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Preliminary insights into the potential of fire-prevention treatments to shape fire-resilient soil fungal communities in Mediterranean high-fire-risk shrublands

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ABSTRACT

Mediterranean ecosystems are frequently affected by wildfires; however, the increasing occurrence of megafires represents a concerning shift in the region's fire regime. Soil fungal communities are among the ecosystem components most affected by fire, with potentially severe consequences for ecosystem functioning and for the local mushroom-based economy. This study evaluates the impact of wildfire on soil fungi and assesses the effectiveness of prescribed burning and total mechanical clearing as fire-prevention strategies in areas at high risk of megafires, with a particular focus on their effects on soil fungal communities. We studied plots that had undergone prescribed burning or total mechanical clearing in 2020, some of which were later affected by the 2022 Sierra de la Culebra megafire. Fungal diversity and community composition were assessed using a metabarcoding approach by amplifying the ITS1 region and identifying operational taxonomic units (OTUs) in soil samples. Soil physicochemical properties, vegetation and substrate surface cover data were also collected. Although no significant differences in species richness were observed between burned and unburned plots, wildfire-affected communities showed greater dominance imbalance. Changes in community composition, significantly correlated with fire occurrence, suggest the emergence of new ecological niches occupied by pyrophilous taxa after the megafire. Several pyrophilous indicator species were identified in wildfire-affected plots; however, some edible taxa had declined in abundance. Although the effects of fire-prevention management in the wildfire-affected area were not statistically significant, prescribed burning appeared to buffer the post-fire loss of fungal diversity more effectively than total mechanical clearing. We conclude that prescribed burning may foster the development of more fire-resilient fungal communities. Furthermore, we suggest that fire-prevention treatments not only help to reduce fuel loads in fire-prone areas but also do not appear to be detrimental to certain valuable edible fungal species that support the mushroom-harvesting economy in these rural landscapes.

1. Introduction

The intensity of wildfires has been increasing in recent years due to climate change, generating megafires (Linley et al., 2022). The Mediterranean region, which is characterized by severe summer droughts and frequent fire events, is adapted to the wildfires that shape these ecosystems (Pausas and Paula, 2012; Trabaud, 1994). However, these wildfire events are becoming much more severe (Ruffault et al., 2020), posing a challenge for fire prevention and forest conservation plans. In particular, areas such as Castilla y León, in northwest Spain, where this study was performed, are characterized by a supra-Mediterranean climate, largescale depopulation and are highly susceptible to wildfires. The lack of people living in rural areas and maintaining traditional land uses has led to an accumulation of forest fuel (Perpiña Castillo et al., 2020; Tárrega et al., 2009), increasing the occurrence of wildfire.

Although the effect of fire on fungal communities is frequently

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neglected, wildfire events can destroy fungal communities (Day et al., 2019), particularly organisms present in the upper layers of the soil. Fungi are an indispensable part of the ecosystem given that they play a key role in nutrient cycling and enhance plant protection and production (Branco et al., 2022; Sun et al., 2015; Tedersoo et al., 2014). In addition, edible mushroom harvesting is a significant economic activity in the Castilla y León region that has boosted the rural economy for a long time (Oria-de-Rueda et al., 2008). Forest management practices therefore need to limit the risk of severe wildfires as much as possible to protect both the fungal community and the ecosystem services it provides and a valuable economic resource for the rural population living in the wildfire-affected areas.

Forest management practices to reduce the spread of wildfire basically consist of reducing the amount of fuel available by undertaking activities such as thinning or clearing to remove most or a large part of the already existing vegetation using mechanical tools (Cañellas et al., 2004; Rodríguez-Calcerrada et al., 2011). However, another commonly used method to reduce the amount of fuel is prescribed burning, which involves the use of low-intensity controlled fires (Plaza-Álvarez et al., 2019; Vázquez-Veloso et al., 2022; Zachmann et al., 2018). The use of prescribed fire is a cost-effective way of managing large areas of fire-prone landscapes (Espinosa et al., 2019). However, in addition to reducing the amount of fuel, the recurrent use of prescribed burning has also been reported to lead to a more fire-adapted fungal community (Oliver et al., 2015). Nevertheless, high frequencies of prescribed burning can drastically alter the microbial community and soil properties (Williams et al., 2012).

As part of a previous study to examine the consequences of implementing prescribed burning or total mechanical clearing as a way of rejuvenating scrublands and reducing the negative impact of any potential wildfires, a set of permanent plots was established in Sierra de la Culebra in northwest Spain in 2020 to gain insight into the impacts of these fire-prevention practices on the fungal community and soil conditions (Martín-Pinto et al., 2023). On the 17th of July 2022, a lightning strike following a dry thunderstorm ignited the largest wildfire ever recorded in Sierra de la Culebra. In total, 31,473.12 ha were burned, of which 11,719.60 ha (37 %) were wooded forest areas, which were dominated by masses of holm oak (*Quercus ilex*), black pine (*Pinus pinaster*) and Scots pine (*Pinus sylvestris*). This wildfire affected some of the experimental fire-prevention treatment sites, resulting in the complete combustion of vegetation; however, some sites remained unaffected. This scenario poses the challenge of potentially encountering spatial autocorrelation at the study sites because they were originally designed to assess the effect of fire-prevention management and the occurrence of a megafire could not be anticipated. However, these series of events also provided an excellent opportunity to compare the different impacts of prescribed burning and total mechanical clearing on soil properties and fungal communities in plots that were either affected or unaffected by a real wildfire.

The main objective of this study was to identify which type of fire-prevention management practice would minimize the impact that wildfires have on the soil fungal community. Given that intense wildfires are expected to become common events in coming years, fire-prevention management will not only become mandatory but also decisive for shaping the future landscape of the territory. Besides the many effects that wildfires have on ecosystems, fire-prevention management practices that take into consideration the protection of fungal communities could serve as a way of protecting both ecosystem functionality and a valuable economic resource for the local population.

Our specific objectives were: (1) to assess whether biodiversity indices differ in wildfire-affected and wildfire-unaffected areas; (2) to assess whether biodiversity indices differ in wildfire-affected areas depending on the type of fire-prevention management that plots had received prior to the wildfire event; and (3) to assess how the community composition varies (if it does) when comparing wildfire-affected and wildfire-unaffected plots, paying special interest to the possible loss of species of culinary interest in wildfire-affected areas.

We hypothesized that: (1) wildfire-unaffected areas would exhibit higher fungal diversity and more balanced dominance values compared with affected areas; (2) plots that received fire-prevention management prior to the occurrence of wildfire would be more diverse and even after the wildfire compared with plots where no management had been carried out, that the intensity of the fire in plots that had received fire-prevention management would be lower, and that low-intensity prescribed burns would have pre-selected some fire-adapted taxa and, hence, that the wildfire would have less impact on the fungal community in these plots; and (3) community composition of wildfire-affected and wildfire-unaffected plots would be different. We expected that fungal species would be differently impacted by wildfire and, hence, that the community assembly would change.

2. Materials and methods

2.1. Study site and experimental design

The sampling sites were located in Sierra de la Culebra, a small mountain range in the northern part of Zamora province, northwest Spain. This region is characterized by a continental Mediterranean climate, with long, cold winters with frequent frost, and short, warm, dry summers.

A set of permanent plots was established in 2020 as part of a previous study of the impact of fire-prevention practices on the fungal community and soil conditions: see Martín-Pinto et al. (2023) for further details about the study site. From the original study area, only two subareas were suitable for use in the present research study because the other areas were irreversibly damaged by heavy machinery during post-fire management operations.

The two studied areas were either affected (F) or not affected (NF) by the historic megafire that occurred in Sierra de la Culebra in 2022. Each area included three control (C), three prescribed burning (PB) and three total mechanical clearing (TC) plots, making a total of 18 sampling plots. The vegetation in the sampling area is dominated by rockrose (*Cistus ladanifer*), a species that has been linked to the occurrence of wildfires (Hernández-Rodríguez et al., 2015). Old rockrose stands in undisturbed plots (NF-C) were approximately 2 m in height, which corresponds to fuel model type 4 (35–40 tn/ha) according to Rothermel's fuel model classification.

Within each plot, a linear transect was established for recording vegetation and substrate surface cover data (i.e., 18 sampling transects in total). Soil samples for determining edaphic variables and for ITS1 metabarcoding analyses were also collected along these linear transects. Sampling was carried out in autumn 2024. Transect lines were 8 m in length and at least 2 m from the edge of the treatment plot to avoid edge effects. Further details about each sampling and data collection method are described in subsections 2.1.1 and 2.1.2.

We acknowledge the limited replication of our experimental setup, which was constrained by our opportunistic use of the available plots. Although this limitation reduces the statistical power of our analyses, we considered this to be a valuable and rare opportunity to investigate the effects of prior fire-prevention management on soil fungal communities in the aftermath of a high-intensity wildfire.

2.1.1. Vegetation transects

All plants, litter, or bare soil in contact with the transect line were recorded and, in the case of plants, their height was also measured. Data obtained using this method were used for complementing the input of some of the analyses performed during our research, which are described in Section 2.3. In addition, ANOVA comparisons of vegetation data recorded in the different types of plots (by wildfire occurrence and by fire-prevention treatment) were performed.

2.1.2. Soil physicochemical analyses

Soil subsamples were collected at a depth of between 2 and 10 cm at five points along each transect line at intervals of 1.6 m. The five subsamples, each comprising approximately 125 mL of soil, were then pooled together to form a single composite sample. Composite samples were kept on ice following collection and stored in a freezer until subsequent physicochemical analysis. A small amount of soil (0.25 g) from each composite sample was used in the metabarcode analyses.

Soil samples were subjected to the following physicochemical analyses: the potentiometric method (1:2.5 soil water ratio) to determine soil pH; a modified Kjeldahl methodology (Bremner, 1960) to determine the total carbon (C, %) and total nitrogen (N, %) content; Olsen's method (Olsen and Khasawneh, 1980) to determine the phosphorus (P, mg kg^{-1}) content; inductively coupled plasma-optical emission spectrometry to determine the potassium (K, mg kg^{-1}) content; and oxidation with potassium dichromate at 105 °C to determine the dry organic matter (OM, %) content.

Data obtained from the physicochemical analyses were used for complementing the input of some of analyses performed in this study, which are described in Section 2.3. In addition, comparisons of the soil parameters of the different types of plots (by wildfire occurrence and by fire-prevention treatment) were performed.

2.2. Genomic DNA analysis and identification

The commercial DNeasy PowerSoil Kit from Qiagen was used to isolate DNA from 0.25 g of each of the composite soil samples following the manufacturer's instructions. Isolated DNA was quantified using Qubit 4 Fluorometer from ThermoFisher and diluted when necessary to adjust the initial DNA concentration to 5 ng μL^{-1}. The library was prepared following the Fungal Metagenomic Sequencing Demonstrated Protocol (Illumina., 2019) by amplifying the ITS1 region using a limited cycle PCR. A pool of the following primers was used to amplify the ITS1 fungal region in a first step known as Amplicon PCR. The forward primer set consisted of:

- ITS_fwd_1 with the sequence CTTGGTCATTTAGAGGAAGTAA;
- ITS_fwd_2 with the sequence CTCGGTCATTTAGAGGAAGTAA;
- ITS_fwd_3 with the sequence CTTGGTCATTTAGAGGAACTAA;
- ITS_fwd_4 with the sequence CCCGGTCATTTAGAGGAAGTAA;
- ITS_fwd_5 with the sequence CTAGGCTATTTAGAGGAAGTAA;
- ITS_fwd_6 with the sequence CTTAGTTATTTAGAGGAAGTAA:
- ITS_fwd_7 with the sequence CTACGTCATTTAGAGGAAGTAA;
- ITS_fwd_8 with the sequence CTTGGTATTTAGAGGTCGTAA.

The reverse primer set consisted of:

- ITS_rev_1 with the sequence GCTGCGTTCTTCATCGATGC;
- ITS_rev_2 with the sequence GCTGCGTTCATCGATGG;
- ITS_rev_3 with the sequence GCTACGTTCTTCATCGATGC;
- ITS_rev_4 with the sequence GCTGCGTTCTTCATCGATGT;
- ITS_rev_5 with the sequence ACTGTGTTCTTCATCGATGC;
- ITS_rev_6 with the sequence GCTGCGTTCTTCATCGTTGC;
- ITS_rev_7 with the sequence GCGTTCTTCATCGATGC.

Amplicon PCR products were purified using AMPure XP beads before performing the second PCR or Index PCR. This step involved adding Illumina sequencing adapters and dual-index barcodes to the amplicon target using a Nextera XT Index Kit v2. Index PCR products were purified as described for the previous step and the fragment library was then quantified, normalized and pooled. Lastly, sequencing was performed following the manufacturer's instructions using the Illumina iSeq100 System using a 2 × 150 bp run.

Raw reads data were processed using the Illumina BaseSpace 16S Metagenomics App. A preliminary taxonomic classification of the amplicon sequencing reads was performed in this app using the UNITE Fungal ITS Database version 7.2. (Abarenkov et al., 2024), displaying classifications at all taxonomic levels. This database encompasses identified fungal sequences with assignments to Species Hypothesis (SH) groups, which are demarcated based on fluctuating sequence similarity thresholds (Kõljalg et al., 2020). Taxonomic assignments were subsequently verified and refined using the PlutoF web workbench (Abarenkov et al., 2010). Operational taxonomic units (OTUs) exhibiting more than 90 % similarity to a fungal SH group with a recognized ecological function were allocated to functional groups in accordance with FungalTraits (Põlme et al., 2020).

2.3. Statistical analysis

We performed all statistical analyses using the sequence count for each OTU as an abundance value of nonsingleton fungal communities. OTUs with fewer than three sequences in the sample in which they were most abundant were removed from the dataset. Subsequent data used for statistical analyses achieved the parametric criteria of normality and homoscedasticity and, therefore, did not need to be transformed.

We assessed differences in fungal and soil physicochemical and surface variables by comparing wildfire affected (F) and unaffected (NF) plots together and also the combined effect of wildfire occurrence with fire-prevention treatments using linear mixed-effects (LME) models, where the plot was defined as random and the occurrence of wildfire or fire-prevention treatments were defined as fixed factors. The adequacy of the mixed models was assessed by verifying normality and homoscedasticity of residuals through graphical inspections and by performing the Shapiro–Wilk test. OTU richness, Shannon diversity index and Pielou evenness values were obtained using the *diversity* function of the vegan package in R. We performed multiple comparisons among groups using the function *emmeans*. This allowed us to obtain pairwise contrasts adjusted for multiple testing and to identify significant differences between factor levels. Data were analysed using R, version 4.4.3 (R Core Team., 2025).

We performed a permutational multivariate analysis of variance (PerMANOVA) using the *adonis2* function to determine both the effect of wildfire alone and the combination of wildfire and fire-prevention treatments on the distribution of soil fungal community composition, which was determined based on the Bray–Curtis dissimilarity after excluding singleton OTUs. We used a Hellinger transformed community matrix and environmental scaled data for the analysis. To assess the variability of community composition within groups, we calculated beta dispersion using the function *betadisper* (vegan package in R). Subsequently, we performed an ANOVA on the distances to centroids to test whether beta dispersions differed significantly among groups. The distribution was visualized using non-metric multidimensional scaling (NMDS) and the analysis of correlation with environmental data was performed using the *envfit* function in R. We performed NMDS analyses for total fungi and for trophic groups. Finally, we used multilevel pattern analysis using the *multipatt* function in R to assign taxa and guilds that were significantly associated with each experimental grouping.

3. Results

3.1. Vegetation and soil physicochemical parameters

Only subsets of the vegetation data and soil variable data were selected for presentation in this results section based on their statistical significance in subsequent analyses and their importance regarding the discussion of this study. Descriptive statistics and statistical differences between these selected variables are shown in Tables 1 and 2. All descriptive statistics and comparisons of vegetation and soil data can be found in Supplementary Table 1 and Supplementary Table 2.

The proportion of litter cover in F and NF areas differed significantly ($p = 0.032$), with a higher proportion of litter cover recorded in F areas. However, the proportion of litter cover in the six plot types did not differ significantly. The proportion of total vegetation cover also differed significantly between F and NF areas ($p < 0.001$), with higher

Table 1
Mean value and standard deviation of vegetation and substrate surface cover in different plots. The complete set of variables and comparisons performed in this study can be found in Supplementary Table 1. Different letters indicate significant differences ($p < 0.05$) between burned and unburned plots. The absence of letters indicates that no statistically significant differences were detected. (NF, wildfire-unaffected plots; F, wildfire-affected plots).

	Cistus height (m)	Surface cover (%)		
		Cistus ladanifer	Litter	Total vegetation
NF	1.08 ± 0.95 (A)	65.82 ± 31.94 (A)	3.03 ± 3.24 (B)	95.56 ± 3.27 (A)
F	0.34 ± 0.09 (B)	60.49 ± 16.33 (B)	9.49 ± 8.00 (A)	79.04 ± 10.59 (B)

Table 2
Mean value and standard deviation of physicochemical soil parameters in different plots. The complete set of variables and comparisons performed in this study can be found in Supplementary Table 2. Different letters indicate significant differences ($p < 0.05$) between burned and unburned plots and between fire-prevention treatments in the wildfire-affected area. The absence of letters indicates that no statistically significant differences were detected. (NF, wildfire-unaffected plots; F, wildfire-affected plots; C, control; PB, prescribed burning; TC, total mechanical clearing; P, phosphorus; OM, dry organic matter).

	P (mg kg^{-1})	OM (%)
NF	6.18 ± 1.81 (B)	2.79 ± 0.61 (B)
F	7.48 ± 1.78 (A)	2.98 ± 0.45 (A)
F-C	6.90 ± 1.71	3.35 ± 0.59 (a)
F-PB	8.90 ± 0.17	2.92 ± 0.15 (ab)
F-TC	6.63 ± 2.26	2.68 ± 0.35 (b)

proportions of vegetation cover in NF areas. Some differences in total vegetation cover were detected between the six types of plot, but none between different treatments in the F area. Lastly, significant differences in *Cistus* height were found between wildfire F and NF areas ($p < 0.001$), with taller *Cistus* plants recorded in NF areas. Some differences in *Cistus* height were detected between the six types of plot, but none between different treatments in the F area (Table 1).

The P content of F plots was significantly higher than that of NF plots ($p = 0.027$). However, comparisons of the six different plot types revealed no significant differences. The organic matter (OM) content of F and NF areas differed significantly ($p = 0.044$), with higher OM content levels in F areas. When comparing the six different plot types, the only difference detected between plots in the F area was that the OM content of F-C plots was significantly higher than that of F-TC ($p < 0.001$) plots (Table 2).

3.2. Effects of fire-prevention treatments and wildfire on fungal diversity

The richness of F and NF plots did not differ significantly ($p = 0.746$) (Fig. 1A). Likewise, the six different treatment–wildfire combinations did not differ in richness (Fig. 1D). A comparison of Shannon diversity indices revealed that diversity was lower in F areas than in NF areas ($p < 0.001$; Fig. 1B). Comparisons of the six different plot types revealed that the lowest Shannon diversity value, which was found in F-TC plots, significantly differed from that of NF-C ($p = 0.026$), NF-PB ($p < 0.001$) and NF-TC ($p < 0.001$) plots (Fig. 1E).

In terms of community evenness, which was analysed using the Pielou evenness index, there were significant differences between F and NF areas ($p < 0.001$), with higher levels of evenness in NF areas (Fig. 1C). Comparisons of the six different plot types revealed that the evenness of NF-PB was significantly higher than that of F-C ($p = 0.046$), and that the evenness of F-TC was significantly lower than that of NF-C ($p = 0.032$), NF-TC ($p = 0.002$) and NF-PB ($p < 0.001$) (Fig. 1F).

3.3. Effects of fire-prevention treatments and wildfire on community composition

NMDS of OTUs produced a good representation of the structure of the fungal community (stress = 0.05). PerMANOVA indicates that the wildfire event significantly influenced the composition of communities ($F = 9.07$; $R^2 = 0.339$; $p = 0.001$) but not their dispersion (ANOVA for β dispersion $p = 0.167$) (Fig. 2A), whereas the combined effect of fire-prevention treatments and wildfire was not statistically significant ($F = 1.43$; $R^2 = 0.107$; $p = 0.133$; ANOVA for β dispersion $p = 0.120$). The *envfit* analysis showed that the proportion of bare soil surface cover ($p = 0.006$), total vegetation surface cover ($p = 0.004$) and *Cistus* height ($p = 0.003$) were significantly correlated with fungal community composition in the NMDS ordination. Furthermore, fungal communities in NF plots, particularly control plots, were more correlated with total vegetation and *Cistus* height, whereas fungal communities in F plots were more correlated with bare soil surface cover (Fig. 2A).

With regards to NMDS of the community structure of fungal guilds (stress = 0.09), PerMANOVA indicated that wildfire had a significant influence on guild composition ($F = 6.75$; $R^2 = 0.291$; $p = 0.001$). The test for beta-dispersion also revealed significant differences in dispersion (ANOVA for β dispersion $p = 0.017$), suggesting that fire affected both the guild composition and the variability among plots (Fig. 2B), whereas the combined effect of fire-prevention treatments and wildfire was not significant ($F = 1.26$; $R^2 = 0.109$; $p = 0.282$; ANOVA for β dispersion $p = 0.325$). The correlation analysis of environmental variables showed that litter surface cover ($p = 0.038$), bare soil surface cover ($p = 0.003$), total vegetation surface cover ($p = 0.001$) and *Cistus* height ($p = 0.010$) were correlated with the NMDS ordination. The soil pH was almost significantly correlated with the ordination ($p = 0.053$). Furthermore, fungal guilds in NF plots were more correlated with a higher proportion of total vegetation and *Cistus* height, whereas fungal guilds in F plots were more correlated with a higher proportion of bare soil cover, pH and litter surface cover (Fig. 2B).

3.4. Fungal indicators

In total, 344 OTUs were significantly associated with the fungal community of either F or NF areas (Supplementary Table 3). Of these, 128 OTUs were associated with F plots, of which 27 were strongly associated with F plots ($p = 0.001$), and 214 OTUs were associated with NF plots, of which 56 were strongly associated with NF plots ($p = 0.001$). Some of the taxa associated with F plots are considered to be pyrophilous, such as *Trichophaea* sp. and *Tephrocybe anthracophila*. Some valuable edible species, such as *Boletus edulis* and *Tricholoma portentosum*, were associated with NF plots, indicating their potential decline after a wildfire. However, several edible species of *Tuber* and *Terfezia* were associated with F plots, indicating that some edible fungi may even increase after the occurrence of fire.

In total, 110 indicator species were associated with the six different types of plot (Supplementary Table S4). Of these, 55 species were associated with NF-C plots, including the edible *T. portentosum*. Only two species were associated with NF-PB plots, *Conioscypha* sp. and *Penicillium cinerascens*, and 11 species were associated with NF-TC plots. In the case of burned plots, 21 species were associated with F-C plots, including the pyrophilous species *Neurospora terricola*; five species were associated with F-PB plots; and 15 species were associated with F-TC plots, including *Terfezia cistophila*, which is associated with *Cistus* plants and has been reported as edible, and *Aspergillus thermomutatus*, which is considered pyrophilous.

Indicator fungal guilds were also analysed. Moss symbionts ($p = 0.001$), animal endosymbionts ($p = 0.005$) and foliar endophytes were associated with F plots, whereas animal parasites ($p = 0.001$), root endophytes ($p = 0.001$), lichenized fungi ($p = 0.001$), mycoparasites ($p = 0.015$), litter saprotrophs ($p = 0.018$), epiphytes ($p = 0.030$) and protistan parasites ($p = 0.037$) were associated with NF plots.

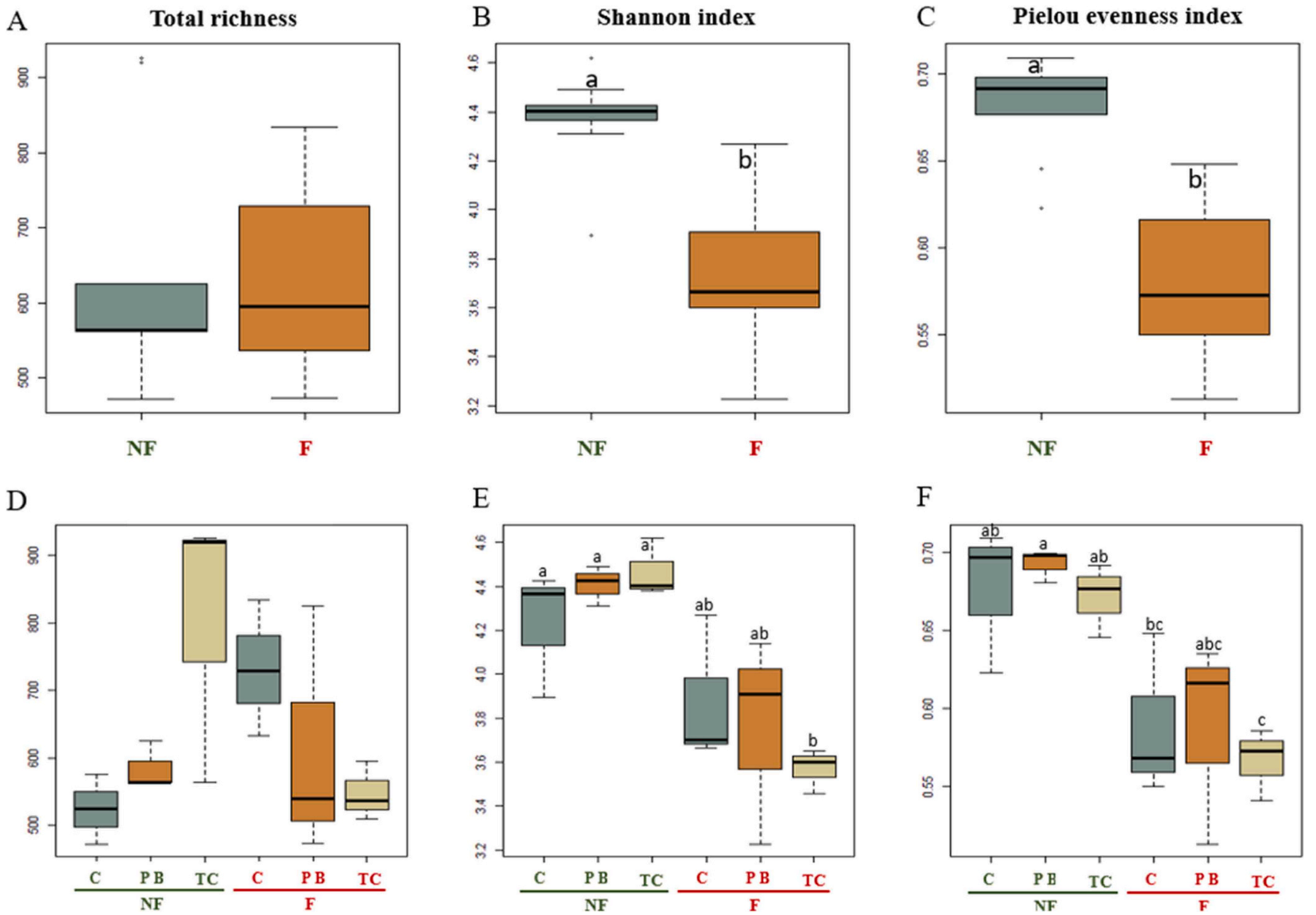

Fig. 1. Effect of wildfire (NF, wildfire-unaffected plots; F, wildfire-affected plots) and fire-prevention treatments (C, control; PB, prescribed burning; TC, total mechanical clearing) on fungal diversity indices. A and D, total richness; B and E, Shannon diversity index; C and F, Pielou evenness index. Different letters indicate a significant difference between burned and unburned plots and/or fire-prevention treatments ($p < 0.05$). The absence of letters indicates no significant differences between comparisons. Note: the Y-axis does not start at zero to improve the visualization of data.

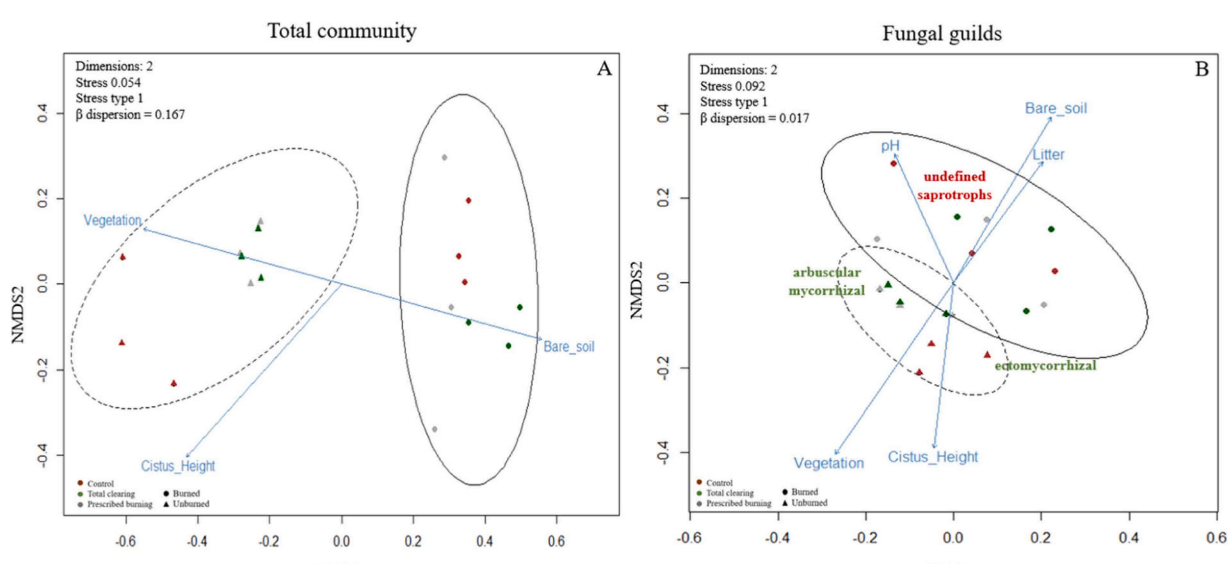

Fig. 2. Non-metric multidimensional scaling (NMDS) of fungal community composition showing the influence of wildfire, fire-prevention treatments and correlations with environmental parameters. A: Total operational taxonomic units; B: Fungal guilds.

4. Discussion

4.1. Effects of fire-prevention treatments and wildfire on fungal diversity

One of the main objectives of this study was to assess changes in soil fungal diversity that may happen after a wildfire event takes place. Our first working hypothesis was that F plots would be less diverse than NF plots. Our second hypothesis was that the control plots in the F area would also be less diverse than managed plots in the same fire-affected area. With regards to OTU richness, our first hypothesis was not supported given that the fungal richness of NF and F plots did not differ significantly. A compilation of the findings of previous research studies showed that fungal richness consistently declined in response to fire, although individual studies involving molecular analysis also showed that species richness does not always differ significantly between burned and unburned areas (Dove and Hart, 2017). This could be due to many context dependencies, such as sampling depth, sampling intensity or analysis method. Furthermore, the use of a purely molecular method may itself pose a limitation because this type of analysis cannot determine whether the organism of origin is alive or dead and because the complete eradication of genetic material from soil is difficult (Bridge and Spooner, 2001). Our findings, in accordance with other studies, suggest that ecosystems do not necessarily shift to an impoverished community following a fire event, at least in terms of species number (Smith et al., 2021). In contrast to our expectations regarding our second working hypothesis, in F plots, fire-prevention treatments did not have a statistically significant effect in terms of preserving richness when compared to control plots. The effects of prescribed burns usually do not imply shifts in the environment as substantial and lasting as those caused by extreme and vast wildfires (Certini et al., 2021), such as the wildfires that affected the study area in 2022. We suspect that the wildfire was so severe in F plots that it made differences between fire-prevention treatments imperceptible.

Shannon diversity and Pielou evenness showed parallel results regarding the expectations we had for our working hypotheses: our first hypothesis was supported by both diversity indices, while our expectations regarding our second hypothesis were not clearly met in either case. For both Shannon and Pielou evenness, significantly higher diversity values were obtained for fungal communities in NF plots than for those in F plots (Day et al., 2019). These results suggest that OTU representation was more balanced in NF plots than in F plots, portraying the existence of a more homogeneous community in the former, as expected. A previous study of soil fungal diversity after fires of different intensity reported a sharp decrease in the Shannon index after a high-intensity fire (Reazin et al., 2016). Furthermore, in wildfire-affected areas, there may be a greater dominance of a particular part of the soil community, the so called pyrodiversity (Fox et al., 2022), comprising species that are more adapted to fire. Contrastingly, our expectations regarding our second hypothesis were not completely met because differences in Shannon index and Pielou evenness values between the control and the fire-prevention treatment plots of the F area were not significant. However, in terms of observed tendencies, mean Shannon index values suggest that F-PB plots host a more balanced community than F-C plots, and that F-C plots, in turn, host a more balanced community than F-TC plots. With regards to Pielou evenness, F-PB plots also exhibited marginally higher values, reflecting a more balanced community compared with that of F-C plots, but this tendency was not observable for F-TC plots compared with F-C plots. Given that fungal communities in F-PB plots had been previously subjected to prescribed burning, they may have been somehow pre-adapted to fire (Oliver et al., 2015). As a consequence of prescribed burning, some fire-adapted species may have been competitively selected, creating a community that was more resilient to subsequent wildfire events (Johnston et al., 2024).

Diversity was more balanced in NF plots, as we anticipated. When considering the fire-prevention treatments applied to the F plots, we did not find robust differences in diversity between treatments, although there was a trend in the medians that suggests that prescribed burning could be the fire-prevention treatment that maintains a higher diversity balance after the occurrence of a wildfire.

4.2. Effects of wildfire on fungal community composition

To assess the impact of wildfire and fire-prevention treatments, besides considering whether the diversity of the soil fungal community changes, we also need to determine if the composition of the communities changes.

The main influence determining the OTU composition of fungal communities was wildfire, which was to be expected. The high temperatures that can be generated during this kind of event can be highly destructive for fungi. Besides this direct impact of fire on fungi, the changes that fire can cause to soil and environmental properties can also subsequently shape the soil fungal community composition (Certini, 2005; Massman et al., 2010). The NMDS analysis of OTUs in F and NF areas showed two distinct communities, which has been previously observed in similar contexts (Hernández-Rodríguez et al., 2013). Fire may have had a strong direct impact on soil fungi survival; however, the community composition of NF and F plots also correlated with some of the environmental variables considered. The environmental correlation analysis showed that total vegetation cover, *Cistus* height and bare soil surface cover significantly correlated with the OTU composition of communities. Communities in F plots correlated with higher values of bare soil cover. This comes as no surprise because we assume that plots that were harshly affected by the wildfire would show a greater proportion of bare soil (Jain et al., 2012). Communities in NF plots showed more correlation with higher levels of vegetation surface cover and rockrose height, as could be predicted. As NF plots did not suffer the effects of wildfire after the fire-prevention treatments, they experienced less plant mass loss and, hence, had greater vegetation surface cover. *Cistus* plants in NF-PB and NF-TC had been growing for a longer period than those in F plots and, hence, were taller. *Cistus* in NF-C plots were several years old and, hence, were much taller than the rest of the plants measured. Although vegetation and bare soil cover showed the direct impact of wildfire on the ecosystem, the lower presence of vegetation *per se* could also cause a change in community composition (Hart et al., 2005). Fungal OTUs that require an association with plants (e.g., endophytes, root symbionts, plant litter decomposers, and plant pathogens) will not thrive in an ecosystem with a depleted plant presence such as those in F plots.

Although they were not found to be statistically correlated with the NMDS ordination, some other environmental variables were also found to be significantly different in F and NF plots. The dispersion of that data was considerable in many cases, which may be why the NMDS environmental analysis could not statistically correlate other environmental variables aside from those already mentioned. Physicochemical analysis of soil revealed that OM and P content were higher in F plots than in NF plots. The higher OM content in F plots may be explained by vegetation remains being integrated into the soil after the fire (González-Pérez et al., 2004). A meta-analysis by Johnson and Curtis (2001) reported an increase in soil C in the A horizon within 0–10 years of a wildfire. Nevertheless, in contrast to our findings, most previous studies have reported that wildfires generally tend to reduce the organic content of the first horizon of the soil (Certini et al., 2011) and worsen soil quality by making it more recalcitrant (Rovira et al., 2012). In the case of P content, previous studies have reported that ash derived from burning can increase the P content (Caon et al., 2014), in accordance with our results.

4.3. Effects of wildfire on community trophic functionality

PerMANOVA analysis of the guild composition of communities revealed that wildfire was statistically determinant of community structure, but dispersions of the two groups (F and NF areas) were statistically different. This implies that although there was an observable difference between communities in both areas, it does not necessarily mean that wildfire occurrence implies a change in guild composition because differences could be due to differences in the dispersion of each group in the NMDS ordination. Comparison of the dispersion of both groups showed that F communities were more heterogeneous than NF communities, meaning that guild proportions were more similar among communities in the NF area.

The environmental correlation analysis showed that total vegetation, litter and bare soil surface cover, as well as *Cistus* height and soil pH significantly correlated with the guild composition of communities. F communities were associated with a greater proportion of litter and bare soil surface cover than communities in NF areas, as well as with higher pH values. The main source of litter in F plots is likely to be derived from the defoliation and deterioration of any vegetation that remained after the fire, as well as charred litter (Merino et al., 2015) and even litter from regrowing vegetation (Fox et al., 2022). Bare soil surface exposure (Jain et al., 2012) and alkalinization of soil pH are also common effects of wildfires (Alexakis et al., 2021; Caon et al., 2014; Fernández-García et al., 2019). NF communities were correlated with a greater proportion of vegetation surface cover as well as with higher *Cistus* height values, parallel to what was observed for the NMDS ordination of OTUs.

The results of the indicator guild analysis did not provide much clarity in terms of general community trophic ecology. Moss symbionts, animal endosymbionts and foliar endophytes were associated with F plots whereas animal parasites, root endophytes, lichenized fungi, mycoparasites, litter saprotrophs, epiphytes and protistan parasites were associated with NF plots. However, the relative abundance of sequence reads of several of these guilds was very low, so it is unlikely that these findings represent a major shift in the trophic ecology of the community. Only foliar endophytes in the case of burned plots, and animal parasites, root endophytes, lichenized fungi, mycoparasites and litter saprotrophs in the case of NF plots, had relative abundances that could potentially represent at least slight differences in the trophic ecology of communities.

One possible explanation for foliar endophytes being associated with F plots may be that there were more fallen leaves on the ground of these plots (Jia et al., 2020), which is supported by the higher proportion of litter found in these plots than in NF plots. With regards to guilds associated with NF plots, animal parasites may be more abundant in these plots because of the habits of their host animals. This makes sense in the case of animals that tend to avoid open habitats such as the one that was formed in F plots after the wildfire, and which was still open at the time of soil sampling. Our personal experience of working in *Cistus ladanifer* shrublands is that older plants are usually covered in lichens, which could explain the association of lichenized fungi with NF plots given that old *Cistus* plants were found exclusively in NF-C plots. We attribute the association of root endophytes with NF plots to the fact that the NF area has more vegetation than the F area, as has been discussed previously. Given that mycoparasites require the presence of their host fungal species and we have observed that community composition changed after the wildfire, we expect that mycoparasites are less likely to thrive in a community where there is a significant possibility that their host species has disappeared (Viterbo and Horwitz, 2010).

Unexpectedly, we did not observe significant statistical correlations between F plots and saprotrophic guilds, whose ecology is usually related to the presence of decomposable matter. Previous studies have shown that saprotrophic fungi tend to respond positively to fire because they can benefit from an increase in the amount of decomposable substrate available following a fire (Espinosa et al., 2023). However, the only correlation observed regarding saprotrophic guilds was between litter saprotrophs and NF plots, which is surprising given that F plots were associated with a greater litter proportion. One possible explanation for these results is that not only is the quantity of decomposable substrate (in this case litter) important but also its quality (Beidler et al., 2020; Joffre et al., 2001).

Furthermore, due to the fire-related mortality of host plants in F plots, we would have expected a greater representation of root symbionts (i.e., ectomycorrhizal and arbuscular mycorrhizal fungi) in NF plots than in F plots and, hence, that root symbionts would be statistically correlated with NF plots. However, in Mediterranean areas, the mycorrhizal community tends to develop a resistance to fire-related disturbance and, hence, requires only a short-term recovery phase to return to a state that does not differ significantly from that of unburned areas (Franco-Manchón et al., 2019).

Although our analysis of fungal communities by guild suggests that communities in F plots differed from those in NF plots, there was no clear involvement of functionally critical and relatively more abundant functional guilds such as saprotrophs, ectomycorrhizal fungi, arbuscular mycorrhizal fungi, or plant pathogens. For these guilds at least, it seems that wildfire did not dramatically change the trophic functional ecology of the whole community.

4.4. Fungal indicators and edible species

Fewer indicator taxa were detected in F plots than in NF plots, likely reflecting wildfire-induced mortality. A greater proportion of the indicator taxa in F plots than in NF plots were pyrophilous species, which is not surprising. The Basidiomycete *Tephrocybe anthracophila*, which has been associated with pyrogenic substrates after burning treatments (Sumorok, 2001), was an indicator of F plots. The Ascomycota genus *Trichophaea*, which is known to be associated with disturbed areas, was also an indicator taxon of F plots. Some species of this genus are considered to be thermotolerant or even heat-resistant (Šimonovičová et al., 2014). As reported in other studies, some gastronomically valuable genera that are associated with post-fire events were statistically associated with our F plots, such as the mycorrhizal desert truffle *Terfezia* (Bordallo et al., 2015; Pérez-Izquierdo et al., 2020). Therefore, at least some economically valuable mushrooms were present in F plots after the megafire event. Another desert truffle indicator species associated with F plots was *Tuber gennadii*, which has been associated with plants of the Cistaceous family (Bonito and Smith, 2016), likewise *Terfezia cistophila* (Bordallo et al., 2015). *Aspergillus thermomutatus*, which was identified as an indicator species in F-TC plots, has also been identified as a heat-resistant fungus (Dijksterhuis, 2019).

Some highly valuable edible species were exclusively associated with NF plots, such as *Boletus edulis* and *Tricholoma portentosum*, indicating that they likely decline after wildfire. Similar findings regarding the decline of edible fungi after wildfire in Mediterranean *Pinus* forests have been previously reported (Gassibe et al., 2014). This might serve as a warning sign that some valuable mycological resources seem to be highly threatened by the occurrence of wildfire given that these species were statistically correlated with unburned areas. However, it is encouraging that fire-prevention treatments alone do not seem to have a negative effect on these species given that they were found to correlate with the whole NF area and not just with NF-C plots. This suggests that fire-prevention treatments do not seem to have a harmful effect on some valuable edible species. Similar findings have been reported in other studies, such as the one by Durán-Manual et al. (2022).

5. Conclusions

As anticipated, areas unaffected by wildfire (NF) exhibited greater fungal diversity, particularly in terms of a more balanced dominance among fungal OTUs. When focusing exclusively on wildfire-affected (F) plots, the use of prescribed burning as a fire-prevention treatment appeared to pre-select fire-adapted OTUs, thereby mitigating post-fire dominance imbalances. This was reflected in higher mean values for both Shannon and Pielou's evenness diversity indices. OTU community composition differed significantly between F and NF plots, likely due to the combined effects of high-temperature impacts on fungi and environmental changes induced by wildfire – such as alterations in vegetation cover and soil characteristics.

The composition of functional guilds also showed statistically significant differences between F and NF areas. However, a drastic shift in the trophic ecology of the fungal community remains uncertain. This uncertainty arises because the guilds associated with either area were, in some cases, of very low abundance, or their presence could be explained by factors other than the direct impact of wildfire. As expected, several fire-adapted species were identified as indicator taxa of F plots. Conversely, some highly prized edible fungi emerged as indicators of NF areas, confirming their sensitivity to wildfire, while also suggesting that fire-prevention treatments alone do not negatively impact these species.

This study underscores the importance of implementing fire-prevention strategies, particularly in the current context of increasing megafire risk. Soil fungal diversity and community composition are once again shown to be highly sensitive to wildfire disturbance. Given that low-severity fire is a relatively common natural occurrence in the Mediterranean Basin, the presence of fire-adapted fungal species suggests that prescribed burning can be an effective management tool to buffer against diversity loss caused by wildfires. Beyond ecological considerations, the conservation of valuable resources such as edible mushrooms, which are also negatively affected by wildfires, further supports the use of fire-prevention management. Our results suggest that such management does not threaten these valuable species, positioning it as a beneficial strategy for both biodiversity conservation and resource protection.

CRediT authorship contribution statement

Claudia Prada-Polo: Writing – review & editing, Investigation, Formal analysis, Data curation. **Scheck Florian:** Writing – review & editing, Investigation. **Martin-Pinto Pablo:** Writing – review & editing, Supervision, Methodology, Investigation, Conceptualization. **Ignacio Sanz-Benito:** Writing – review & editing, Writing – original draft, Investigation, Data curation. **Juan Andrés Oria-de-Rueda:** Validation, Supervision, Conceptualization.

Declaration of Competing Interest

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

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.123363.

Data availability

Data will be made available on request.

References

Abarenkov, K., Tedersoo, L., Nilsson, R.H., Vellak, K., Saar, I., Veldre, V., Parmasto, E., Prous, M., Aan, A., Ots, M., Kurina, O., Ostonen, I., Jõgeva, J., Halapuu, S., Põldmaa, K., Toots, M., Truu, J., Larsson, K.H., Kõljalg, U., 2010. PlutoF-a web based workbench for ecological and taxonomic research, with an online implementation for fungal its sequences. Evolut. Bioinforma. 2010 (6), 189–196. https://doi.org/10.4137/EBO.S6271/ASSET/884BDAE8-5B33-483D-8630-988B2944CF2E/ASSETS/IMAGES/LARGE/10.4137_EBO.S6271-FIG1.JPG.

Abarenkov, K., Nilsson, R.H., Larsson, K.H., Taylor, A.F.S., May, T.W., Frøslev, T.G., Pawlowska, J., Lindahl, B., Põldmaa, K., Truong, C., Vu, D., Hosoya, T., Niskanen, T., Piirmann, T., Ivanov, F., Zirk, A., Peterson, M., Cheeke, T.E., Ishigami, Y., Kõljalg, U., 2024. The UNITE database for molecular identification and taxonomic communication of fungi and other eukaryotes: sequences, taxa and classifications reconsidered. Nucleic Acids Res. 52 (D1), D791–D797. https://doi.org/10.1093/NAR/GKAD1039.

Alexakis, D., Kokmotos, I., Gamvroula, D., Varelidis, G., 2021. Wildfire effects on soil quality: application on a suburban area of West Attica (Greece). Geosci. J. 25 (2), 243–253. https://doi.org/10.1007/s12303-020-0011-1.

Beidler, K.V., Phillips, R.P., Andrews, E., Maillard, F., Mushinski, R.M., Kennedy, P.G., 2020. Substrate quality drives fungal necromass decay and decomposer community structure under contrasting vegetation types. J. Ecol. 108 (5), 1845–1859. https://doi.org/10.1111/1365-2745.13385.

Bonito, G.M., Smith, M.E., 2016. General systematic position of the truffles: Evolutionary theories. In: Zambonelli, A., Iotti, M., Murat, C. (Eds.), True Truffle (Tuber spp.) in the World. Soil Biology series, first ed., 47. Springer International Publishing, pp. 3–18. https://doi.org/10.1007/978-3-319-31436-5-1.

Bordallo, J.J., Rodríguez, A., Kounas, V., Camello, F., Honrubia, M., Morte, A., 2015. Two new *Terfezia* species from Southern Europe. Phytotaxa 230 (3), 239–249. https://doi.org/10.11646/phytotaxa.230.3.2.

Branco, S., Schauster, A., Liao, H., Ruytinx, J., 2022. Mechanisms of stress tolerance and their effects on the ecology and evolution of mycorrhizal fungi. N. Phytol. 235 (6), 2158–2175. https://doi.org/10.1111/nph.18308.

Bremner, J.M., 1960. Determination of Nitrogen in soil by the Kjeldahl method. J. Agric. Sci. 55 (1), 11–33. https://doi.org/10.1017/S0021859600021572.

Bridge, P., Spooner, B., 2001. Soil fungi: diversity and detection. Plant Soil 232 (1–2), 147–154. https://doi.org/10.1023/A:1010346305799/METRICS.

Cañellas, I., Del Río, M., Roig, S., Montero, G., 2004. Growth response to thinning in *Quercus pyrenaica* Willd. coppice stands in Spanish central mountain. Ann. For. Sci. 61 (3), 243–250. https://doi.org/10.1051/forest:2004017.

Caon, L., Vallejo, V.R., Ritsema, C.J., Geissen, V., 2014. Effects of wildfire on soil nutrients in Mediterranean ecosystems. EarthSci. Rev. 139, 47–58. https://doi.org/10.1016/j.earscirev.2014.09.001.

Certini, G., 2005. Effects of fire on properties of forest soils: a review. Oecologia 143 (1), 1–10. https://doi.org/10.1007/S00442-004-1788-8/TABLES/2.

Certini, G., Nocentini, C., Knicker, H., Arfaioli, P., Rumpel, C., 2011. Wildfire effects on soil organic matter quantity and quality in two fire-prone Mediterranean pine forests. *168* Geoderma 167, 148–155. https://doi.org/10.1016/j.geoderma.2011.09.005.

Certini, G., Moya, D., Lucas-Borja, M.E., Mastrolonardo, G., 2021. The impact of fire on soil-dwelling biota: a review. For. Ecol. Manag. 488, 118989. https://doi.org/10.1016/J.FORECO.2021.118989.

Day, N.J., Dunfield, K.E., Johnstone, J.F., Mack, M.C., Turetsky, M.R., Walker, X.J., White, A.L., Baltzer, J.L., 2019. Wildfire severity reduces richness and alters composition of soil fungal communities in boreal forests of western Canada. Glob. Change Biol. 25 (7), 2310–2324. https://doi.org/10.1111/gcb.14641.

Dijksterhuis, J., 2019. Fungal spores: Highly variable and stress-resistant vehicles for distribution and spoilage. Food Microbiol. 81, 2–11. https://doi.org/10.1016/j.fm.2018.11.006.

Dove, N.C., Hart, S.C., 2017. Fire reduces fungal species richness and *in situ* mycorrhizal colonization: A meta-analysis. Fire Ecol. 13 (2), 37–65. https://doi.org/10.4996/FIREECOLOGY.130237746.

Durán-Manual, F., Espinosa, J., Pérez-Pereda, E., Mediavilla, O., Geada-López, G., Dejene, T., Sanz-Benito, I., Martín-Pinto, P., Martínez-Becerra, L.W., 2022. Prescribed burning in *Pinus cubensis*-dominated tropical natural forests: a myco-friendly fire-prevention tool. For. Syst. 31 (2). https://doi.org/10.5424/fs/2022312-19318.

Espinosa, J., Palheiro, P., Loureiro, C., Ascoli, D., Esposito, A., Fernandes, P.M., 2019. Fire-severity mitigation by prescribed burning assessed from fire-treatment encounters in maritime pine stands. Can. J. For. Res. 49 (2), 205–211. https://doi.org/10.1139/cjfr-2018-0263.

Espinosa, J., Dejene, T., Guijarro, M., Cerdá, X., Madrigal, J., Martín-Pinto, P., 2023. Fungal diversity and community composition responses to the reintroduction of fire in a non-managed Mediterranean shrubland ecosystem. For. Ecosyst. 10, 100110. https://doi.org/10.1016/j.fecs.2023.100110.

Fernández-García, V., Miesel, J., Baeza, M.J., Marcos, E., Calvo, L., 2019. Wildfire effects on soil properties in fire-prone pine ecosystems: Indicators of burn severity legacy over the medium term after fire. Appl. Soil Ecol. 135, 147–156. https://doi.org/10.1016/j.apsoil.2018.12.002.

Fox, S., Sikes, B.A., Brown, S.P., Cripps, C.L., Glassman, S.I., Hughes, K., Semenova-Nelsen, T., Jumpponen, A., 2022. Fire as a driver of fungal diversity — A synthesis of current knowledge. Mycologia 114 (2), 215–241. https://doi.org/10.1080/00275514.2021.2024422.

Franco-Manchón, I., Salo, K., Oria-de-Rueda, J.A., Bonet, J.A., Martín-Pinto, P., 2019. Are wildfires a threat to fungi in European *Pinus* forests? A case study of Boreal and Mediterranean forests. Forests 10 (4), 309. https://doi.org/10.3390/F10040309.

Gassibe, P.V., Fabero, R.F., Hernández-Rodríguez, M., Oria-de-Rueda, J.A., Oviedo, F.B., Martín-Pinto, P., 2014. Post-fire production of mushrooms in *Pinus pinaster* forests using classificatory models. J. For. Res. 19 (3), 348–356. https://doi.org/10.1007/S10310-013-0419-9/TABLES/7.

González-Pérez, J.A., González-Vila, F.J., Almendros, G., Knicker, H., 2004. The effect of fire on soil organic matter—a review. Environ. Int. 30 (6), 855–870. https://doi.org/10.1016/j.envint.2004.02.003.

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

Hernández-Rodríguez, M., Oria-de-Rueda, J.A., Martín-Pinto, P., 2013. Post-fire fungal succession in a Mediterranean ecosystem dominated by *Cistus ladanifer* L. For. Ecol. Manag. 289, 48–57. https://doi.org/10.1016/J.FORECO.2012.10.009.

Hernández-Rodríguez, M., Oria-de-Rueda, J.A., Pando, V., Martín-Pinto, P., 2015. Impact of fuel reduction treatments on fungal sporocarp production and diversity associated with *Cistus ladanifer* L. ecosystems. For. Ecol. Manag. 353, 10–20. https://doi.org/10.1016/j.foreco.2015.05.007.

Illumina, 2019. Fungal metagenomic sequencing demonstrated protocol preparing ITS amplicons for sequencing on Illumina sequencing systems.
Jain, T.B., Pilliod, D.S., Graham, R.T., Lentile, L.B., Sandquist, J.E., 2012. Index for Characterizing Post-Fire Soil Environments in Temperate Coniferous Forests. Forests 3, 445–466. https://doi.org/10.3390/F3030445.
Jia, Q., Qu, J., Mu, H., Sun, H., Wu, C., 2020. Foliar endophytic fungi: diversity in species and functions in forest ecosystems. Symbiosis 80 (2), 103–132. https://doi.org/10.1007/S13199-019-00663-X/FIGURES/1.
Joffre, R., Agren, G.I., Gillon, D., Bosatta, E., 2001. Organic matter quality in ecological studies: theory meets experiment. Oikos 93 (3), 451–458. https://doi.org/10.1034/j.1600-0706.2001.930310.x.
Johnson, D.W., Curtis, P.S., 2001. Effects of forest management on soil C and N storage: meta analysis. For. Ecol. Manag. 140 (2–3), 227–238. https://doi.org/10.1016/S0378-1127(00)00282-6.
Johnston, M.T., Miller, A.D., Holland, O.J., Clark, Z., Wevill, T., 2024. Impacts of planned burning on the fungal diversity and vascular plants in a heathy woodland. For. Ecol. Manag. 563, 121958. https://doi.org/10.1016/j.foreco.2024.121958.
Kõljalg, U., Nilsson, H.R., Schigel, D., Tedersoo, L., Larsson, K.H., May, T.W., Taylor, A.F.S., Jeppesen, T.S., Frøslev, T.G., Lindahl, B.D., Põldmaa, K., Saar, I., Suija, A., Savchenko, A., Yatsiuk, I., Adojaan, K., Ivanov, F., Piirmann, T., Pöhönen, R., Abarenkov, K., 2020. The Taxon Hypothesis Paradigm—On the unambiguous detection and communication of taxa. Microorganisms 8, 1910. https://doi.org/10.3390/MICROORGANISMS8121910.
Linley, G.D., Jolly, C.J., Doherty, T.S., Geary, W.L., Armenteras, D., Belcher, C.M., Bliege Bird, R., Duane, A., Fletcher, M.S., Giorgis, M.A., Haslem, A., Jones, G.M., Kelly, L.T., Lee, C.K.F., Nolan, R.H., Parr, C.L., Pausas, J.G., Price, J.N., Regos, A., Nimmo, D.G., 2022. What do you mean, 'megafire'? Glob. Ecol. Biogeogr. 31 (10), 1906–1922. https://doi.org/10.1111/GEB.13499.
Martín-Pinto, P., Dejene, T., Benucci, G.M.N., Mediavilla, O., Hernández-Rodríguez, M., Geml, J., Baldrian, P., Sanz-Benito, I., Olaizola, J., Bonito, G., Oria-de-Rueda, J.A., 2023. Co-responses of bacterial and fungal communities to fire management treatments in Mediterranean pyrophytic ecosystems. Sci. Total Environ. 875, 162676. https://doi.org/10.1016/J.SCITOTENV.2023.162676.
Massman, W.J., Frank, J.M., Mooney, S.J., 2010. Advancing investigation and physical modeling of first-order fire effects on soils. Fire Ecol. 6 (1), 36–54. https://doi.org/10.4996/FIREECOLOGY.0601036/FIGURES/8.
Merino, A., Chávez-Vergara, B., Salgado, J., Fonturbel, M.T., García-Oliva, F., Vega, J.A., 2015. Variability in the composition of charred litter generated by wildfire in different ecosystems. CATENA 133, 52–63. https://doi.org/10.1016/j.catena.2015.04.016.
Oliver, A.K., Callaham, M.A., Jumpponen, A., 2015. Soil fungal communities respond compositionally to recurring frequent prescribed burning in a managed Southeastern US forest ecosystem. For. Ecol. Manag. 345, 1–9. https://doi.org/10.1016/j.foreco.2015.02.020.
Olsen, S.R., Khasawneh, F.E., 1980. Use and limitations of physical chemical criteria for assessing the status of Phosphorus in soils. In: Khasawneh, F.E., Sample, E.C., Kamprath, E.J. (Eds.), The role of Phosphorus in agriculture. ASA-CSSA-SSSA., pp. 361–410. https://doi.org/10.2134/1980.ROLEOFPHOSPHORUS.C15;WGROUP:STRING:PUBLICATION
Oria-de-Rueda, J.A., Martín-Pinto, P., Olaizola, J., 2008. Bolete productivity of cistaceous scrublands in Northwestern Spain. Econ. Bot. 62 (3), 323–330. https://doi.org/10.1007/s12231-008-9031-x.
Pausas, J.G., Paula, S., 2012. Fuel shapes the fire–climate relationship: evidence from Mediterranean ecosystems. Glob. Ecol. Biogeogr. 21 (11), 1074–1082. https://doi.org/10.1111/j.1466-8238.2012.00769.x.
Pérez-Izquierdo, L., Zabal-Aguirre, M., Verdú, M., Buée, M., Rincón, A., 2020. Ectomycorrhizal fungal diversity decreases in Mediterranean pine forests adapted to recurrent fires. Mol. Ecol. 29 (13), 2463–2476. https://doi.org/10.1111/mec.15493.
Perpiña Castillo, C., Coll Aliaga, E., Lavalle, C., Martínez Llario, J.C., 2020. An Assessment and spatial modelling of agricultural land abandonment in Spain (2015–2030). Sustainability 12 (2), 560. https://doi.org/10.3390/su12020560.
Plaza-Álvarez, P.A., Lucas-Borja, M.E., Sagra, J., Zema, D.A., González-Romero, J., Moya, D., De las Heras, J., 2019. Changes in soil hydraulic conductivity after prescribed fires in Mediterranean pine forests. J. Environ. Manag. 232, 1021–1027. https://doi.org/10.1016/j.jenvman.2018.12.012.
Põlme, S., Abarenkov, K., Henrik Nilsson, R., Lindahl, B.D., Clemmensen, K.E., Kauserud, H., Nguyen, N., Kjøller, R., Bates, S.T., Baldrian, P., Frøslev, T.G., Adojaan, K., Vizzini, A., Suija, A., Pfister, D., Baral, H.O., Järv, H., Madrid, H., Nordén, J., Tedersoo, L., 2020. FungalTraits: a user-friendly traits database of fungi and fungus-like stramenopiles. Fungal Divers. 105 (1), 1–16. https://doi.org/10.1007/S13225-020-00466-2/FIGURES/3.
R Core Team, 2025. R: A Language and Environment for Statistical Computing. ⟨https://www.R-project.org/⟩.
Reazin, C., Morris, S., Smith, J.E., Cowan, A.D., Jumpponen, A., 2016. Fires of differing intensities rapidly select distinct soil fungal communities in a Northwest US ponderosa pine forest ecosystem. For. Ecol. Manag. 377, 118–127. https://doi.org/10.1016/J.FORECO.2016.07.002.
Rodríguez-Calcerrada, J., Pérez-Ramos, I.M., Ourcival, J.-M., Limousin, J.-M., Joffre, R., Rambal, S., 2011. Is selective thinning an adequate practice for adapting *Quercus ilex* coppices to climate change? Ann. For. Sci. 68 (3), 575. https://doi.org/10.1007/s13595-011-0050-x.
Rovira, P., Romanyà, J., Duguy, B., 2012. Long-term effects of wildfires on the biochemical quality of soil organic matter: A study on Mediterranean shrublands. Geoderma 179, 9–19. https://doi.org/10.1016/j.geoderma.2012.02.011.
Ruffault, J., Curt, T., Moron, V., Trigo, R.M., Mouillot, F., Koutsias, N., Pimont, F., Martin-StPaul, N., Barbero, R., Dupuy, J.-L., Russo, A., Belhadj-Khedher, C., 2020. Increased likelihood of heat-induced large wildfires in the Mediterranean Basin. Sci. Rep. 10 (1), 13790. https://doi.org/10.1038/s41598-020-70069-z.
Šimonovičová, A., Nováková, A., Pangallo, D., Hnátová, V., Hubka, V., 2014. The occurrence of heat-resistant species of *Trichophaea abundans* in different types of soil in Slovakia and Czech Republic. Biologia 69 (2), 168–172. https://doi.org/10.2478/s11756-013-0300-5.
Smith, G.R., Edy, L.C., Peay, K.G., 2021. Contrasting fungal responses to wildfire across different ecosystem types. Mol. Ecol. 30 (3), 844–854. https://doi.org/10.1111/mec.15767.
Sumorok, B., 2001. Post-fire macrofungi in the burnt area in the Jelonka reserve (Białowieża region, NE Poland). Acta Mycol. 36 (1), 149–158. https://doi.org/10.5586/am.2001.010.
Sun, H., Santalahti, M., Pumpanen, J., Köster, K., Berninger, F., Raffaello, T., Jumpponen, A., Asiegbu, F.O., Heinonsalo, J., 2015. Fungal community shifts in structure and function across a boreal forest fire chronosequence. Appl. Environ. Microbiol. 81 (22), 7869–7880. https://doi.org/10.1128/AEM.02063-15/SUPPL_FILE/ZAM999116731SO1.PDF.
Tárrega, R., Calvo, L., Taboada, Á., García-Tejero, S., Marcos, E., 2009. Abandonment and management in Spanish dehesa systems: Effects on soil features and plant species richness and composition. For. Ecol. Manag. 257 (2), 731–738. https://doi.org/10.1016/j.foreco.2008.10.004.
Tedersoo, L., Bahram, M., Põlme, S., Kõljalg, U., Yorou, N.S., Wijesundera, R., Ruiz, L.V., Vasco-Palacios, A.M., Thu, P.Q., Suija, A., Smith, M.E., Sharp, C., Saluveer, E., Saitta, A., Rosas, M., Riit, T., Ratkowsky, D., Pritsch, K., Põldmaa, K., Abarenkov, K., 2014. Global diversity and geography of soil fungi. Science 346 (6213), 1256688. https://doi.org/10.1126/SCIENCE.1256688/SUPPL_FILE/TEDERSOO-SM.PDF.
Trabaud, L., 1994. Postfire plant community dynamics in the Mediterranean Basin. In: Moreno, J.M., Oechel, W.C. (Eds.), The Role of Fire in Mediterranean-Type Ecosystems, 107. Springer New York, pp. 1–15. https://doi.org/10.1007/978-1-4613-8395-6.
Vázquez-Veloso, A., Dejene, T., Oria-de-Rueda, J.A., Guijarro, M., Hernando, C., Espinosa, J., Madrigal, J., Martín-Pinto, P., 2022. Prescribed burning in spring or autumn did not affect the soil fungal community in Mediterranean *Pinus nigra* natural forests. For. Ecol. Manag. 512, 120161. https://doi.org/10.1016/J.FORECO.2022.120161.
Viterbo, A., Horwitz, B.A., 2010. Mycoparasitism. In: Borkovich, K.A., Ebbole, D.J. (Eds.), Cellular and Molecular Biology of Filamentous Fungi. ASM Press, pp. 676–693. https://doi.org/10.1128/9781555816636.CH42.
Williams, R.J., Hallgren, S.W., Wilson, G.W.T., 2012. Frequency of prescribed burning in an upland oak forest determines soil and litter properties and alters the soil microbial community. For. Ecol. Manag. 265, 241–247. https://doi.org/10.1016/j.foreco.2011.10.032.
Zachmann, L.J., Shaw, D.W.H., Dickson, B.G., 2018. Prescribed fire and natural recovery produce similar long-term patterns of change in forest structure in the Lake Tahoe basin, California. For. Ecol. Manag. 409, 276–287. https://doi.org/10.1016/j.foreco.2017.11.013.