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# Does helimulching after severe wildfire affect soil fungal diversity and community composition in a Mediterranean ecosystem?



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# HIGHLIGHTS

- Fungal diversity and community composition were analysed after helimulching treatment.
- It was not observed changes in fungal richness between mulched and non-mulched plots.
- There was an increase in richness of litter and wood saprotrophs and plant pathogens.
- Fungal composition at the OTUs level correlated with pH, organic matter and soil nitrogen content.
- Fungal composition by trophic groups was correlated with soil potassium content.

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# GRAPHICAL ABSTRACT



# ABSTRACT

Straw helimulching was applied to an area with a high soil erosion risk one month after the Navalacruz megafire (Iberian Central System, Ávila, Spain) to mitigate soil erosion and to maintain soil quality. To determine whether the soil fungal community, which is key to soil and vegetation recovery after fire, is altered by straw mulching, we examined the effect of helimulching one year after its application. Three hillside zones were chosen with two treatments in each zone (mulched and non-mulched plots), with three replicates of each treatment. Chemical and genomic DNA analyses of soil samples from mulched and non-mulched plots were performed to assess the soil characteristics and the soil fungal community composition and abundance. The total fungal operational taxonomic unit richness and abundance did not differ between treatments. However, there was an increase in the richness of litter saprotrophs, plant pathogens and wood saprotrophs associated with the application of straw mulch. The total fungal composition of mulched and non-mulched plots differed significantly. Fungal composition at the phylum level correlated with the soil potassium content and marginally with the PH and phosphorus content. The application of mulch promoted the dominance of saprotrophic functional groups. Fungal composition according to guilds was also significantly different between treatments. As conclusion, the application of mulch could mean a faster recovery of saprotrophic functional groups that will be responsible for decomposing the available dead fine fuel.

# 1. Introduction

\* Corresponding author. *E-mail address:* pmpinto@uva.es (P. Martín-Pinto). Wildfires, depending on the burn severity and frequency, may drastically remove the plant cover, cause partial or complete combustion of

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organic matter, alter pH and bulk density, and modify the porosity (Shakesby, 2011; Agbeshie et al., 2022). They may also alter aggregate stability or water repellency (e.g., Doerr and Shakesby, 2009; Jordán et al., 2011; Mataix-Solera et al., 2011; Varela et al., 2015), causing nutrient depletion (Shakesby, 2011), together with marked alterations in the numbers and composition of soil microbes and soil-dwelling invertebrates (Certini et al., 2021). Many of these changes potentially make the soil more susceptible to removal by water erosion and/or less likely to allow infiltration and more likely to promote overland flow (Shakesby, 2011; Díaz et al., 2022). In the Mediterranean basin, which has hot, dry summers (when most fires occur) followed by frequent and intense rainstorms in autumn (70–80 % of the annual rainfall occurs in autumn), and shallow forest soils with low levels of organic matter (Díaz et al., 2022), the negative impacts of soil erosion are aggravated following a wildfire (Shakesby, 2011; Panagos et al., 2015; Lucas-Borja, 2021).

Mulching is one of the most common post-fire management techniques used to reduce post-fire soil erosion (e.g., Robichaud et al., 2013; Fernández and Vega, 2014; Prosdocimi et al., 2016; Keizer et al., 2018; Lucas-Borja et al., 2019; Zituni et al., 2019). Agricultural straw is a particularly useful mulching material because it is light, has a high soil-covering capacity, is readily available at relatively low cost and can be applied from the air (helimulching), thus enabling extensive burned areas to be treated in a relatively short time (Fernández et al., 2016a). Several studies have evaluated the impact of mulching on: the understory plant species cover, richness, and diversity (e.g., Fernández et al., 2016b; Bontrager et al., 2019); soil infiltration (e.g., Lucas-Borja et al., 2021); nutrient availability, particularly soil gross nitrogen (N) rates (e.g., Gómez-Rey and González-Prieto, 2015; Fernández-Fernández et al., 2017); and microbial populations (Fontúrbel et al., 2012; Barreiro et al., 2015). However, even though the fungal community is known to play a key role in the post-fire establishment, growth and survival of vegetation (Smith and Read, 2008), to our knowledge, the impact of mulching on the fungal diversity and community composition after a fire has not been studied. In addition, the effect of forest management practices on soil-inhabiting fungi has been mostly inferred based on sporocarp occurrence, which can underestimate the fungal richness and diversity (Tomao et al., 2020), whereas studies involving genomic DNA analyses of the soil may be more accurate (Espinosa et al., 2023).

During August 2021, an area of high pressure in the upper troposphere affected a large part of the Mediterranean basin. This atmospheric configuration induced a severe heat wave over the Mediterranean region (Faranda et al., 2022). This, combined with the type of Mediterranean ecosystems that occur in this region, a mosaic of shrublands, woodlands, pastures and fields that have a great biomass accumulation of dry and flammable vegetation (Keeley et al., 2011; Moreira et al., 2020), resulted in extensive wildfires, including the Navalacruz megafire in Spain (the fire started on August 14, 2021). This large wildfire in the Navalacruz area (Iberian Central System, Ávila) had a perimeter of 90 km. The megafire burned approximately 22,000 ha of vegetation (approximately 50 % of which belonged to the Natura 2000 Network, which at the time made it the largest wildfire in this Autonomous Community (Junta de Castilla y León, 2021). To reduce the risk of post-fire hydrologic and soil erosion hazards, helimulching using straw was applied to areas with a high soil erosion potential one month after the fire. Straw mulching reduces soil post-fire erosion and, therefore, nutrients are retained in the soil, dampening the negative effect of fire on the physical, chemical and biochemical characteristics of the soil (Díaz-Raviña et al., 2012). In addition, the organic matter provided by the straw (Lucas-Borja et al., 2021; Navidi et al., 2022) and dead matter created as a result of the effects of the fire may favour the growth of certain fungal guilds. For example, saprotrophic fungi could benefit from decomposing dead organic matter, including dead wood, coarse woody debris and litter after the fire. Although the richness and abundance of ectomycorrhizal (ECM) fungi may be reduced in the short term due to a lack of hosts, if nutrient retention is sufficient to promote vegetation regeneration, this would have a positive effect on this guild. On this basis, we hypothesized that helimulching would significantly improve the richness and diversity of the fungal community and would contribute to the

improvement of post-fire soil properties. To test this hypothesis, our specific objectives were: (i) to analyse whether the soil fungal richness and abundance were similar in plots with and without mulch; (ii) to identify edaphic variables that significantly drive the composition of the total fungi and the different fungal guilds; and (iii) to ascertain the effect of helimulching on different guilds. Thus, the information generated from this study should help to guide post-fire management strategies after large wildfires and supplement our knowledge of postfire management effects on soil fungal community dynamics.

# 2. Material and methods

# 2.1. Study site

The study is located in the municipality of Sotalbo (Iberian Central System, Ávila), within the boundary of the Natura 2000 network "Sierra de la Paramera y Serrota". The coordinates are 40° 29' 25" N and 004° 59' 52" W (WGS84) (Fig. 1a). The mean altitude is 1400 m a.s.l. The mean slope in the area ranges from 25 % to 75 %. The bedrock is composed of siliceous rocks, primarily granites and gneisses that were geomorphologically moulded by horst-graben tectonics (Rubiales and Génova, 2015). In terms of the edaphology, the altitude, topography and climatic conditions of the Iberian Central System have hindered the evolution of soils. Steep slopes and anthropological actions also favour soil erosion. As a result, there is a predominance of poorly developed soils. The climate is montane Mediterranean, with an intense summer drought and great seasonal temperature oscillations (Rubiales and Génova, 2015). The mean annual precipitation is 554 mm, with most precipitation occurring in spring and in autumn, and with a 2month period of hydric deficit (July and August). The mean annual temperature is 11.5 °C (Génova and Moya, 2012).

The vegetation includes evergreen and deciduous species: *Quercus ilex* subsp. *ballota* (Desf.) Samp. and *Quercus suber* L. and pines, mainly *Pinus pinaster* Aiton and *P. pinea* L. The tree line reaches approximately 1800 m a.s.l. with isolated and dispersed stands of *Pinus sylvestris* L. and *Pinus nigra* subsp. *salzmannii* (Dunal) Franco (Génova et al., 1988; Génova and Moya, 2012). Ridges are composed by a shrubland of *Cytisus oromediterraneus* Rivas Mart. and *Juniperus communis* subsp. *alpina* (Suter) Celak is dominant at the highest altitudes, along with alpine pastures (Ruiz de la Torre, 2002; Gómez Manzaneque et al., 2009).

### 2.2. Experimental design

We established three blocks (B1, B2 and B3). In each block, three mulched and three non-mulched plots of 90 m<sup>2</sup> (3 m × 30 m; n = 18 plots) were sampled (Fig. 1b). The plots were representative of the study area and homogeneous in terms of slope (65–75 %) and exposure (north-eastern), in an area with a shrub community of *Cytisus* sp., *J. communis* subsp. *alpina* and alpine pastures. The burn severity of all experimental plots was characterized as high by the forest service of Castilla y León. The mean chemical properties of soil samples collected from mulched and non-mulched plots are shown in Table 1 and Fig. S1.

# 2.3. Helimulching

Helimulching was conducted by the Forest Service of Castilla y León in the last week of September 2021 (one month after the wildfire of Navalacruz) to explore the potential of applying agricultural straw from the air using a helicopter as a tool to minimize erosive impacts on the soil in high severity areas (levels higher than 4 in the classification proposed by Vega et al., 2013). Wheat straw mulching was applied at a rate of 3.0-3.5 Mg ha<sup>-1</sup> (Fig. 2) to form a layer of mulch 2 to 3 cm thick. Due to the expense, helimulching was used as a strategic treatment in areas of high soil erosion potential and where there was a risk of loss of downstream values, such as aquatic ecosystems, infrastructure and property. (Fig. 2) (Robichaud, 2010; Fernández et al., 2016a).



Fig. 1. (a) Location of the study area in the Iberian Central System, Ávila, Spain (1:150000). (b) Location of the three study blocks (B1, B2 and B3) (1:7000).

Fifteen days after the Navalacruz fire started (August 14, 2021), rainfall occurred for five days in the study area (total precipitation of 6.3 mm). In addition, prior to the application of helimulching, storms occurred in the area during the second half of September 2021 (total precipitation of 35.4 mm). The weather during the study year was characterized by a mean annual temperature of 12  $^{\circ}$ C, with a mean maximum temperature of 20  $^{\circ}$ C and an accumulated precipitation of 211 mm (from August, 14 to September 30, 2022).

#### 2.4. Soil samples and molecular work

Soil samples were collected from plots (September 24–25, 2022) one year after the helimulching treatment was applied. Plots were analysed as independent samples (Ruiz-Almenara et al., 2019). To collect samples with spatial variability while minimizing the likelihood of repeatedly sampling the same genet, soil cores of topsoil (10–15 cm in depth) taken from underneath the litter or mulch layer were extracted 5 m apart at 10 sampling points along the centrelines of each plot (250 cm<sup>3</sup>) (De la Varga et al., 2012). Litter, twigs and mulch were removed from the surface before soil samples were taken (Voříšková and Baldrian, 2013). The 10 cores were pooled to produce a composite soil sample for each plot. The samples were transported to the laboratory in sterile plastic bags and stored at 4 °C. Within the following 24 h, samples were air dried, sieved through a 1 mm<sup>2</sup> mesh, and then ground to a fine powder using a mortar and pestle (Martín-Pinto et al., 2021; Alem et al., 2022). Each soil composite sample was subjected to chemical and genomic DNA analyses. Soil samples for sequencing were frozen (-80 °C) to conserve them until ready for processing.

Chemical analyses were performed to determine soil pH using potentiometry method (1:2.5 soil water ratio); dry matter (%) using a 105 °C heater; total nitrogen (N, %) using a modified Kjeldahl methodology; phosphorus (P, mg kg<sup>-1</sup>) content using Olsen's method (Olsen, 1954).; potassium (K, mg kg<sup>-1</sup>) content using ICP-OES (inductively coupled plasma-optical emission spectrometry); and organic matter (%) using the modified Walkley-Black method.

Available phosphorus (P) was determined using Olsen's sodium bicarbonate extraction method (Olsen, 1954).

The internal transcribed spacer 2 (ITS2) region (ca. 250 bp) of the nuclear ribosomal DNA repeat was PCR amplified using the forward primer fITS7 (GTGARTCATCGAATCTTTG) (Ihrmark et al., 2012) and the reverse primer ITS4 (TCCTCCGCTTATTGATATGC) (White et al., 1990). Amplification was performed using the following amplification program: a first cycle of 95 °C for 5 min, followed by 37 cycles of 95 °C for 20 s, 56 °C for 30 s, and 72 °C for 1.5 min, and a final cycle of 72 °C for 7 min (Alem et al., 2022). Afterwards, a second PCR was performed to generate barcoded amplicons for sequencing using the Illumina MiSeq platform at BaseClear B.V. company (The Netherlands) BaseClear (Naturalis).

Table 1

Mean chemical properties of soil samples from mulched and non-mulched plots (mean  $\pm$  standard deviation).

|       |              | -               | -                  |                 |                                  |                                   |
|-------|--------------|-----------------|--------------------|-----------------|----------------------------------|-----------------------------------|
| Block | Treatment    | pH              | Organic matter (%) | Nitrogen (%)    | Potassium (mg kg <sup>-1</sup> ) | Phosphorus (mg kg <sup>-1</sup> ) |
| B1    | Mulching     | $4.74 \pm 0.06$ | $7.72 \pm 0.55$    | $0.35 \pm 0.03$ | $27.13 \pm 1.91$                 | 163.67 ± 26.31                    |
| B1    | Non-mulching | $5.04 \pm 0.17$ | $6.17 \pm 0.12$    | $0.30 \pm 0.03$ | $23.40 \pm 7.28$                 | $79.67 \pm 13.58$                 |
| B2    | Mulching     | $4.74 \pm 0.33$ | $11.78 \pm 1.91$   | $0.56 \pm 0.10$ | $33.63 \pm 12.71$                | 98.67 ± 30.89                     |
| B2    | Non-mulching | $4.64 \pm 0.30$ | $9.96 \pm 0.82$    | $0.49 \pm 0.09$ | $22.23 \pm 4.93$                 | $41.00 \pm 17.09$                 |
| B3    | Mulching     | $4.47 \pm 0.01$ | $10.26 \pm 0.94$   | $0.47 \pm 0.04$ | $23.23 \pm 7.22$                 | $110.67 \pm 46.48$                |
| B3    | Non-mulching | $4.86 \pm 0.32$ | $9.41 \pm 1.01$    | $0.46 \pm 0.06$ | $27.07 \pm 3.52$                 | $48.00 \pm 14.14$                 |
|       |              |                 |                    |                 |                                  |                                   |



Fig. 2. (a) Application of aerial mulching in the study plots during the last week of September 2021, one month after the Navalacruz fire. (b) Mulching applied in block B of the study area; (c) detail of the mulch applied in a study plot.

# 2.5. Bioinformatic analysis

Primers and poor-quality ends were removed using Cutadapt, which was set with a quality score of 5 and a minimum sequence length of 200 bp. Primer pairs were trimmed and sequences with an expected error of >1 were removed. The remaining sequences were merged into unique sequence types on a per-sample basis using USEARCH v.8.0 (Edgar, 2010) while preserving read counts. High-quality sequences were grouped with USEARCH at 97 % sequence similarity to generate operational taxonomic units (OTUs) while simultaneously excluding sequences representing OTUs with <70 % similarity or < 200 bp pairwise alignment to a fungal sequence. Sequences were assigned to taxonomic groups based on pairwise similarity searches against the curated UNITE + INSD fungal ITS sequence database (version v.8.0), which contains identified and unidentified sequences assigned to species hypothesis groups defined based on dynamic sequence similarity thresholds (Kõljalg et al., 2013). Functional groups were assigned to each OTU using Fungal Traits (Põlme et al., 2020).

# 2.6. Statistical analysis

All statistical analyses were carried out using the sequence count for each OTU as an abundance value (Danzeisen et al., 2011) of nonsingleton fungal communities. Data used for statistical analyses were not transformed because they achieved the parametric criteria of normality and homoscedasticity. Differences in fungal and soil variables across the treatments were assessed using linear mixed-effects (LME) models (Pinheiro et al., 2016), where the plot was defined as random and the mulching treatment was defined as a fixed factor. A Tukey test was subsequently performed to check significant differences ( $p \le 0.05$ ) between treatments. Data were analysed using R, version 2.13.2 (R Core Team, 2020). Krona charts were used to visualize the taxonomic distribution of all fungi and guilds based on OTU richness following Tedersoo et al. (2020).

The fungal community structures of mulched and non-mulched soils were compared similarities in the fungal community structure between the two treatments were analysed using a permutational multivariate ANOVA (PerMANOVA) based on 999 permutations and Bray–Curtis distance using the *adonis2* function in the vegan package.

Relationships between soil chemical variables and soil fungal community composition were determined based on the Bray–Curtis dissimilarity after excluding singleton OTUs and were visualized using Non-metric Multidimensional Scaling (NMDS) based on a Hellinger transformed OTU abundance data matrix and environmental scaled data. The correlation of NMDS axes scores with explanatory variables was assessed using the *envfit* function in R (R Core Team, 2020). NMDS analyses were performed for total fungi and trophic groups.





Fig. 3. Krona charts showing the relative abundance of: (a) the total fungal taxa in each division, class, order, family and genus; and (b) each fungal guild based on sequence abundance.

An analysis of similarity percentages (SIMPER) was also performed to identify fungal OTUs that were most responsible for the observed community patterns and to determine the percentage contributions of these OTUs to significant dissimilarities between treatments (Parravicini et al., 2010). The analysis was conducted using PAST software (Hammer et al., 2001).

# 3. Results

# 3.1. Taxonomic composition of fungal communities

Between 14,914 and 23,308 high-quality reads were obtained from each sample. In total, 19,520 high-quality sequences were grouped into 933 OTUs, which were assigned to 15 fungal phyla (Fig. 3). Taxonomic classification revealed that the majority of OTUs belonged to Ascomycota (46.6 %) or Basidiomycota (21.3 %). In total, 419 OTUs (44.9 %) were resolved to genus level and were assigned to 231 different genera. In addition, 418 OTUs were assigned to 21 trophic groups, of which 0.64 % were ECM fungi. Unidentified fungi were classified down to kingdom level and represented 12.6 % of the total OTUs. The relative abundance of fungal taxa in each division, class, order, family and genus and in each guild is shown in Fig. 3.

# 3.2. Impact of straw helimulching on fungal richness

**Total fungal OTU richness and abundance** values in mulched and non-mulched plots were not significantly different (F = 1.705; *p* = 0.210; F = 1.849; *p* = 0.193; Fig. 4), suggesting that fungal richness and abundance were not affected by the mulching treatment one-year after the treatment.



Fig. 4. Total richness (left) and abundance (right) of operational taxonomic units in soil collected in mulched and non-mulched plots. Means and the interval distribution of the data are shown.

At the **phylum level**, Ascomycota and Basidiomycota were considered the dominant phyla (Fig. 3). Only marginally significant differences (p < 0.1) were detected in the richness of basidiomycetes following the mulching treatment (p = 0.053; Table S1). No significant differences were found in the richness and abundance of the other phylum (Table S1).

Analysis of specific **guilds** revealed that the richness of <u>litter</u> saprotrophs, plant pathogens and wood saprotrophs were marginally affected by mulching (p < 0.1; Table 2), which was higher after mulching. No differences between treatments were observed for animal parasites, dung saprotrophs, mycoparasites, lichenized fungi or root endophytes.

## 3.3. Effect of straw helimulching treatment on fungal composition

The perMANOVA analyses indicated that the total fungal composition differed significantly between mulched and non-mulched plots (F = 1.859,  $R^2 = 0.104$ , p = 0.013). Chemical properties of soil such as pH, organic matter and N were significantly correlated with the composition of total fungal OTUs and P was marginally correlated as well (Fig. 5; Table 3).

The perMANOVA analysis also indicated that the fungal composition at the phylum level was significantly different between treatments (F = 4.300,  $R^2 = 0.211$ , p = 0.002). Furthermore, K and marginally pH and P (Fig. 6; Table 3) were significantly correlated with the composition of the fungal community at the phylum level.

The SIMPER analysis identified fungal OTUs that were responsible for differences in fungal composition under the different treatments. The cumulative contribution of the most influential OTUs for the dissimilarity between sampling treatments is shown in Table S2. Some fungi that form

#### Table 2

Influence of the mulching treatment on the richness of specific fungal guilds. Values in bold indicate marginally significant differences (p < 0.1). Coeff.: a positive coefficient indicates an increase in the richness associated with the application of mulch.

| Guilds                  | Richness |              |        |       |                 |  |  |
|-------------------------|----------|--------------|--------|-------|-----------------|--|--|
|                         | Mulching | Non-mulching | Coeff. | F     | <i>p</i> -value |  |  |
| Arbuscular mycorrhizae  | 0.0      | 0.1          | 0.111  | 1.000 | 0.332           |  |  |
| Animal parasites        | 3.4      | 3.7          | 0.222  | 0.059 | 0.811           |  |  |
| Dung saprotrophs        | 1.2      | 1.2          | 0.000  | 0.000 | 1.000           |  |  |
| Ectomycorrhizal fungi   | 1.3      | 1.4          | 0.111  | 0.087 | 0.772           |  |  |
| Mycoparasites           | 5.4      | 5.2          | -0.222 | 0.085 | 0.774           |  |  |
| Lichenized fungi        | 0.6      | 0.6          | 0.000  | 0.000 | 1.000           |  |  |
| Litter saprotrophs      | 8.0      | 12.6         | 4.555  | 4.366 | 0.053           |  |  |
| Plant pathogens         | 10.4     | 15.4         | 5.000  | 4.451 | 0.051           |  |  |
| Root endophytes         | 0.9      | 0.8          | -0.111 | 0.085 | 0.774           |  |  |
| Unspecified saprotrophs | 20.9     | 22.1         | 1.222  | 0.869 | 0.365           |  |  |
| Soil saprotrophs        | 38.8     | 46.7         | 7.888  | 2.026 | 0.174           |  |  |
| Wood saprotrophs        | 6.0      | 8.6          | 2.555  | 3.785 | 0.069           |  |  |

characteristic mycorrhizal associations with members of the Ericaceae family were identified: Helotiales sp. and *Oidiodendron griseum*. The saprotrophic fungi were mainly *Umbelopsis changbaiensis*, Pleosporaceae sp., *Mortierella humilis* or *Rhodotorula* sp. Some saprotrophs that may be associated with damp straw were identified as *Cladosporium* sp., as well as rare parasites, such as *Saitoella coloradoensis*, and tree pathogens, such as *Coniochaeta decumbens*. We also distinguished fungi associated with charcoal remnants (*Pyronema domesticum*) and some directly associated with grass (*Naganishia cerealis*).

# 4. Discussion

Straw mulch is an emergency treatment that has been recognized as an effective method of mitigating post-fire soil erosion (Robichaud et al., 2013; Fernández et al., 2016a; Fernández et al., 2020a). Mulching practices can alter microbial community composition and diversity by improving the soil chemical environment (Wang et al., 2020), favouring fungal growth (Rousk and Bååth, 2007). However, this is the first study to assess the impact of a straw mulch layer applied to burned soils on soil microbial community composition. However, under the environmental conditions experienced in the study plots, one year was not sufficient for the straw mulch to decompose completely and improve the soil conditions to enhance changes in the diversity of the fungal community. In this regard, the mulch depth was still >2 cm thick one year after application, as was also observed in NW Spain one year after helimulching at an application rate of 3.5-4.0 Mg ha-1 (Fernández et al., 2020b). Similarly, Liu et al. (2021) did not detect changes in the richness and abundance of the fungal community after applying straw mulch to a one-year abandoned pasture in a mid-temperate continental monsoon climate zone.

Post-fire mulching also did not significantly affect phylum diversity and only basidiomycete richness responded positively to the treatment. This indicates that straw mulch, which has a high cellulose, hemicellulose and lignin content (Rousk and Bååth, 2007; Niu et al., 2014), could enhance the growth of basidiomycetes, many of which are effective decomposers (Semenova-Nelsen et al., 2019). Saprotrophic fungi are sensitive to fire and may decline in richness and abundance after a fire (Semenova-Nelsen et al., 2019). However, as mentioned, mulch may enhance the growth conditions of this functional group. In this study, we observed a significant increase in litter saprotrophs and wood saprotrophs. This might temporarily increase fine fuel decomposition and reduce the amount of available fuel for future fires (Semenova-Nelsen et al., 2019). In addition, since the mulch cover is described to retain soil moisture (Fernández, 2021) and decrease soil temperature variations (Yin et al., 2023), this could improve soil properties for these functional groups at long-term. Another key guild responsible for the resilience of Mediterranean ecosystems is ECM fungi



Fig. 5. Non-metric multidimensional scaling (NMDS-stress 0.1522) ordination graph of the soil fungal community composition of the total operational taxonomic units (OTUs) in mulched (green polygon) and non-mulched (brown polygon) plots. Soil chemical properties that were significantly correlated with OTU composition are shown in blue. OM: organic matter.

(Izzo et al., 2006; Buscardo et al., 2012). Although we expected straw mulching to improve the ECM fungal richness of treated plots, this did not occur in this study. This could be partly because the fire completely destroyed host plant biomass and the existing functional roots in the study area. In addition, the dominance of non-ECM hosts, Cytisus and Juniperus, and alpine pastures in the study area could also explain this result. A longer-term study could help to establish the time needed for ECM fungi from nearby plantations to invade an area treated with mulch following a vegetation-replacing fire. Conversely, a significant increase in plant pathogens was detected in plots where straw mulch was added. Therefore, straw mulch could increase plant pathogens in soils that have been completely devastated by wildfire and then treated immediately with straw mulch. This increase in plant pathogens could also be due to changes in the functional characteristics of the guild, which can respond to changes in the environment (Albornoz et al., 2022). In this sense, many plant pathogens possess facultative saprotrophic traits (Zanne et al., 2020) which would be enhanced by the availability of straw and lack of host vegetation to parasitize after a high severity fire.

## Table 3

Significance of soil chemical properties on total operational taxonomic unit (OTU) and guild community composition using *envfit* function in R. Values in bold indicate significant differences (p < 0.05). Italicized values showed marginal differences.

| Chemical properties      | Total OTUs |       | Guilds |       |
|--------------------------|------------|-------|--------|-------|
|                          | $R^2$      | р     | $R^2$  | р     |
| pH                       | 0.533      | 0.003 | 0.298  | 0.064 |
| Organic matter           | 0.497      | 0.006 | 0.002  | 0.991 |
| Nitrogen                 | 0.434      | 0.017 | 0.024  | 0.843 |
| Phosphorus               | 0.281      | 0.084 | 0.330  | 0.055 |
| Potassium                | 0.061      | 0.622 | 0.581  | 0.003 |
| Carbon-to-nitrogen ratio | 0.156      | 0.266 | 0.115  | 0.403 |

The addition of mulch did not significantly change the pH, organic matter, carbon (C), macronutrients, or C:N ratio of the soil. Mulching only significantly affected the soil K levels, which is likely to be because it is rapidly liberated during the decomposition process (Aponte et al., 2012). The absence of short-term effects on soil chemical and biochemical properties after using straw as a stabilization treatment on burned soil has already been noted by Díaz-Raviña et al. (2012) and by Liu et al. (2021) after the application of straw to pasture that had been abandoned for a year. Neither Lucas-Borja et al. (2021) found long-term significant differences in the pH between plots treated with straw mulch and non-treated plots. Although the use of mulch is effective for reducing soil loss in severely burned areas, it did not seem to have any effects on the soil physicochemical properties (Norland, 2000). However, other authors describe changes in soil chemical after mulching (Prats et al., 2022).

In this study, we found that the soil properties had a significant effect on the overall composition of fungal OTUs. The analysis showed that soil pH, organic matter, C and N were correlated with the overall composition of fungal OTUs. Among these, pH is known to be the most important soil characteristic affecting fungal community composition and structure (Zhang et al., 2016), as also observed in this study. This may be due to the soil pH directly affects fungal community composition by providing a physiological constraint on fungal survival and growth as some fungal taxa cannot grow or survive when the soil pH is outside a certain range. Although fungi generally grow well under acidic conditions, some fungi also grow well under neutral to slightly alkaline conditions (Yamanaka, 2003). Our analysis also showed that the soil organic matter correlated with the overall fungal composition in the study area. This might be explained by the mulching increases the amount of decomposable material (Marinari et al., 2015), as the application of mulch increases the soil organic C content (Saroa and Lal, 2003) and improves soil moisture retention (Ji and Unger, 2001), although this was not measured in this study. Thus, mulching could affect



Fig. 6. Non-metric multidimensional scaling (NMDS-stress 0.1530) ordination graph of the soil fungal community composition of guilds in mulched (green polygon) and nonmulched (brown polygon) plots. Soil chemical properties that were significantly correlated with guilds are shown in blue.

mycelial growth, especially of saprophytic fungal species. The soil N content was also correlated with the total fungal OTU composition. This finding is consistent with the findings of Reverchon et al. (2010), who reported that fungal composition may increase along soil N gradients because N can affect mycelial growth in soil (Trudell, 2004). In addition, many fungal species can adapt to more N-rich sites (Toljander et al., 2006).

The SIMPER analysis revealed that the first eleven species listed in Table S2, including Helotiales sp., Calyptrozyma sp., Oidiodendron griseum, Umbelopsis changbaiensis, Naganishia cerealis, Saitoella coloradoensis, Coniochaeta decumbens, Solicoccozyma terrea, and Holtermanniella wattica, contributed to >50 % of the dissimilarity between the two treatments. Genera of these species are known to be saprotrophic and include ecologically diverse species specialized in using carbon from cellulose in organic matter (Boekhout et al., 1995; Meyer and Walter, 2003; Andrew et al., 2016; Rice and Currah, 2005; Gladieux et al., 2011; Wuczkowski et al., 2011; Harrington et al., 2019; Müller et al., 2020; Čadež et al., 2021). Thus, they are heavily involved in the decomposition of dead plant materials, which could explain their contribution to the dissimilarity between the two treatments (Štursová et al., 2012). Furthermore, the dead organic material in the form of straw in the mulching treatment, in addition to the available materials left after the fire or dead woody materials could serve as a carbon source (Barnhill et al., 2023), which may have attracted these saprophytic species and could explain the observed dissimilarity in terms of species abundance between the two treatments in the study area.

#### 5. Conclusions

One year after helimulching was applied on three hillside zones affected by a severe wildfire, we did not observe changes in fungal diversity (richness and abundance) between treated and non-treated plots, which does not confirm our initial hypothesis. Under this type of montane Mediterranean climate, one year is unlikely to be sufficient for the straw to decompose. Thus, a longer-term study should be contemplated. The application of mulch could mean a faster recovery of saprotrophic functional groups that will be responsible for decomposing the available dead fine fuel. The straw mulching was not improving the ECM fungal community of treated plots. Partly because the fire completely destroyed the host plant biomass and also by the dominance of non-ECM host in the study area. Conversely, an increase in the number of plant pathogens in soils that have been severely burned was expected. Although the use of a mulch is prescribed in severely burned areas to reduce soil erosion after fire, it did not seem to have a positive impact on soil chemical properties in the short-term; thus, a longer-term study could help to better assess the effects on the soil chemical properties. However, the total OTU and guild composition of mulched and non-mulching plots differed significantly.

#### CRediT authorship contribution statement

J.E.: conceptualization, methodology, investigation, fieldwork, data curation, and writing the original draft. T.D.: fieldwork, statistical analysis, and reviewing and editing the manuscript. C.F.: supervision, reviewing and editing the manuscript. C.A.: supervision, reviewing and editing the manuscript. C.A.: supervision, reviewing and editing the manuscript. C.A.: supervision, reviewing and editing the manuscript P.M-P.: conceptualization, methodology, fieldwork, statistical analysis, and writing, reviewing and editing the manuscript. All authors have read the manuscript and agree with the published version of the manuscript.

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#### Data availability

The data are available from the corresponding author upon request.

# Declaration of competing interest

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

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# Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi. org/10.1016/j.scitotenv.2023.164752.

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