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The Recovery of Mediterranean Soils After Post-Fire Management: The Role of Biocrusts and Soil Microbial Communities

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Although Mediterranean ecosystems are adapted to fire disturbances, soils are prone to degradation. Therefore, post-fire forest management is a critical step for ecosystem recovery: it 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, 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.

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INTRODUCTION

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 and 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 thanks to the climatic seasonality, precipitation in the mild winters that enable plant growth which became highly flammable during the dry and hot summers. Thus, several species have developed adaptive strategies to resist, promote, or recover from recurrent fires (Keeley et al., 2011). Land-use

change, fire suppression policies, and climate predictions that point to intensification in drought frequency and warmer conditions, have the potential to magnify the wildfire impacts (Pausas, 2004; IPCC, 2018), threatening the resilience of ecosystems (Flannigan et al., 2009).

Intensification in frequency and severity of fire events is expected to result in detrimental effects on soils (Guénon et al., 2013; Pellegrini et al., 2018), through the magnification of the hydrological response, destruction of soil structure, modification of soil organic matter and soil biochemistry, and loss in soil biodiversity (Neary et al., 1999; DeBano, 2000; González-Pérez et al., 2004; Certini et al., 2021; Doerr et al., 2022). Fire effects on soils are coupled with changes aboveground. Rapid vegetation recovery is critical to guarantee soil protection against erosive forces, the main threat to Mediterranean soils after fires (Cerdà and Robichaud, 2009). Nonetheless, above-belowground interactions may suffer alterations under changing fire regimes, e.g., changing soil nutrient pools over time (Caon et al., 2014; Pellegrini et al., 2018; Dove et al., 2020). Understanding how vegetation regenerates is essential for mitigating the escalating fire effects in vulnerable ecosystems (Fernández-García et al., 2019).

Aboveground and belowground soil components are strongly linked; therefore, 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). Given the critical ecosystem processes soil microorganisms are involved in, including nutrient cycling, physical stability, carbon sequestration, or support for plant growth (Fultz et al., 2016), modifications in fire regimen could profoundly alter the microbial communities and lead to a great impact on soil functioning (Ferrenberg et al., 2013; Dove and Hart, 2017; Whitman et al., 2019; Sáenz De Miera et al., 2020). Considering the global change projections and new wildfire scenarios, additional work is necessary to better understand the resilience of fire-affected ecosystems exposed to additional disturbances such as human intervention through forest management, of major relevance to support strategies that preserve soils against functionality loss (Pereira et al., 2018; Tomao et al., 2020; Lucas-Borja et al., 2021; Averill et al., 2022).

Biocrust-Forming Mosses: Their Role in Soil Recovery

Biological soil crust, hereafter “biocrust,” is a diverse community of photoautotrophic (e.g., cyanobacteria, algae, lichens, bryophytes) and heterotrophic (e.g., bacteria, fungi, archaea) organisms, living within the first centimeters of the soil surface. Soil particles are aggregated through their presence and activity, and the resultant living crust covers the surface of the ground as a coherent layer (Weber et al., 2022). Around 12% of Earth’s terrestrial surface is covered by biocrust (Rodríguez-Caballero et al., 2018), dominating the plant interspace in many drylands thanks to specific adaptations to survive in unfavorable and often extreme environments (Belnap and Büdel, 2016). While mosses are typically found creating carpets in habitats where water is not a limiting factor (Weber

et al., 2022), biocrust-forming mosses developed in drylands are adapted to cope with high insolation, low rainfall, and drought. In the semiarid Mediterranean region, biocrusts are dominated by lichens and bryophytes due to their physiological and morphological characteristics (Maestre et al., 2021; Ladrón De Guevara and Maestre, 2022).

Biocrust-forming mosses are ecosystem engineers: modulate 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 (i.e., fine rhizoids and protonema mats) allows strong cohesion of soil particles providing high stability (Seppelt et al., 2016). This high resistance enables effective mitigation of soil erosion, directly, by creating a physical barrier and roughening the surface, and indirectly, by affecting soil properties mainly by increasing the organic matter content (Gao et al., 2020; Zhang et al., 2022). The biocrust effect on soil stability is subordinated to its development stage, which is influenced as well by the extent, intensity, and time since disturbances (Belnap and Büdel, 2016). Due to their implication in distributing surface flows, infiltration and runoff, and regulating soil moisture, biocrust have a major role in controlling local hydrological cycles in drylands (Eldridge et al., 2020). Biocrusts represent islands of fertility for plants and microorganisms through the concentration of essential elements in soils (Ferrenberg et al., 2018), 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), and contribute indirectly by acting as dust particle trappers (Reynolds et al., 2001). 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).

Natural recovery rates of biocrust after disturbances are known to be slow, especially after wildfire events, which can involve long-lasting consequences for biocrust community structure and diversity recovery (Johansen, 2001; Root et al., 2017). However, there is not a general consensus on how biocrusts respond to fire disturbances since it highly 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). Under favorable climate conditions and soil stability, the initial cyanobacteria-dominated succession stages may be omitted to start with biocrust-forming mosses (Weber et al., 2016). This succession pattern is highly observed in fire-affected semiarid or temperate ecosystems (Bowker et al., 2004; Grover et al., 2020; Weber et al., 2022). Fire disturbances provide an opportunity for biocrust to develop, and demine temporarily, in areas that are commonly covered with vascular plants and plant litter. Eventually, biocrust will be diminished in abundance or replaced by vascular plant vegetation with natural recovery succession; however, persistent



FIGURE 1 | Patch of moss biocrust emerged after a wildfire stabilizing soils surrounded by bare soils exhibiting erosion symptoms.

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., 2022a).

Bryophytes are recurrent elements in the post-fire vegetation succession in Mediterranean forests (During, 1979; De las Heras et al., 1994; Esposito et al., 1999; Castoldi et al., 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 after high-intensity fires, in which ecosystems are largely dominated by ruderal mosses 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 spores, 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 such as *Funaria hygrometrica*, a specie that shows a very fast protonema development able to survive the desiccation that typically occurs in recently burned soils (During, 1979; De las Heras et al., 1994; Esposito et al., 1999).

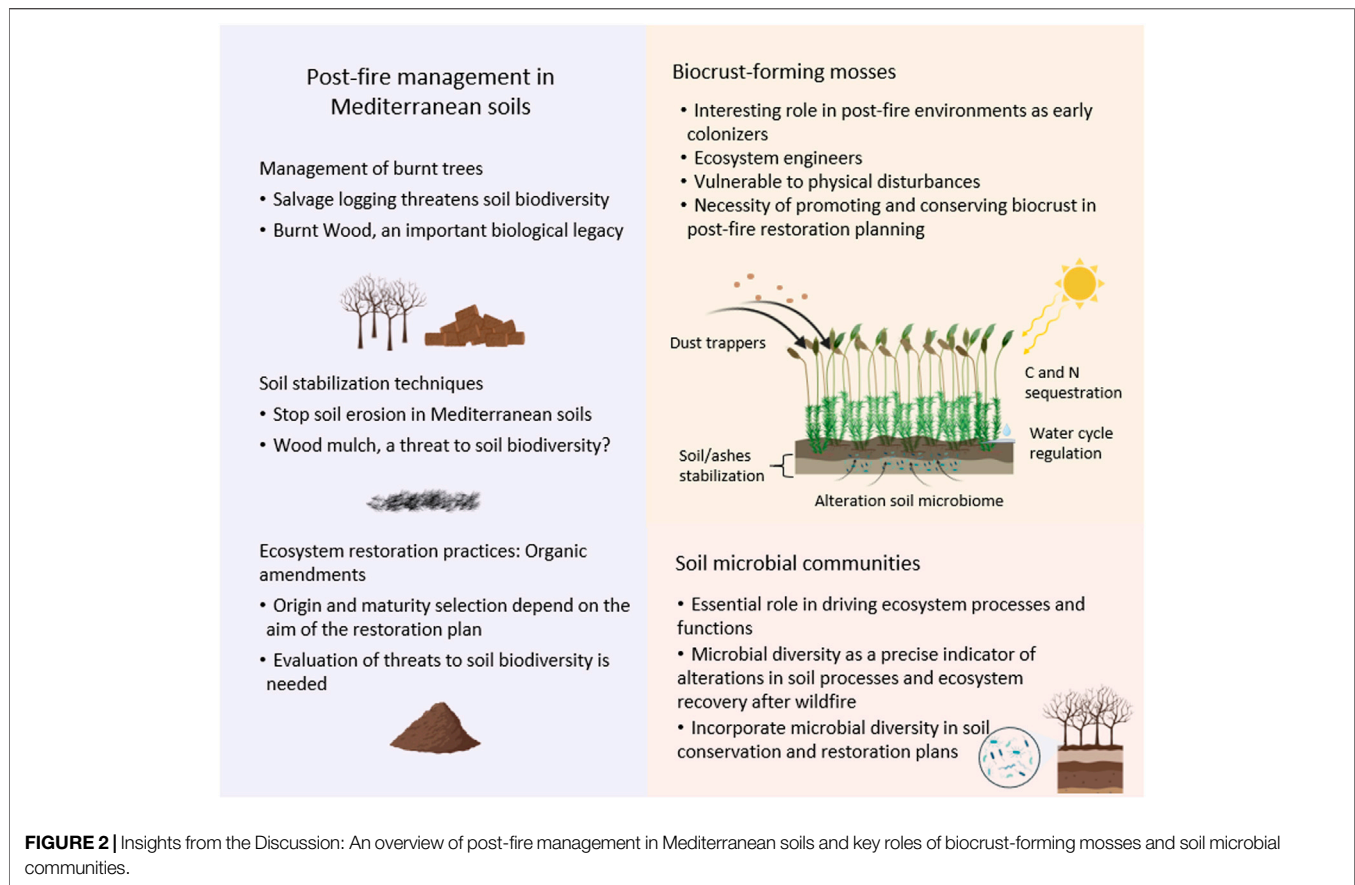
Biocrust-forming mosses have received attention recently due to their efficiency in stabilizing the soil surface and controlling soil water erosion after wildfires (Figure 1) (Silva et al., 2019; Gall et al., 2022b), which makes them a promising technique to rehabilitate fire-affected soils (Grover et al., 2020; Muñoz-Rojas et al., 2021). 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. The burgeoning biocrust is a valuable component in post-fire environments beyond soil stabilization. The early colonization of mosses mitigates the harsh conditions on the surface (e.g., desiccation, high temperature, and solar

radiation), thereby facilitating microbial growth in biomass and diversity, 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 (García-Carmona et al., 2020; 2022). However, biocrust are highly vulnerable to physical disturbances and climate change (Rodríguez-Caballero et al., 2018; García-Carmona et al., 2020), thus more studies are needed to understand how biocrust-forming mosses will respond to the intensification of fire events in a scenario of climate change.

The Soil Microbial Response to Fire Disturbances

Soil microbial communities play an essential role in driving 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). Therefore, microbial diversity act as a precise indicator of soil process alterations and ecosystem recovery after wildfires (Muñoz-Rojas and Bárcenas-Moreno, 2019). Fire disturbances induce 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). In Mediterranean soils, microbial communities generally show high resilience to wildfires, 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). The study of microbial communities (i.e., population abundance and taxonomic and functional diversity) and their relationship with soil properties (i.e., indicators of soil health, nutrient cycling, or soil carbon stock) becomes strategic to evaluate the recovery process after fires, monitor the soil biodiversity conservation, and to predict the ecosystem's resilience to further disturbances (Adkins et al., 2020; Dove et al., 2020; Guerra et al., 2021).

Fire profoundly alters the assembly of microbial communities, which are strongly affected by fire severity (Whitman et al., 2019), and with long-lasting consequences on the community complexity (Treseder et al., 2004; Holden et al., 2016; Cutler et al., 2017; Su et al., 2022). As warned in several meta-analyses, 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 (Dooley and Treseder, 2012; Pressler et al., 2019). After wildfires, the taxonomic structure is dominated by some groups as a response to their ecological strategy (Prendergast-Miller et al., 2017; Pérez-Valera et al., 2018). For instance, the



identification of responsive taxa to fire disturbances provides valuable information in order to predict the recovery of microbial functionality. In this sense, pyrophilous fungi are interesting indicator taxa after fires, which fruit abundantly 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; Fox et al., 2022). Pyrophilous fungi have been recently recognized for aggregating particles and increasing moisture in soils (Filialuna and Cripps, 2021), accelerating the ecosystem recovery process following a fire disturbance.

In drylands, biocrust promote soil microbial diversity (Delgado-Baquerizo et al., 2016; Zhang et al., 2022), being the macro component, either cyanobacteria, lichen, or bryophyte, the main driver of microbiome assembly (Maier et al., 2016; 2018). Moss biocrust is known to harbor a high diversity of bacteria and fungi beneath it, but communities are highly sensitive to disturbances (Xiao and Veste, 2017; Bao et al., 2019; Cheng et al., 2021). Whether new wildfire scenarios coupled with climatic projections may shift the structure of biocrust, switching to early-successional cyanobacteria, is relevant for microbial biodiversity conservation. Those shifts may strongly impact the functioning of recently fire-affected ecosystems through the profound alteration of soil microbial communities and biochemical processes (Maestre et al., 2015; Delgado-Baquerizo et al., 2018; Tucker et al., 2020; Tian et al., 2022). Those questions remain unanswered, but new approaches in the

study of soil microbiome are expected to reveal valuable information in this regard.

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. While Mediterranean ecosystems are resilient to fire events, soils are prone to degradation. Therefore, the management 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 planning in a Mediterranean burnt forest includes interventions with contrasting approaches, including the management of burnt trees, soil protection, or practices devoted to ecosystem restoration. The consequences of forest management in soils, especially in soil biology, are particularly complex and conditioned by multiple factors, often overlooked in the decision-making process (Figure 2).

Salvage logging is the most common post-fire management strategy in Mediterranean coniferous forests. Intensive salvage logging trigger soil degradation processes: soil compaction, 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), reducing the cover of biocrust-forming mosses (García-Carmona et al., 2020), or altering the soil microbial communities (García-Carmona et al., 2021a). 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). On the other hand, burnt wood is a biological legacy of key relevance in burned forests (Thorn et al., 2018). The burnt wood act as a barrier for sediments against water erosion, constitutes a stock of nutrients that slowly fertilize soil through decomposition, and ameliorates the stress conditions by increasing soil moisture, enabling vegetation and microbial development and sustaining biodiversity and ecosystem services (Baldrian, 2017; Thorn et al., 2018; 2020; García-Carmona et al., 2021a; Juan-Ovejero et al., 2021). However, timber activities in Mediterranean forests are important from a social perspective, being non-interventionism is highly controversial (Castro, 2021). The creation of land diversification via patches of different wood extraction intensities could increase the forest's resilience to future disturbances (FAO et al., 2020).

Among the emergency stabilization techniques to face the risk of soil erosion, mulching is considered the most cost-effective intervention after wildfires (Robichaud et al., 2013; Girona-García et al., 2021). Straw mulches, the most commonly applied materials, are highly effective (Lucas-Borja et al., 2019), but their application presents some drawbacks like the introduction of non-native 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). However, vegetation regrowth can be hindered under a thick layer of mulch (Bautista et al., 2009), and thus endangered its crucial role in soil protection and recovery. While preventing soil loss in Mediterranean forests must be the main goal in post-fire planning, more research is needed regarding the potential threat to soil biodiversity conservation of wood-mulching if incorrectly performed. Multiple recommendations or guidelines exist in this aspect (Vallejo et al., 2012; Robichaud et al., 2013; Pereira et al., 2018; Castro, 2021): interventions should be limited to very specific situations, i.e., high risk of erosion, slow vascular plant recovery rate, risk downslope, *etc.* For instance, wood residues generated in the framework of logging operations are often applied where intensive logging operations may have created the necessity of the mulch application after triggering erosion processes (Castro, 2021). Wood-based mulch in soils is expected to produce positive effects in soils related to microclimatic improvement and nutrient supply, although the biological soil response and functionality recovery are still rather unexplored.

Restoration practices act on components or processes in the affected ecosystem in order to recover its functionality, for

example, via the application of organic amendments (Hueso-González et al., 2018; Muñoz-Rojas, 2018). After the strong consumption of organic carbon in high-severity fires, the additional source of organic matter induces a cascade of effects in multiple components of the perturbed ecosystem (Heneghan et al., 2008; Costantini et al., 2016). The amendment selection, in relation to the decomposition rates of the organic materials, depends on the goals of the soil restoration plan in terms of the durability of effects on the soil response (Tejada et al., 2009; González-Ubierna et al., 2012; Larney and Angers, 2012; García-Carmona et al., 2021b). Studying the application effects on soil microbial diversity is highly necessary to identify possible threats to soil biodiversity, related to the introduction of new taxa, in order to correctly address biodiversity protection plans.

CONCLUSION

In order to support management practices that boost soil biodiversity and preserve ecosystem functionality, threats must be identified to formulate strategies that prioritize soil conservation (Guerra et al., 2021; Averill et al., 2022). In this sense, biocrust and soil microbial communities are highly vulnerable to post-fire physical disturbances, thus land diversification through different management intensities could be strategic for increasing the ecosystem's resilience. In the context of intensification of fire events and climate change scenarios, the investigation of two key components for soil recovery, i.e., microbial diversity and biocrust-forming mosses, might be key to guiding forest strategies toward accelerating recovery and resilience of semi-arid ecosystems prone to degradation.

AUTHOR CONTRIBUTIONS

MG-C conduct the study and wrote the manuscript, JM-S and FG-O lead the funding acquisition. All authors contributed to the article and approved the submitted version.

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CONFLICT OF INTEREST

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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