time) hinders scaling up fine information to larger ones. Working at small scales in space is again a result of working with fires since complexity is characteristic in fire-affected ecosystems, where mosaics of burned and unburned areas and different patches of fire severity are intermixed at landscape scales. In relation to this fact, the post-fire techniques studied in Chapters 6 and 7 were carried out manually at the small plot level for operative reasons. The manual application of mulch and organic amendments in a localized and homogeneous area without machinery operations allows us to isolate the effects of the materials applied on soils, although this does not completely represent a reality. The machinery needed could represent an additional disturbance for soils, especially relevant in mulching, a technique often performed to prevent soil erosion occasioned by logging operations. Results from Chapters 3 and 4 confirm the impact of machinery operations on several components of the ecosystem; thus, additional disturbances are expected in the already disturbed soils. Moreover, studies on fire-affected systems often evaluate the first years after the disturbance, when soils are more vulnerable and express immediate results, but limit our comprehension of the ecosystem response to management mid and long-term.

Third, some limitations are associated with metrics not performed in the studies. One fundamental role of moss biocrust is soil stabilization, which drives multiple beneficial processes for soils and ecosystems after disturbances. Despite being appropriate for the results in Chapter 6, the potential of mosses retaining soils in early post-fire stages was not directly measured. The evaluation of sediment loss in plots from Chapter 6 would provide valuable information regarding the role of mosses in counteracting soil erosion in contrast to the wood mulch post-fire technique.

Future perspectives

New research opportunities arise from the relevance of biocrust-forming mosses for the ecosystem succession development after wildfires.

It is necessary to understand how biocrust-forming mosses will respond to the intensification of fire events in a scenario of climate change. Evidence suggests that biocrust is highly susceptible to both climate change and physical disturbances (Rodriguez-Caballero et al., 2018), and increasing aridity in drylands is expected to shift the biocrust composition, from late-successional mosses and lichens to early-successional cyanobacteria (Maestre et al., 2015; Reed et al., 2016). Whether new wildfire scenarios, while undergoing warming and aridification, may shift the structure of biocrust in fire-affected ecosystems, progressing from bare soils to cyanobacteria and not to moss biocrust, is relevant and remain unanswered. Those shifts may strongly impact the functioning of recently fire-affected ecosystems through the profound alteration of biochemical processes and soil microbial communities (Maestre et al., 2015; Delgado-Baquerizo et al., 2018; Tucker et al., 2020). New approaches in the study of soil microbiome can assist in this research purpose. For instance, studying the metabolic processes through the biocrust succession, which is known to differ (Tian et al., 2022), might reveal valuable information in the understanding of nutrient cycling in new scenarios of climate change and the intensification of wildfires. Strong modifications of soil physicochemical properties are plausible under these new scenarios, where soil water repellency is especially relevant since it could be a key factor controlling the biocrust spreading in fire-affected soils, completely unknown and worth studying.

Another needed line of research is related to active biocrust restoration, which has great potential to restore important ecosystem functions and increase resilience (Bowker, 2007; Antoninka et al., 2020; Muñoz-Rojas et al., 2021). Developing effective restoration methods (e.g., achieve inoculation success) highly depends on the type of disturbance and the possible interactions of the biocrust with the microbiology and vascular plants (Antoninka et al., 2020), which are still to be fully understood in post-fire systems exposing new challenges and opportunities in ecosystem restoration (Grover et al., 2020).

Throughout this dissertation, it is emphasized the necessity of including biocrust and microbial diversity in post-fire management planning to protect and promote fundamental ecological functions, thereby creating healthy and resilient managed ecosystems. To effectively achieve this purpose, more information is required, including the identification of threats, priorities, and strategies in order to face the new paradigm of post-fire management. The debate about the management of burned areas will benefit from the collaboration of relevant actors including managers, researchers, the local community, and other stakeholders. Apart from that, future work should explore the diversification of forest management performances, focusing particularly on the study of different intensities of burnt wood management at landscape scale, in which additional disturbances are considered. Regarding the utilization of organic amendments, studying the application effects on soil microbial diversity is highly necessary to identify possible threats related to the introduction of new taxa and correctly address microbial diversity protection.

CHAPTER 9

Conclusions

1. Biocrust-forming mosses play an important role in the recovery of multiple functions of soils in post-fire ecosystems, mitigating the degradation threats of wildfires and disruptive post-fire management. The developmental stage of the moss biocrust controls the effects on soils; while advanced stages profoundly impact nutrient cycling, critical biochemical processes, soil stability, and microbial development, the major contribution of the moss biocrust in early post-fire stages is to accelerate the recovery of soil microbial communities, improving their resilience to fire disturbances.

2. The post-fire management salvage logging and wood-mulch application negatively affect the biocrust spreading, decreasing the soil covered by mosses. The reduction in moss biocrust leads to negative cascade effects in the mid-term on ecosystem functionality, hindering forest recovery. The protection of biocrust that emerge after fires contributes to the recovery and resilience of ecosystems to future disturbances.

3. Salvage logging, involving strong interventionism and performed in highly erodible soils, profoundly alters the resistance and resilience of soil microbial communities, with the degradation of soil structure being the main driver of microbial community shifts. In contrast, burnt wood maintenance ameliorates stressful conditions on the soil surface and promotes microbial abundance in response to higher resource availability.

4. Wood mulch application results in a low impact on physicochemical soil properties, but an incipient acceleration of biochemical processes, especially at mulch rates that do not totally cover the soil surface. Regardless of the application rate, microbial communities under mulch become transitorily highly homogeneous and less diverse, being fungi highly responsive to the wood mulch.

5. Organic amendments application, designed to promote the recovery of ecosystem functionality, results in contrasting responses in soils depending on the origin and stability of materials: fresh materials express immediate effects on microbial growth, whereas stable materials have more durable effects on soil fertility. The selection of the organic material ultimately depends on the restoration goals over time.

6. In order to seek the restoration of ecosystem functionality, post-fire management planning must incorporate the protection and promotion of two active agents of post-fire soil recovery: microbial diversity and biocrust-forming mosses.

1. Los musgos formadores de biocostras juegan un papel importante en la recuperación de múltiples funciones de los suelos en los ecosistemas post-incendio, mitigando las amenazas de degradación de los incendios y de las gestiones disruptivas post-incendio. La etapa de desarrollo de la biocostra de musgo controla los efectos sobre los suelos; mientras que las etapas avanzadas tienen un impacto profundo en el ciclo de nutrientes, procesos bioquímicos críticos, la estabilidad del suelo y el desarrollo microbiano, la principal contribución de la biocostra de musgo en las primeras etapas posteriores al incendio es acelerar la recuperación de las comunidades microbianas del suelo, mejorando su resiliencia ante las perturbaciones del fuego.

2. Los manejos post-incendio tala y saca de madera y aplicación de mulch de madera afectan negativamente la expansión de la biocostra, reduciendo el suelo que es cubierto por musgos. La reducción de la biocostra de musgo lleva a efectos negativos en cascada a medio plazo sobre la funcionalidad de los ecosistemas, lo que dificulta la recuperación de los bosques. Proteger la biocostra que emerge después de los incendios contribuye a la recuperación y resiliencia de los ecosistemas ante futuras perturbaciones.

3. La tala y saca de madera que involucra un fuerte intervencionismo y se realiza en suelos altamente erosionables, altera profundamente la resistencia y resiliencia de las comunidades microbianas del suelo, siendo la degradación de la estructura del suelo el principal impulsor de los cambios en la comunidad microbiana. Por el contrario, el mantenimiento de la madera quemada mejora las condiciones estresantes en la superficie del suelo y promueve la abundancia microbiana en respuesta a una mayor disponibilidad de recursos.

4. La aplicación de mulch de madera tiene un bajo impacto en las propiedades fisicoquímicas del suelo, pero una incipiente aceleración de los procesos bioquímicos, especialmente a tasas de mulch que no cubren totalmente la superficie del suelo. Independientemente de la tasa de aplicación, las comunidades microbianas debajo del mulch se vuelven transitoriamente altamente homogéneas y menos diversas, siendo los hongos altamente sensibles al mulch de madera.

5. La aplicación de enmiendas orgánicas, diseñadas para promover la recuperación de la funcionalidad de los ecosistemas, produce respuestas contrastantes en los suelos según el origen y la estabilidad de los materiales: los materiales frescos expresan efectos inmediatos sobre el crecimiento microbiano, mientras que los materiales estables tienen efectos más duraderos sobre la fertilidad del suelo. La selección del material orgánico depende en última instancia de los objetivos de restauración a lo largo del tiempo.

6. Para buscar la restauración de la funcionalidad de los ecosistemas, la planificación de gestión post-incendio debe incorporar la protección y promoción de dos agentes activos de recuperación del suelo post-incendio: la diversidad microbiana y los musgos formadores de biocostras.

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APPENDICES

Appendix A:

Chapter 3 “Salvage logging alters microbial community structure and functioning after a wildfire in a Mediterranean forest”

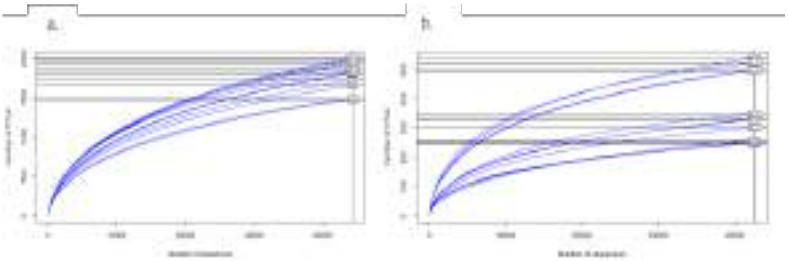


Fig.A1. Rarefaction curves on the rarefied bacterial OTU dataset at 44245 sequences per sample (a.), and on the rarefied fungal OTU dataset at 42529 sequences per sample (b.), of control (C) and salvage logging (SL) soils.

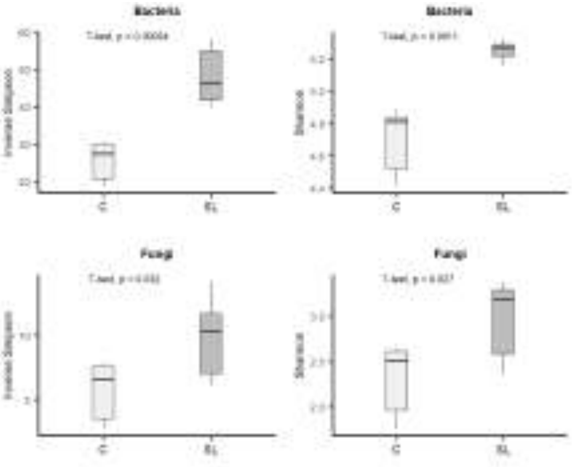


Fig. A2. Shannon and Inverse of Simpson alpha-diversity indices on the OTU dataset for bacteria and fungi communities for control (C) and salvage logging (SL) soils. Significant differences at P < 0.05 determined by t-test.

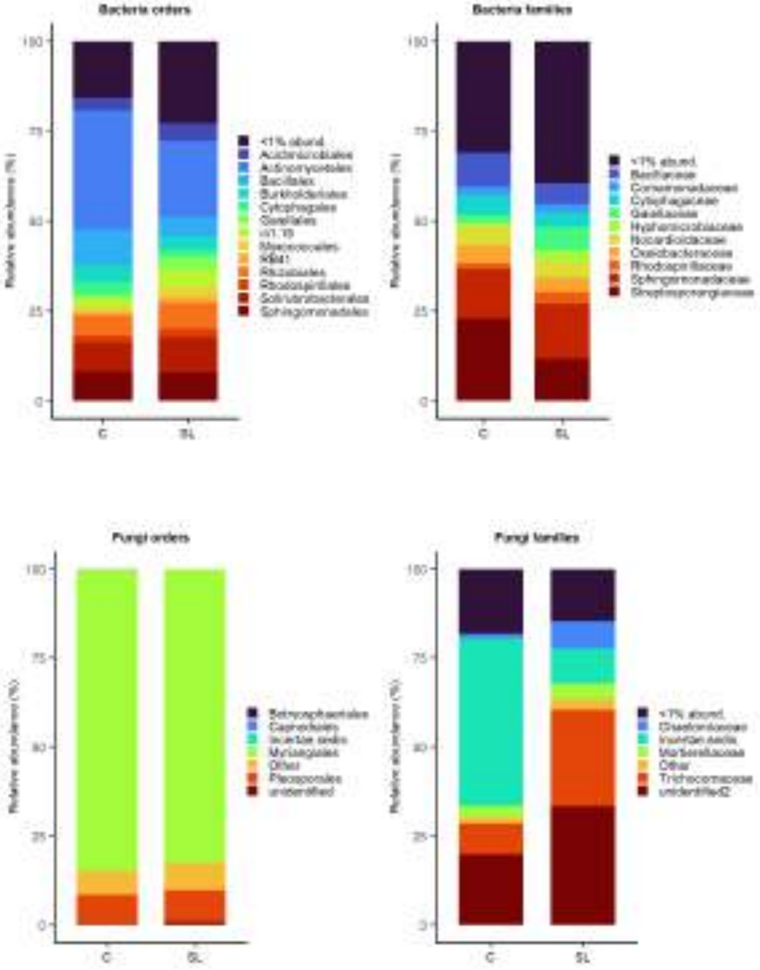


Fig. A3. Relative abundances of the dominant orders and families for bacterial and fungal of control (C) and salvage logging (SL) soils.

Table A1. Indicator Species Analysis (IndVal and p-value) at bacterial family level for bacterial community of control (C) and salvage logging (SL) soils. C-RA = relative abundance in control soils, SL-RA = relative abundance in salvage logging soils.

Indicator families for Control soils (displayed 30)

Phylum	Class	Order	Family	IndVal	p-value	C -RA (%)	SL -RA (%)
Proteobacteria	Betaproteobacteria	Burkholderiales	Alcaligenaceae	0.942	0.004	0.007	0.001
Proteobacteria	Deltaproteobacteria	Desulfuromonadales	Geobacteraceae	0.899	0.020	0.003	0.001
Planctomycetes	C6	d113	Unclassified140	0.897	0.005	0.000	0.003
Actinobacteria	Acidimicrobiia	Acidimicrobiales	Acidimicrobiaceae	0.893	0.004	0.024	0.006
Actinobacteria	Actinobacteria	Actinomycetales	Mycobacteriaceae	0.883	0.020	0.002	0.000
TM7	TM7-3	I025	Unclassified196	0.874	0.023	0.004	0.006
Firmicutes	Clostridia	Natranaerobiales	ML1228J.1	0.871	0.016	0.013	0.004
Acidobacteria	Acidobacteriia	Acidobacteriales	Koribacteraceae	0.859	0.041	0.134	0.048
Bacteroidetes	Sphingobacteriia	Sphingobacteriales	Sphingobacteriaceae	0.854	0.006	0.149	0.055
TM7	SC3	unclassified	Unclassified192	0.854	0.032	0.007	0.017
Actinobacteria	Acidimicrobiia	Acidimicrobiales	SC3.41	0.853	0.042	0.002	0.000
Proteobacteria	unidentified	unidentified	Unidentified.46	0.848	0.030	0.008	0.009
Cyanobacteria	Oscillatoriophycideae	Chroococcales	Xenococcaceae	0.847	0.044	0.011	0.004
unidentified	unidentified	unidentified	Unclassified2	0.847	0.044	0.258	0.344
Firmicutes	Clostridia	Clostridiales	Veillonellaceae	0.844	0.004	0.070	0.028
Acidobacteria	Acidobacteria-5	unclassified	Unclassified6	0.840	0.023	0.008	0.058
Planctomycetes	unidentified	unidentified	Unidentified.44	0.840	0.004	0.001	0.000
Actinobacteria	Actinobacteria	Actinomycetales	Streptosporangiaceae	0.838	0.004	12.639	5.350
Actinobacteria	Actinobacteria	Bifidobacteriales	Bifidobacteriaceae	0.838	0.004	0.988	0.420
Actinobacteria	Actinobacteria	Actinomycetales	Geodermatophilaceae	0.837	0.004	0.147	0.063
Firmicutes	Bacilli	Bacillales	Paenibacillaceae	0.836	0.006	0.709	0.306
Actinobacteria	unidentified	unidentified	Unidentified.7	0.835	0.009	0.134	0.366
Bacteroidetes	Cytophagia	Cytophagales	Unclassified40	0.831	0.004	0.037	0.017
Actinobacteria	Acidimicrobiia	Acidimicrobiales	wb1_P06	0.827	0.005	0.039	0.018
Proteobacteria	Alphaproteobacteria	Rhodospirillales	Unidentified.50	0.824	0.027	0.002	0.003
Firmicutes	Clostridia	Halanaerobiales	Halanaerobiaceae	0.824	0.005	0.023	0.011
Proteobacteria	Betaproteobacteria	Burkholderiales	Burkholderiaceae	0.815	0.049	0.102	0.052
Proteobacteria	Alphaproteobacteria	Kiloniellales	Kiloniellaceae	0.815	0.038	0.009	0.005
Firmicutes	Bacilli	Bacillales	Bacillaceae	0.813	0.009	5.208	2.662
OD1	unidentified	unidentified	Unidentified.42	0.813	0.004	0.001	0.005

Indicator families for Salvage logging soils (displayed 30)

Phylum	Class	Order	Family	IndVal	p-value	C - RA (%)	SL - RA (%)
Actinobacteria	Actinobacteria	Micrococcales	Unclassified28	1.000	0.004	0.010	0.032
Firmicutes	Bacilli	Bacillales	Unclassified97	1.000	0.004	0.001	0.000
Gemmatimonadetes	Gemmatimonadetes	Ellin5290	Unclassified117	0.989	0.004	0.164	0.159
unidentified	unidentified	unidentified	Unidentified.1	0.985	0.004	0.258	0.344
Acidobacteria	EC1113	unidentified	Unclassified13	0.978	0.004	0.001	0.007
Chloroflexi	TK17	unclassified	Unclassified73	0.972	0.010	0.023	0.069
Bacteroidetes	Saprospirae	Saprospirales	Saprospiraceae	0.969	0.004	0.006	0.099
Crenarchaeota	Thaumarchaeota	Nitrososphaerales	Nitrososphaeraceae	0.968	0.004	0.001	0.019

Proteobacteria	Alphaproteobacteria	Sphingomonadales	Unclassified159	0.961	0.006	0.000	0.000
Chloroflexi	Gitt-GS-136	unclassified	Unclassified65	0.961	0.004	0.306	1.027
BRC1	PRR-11	unclassified	Unclassified35	0.959	0.005	0.032	0.034
Proteobacteria	Betaproteobacteria	Thiobacterales	Unclassified146	0.957	0.004	0.004	0.003
Actinobacteria	Acidimicrobiia	Acidimicrobiales	Unclassified26	0.957	0.004	0.001	0.003
Chloroflexi	Anaerolinea	envOPS12	Unclassified58	0.956	0.017	0.000	0.004
Nitrospirae	Nitrospira	Nitrospirales	Nitrospiraceae	0.953	0.004	0.007	0.075
Therm	Deinococci	Deinococcales	Trueperaceae	0.952	0.007	0.001	0.006
Lentisphaerae	Lentisphaeria	Z20	Unclassified122	0.951	0.004	0.002	0.003
Unassigned	Unassigned	Unassigned	Unassigned	0.950	0.004	0.024	0.220
Proteobacteria	Alphaproteobacteria	Ellin329	Unclassified155	0.939	0.004	0.089	0.283
Acidobacteria	Sva0725	Sva0725	Unclassified18	0.938	0.004	0.156	0.499
Cyanobacteria	Chloroplast	Chlorophyta	Unclassified84	0.935	0.004	0.041	0.017
Chlorobi	OPB56	unclassified	Unclassified49	0.931	0.005	0.040	0.061
Nitrospirae	Nitrospira	Nitrospirales	Unclassified 42	0.931	0.004	0.001	0.004
Chloroflexi	SHA-26	unclassified	Unclassified69	0.929	0.004	0.001	0.003
Proteobacteria	Gammaproteobacteria	Legionellales	Unclassified182	0.927	0.004	0.000	0.002
OP8	OP8_1	unclassified	Unclassified135	0.926	0.005	0.003	0.001
Proteobacteria	Deltaproteobacteria	Myxococcales	Unclassified172	0.926	0.004	0.984	1.609
Chloroflexi	Chloroflexi	unidentified	Unidentified.21	0.923	0.005	0.050	0.069
Firmicutes	Bacilli	Bacillales	Unidentified.35	0.922	0.004	2.497	1.277
Chloroflexi	TK10	unclassified	Unclassified70	0.921	0.019	0.007	0.031

Table A2. Indicator Species Analysis (IndVal and p-value) at fungi family level for fungal community of control (C) and salvage logging (SL) soils. C-RA = relative abundance in control soils, SL-RA = relative abundance in salvage logging soils.

Indicator families for Control soils							
Phylum	Class	Order	Family	IndVal	p-value	C - RA (%)	SL - RA (%)
Basidiomycota	Agaricomycetes	Thelephorales	Thelephoraceae	0.981	0.004	1.984	0.079
Basidiomycota	Tremellomycetes	Tremellales	Incertae.sedis.8	0.909	0.004	0.001	0.000

Indicator families for Salvage Logging soils							
Phylum	Class	Order	Family	IndVal	p-value	C - RA (%)	SL - RA (%)
Ascomycota	Eurotiomycetes	Chaetothyriales	Chaetothyriaceae	1.000	0.004	0.000	0.008
Basidiomycota	Agaricomycetes	Agaricales	Inocybaceae	0.998	0.007	0.003	0.971
Ascomycota	Sordariomycetes	unidentified	unidentified14	0.998	0.005	0.017	0.021
Ascomycota	Pezizomycetes	Pezizales	Pezizaceae	0.990	0.009	0.018	0.921
Ascomycota	Sordariomycetes	Sordariales	Lasiosphaeriaceae	0.989	0.009	0.025	1.163
Ascomycota	Leotiomycetes	Helotiales	Hyaloscyphaceae	0.989	0.004	0.000	0.011
Ascomycota	Dothideomycetes	Pleosporales	Incertae.sedis.3	0.984	0.004	0.007	0.032
Ascomycota	Dothideomycetes	Pleosporales	unidentified3	0.976	0.004	0.198	0.183
Basidiomycota	Microbotryomycete	unidentified	unidentified19	0.974	0.004	0.000	0.001
Ascomycota	Dothideomycetes	Incertae sedis	Myxotrichaceae	0.965	0.004	0.000	0.007
Ascomycota	Leotiomycetes	Geoglossales	Geoglossaceae	0.962	0.004	0.011	0.139
Ascomycota	Eurotiomycetes	Chaetothyriales	Herpotrichiellaceae	0.956	0.004	0.020	0.209
Ascomycota	Sordariomycetes	Xylariales	unidentified13	0.953	0.004	0.012	0.060

Ascomycota	Dothideomycetes	unidentified	unidentified4	0.948	0.007	0.049	0.319
Ascomycota	Lecanoromycetes	Incertae sedis	Coniocybaceae	0.947	0.004	0.040	0.348
Ascomycota	Sordariomycetes	Hypocreales	Nectriaceae	0.939	0.006	0.006	0.048
Ascomycota	Sordariomycetes	Sordariales	Chaetomiaceae	0.919	0.010	1.400	7.655
Ascomycota	Sordariomycetes	Hypocreales	Hypocreaceae	0.917	0.030	0.028	0.148
Ascomycota	Sordariomycetes	Hypocreales	Ophiocordycipitaceae	0.913	0.018	0.000	0.013
Basidiomycota	Agaricomycetes	Cantharellales	Ceratobasidiaceae	0.912	0.023	0.001	0.498
unidentified	unidentified	unidentified	unidentified24	0.912	0.016	0.133	0.489
Ascomycota	Eurotiomycetes	Verrucariales	Verrucariaceae	0.909	0.013	0.000	0.016
Ascomycota	Dothideomycetes	Capnodiales	Incertae.sedis.2	0.904	0.010	0.012	0.007
Ascomycota	Sordariomycetes	Hypocreales	Incertae.sedis.7	0.901	0.010	0.002	0.074
Ascomycota	Lecanoromycetes	Lecanorales	unidentified6	0.899	0.024	0.000	0.001
Zygomycota	Incertae sedis	Mortierellales	unidentified23	0.887	0.005	0.000	0.000
Basidiomycota	unidentified	unidentified	unidentified21	0.876	0.029	0.001	0.016
Ascomycota	Sordariomycetes	Hypocreales	Cordycipitaceae	0.876	0.023	0.036	0.119
Ascomycota	Eurotiomycetes	Eurotiales	Trichocomaceae	0.869	0.004	8.795	27.018
Ascomycota	Sordariomycetes	Sordariales	Cephalothecaceae	0.816	0.047	0.000	0.004
Basidiomycota	Agaricomycetes	Agaricales	Cortinariaceae	0.815	0.047	0.000	0.058

Appendix B

Chapter 4 "The role of mosses in soil stability, fertility and microbiology six years after a post-fire salvage logging management"

Table B1. Mean, standard deviation (sd), minimum and maximum values of cover in the Control and Salvage logging areas. Significant differences (sig) by U Mann-Whitney at p<0.05*.

		Control				**Salvage logging**			
Cover (%)	sig	Mean	*sd*	Min	Max	Mean	*sd*	Min	Max
Total	*	99.8	*0.6*	97	100	96.6	*4.7*	85	100
Mosses	*	78.4	*29.7*	0	100	56.0	*30.7*	0	98
Herbaceous		51.7	*31.4*	0	100	64.6	*34.5*	0	100
Vascular		61.8	*29.3*	10	100	48.8	*29.6*	0	98
Pinus halepensis	*	34.5	*24.4*	0	76	19.4	*20.5*	0	64

Appendix C

Chapter 5 "Moss biocrust accelerates the recovery and resilience of soil microbial communities in fire-affected semi-arid Mediterranean soils"

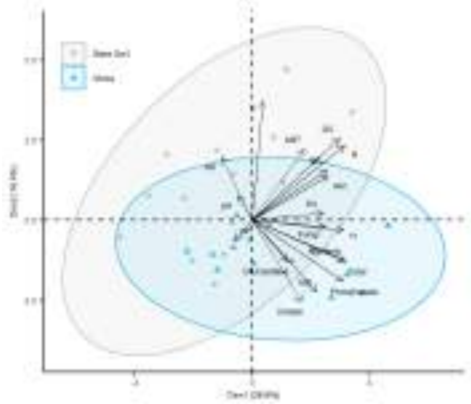


Fig. C1. Scores and loadings for PCA performed using all soil properties and PLFAs and NLFA biomarkers, for burned soils under moss biocrust and bare soils. (AS: aggregate stability; OC: organic carbon; N: total nitrogen; P: available phosphorous; MB: microbial biomass carbon; BR: basal respiration; AM: arbuscular mycorrhiza; AMT: arbuscular mycorrhiza/total PLFAs ratio; BF: bacteria/fungi ratio; Total: total PLFAs).

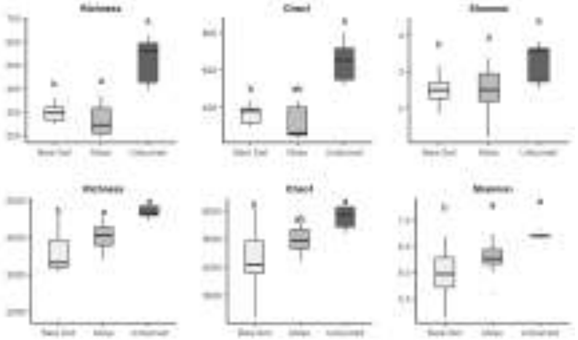


Fig. C2. Alpha indices Richness, Chao1 and Shannon based on OTU dataset for fungal (upper part) and bacterial (bottom part) communities, in soils under mosses, bare soils and unburned soils. Significant differences at p-value < 0.05.

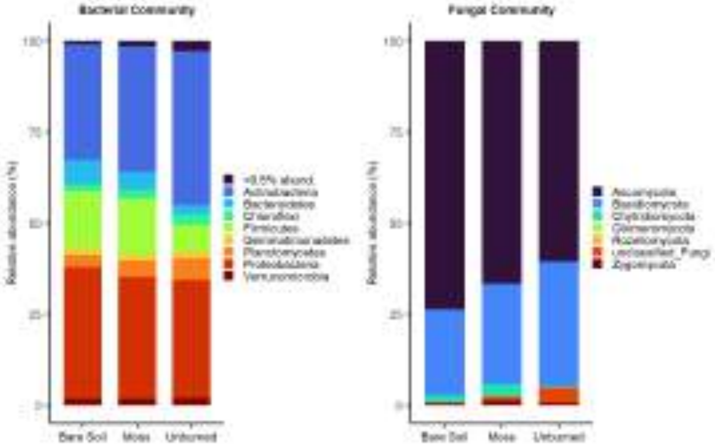


Fig. C3. Relative abundances of the dominant bacterial and fungal phyla in soils under mosses, bare soils and unburned soils

Table C1. Indicator Species Analysis (IndVal and p-value) for bacteria community at genus level for soils under mosses, bare soils and unburned soils. Values represent relative abundance in soils.

Indicator genera for Mosses (display 30 of #60)					
Genus	IndVal	P-value	Unburned	Bare Soils	Moss
Arthrobacter	0.738	0.014*	0.158	3.227	7.967
Blastopirellula	0.647	0.041*	0.585	0.362	0.795
Lysinibacillus	0.671	0.020*	0.467	0.349	0.773
Fictibacillus	0.749	0.029*	0.013	0.229	0.400
Acinetobacter	0.732	0.009**	0.089	0.091	0.375
Phycisphaera	0.669	0.029*	0.127	0.087	0.218
Hyphomicrobium	0.703	0.008**	0.079	0.097	0.207
Oligoflexus	0.779	0.001***	0.022	0.068	0.250
Fimbriimonas	0.660	0.010**	0.084	0.102	0.137
Steroidobacter	0.667	0.037*	0.059	0.067	0.119
Lysobacter	0.749	0.001***	0.015	0.064	0.154
Nitrospira	0.666	0.002**	0.053	0.060	0.101
Pelobacter	0.659	0.044*	0.067	0.076	0.134
Litorilinea	0.652	0.029*	0.074	0.059	0.101
Planctomicrobium	0.681	0.050*	0.044	0.058	0.085
Pedomicrobium	0.716	0.041*	0.050	0.048	0.142
Amorphus	0.700	0.006**	0.032	0.030	0.070

Gelria	0.691	0.013*	0.028	0.038	0.063
Nitrosomonas	0.705	0.008**	0.020	0.033	0.054
Methyloceanibacter	0.736	0.001***	0.010	0.030	0.064
Kofleria	0.679	0.045*	0.043	0.025	0.066
Pseudobacteriovorax	0.697	0.014*	0.010	0.021	0.053
Pelolinea	0.697	0.017*	0.026	0.043	0.060
Vampirovibrio	0.703	0.003**	0.028	0.024	0.048
Shinella	0.751	0.003**	0.020	0.010	0.052
Byssovorax	0.750	0.019*	0.020	0.014	0.066
Megasphaera	0.723	0.010**	0.006	0.031	0.060
Arenimonas	0.724	0.033*	0.016	0.011	0.044
Vasilyevaea	0.700	0.043*	0.012	0.017	0.037
Legionella	0.726	0.003**	0.011	0.008	0.029
Indicator genera for Bare Soil (display 30 of #81)					
Genus	**IndVal**	**P-value**	**Unburned**	**Bare Soils**	**Moss**
Blastococcus	0.713	0.006**	2.994	6.391	3.200
Bacillus	0.679	0.046*	0.851	4.415	4.303
Massilia	0.767	0.001***	0.340	4.546	2.844
Comamonas	0.829	0.001***	0.122	4.807	2.070
Sphingomonas	0.634	0.001***	2.191	3.308	2.730
Paenisporosarcina	0.705	0.017*	0.320	2.736	2.456
Adhaeribacter	0.755	0.001***	0.161	2.522	1.746
Domibacillus	0.829	0.001***	0.017	2.042	0.912
Nocardioides	0.730	0.001***	0.515	1.462	0.770
Ramlibacter	0.670	0.013*	0.397	1.194	1.069
Devosia	0.704	0.001***	0.394	1.279	0.906
Paenibacillus	0.685	0.005**	0.323	1.109	0.930
Pedobacter	0.720	0.013*	0.136	1.085	0.871
Flavisolibacter	0.731	0.001***	0.315	0.981	0.542
Phenylobacterium	0.651	0.001***	0.393	0.718	0.584
Rhizobium	0.670	0.033*	0.127	0.468	0.446
Geodermatophilus	0.669	0.022*	0.331	0.473	0.253
Ensifer	0.700	0.011*	0.112	0.428	0.333
Cohnella	0.690	0.049*	0.117	0.405	0.327
Noviherbaspirillum	0.778	0.001***	0.049	0.462	0.252
Planomicrobium	0.705	0.008**	0.018	0.294	0.281
Lysinimonas	0.683	0.016*	0.131	0.306	0.219
Peredibacter	0.714	0.001***	0.029	0.247	0.209
Flavitalea	0.664	0.004**	0.096	0.200	0.157

Erythrobacter	0.703	0.001***	0.091	0.220	0.135
Cytophaga	0.671	0.019*	0.113	0.205	0.136
Bdellovibrio	0.657	0.005**	0.080	0.186	0.164
Novosphingobium	0.718	0.002**	0.089	0.211	0.109
Herbaspirillum	0.793	0.001***	0.004	0.218	0.124
Nibribacter	0.683	0.027*	0.075	0.173	0.123
Indicator genera for Unburned soils (display 30 of #219)					
Genus	**IndVal**	**P-value**	**Unburned**	**Bare Soils**	**Moss**
Conexibacter	0.681	0.003**	7.477	5.030	6.033
Solirubrobacter	0.734	0.001***	8.608	3.776	5.461
Microvirga	0.633	0.050*	3.259	2.841	1.964
Rubrobacter	0.835	0.001***	5.500	1.449	1.511
Nitrolancea	0.653	0.004**	1.657	1.174	1.581
Pseudonocardia	0.672	0.011*	1.307	0.871	0.710
Methylobacterium	0.715	0.001***	1.351	0.785	0.674
Mycobacterium	0.683	0.030*	1.153	0.567	0.868
Aminivibrio	0.798	0.001***	1.589	0.451	0.736
Singulisphaera	0.764	0.001***	1.348	0.406	0.537
Aciditerrimonas	0.646	0.012*	0.807	0.543	0.773
Gemmata	0.763	0.001***	1.310	0.385	0.627
Kosakonia	0.641	0.007**	0.764	0.413	0.645
Aquihabitans	0.635	0.008**	0.743	0.561	0.635
Pseudolabrys	0.693	0.002**	0.899	0.340	0.653
Nitrospirillum	0.738	0.001***	0.929	0.507	0.436
Prosthecobacter	0.694	0.001***	0.697	0.381	0.367
Chelatococcus	0.789	0.001***	0.839	0.346	0.226
Modestobacter	0.676	0.043*	0.498	0.481	0.131
Halochromatium	0.719	0.001***	0.581	0.218	0.405
Povalibacter	0.673	0.031*	0.460	0.200	0.350
Hydrogenispora	0.704	0.016*	0.525	0.215	0.399
Kallotenue	0.704	0.001***	0.498	0.295	0.240
Thermogutta	0.672	0.008**	0.419	0.193	0.340
Rhodoplanes	0.637	0.046*	0.360	0.208	0.272
Belnapia	0.735	0.001***	0.515	0.225	0.164
Desulfosalsimonas	0.658	0.017*	0.368	0.173	0.325
Polyangium	0.708	0.029*	0.411	0.210	0.283
Dongia	0.712	0.002**	0.409	0.124	0.267
Desulfomonile	0.671	0.015*	0.340	0.173	0.274

Table C2. Indicator Species Analysis (IndVal and p-value) for bacteria community at OTU level for soils under mosses, bare soils and unburned soils. Values represent relative abundance in soils.

Indicator OTU for Mosses (display 30 of #318)							
OTU	Phyla	Genus	IndVal	P-value	Unburned	Bare Soils	Moss
OTU00002	Actinobacteria	Arthrobacter	0.776	0.004**	0.600	3.715	5.988
OTU00005	Firmicutes	Bacillus	0.708	0.038*	0.490	1.957	2.244
OTU00019	Firmicutes	Lysinibacillus	0.674	0.043*	0.381	0.271	0.536
OTU00022	Proteobacteria	Sphingomonas	0.682	0.038*	0.152	0.445	0.487
OTU00045	Bacteroidetes	Pedobacter	0.739	0.023*	0.044	0.401	0.506
OTU00153	Actinobacteria	Conexibacter	0.722	0.006**	0.175	0.210	0.394
OTU00017	Firmicutes	Fictibacillus	0.748	0.029*	0.095	0.219	0.338
OTU00498	Proteobacteria	Sphingosinicella	0.636	0.041*	0.188	0.162	0.226
OTU00245	Proteobacteria	Sphingomonas	0.701	0.006**	0.118	0.086	0.187
OTU00204	Proteobacteria	Acinetobacter	0.785	0.007**	0.007	0.102	0.203
OTU00273	Proteobacteria	Rhizobium	0.728	0.005**	0.028	0.110	0.147
OTU00377	Proteobacteria	Devosia	0.714	0.005**	0.049	0.085	0.138
OTU00298	Firmicutes	Paenibacillus	0.749	0.001***	0.014	0.084	0.115
OTU00439	Proteobacteria	Sphingomonas	0.699	0.010**	0.044	0.062	0.098
OTU00508	Proteobacteria	Devosia	0.689	0.023*	0.040	0.064	0.096
OTU00407	Proteobacteria	Oligoflexus	0.835	0.001***	0.013	0.043	0.123
OTU00673	Bacteroidetes	Adhaeribacter	0.731	0.004**	0.008	0.067	0.081
OTU00403	Firmicutes	Bacillus	0.708	0.043*	0.012	0.067	0.071
OTU00275	Proteobacteria	Haliangium	0.699	0.014*	0.021	0.057	0.076
OTU00254	Proteobacteria	Steroidobacter	0.710	0.019*	0.020	0.057	0.073
OTU00112	Firmicutes	Paenibacillus	0.704	0.020*	0.012	0.061	0.064
OTU00405	Gemmatimonadetes	Gemmatimonas	0.704	0.011*	0.042	0.036	0.073
OTU01374	Actinobacteria	Conexibacter	0.710	0.019*	0.037	0.034	0.069
OTU00468	Bacteroidetes	Adhaeribacter	0.690	0.023*	0.013	0.052	0.057
OTU01135	Verrucomicrobia	Luteolibacter	0.789	0.007**	0.011	0.030	0.078

OTU00274	Proteobacteria	Amorphus	0.729	0.002**	0.022	0.033	0.059
OTU00195	Firmicutes	Gelria	0.696	0.012*	0.030	0.031	0.057
OTU00568	Verrucomicrobia	Roseimicrobium	0.673	0.028*	0.017	0.044	0.047
OTU00446	Proteobacteria	Devosia	0.732	0.044*	0.023	0.024	0.057
OTU06198	Actinobacteria	Arthrobacter	0.792	0.002**	0.007	0.034	0.061
Indicator OTU for Bare Soils (display 30 of #441)							
OTU	**Phyla**	**Genus**	**IndVal**	**P-value**	**Unburned**	**Bare Soils**	**Moss**
OTU00006	Proteobacteria	Comamonas	0.829	0.001***	0.620	4.891	2.180
OTU00003	Proteobacteria	Massilia	0.777	0.001***	0.523	3.922	2.502
OTU00008	Firmicutes	Domibacillus	0.831	0.001***	0.134	1.897	0.822
OTU00030	Actinobacteria	Arthrobacter	0.782	0.002**	0.144	1.446	0.880
OTU00009	Bacteroidetes	Adhaeribacter	0.762	0.001***	0.164	1.248	0.899
OTU00054	Bacteroidetes	Adhaeribacter	0.753	0.001***	0.137	0.776	0.599
OTU00050	Proteobacteria	Devosia	0.736	0.001***	0.247	0.597	0.369
OTU00092	Actinobacteria	Arthrobacter	0.765	0.008**	0.060	0.606	0.431
OTU00038	Actinobacteria	Blastococcus	0.830	0.001***	0.212	0.712	0.178
OTU00042	Actinobacteria	Nocardioides	0.804	0.001***	0.218	0.521	0.209
OTU00059	Proteobacteria	Massilia	0.711	0.001***	0.164	0.419	0.280
OTU00083	Firmicutes	Bacillus	0.811	0.001***	0.038	0.476	0.246
OTU00209	Proteobacteria	Noviherbaspirillum	0.785	0.001***	0.095	0.403	0.228
OTU00158	Firmicutes	Bacillus	0.738	0.007**	0.060	0.346	0.279
OTU00131	Proteobacteria	Ensifer	0.731	0.005**	0.115	0.321	0.237
OTU00099	Bacteroidetes	Flavisolibacter	0.732	0.001***	0.110	0.322	0.203
OTU00123	Verrucomicrobia	Brevifollis	0.740	0.001***	0.073	0.279	0.209
OTU00055	Actinobacteria	Nocardioides	0.760	0.001***	0.104	0.257	0.174
OTU00117	Firmicutes	Tumebacillus	0.831	0.012*	0.033	0.263	0.079
OTU00170	Proteobacteria	Sphingomonas	0.739	0.001***	0.074	0.190	0.122
OTU24775	Proteobacteria	Massilia	0.772	0.001***	0.021	0.186	0.119
OTU00198	Bacteroidetes	Pedobacter	0.784	0.001***	0.031	0.176	0.109

OTU00156	Proteobacteria	Brevundimonas	0.753	0.001***	0.047	0.167	0.108
OTU00062	Chloroflexi	Nitrolancea	0.709	0.049*	0.070	0.138	0.120
OTU00444	Firmicutes	Domibacillus	0.801	0.001***	0.012	0.176	0.083
OTU00080	Proteobacteria	Rhizobium	0.765	0.001***	0.033	0.154	0.102
OTU00289	Verrucomicrobia	Brevifollis	0.742	0.001***	0.044	0.140	0.094
OTU00064	Firmicutes	Bacillus	0.714	0.038*	0.034	0.123	0.109
OTU00272	Bacteroidetes	Flavisolibacter	0.760	0.001***	0.027	0.150	0.091
OTU00074	Actinobacteria	Cryptosporangium	0.874	0.001***	0.019	0.177	0.052
Indicator OTU for Unburned soils (display 30 of #2152)							
OTU	Phyla	Genus	IndVal	P-value	Unburned	Bare Soils	Moss
OTU00015	Actinobacteria	Rubrobacter	0.854	0.001***	1.849	0.308	0.453
OTU00023	Actinobacteria	Rubrobacter	0.851	0.001***	0.908	0.188	0.203
OTU00136	Proteobacteria	Desulfopila	0.877	0.001***	0.272	0.058	0.038
OTU00163	Proteobacteria	Desulfococcus	0.874	0.001***	0.225	0.033	0.048
OTU00375	Verrucomicrobia	Prosthecobacter	0.903	0.001***	0.253	0.029	0.038
OTU00266	Proteobacteria	Belnapia	0.838	0.001***	0.174	0.045	0.041
OTU00291	Proteobacteria	Craurococcus	0.839	0.001***	0.151	0.033	0.037
OTU00237	Actinobacteria	Conexibacter	0.832	0.001***	0.146	0.036	0.035
OTU00122	Actinobacteria	Actinomycetospora	0.838	0.001***	0.147	0.034	0.037
OTU01999	Actinobacteria	Plantactinospora	0.843	0.001***	0.133	0.024	0.036
OTU00464	Proteobacteria	Novispirillum	0.835	0.007**	0.121	0.021	0.025
OTU00115	Cyanobacteria	GpXIII	0.889	0.001***	0.256	0.004	0.000
OTU00178	Proteobacteria	Desulfobacca	0.864	0.001***	0.127	0.018	0.028
OTU00411	Proteobacteria	Craurococcus	0.843	0.001***	0.092	0.020	0.023
OTU00868	Actinobacteria	Rubrobacter	0.889	0.001***	0.112	0.018	0.016
OTU00808	Proteobacteria	Belnapia	0.888	0.001***	0.107	0.020	0.015
OTU01371	Actinobacteria	Solirubrobacter	0.854	0.001***	0.091	0.015	0.021
OTU00102	Proteobacteria	Desulfohalobium	0.836	0.002**	0.081	0.017	0.023
OTU00600	Proteobacteria	Pelagibius	0.835	0.001***	0.070	0.012	0.025

OTU00866	Synergistetes	Aminivibrio	0.867	0.001***	0.078	0.012	0.018
OTU00857	Verrucomicrobia	Brevifollis	0.862	0.001***	0.076	0.012	0.016
OTU00739	Actinobacteria	Conexibacter	0.897	0.001***	0.088	0.009	0.016
OTU01364	Actinobacteria	Gaiella	0.833	0.001***	0.063	0.012	0.020
OTU00530	Actinobacteria	Rubrobacter	0.872	0.001***	0.071	0.013	0.013
OTU01064	Firmicutes	Oceanobacillus	0.952	0.020*	0.100	0.005	0.007
OTU01090	Proteobacteria	Nitrospirillum	0.870	0.001***	0.067	0.012	0.014
OTU00905	Actinobacteria	Streptomyces	0.939	0.001***	0.094	0.007	0.006
OTU00496	Proteobacteria	Rhodopila	0.883	0.001***	0.069	0.012	0.011
OTU00445	Proteobacteria	Rhodopila	0.840	0.001***	0.055	0.011	0.014
OTU00342	Actinobacteria	Pseudonocardia	0.893	0.001***	0.070	0.014	0.007

Table C3. Indicator Species Analysis (IndVal and p-value) for fungal community at genus level for soils under mosses, bare soils and unburned soils. Values represent relative abundance in soils.

Indicator genera for Mosses					
Genus	**IndVal**	**P-value**	**Unburned**	**Bare Soils**	**Moss**
Penicillium	0.714	0.024*	7.159	23.501	31.892
Clonostachys	0.793	0.024*	0.015	0.372	0.655
Sesquicillium	0.801	0.037*	0.008	0.060	0.196
Oidiodendron	0.846	0.004**	0.010	0.012	0.106
Dicranophora	0.894	0.008**	0.001	0.003	0.051
Phialocephala	0.691	0.041*	0.000	0.002	0.020
Absidia	0.708	0.036*	0.000	0.001	0.018
Lophiotrema	0.681	0.028*	0.000	0.001	0.006
Hormococcus	0.577	0.028*	0.000	0.000	0.004
Indicator genera for Bare soil					
Genus	**IndVal**	**P-value**	**Unburned**	**Bare Soils**	**Moss**
Coniothyrium	0.881	0.001***	0.145	4.149	1.054
Papiliotrema	0.859	0.010**	0.002	0.937	0.332
Pyronema	0.923	0.003**	0.000	0.913	0.086
unclassified_Chytridiomycota	0.841	0.002**	0.006	0.337	0.133

Filobasidium	0.900	0.001***	0.002	0.361	0.083
Saitoella	0.820	0.010**	0.000	0.209	0.102
Venturia	0.766	0.023*	0.002	0.266	0.004
Rhodotorula	0.847	0.003**	0.000	0.109	0.043
Hannaella	0.900	0.006**	0.000	0.084	0.013
Holtermanniella	0.800	0.006**	0.000	0.052	0.024
Cystobasidium	0.821	0.002**	0.005	0.035	0.009
Allophoma	0.731	0.033*	0.002	0.024	0.013
Vishniacozyma	0.772	0.029*	0.001	0.027	0.006
Rhodosporidiobolus	0.773	0.014*	0.000	0.014	0.003
Thelebolus	0.670	0.038*	0.001	0.013	0.002
Sporidiobolus	0.632	0.049*	0.000	0.004	0.001
Indicator genera for Unburned soils (display 30 of #172)					
Genus	**IndVal**	**P-value**	**Unburned**	**Bare Soils**	**Moss**
Geopora	0.882	0.038*	13.467	0.296	0.081
Solicoccozyma	0.871	0.002**	3.401	0.313	0.769
Tomentella	0.997	0.001***	6.183	0.018	0.022
unclassified_Ascomycota	0.973	0.001***	5.083	0.071	0.212
unclassified_Dothideomycetes	0.974	0.001***	2.626	0.034	0.110
Knufia	0.968	0.001***	2.172	0.049	0.099
Preussia	0.982	0.001***	2.214	0.046	0.037
Chaetomium	0.817	0.005**	0.622	0.204	0.106
Sebacina	0.996	0.001***	1.340	0.004	0.007
Gibberella	0.855	0.001***	0.530	0.144	0.051
Leohumicola	0.930	0.016*	0.728	0.015	0.100
Ophiocordyceps	0.882	0.021*	0.509	0.095	0.050
unclassified_Onygenales	0.974	0.001***	0.547	0.001	0.029
Paraconiothyrium	0.887	0.001***	0.333	0.033	0.057
Darksidea	0.903	0.001***	0.346	0.034	0.045
Oliveonia	0.774	0.005**	0.543	0.000	0.000
Verrucaria	0.782	0.024*	0.166	0.061	0.044
Heterospora	0.994	0.001***	0.450	0.005	0.000
Exophiala	0.816	0.003**	0.167	0.054	0.030
Tuber	0.612	0.040*	0.348	0.020	0.003

Sphaceloma	1.000	0.001***	0.372	0.000	0.000
Schizothecium	0.898	0.002**	0.214	0.048	0.004
Meristemomyces	0.632	0.014*	0.337	0.000	0.000
Tylospora	0.984	0.001***	0.266	0.003	0.006
Staninwardia	1.000	0.001***	0.277	0.000	0.000
Pseudorobillarda	0.894	0.001***	0.268	0.000	0.000
Polyblastia	0.860	0.003**	0.129	0.013	0.032
Stereocaulon	0.893	0.003**	0.143	0.009	0.028
unclassified_Eurotiomycetes	0.869	0.002**	0.197	0.000	0.011
Guttulispora	0.982	0.001***	0.208	0.002	0.006

Table C4. Indicator Species Analysis (IndVal and p-value) for fungal community at OTU level for soils under mosses, bare soils and unburned soils. Values represent relative abundance in soils.

Indicator OTU for Mosses								
OTU	Phyla	Genus	Ecology	IndVal	P-value	Unburned	Bare Soils	Moss
OTU00012	Ascomycota	Penicillium	saprotroph	0.870	0.004**	0.204	0.995	3.732
OTU00037	Ascomycota	Clonostachys	saprotroph	0.793	0.025*	0.015	0.371	0.654
OTU00090	unclas_Fungi	unclas_Fungi	unknown	0.668	0.032*	0.000	0.036	0.778
OTU00126	Ascomycota	Penicillium	saprotroph	0.949	0.043*	0.001	0.021	0.609
OTU00142	Basidiomycota	Geminibasidium	saprotroph	0.826	0.013*	0.012	0.103	0.313
OTU00257	Ascomycota	Penicillium	saprotroph	0.803	0.022*	0.003	0.108	0.202
OTU00129	unclas_Fungi	unclas_Fungi	unknown	0.725	0.048*	0.000	0.004	0.270
OTU00165	Ascomycota	Sesquicillium	saprotroph	0.801	0.038*	0.008	0.060	0.196
OTU00158	Ascomycota	Acremonium	saprotroph	0.920	0.001***	0.012	0.023	0.194
OTU00264	Ascomycota	Penicillium	saprotroph	0.847	0.011*	0.001	0.053	0.139
OTU00371	Ascomycota	Penicillium	saprotroph	0.724	0.050*	0.000	0.001	0.083
OTU00325	Ascomycota	Penicillium	saprotroph	0.779	0.048*	0.000	0.020	0.063
OTU00060	Ascomycota	Oidiodendron	saprotroph	0.872	0.003**	0.006	0.004	0.073

OTU00705	Zygomycota	Dicranophora	fungal parasite/ decomposer	0.753	0.023*	0.000	0.001	0.024
OTU02032	Basidiomycota	un_Agaricomycetes	unknown	0.812	0.024*	0.000	0.006	0.019
OTU00536	Ascomycota	Phialocephala	saprotroph	0.675	0.036*	0.000	0.000	0.017
OTU00241	Ascomycota	Slimacomyces	saprotroph	0.675	0.032*	0.000	0.002	0.012
OTU00783	Ascomycota	Penicillium	saprotroph	0.671	0.038*	0.000	0.000	0.011
OTU00603	Ascomycota	Lophiotrema	saprotroph	0.681	0.027*	0.000	0.001	0.006
OTU01662	Ascomycota	Hormococcus	saprotroph	0.577	0.026*	0.000	0.000	0.004
Indicator OTU for Bare Soils (display 30 of #39)								
OTU	**Phyla**	**Genus**	**Ecology**	**IndVal**	**P-value**	**Unburned**	**Bare Soils**	**Moss**
OTU00015	Ascomycota	Coniothyrium	saprotroph	0.891	0.001***	0.000	3.711	0.960
OTU00061	Basidiomycota	Papiliotrema	fungal parasite/ decomposer	0.859	0.010**	0.002	0.930	0.330
OTU00057	Ascomycota	Pyronema	saprotroph	0.923	0.003**	0.000	0.905	0.086
OTU00024	Ascomycota	Fusarium	saprotroph	0.869	0.004**	0.044	0.738	0.129
OTU00074	Ascomycota	Aureobasidium	saprotroph	0.827	0.034*	0.014	0.557	0.243
OTU00027	Ascomycota	Coniothyrium	saprotroph	0.831	0.027*	0.093	0.360	0.068
OTU00178	Basidiomycota	Naganishia	yeast	0.768	0.019*	0.011	0.239	0.156
OTU00040	Ascomycota	Fusarium	saprotroph	0.838	0.006**	0.049	0.299	0.078
OTU00145	Ascomycota	Saitoella	yeast	0.820	0.010**	0.000	0.209	0.102
OTU00201	Basidiomycota	Filobasidium	saprotroph	0.934	0.001***	0.002	0.263	0.037
OTU00092	Basidiomycota	Cryptococcus	yeast	0.897	0.001***	0.004	0.189	0.042
OTU00309	Basidiomycota	Rhodotorula	yeast	0.847	0.003**	0.000	0.103	0.041
OTU00367	Basidiomycota	Filobasidium	saprotroph	0.824	0.006**	0.000	0.096	0.045
OTU00153	Ascomycota	Venturia	saprotroph	0.677	0.032*	0.000	0.118	0.002
OTU00155	Basidiomycota	Cryptococcus	yeast	0.789	0.009**	0.025	0.070	0.017
OTU00339	Basidiomycota	Hannaella	yeast	0.864	0.003**	0.000	0.078	0.013

OTU00389	Chytridiomycota	un_Chytridiomycota	unknown	0.856	0.001***	0.000	0.088	0.000
OTU00395	unclas_Fungi	unclas_Fungi	unknown	0.774	0.026*	0.006	0.058	0.014
OTU00490	Basidiomycota	Holtermanniella	saprotroph	0.794	0.010**	0.000	0.047	0.022
OTU00267	Chytridiomycota	Spizellomyces	saprotroph	0.829	0.003**	0.000	0.056	0.009
OTU00202	Ascomycota	Phoma	saprotroph	0.748	0.024*	0.001	0.043	0.018
OTU00486	Ascomycota	Sporormiella	saprotroph	0.736	0.033*	0.000	0.036	0.017
OTU00148	Ascomycota	Penicillium	saprotroph	0.872	0.048*	0.001	0.039	0.008
OTU00394	unclas_Fungi	unclas_Fungi	unknown	0.764	0.023*	0.001	0.034	0.008
OTU00707	Ascomycota	Epicoccum	saprotroph	0.782	0.006**	0.000	0.035	0.003
OTU00343	Ascomycota	Allophoma	plant-pathogen	0.731	0.034*	0.002	0.024	0.013
OTU00613	Basidiomycota	Vishniacozyma	yeast	0.785	0.023*	0.001	0.027	0.004
OTU00672	Basidiomycota	Cystofilobasidium	yeast	0.754	0.015*	0.001	0.015	0.004
OTU01222	Ascomycota	Coniothyrium	saprotroph	0.894	0.001***	0.000	0.013	0.002
OTU10432	Basidiomycota	Cryptococcus	yeast	0.677	0.039*	0.000	0.009	0.004
Indicator OTU for Unburned soils (display 30 of #172)								
OTU	**Phyla**	**Genus**	**Ecology**	**IndVal**	**P-value**	**Unburned**	**Bare Soils**	**Moss**
OTU00025	Basidiomycota	Solicoccozyma	yeast	0.871	0.002**	3.401	0.313	0.769
OTU00051	Ascomycota	unclas_Ascomycota	unknown	0.969	0.001***	3.687	0.048	0.194
OTU00072	unclas_Fungi	unclas_Fungi	unknown	0.985	0.004**	3.886	0.091	0.028
OTU00058	Ascomycota	Geopora	ectomycorrhizal	0.773	0.003**	3.974	0.011	0.001
OTU00268	Ascomycota	un_Dothideomycetes	unknown	0.977	0.001***	1.817	0.013	0.075
OTU00033	Ascomycota	Fusarium	saprotroph	0.793	0.025*	0.581	0.166	0.177
OTU00113	Ascomycota	Knufia	saprotroph	0.979	0.001***	1.221	0.008	0.044
OTU00004	Basidiomycota	Suillus	ectomycorrhizal	0.909	0.021*	0.729	0.006	0.148
OTU00013	Ascomycota	Gibberella	unknown	0.856	0.001***	0.530	0.144	0.050
OTU00167	Ascomycota	un_Ascomycota	unknown	0.995	0.001***	1.021	0.005	0.006

OTU00099	Ascomycota	Paraphoma	saprotroph	0.879	0.004**	0.493	0.078	0.066
OTU00042	Basidiomycota	Tomentella	ectomycorrhizal	0.993	0.001***	0.884	0.006	0.006
OTU00109	Ascomycota	Ophiocordyceps	animal parasite/ decomposer	0.816	0.038*	0.474	0.059	0.037
OTU00068	Basidiomycota	Sebacina	ectomycorrhizal	0.894	0.001***	0.757	0.000	0.000
OTU00197	Ascomycota	Preussia	saprotroph	0.632	0.020*	0.601	0.000	0.000
OTU00102	Ascomycota	Paraconiothyrium	saprotroph	0.888	0.001***	0.333	0.033	0.057
OTU00112	Ascomycota	Preussia	saprotroph	0.997	0.001***	0.540	0.002	0.002
OTU00352	Ascomycota	un_Dothideomycetes	unknown	0.970	0.001***	0.462	0.010	0.020
OTU00353	Ascomycota	Leohumicola	saprotroph	0.993	0.001***	0.508	0.007	0.000
OTU00170	Ascomycota	Knufia	saprotroph	0.939	0.003**	0.372	0.008	0.042
OTU00218	Basidiomycota	Oliveonia	saprotroph	0.632	0.016*	0.507	0.000	0.000
OTU00403	Ascomycota	un_Onygenales	unknown	0.965	0.001***	0.404	0.001	0.029
OTU00091	Ascomycota	Leohumicola	saprotroph	0.809	0.017*	0.184	0.006	0.092
OTU00162	Ascomycota	Heterospora	saprotroph	0.994	0.001***	0.450	0.005	0.000
OTU00289	Basidiomycota	Tomentella	ectomycorrhizal	0.893	0.001***	0.450	0.001	0.000
OTU00189	Ascomycota	Darksidea	saprotroph	0.868	0.001***	0.225	0.032	0.042
OTU00166	Ascomycota	Fusarium	saprotroph	0.936	0.001***	0.239	0.018	0.016
OTU00355	Ascomycota	Meristemomyces	saprotroph	0.632	0.014*	0.337	0.000	0.000
OTU00159	Ascomycota	Aspergillus	saprotroph	0.951	0.002**	0.248	0.015	0.011
OTU00221	Ascomycota	Preussia	saprotroph	0.956	0.001***	0.254	0.016	0.008

Appendix D

Chapter 6 “Post-fire wood mulch modulates the biocrust-forming mosses response and the soil fungal community composition.”

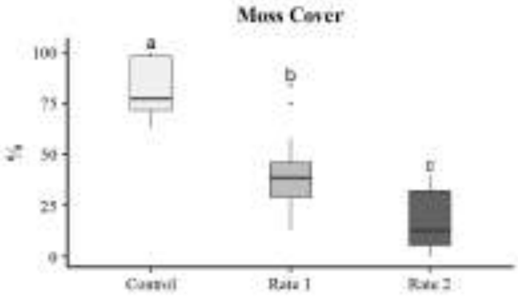


Fig. D1. Moss cover in soils after one year of mulch application. Different lowercase letters indicate significant differences among treatments (p-value <0.05, Tukey test).

Table D1. Microbial biomass in fire-affected and unburned soils. Mean and standard deviation of biomarkers (PLFA and NLFA) reflecting microbial biomass in soils during the study "Time" (T0, and T1, one year after the treatments application), and the "Treatment" application (unburned soils, control soils, Rate 1, and Rate 2), differentiated by "Crust" (uncrusted soils and moss biocrust soils). Significance of factors in models are shown, including "Time", "Crust", and "Mulch" (control soils and soils under mulch application), and the interaction between factors when relevant (n.s. not significant at p-value >0.05). (Total: total microbial biomass).

Treatment	Crust	Time	Fungi (µg g^{-1})	Arbuscular Mycorrhiza (µg g^{-1})	Bacteria (µg g^{-1})	Total (µg g^{-1})
Unburned			0.33 ± 0.11	4.96 ± 1.13	8.68 ± 1.25	13.3 ± 1.92
Control	Uncrusted	T0	0.20 ± 0.09	1.55 ± 1.15	4.49 ± 1.00	6.97 ± 1.64
		T1	0.24 ± 0.08	1.60 ± 0.82	6.47 ± 2.19	9.66 ± 3.17
	Mosses	T0	0.28 ± 0.08	2.46 ± 1.99	5.43 ± 2.05	8.52 ± 3.01
		T1	0.26 ± 0.18	1.60 ± 1.25	8.66 ± 7.42	12.7 ± 10.7
Rate1	Uncrusted	T0	0.18 ± 0.05	1.01 ± 0.67	5.78 ± 1.59	8.80 ± 2.25
		T1	0.20 ± 0.03	1.84 ± 0.53	6.82 ± 1.17	9.99 ± 1.69
	Mosses	T0	0.22 ± 0.06	1.94 ± 0.96	5.21 ± 1.17	8.19 ± 1.89
		T1	0.17 ± 0.06	0.89 ± 0.36	5.18 ± 1.03	7.73 ± 1.50
Rate2	Uncrusted	T0	0.18 ± 0.05	1.21 ± 0.56	4.56 ± 0.95	7.14 ± 1.47
		T1	0.16 ± 0.02	1.79 ± 1.11	5.58 ± 0.99	8.29 ± 1.39
	Mosses	T0	0.16 ± 0.07	0.97 ± 0.25	5.49 ± 1.87	8.29 ± 2.78
		T1	0.23 ± 0.14	2.51 ± 2.35	6.91 ± 1.99	10.2 ± 3.04
Factors	Time		n.s.	n.s.	0.03	n.s.
	Crust		n.s.	n.s.	n.s.	n.s.
	Mulch		0.04	n.s.	n.s.	n.s.
	Crust:Mulch		n.s.	n.s.	n.s.	n.s.
	Crust:Time		n.s.	n.s.	n.s.	n.s.
	Mulch:Time		n.s.	n.s.	n.s.	n.s.
	Crust:Mulch:Time		n.s.	n.s.	n.s.	n.s.

Table D2. Effects of mulch treatments over time on the microbial community composition in fire-affected soils. The studied effects include “Time” (T0, and T1, one year after the treatments application), “Treatment” (Control, Rate 1, and Rate 2), “Mulch” (control soils and soils under mulch application), and “Crust” (uncrusted soils and moss biocrust soils). Results of PERMANOVA test based on OTU tables (Significant codes: p<0.001, “***”; p<0.01, “**”; p<0.05, “*”).

	Fungal community					Bacterial community				
Factors	Df	Sum of squares	R2	F	p-value	Df	Sum of squares	R2	F	p-value
Time	1	1.23	0.12	8.17	0.0001***	1	0.57	0.10	6.62	0.0001***
Mulch	1	0.31	0.03	2.05	0.0055**	1	0.18	0.03	2.04	0.011*
Treat	1	0.17	0.02	1.13	0.244	1	0.08	0.01	0.92	0.510
Crust	1	0.24	0.02	1.58	0.036*	1	0.20	0.03	2.34	0.004**
Time:Mulch	1	0.24	0.02	1.61	0.028*	1	0.10	0.02	1.14	0.239
Time:Treat	1	0.12	0.01	0.82	0.744	1	0.07	0.01	0.87	0.593
Time:Crust	1	0.28	0.03	1.83	0.011*	1	0.20	0.03	2.27	0.0056**
Mulch:Crust	1	0.18	0.02	1.22	0.171	52	0.09	0.02	1.02	0.359
Treat:Crust	1	0.10	0.01	0.63	0.979	59	0.06	0.01	0.70	0.930
Time:Mulch:Crust	1	0.16	0.02	1.03	0.362		0.08	0.01	0.96	0.432
Time:Treat:Crust	1	0.11	0.01	0.8	0.783		0.06	0.01	0.69	0.935
Residual	48	7.72	0.70				4.14	0.71		
Total	59	10.35	1				5.82	1		

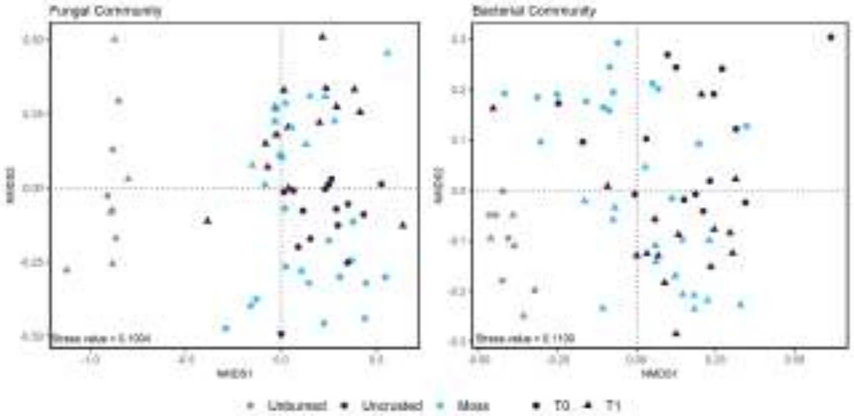


Fig. D2. Impact of the moss biocrust presence over time in the composition of the microbial communities. Ordination plots represent two-dimensional non-metric multidimensional scaling (NMDS) ordination based on Bray-Curtis dissimilarities at OTU level for fungal and bacterial communities, representing differences at "Time" (T0 and T1) and "Crust" presence (uncrusted and moss soils).

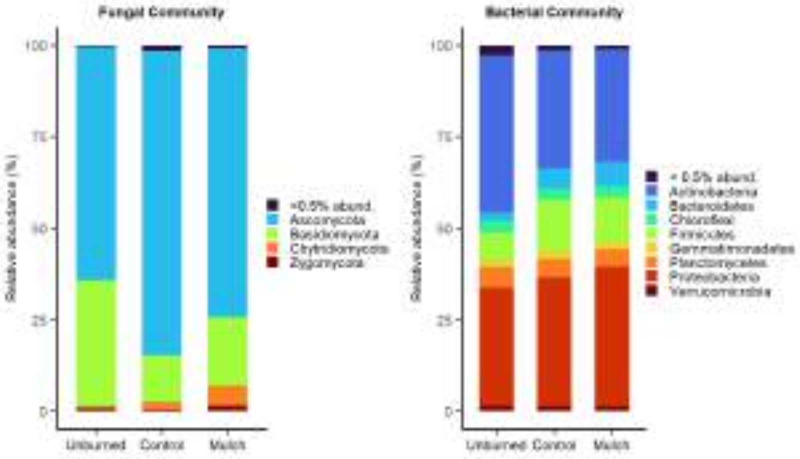
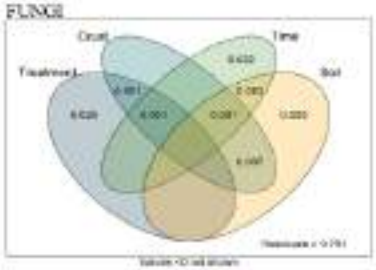
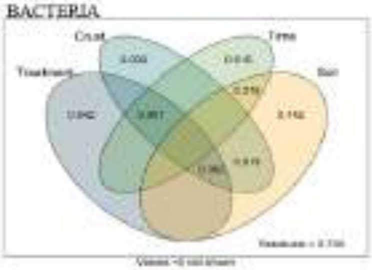


Fig. D3. Effects of mulch treatment on the dominant fungal and bacterial phyla at the end of the experiment. Data represent the relative abundance for soils under "Mulch" application (unburned soils, controls and soils under mulch application).

Table D4. Impact of the mulch treatments and crust presence over time in the composition of the microbial communities and soil parameters related. Variation partitioning are performed from the OTU tables for fungal and bacterial communities, considering all factors including "Soil" characterized by the soil physicochemical and biological parameters. (Significant codes: p<0.001, "***"; p<0.01, "**"; p<0.05, "*"). Venn diagrams are included for both microbial communities.

	Fungal Community				**Bacterial Community**			
Models	df	Adjusted R2	F	p-value	df	Adjusted R2	F	p-value
Treatment + Crust + Time + Soil	15	0.174	1.901	0.001***	15	0.090	2.322	0.001***
Treatment	2	0.022	1.451	0.049*	2	0.009	1.339	0.097
Crust	1	0.009	1.180	0.247	1	0.007	2.160	0.015*
Time	1	0.05	7.484	0.001***	1	0.021	6.630	0.001***
Soil	12	0.149	1.985	0.001***	12	0.076	2.326	0.001***
Treatment (Crust + Time + Soil)	2	0.021	1.738	0.004**	2	0.011	2.276	0.001***
Crust (Treatment + Time + Soil)	1	0.006	0.926	0.525	1	0.003	1.210	0.157
Time (Crust + Treatment + Soil)	1	0.107	1.494	0.003**	1	0.005	1.870	0.009**
Soil (Crust + Treatment + Time)	12	0.107	1.494	0.001***	12	0.057	1.888	0.001***





Appendix E

Chapter 7"Contrasting Organic Amendments Induce Different Short-Term Responses in Soil Abiotic and Biotic Properties in a Fire-Affected Native Mediterranean Forest in Chile."

Table E1. Total content of organic matter (OM), organic carbon (OC), and total nitrogen added to the soil by the organic amendments (dry weight) in a volume of 200 m^3 ha^{-1} of amendment.

Organic amendment	Amendment (t ha^{-1})	OM (t ha^{-1})	OC (t ha^{-1})	N (t ha^{-1})
Compost	78,77	14,7	8,18	0,65
Poultry manure	150,91	63,7	35,41	2,89
Swine manure	95,67	22,2	27,64	0,717

Table E2. Linear models resulting of stepwise linear regressions for basal respiration, microbial biomass, microbial metabolic coefficient (qCO_2), and coefficient of carbon mineralization, independently of treatment. The order of the variables indicates their importance (OC: organic carbon; N: total nitrogen; P: available phosphorous; EC, electrical conductivity).

Response	Model	AIC
Basal respiration	EC+Cu+Mn+Fe+Cr+Pb+Cd	157.68
Microbial biomass	pH+EC+N+Mn+Fe+Cr+Pb	536.07
Coefficient of C mineralization	EC+OC+Mn+Fe+Cr+Pb+Cd	-108.38
qCO_2	pH+EC+Cu+Mn+Fe+Ni+Pb	-1198.52

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Sin duda, soy toda una privilegiada.

TESIS DOCTORAL

Minerva García Carmona

Role of biological soil crust and soil microbial communities in the recovery of burned soils exposed to post-fire management

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El papel de las costras biológicas y comunidades microbianas edáficas en la recuperación de suelos quemados sometidos a manejos post-incendio

Programa de Doctorado en Medio Ambiente y Sostenibilidad
Universidad Miguel Hernández de Elche
Director de la tesis: Dr. Jorge Mataix Solera
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