



Fungal diversity and community composition responses to the reintroduction of fire in a non-managed Mediterranean shrubland ecosystem



Juncal Espinosa^{a,b,*}, Tatek Dejene^c, Mercedes Guijarro^d, Xim Cerdá^e, Javier Madrigal^{d,f,1}, Pablo Martín-Pinto^{b,1}

^a Centre for the Research and Technology of Agro-Environmental and Biological Sciences, University of Trás-os-Montes e Alto Douro, Vila Real, Portugal

^b Sustainable Forest Management Research Institute, University of Valladolid, Palencia, Spain

^c Ethiopian Forestry Development, Addis Ababa, Ethiopia

^d Instituto de Ciencias Forestales (ICIFOR-INIA), CSIC, Madrid, Spain

^e Estación Biológica de Doñana, CSIC, Sevilla, Spain

^f University Polytechnic of Madrid, ETSI Montes, Forestal y Medio Natural, Madrid, Spain

ARTICLE INFO

Keywords:

Doñana National Park
Ectomycorrhizal fungi
Fire ecology
Forest management
Global change
Prescribed burning
Wildfire
Saprotrophic fungi

ABSTRACT

Background: More than a decade of fire suppression has changed the structure of fire-adapted shrubland ecosystems in Spain's National Parks, which are now at extreme risk of uncontrolled wildfires. Prescribed burning can mitigate the risk of wildfires by reducing the fuel load but prescribed burning may also alter the soil properties and reduce microbial and fungal activity, causing changes in the availability of nutrients deep in the soil layer. Although fungal communities are a vital part of post-fire restoration, some fire effects remain unclear. To examine the short-term effects of prescribed burning on soil fungal communities in Doñana Biological Reserve (SW Spain), we collected soil samples pre-burn and 1 day, 6 and 12 months post-burn from burned plots to perform physicochemical and metabarcoding DNA analyses.

Results: Prescribed burning had no significant effect on the total fungal operational taxonomic unit richness and abundance. However, changes in soil pH, nitrogen and potassium content post-burn affected fungal community composition. Small non-significant changes in pH and phosphorous affected the composition of ectomycorrhizal fungi.

Conclusions: The ectomycorrhizal fungal community appears to be resilient to the effects of low-to moderate-intensity fires and saprotrophic taxa may benefit from this kind of fire. This finding revealed that prescribed burning is a potentially valuable management tool for reducing fire hazards in shrublands that has little effect on the total richness and abundance of fungal communities.

1. Background

In the last decade, the reduction of fire management in shrubland ecosystems adapted to a recurrent regimen of fire, has altered their forest structure (e.g., Airey-Lauvaux et al., 2022; Rodrigues et al., 2022). In the absence of fire, this type of ecosystem is characterized by a greater fuel load and more horizontal continuity. Indeed, lack of management often causes habitat loss and degradation in these areas (Fontúrbel et al., 2016) owing to the increased risk of a high-severity wildfire. In this regard,

prescribed burning (PB) can be considered a management tool for mitigating fire hazards by reducing fuel load (Fernández et al., 2008; Marino et al., 2011). Prescribed burning also maintains the landscape in a mosaic of different age classes (Keeley, 2002), which helps to develop stages of post-fire succession dominated by herbaceous plants, which favours animal species typical of these open habitats (Rollan and Real, 2011). Despite the benefits, PB may alter the soil properties and reduce microbial and fungal activity, causing changes in the availability of nutrients deep in the soil layer and directly influencing vegetation recovery

Abbreviations: ANOSIM, Analysis of similarity; C, carbon; DBR, Doñana Biological Reserve; DNP, Doñana National Park; ECM, Ectomycorrhizal; LME, Linear mixed-effect; N, nitrogen; NMDS, Non-metric multidimensional scaling; OUT, operational taxonomic unit; P, phosphorus; PERMANOVA, permutational multivariate analysis of variance; PB, Prescribed burning; SIMPER, Similarity percentages.

* Corresponding author. Sustainable Forest Management Research Institute, University of Valladolid, Palencia, Spain.

E-mail address: juncal.espinosa@uva.es (J. Espinosa).

¹ Both authors contributed equally to manuscript as senior researchers and coordinators.

<https://doi.org/10.1016/j.fecs.2023.100110>

Received 31 January 2023; Received in revised form 27 March 2023; Accepted 1 April 2023

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(Reverchon et al., 2010; Hernández-Rodríguez et al., 2013; Parks et al., 2016). To date, there has been limited evaluation of the effects of prescribed burning on soil fungal communities, particularly in Mediterranean ecosystems where fire-adapted shrublands are abundant (Lauber et al., 2008). Conservation of fungal diversity is important for maintaining the provision of multiple ecosystem services that are crucial to both forest ecosystem functioning and human well-being (Tomao et al., 2020). For example, ectomycorrhizal (ECM) fungi can increase their host's resistance to abiotic stresses by enhancing water uptake and the mobilization, uptake and translocation of nutrients in forest soils (Van Der Heijden et al., 2008; Pietras et al., 2013), whereas saprotrophic fungi are mainly responsible for the hydrolytic degradation of organic matter (Hobbie et al., 1999). In addition, root-associated beneficial symbionts are expected to improve the ability of their host to adapt to stressors associated with climate change (van der Linde et al., 2018). Indeed, it is thought that the high resilience of Mediterranean ecosystems (Bradshaw et al., 2011) is partly due to the presence of active ECM fungal propagules in the soil (Izzo et al., 2006; Buscardo et al., 2012).

Fire is known to affect soil fungal communities to a greater or lesser extent, which mainly depends on burn severity (Dooley and Treseder, 2012; Wang et al., 2012; Parks et al., 2016). Many studies have been conducted after wildfire events (e.g., Sun et al., 2015; Whitman et al., 2019; Brown et al., 2019; Smith et al., 2021). However, prescribed burning, which is typically less intense and less severe than a wildfire event, is generally expected to have less impact on the soil fungal community than wildfire (Oliver et al., 2015; Hart et al., 2018; Giuditta et al., 2019; Vázquez-Veloso et al., 2022). In this sense, different responses have been reported in soil fungal communities in high forests and shrublands after low-severity experimental fires, ranging from a decrease in diversity and sporocarp production levels (Martín-Pinto et al., 2006; Taudière et al., 2017), to no effect (Oliver et al., 2015; Vázquez-Veloso et al., 2022) to a slight increase when compared with the effect of other forest management methods (Hernández-Rodríguez et al., 2013).

Many studies have mainly focused in high forests (e.g., Oliver et al., 2015; Hart et al., 2018; Vázquez-Veloso et al., 2022); however, little is known about the impact on diversity and composition of fungal communities after silvicultural treatments in shrublands, even though shrublands are the typical ecosystem where prescribed burning is carried out in Spain and they play a key role in the stabilization and protection of soils in stress- and fire-prone environments (Castaño et al., 2020).

In addition, to date most studies have focused on non-Mediterranean ecosystems (e.g., Reazin et al., 2016; Day et al., 2019; Wang et al., 2020; Durán-Manuel et al., 2022). However, in recent years, there has been growing interest in studying the impact of fire on fungal communities in Mediterranean ecosystems (e.g., Borgogni et al., 2019; Castaño et al., 2020; Martín-Pinto et al., 2022; Vázquez-Veloso et al., 2022), partly because the Mediterranean area has witnessed an increase in both the frequency and severity of large fires (Lionello and Scarascia, 2018; Dupuy et al., 2020). Overall, we need a better understanding of the impact of forest management-related disturbances on fungal communities. Most studies have been conducted after thinning (e.g., Müller et al., 2007; Castaño et al., 2018), clear-cutting or the implementation of shelterwood systems (e.g., Chaudhary et al., 2016; Kohout et al., 2018). However, the findings after prescribed burning in shrubland remain unspecific. 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 using physicochemical and genomic DNA analyses may be more accurate.

Conservation strategies in the emblematic Doñana National Park (DNP) (Andalusia, SW Spain), have been based on non-intervention for more than a decade. The policy of fire suppression in this protected area has changed fundamental aspects of the structure and functioning of the fire-adapted shrubland forests and has led to an extreme risk of uncontrolled wildfires (Keeley, 2002). However, following a large wildfire in the park in 2017, in which 10,339 ha were burnt (88% of which were

protected areas) (Adame et al., 2018), an important effort has been made to re-introduce the natural disturbance of fire to the park. In October 2020, a pioneering experimental prescribed burning treatment was carried out in Doñana National Park with many agencies and stakeholders engaged in the management of this area that are involved in assessing the viability of prescribed burning and its associated impacts.

The main aim of this study was to assess the response of the soil fungal community to the potential use of fire in the Doñana Biological Reserve (DBR). This management tool was used to favour the rejuvenation of shrubland species such as herbaceous plants, which potentially improves the habitat of rabbits (*Oryctolagus cuniculus* L.), the main diet of *Lynx pardinus* Temminck (Iberian lynx) and *Aquila adalberti* C. L. Brehm (Iberian imperial eagle) (Molina et al., 2019). The composition and abundance of fungal community in the soil was assessed using physicochemical and genomic DNA analyses. We hypothesized that the diversity of fungi could be improved via forestry practices if structural complexity and forest characteristics were enhanced (Tomao et al., 2020) through prescribed burnings. To test this hypothesis, the specific research objectives were: (i) to determine the evolution of soil fungal richness and abundance at three sampling intervals following the prescribed burning treatment; (ii) to identify edaphic variables that significantly drive the composition of the total fungi, the different fungal guilds, and ECM fungi. Thus, the information generated from this study should help to guide management strategies for Doñana National Park and supplement our knowledge of the soil fungal communities in similar conservation areas in Spain.

2. Methods

2.1. Study site

The study area is located in the stabilized dunes of the Doñana Biological Reserve in the Doñana National Park in Andalusia in SW Spain (37°01'13" N and 6°28'48" W) (Fig. 1). The area of Doñana (of which 116,487 ha are protected park) is considered to be a major biodiversity hot spot (Martín-López et al., 2010) and is one of the most important wetlands in Europe. The study area is at a mean altitude of 20 m above sea level and has a Mediterranean climate type with some oceanic influence (Muñoz and García, 2005). The mean annual precipitation is 550–570 mm, with 80% of precipitation occurring between October and March. The mean annual temperature is between 16 °C and 17 °C. The summer is dry with the highest temperatures occurring in July and August (25 °C) and the lowest in December and January (9 °C) (Hernández and Muñoz, 2005). The soil is sandy with an undulating topography (Siljeström and Clemente, 1987), which has its origin in old dune fronts generated by the prevailing westerly winds.

The study site is mainly dominated by Mediterranean shrublands, with the dominant species belonging to the families Ericaceae, Lamiaceae and Cistaceae. Senescence is a serious problem in these shrublands, with high levels of accumulated dead biomass, which may generate a high risk of fires. In addition, shrublands prevent the growth of herbaceous plants that are the food base of herbivores. According to Hernández and Muñoz (2005), there are three main units of vegetation: (i) white shrub, which constitutes a stage of degradation of the *Juniperus* forest by fires and clearing, dominated by *Salvia rosmarinus* Spenn. and *Halimium halimifolium* (L.) Willk., together with other species (e.g., *Cistus libanotis* (L.), *H. calycinum*, *Lavandula stoechas* L., and *Stauracanthus genistoides* (Brot.) Samp.); (ii) black shrub, which is hygrophilous shrub, dominated by *Erica scoparia* L., and *Calluna vulgaris* (L.) Hull accompanied by *Cistus salvifolius* L.; (iii) intermediate shrub, which is a transition phase located between white shrub and black shrub vegetation along the gradient topography and water availability, and which is characterized by the presence of *Ulex australis* Clemente together with *H. halimifolium* and *S. officinalis*.

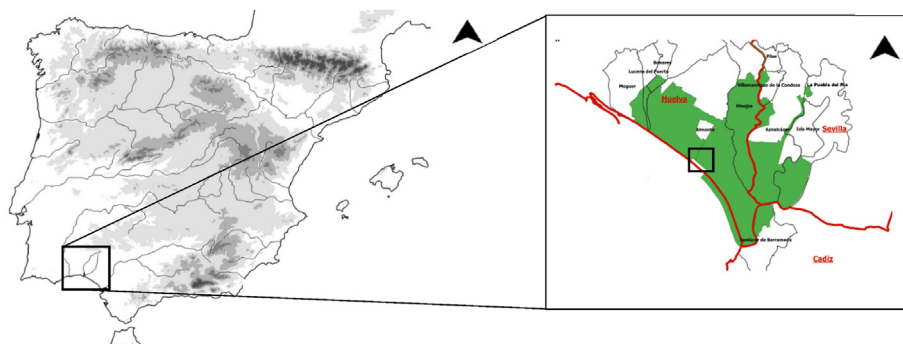


Fig. 1. Location of Doñana National Park in the Iberian Peninsula (1:5,000,000). The inset shows the limits of Doñana National Park (green) in Southwestern Andalusia (1:500,000). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

2.2. Experimental design

We established three blocks (B1, B2 and B3). In each block, three burned plots of 90 m² were sampled (3 m × 30 m; $n = 9$ plots) (Fig. 2). For the samples to be representative of the predominant types of shrublands found in the Doñana Biological Reserve, blocks of white shrub (B1), intermediate shrub (B2) and black shrub (B3) were included. We collected soil samples pre-burn and 1 day, 6 and 12 months post-burn from burned plots to perform physicochemical and genomic DNA analyses. Due to sampling limitations, we considered pre-burn status as the reference for further comparisons of evolution of fungal community.

2.3. Prescribed burning

The prescribed burnings were conducted by INFOCA Forest Service (October 2020) to explore the potential use of fire as a tool for the restoration of shrubland ecosystems. The shrub layer was the main fire-spread vector. The temperature (T , °C), relative humidity (RH, %), and wind speed (WS, m·s⁻¹) were recorded every 10 min at mobile meteorological station located at adjacent point to the plots (Table 1). The rate of spread (RS, m·min⁻¹) was calculated as the mean of several measurements of the time taken for the fire front to travel between two locations of known separation (Gould and Sullivan, 2020). Flame height (FH, cm) was measured from the base of the flame to the height above the flaming object using images taken during the prescribed burning treatment (Table 1).

Green, dead and total aboveground biomass (biomass in dry weight per unit area) were determined in burned plots before prescribed burnings were carried out. This variable is the most used variable in fuel description systems (Keane, 2012). The fuel load (equivalent to biomass) provides the necessary energy for fire ignition and propagation, thus modulating the intensity and severity of the fire (Vega et al., 2022). To

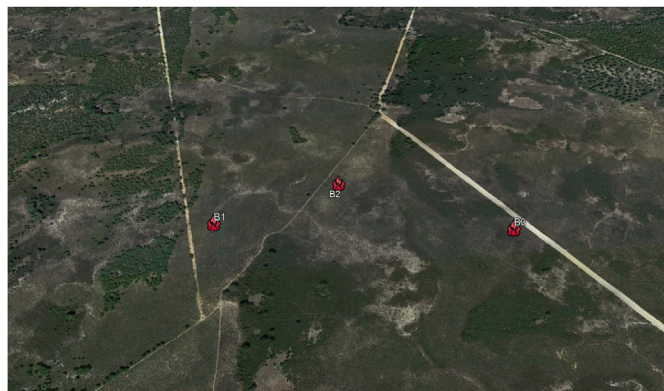


Fig. 2. Distribution of burning blocks (B1–B3) in the Doñana Biological Reserve.

Table 1

Main parameters measured during the execution of PB in burned blocks (mean and standard deviation).

Parameters	Unit	B1	B2	B3
Temperature (T)	°C	23.5 ± 2.1	25.4 ± 3.7	22.4 ± 2.1
Relative humidity (RH)	%	54.0 ± 0.0	–	59.5 ± 9.5
Wind speed (WS)	m·s ⁻¹	2.2 ± 0.0	2.4 ± 0.7	2.0 ± 0.5
Rate of spread (RS)	m·min ⁻¹	9.3 ± 5.5	8.3 ± 4.0	5.9 ± 3.0

determine the green, dead and total aboveground biomass, destructive sampling was carried out at five points along the two diagonals of each plot. The samples were taken to the laboratory, weighed and then dried in an oven at 60 °C until a constant weight was reached. According to the Rothermel Model (Rothermel, 1972), the plots were classified as model 6 (i.e., continuous shrubland up to a mean height of 1.6 m with biomass of between 11 and 19 t·ha⁻¹; Table 2), with dead biomass in burned plots comprising between 80% and 84% of the total biomass (Table 2).

2.4. Soil samples and molecular work

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 samples of topsoil were taken from underneath the litter layer were extracted 5 m apart at 10 sampling points along the centrelines of each plot (250 cm³) (De la Varga et al., 2012). Litter and twigs were removed from the surface before soil samples were taken (Voríšková 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 -80 °C. Next, the samples were air dried, sieved through a 1-mm² 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 physicochemical and genomic DNA analyses.

Chemical analyses were performed to determine soil pH using potentiometry; dry matter (%) using a 105 °C heater; total phosphorus (P) content using the Olsen method; total nitrogen (N) and total carbon (C) content (%) using a modified Kjeldahl methodology; and organic matter (%) using the relationship 1:0.5 between organic matter and C content (Bianchi et al., 2008).

In addition, the internal transcribed spacer 2 (ITS2) region (ca. 250

Table 2

Green, dead and total aboveground biomass in dry weight (t·ha⁻¹) estimated in burned blocks (B1, B2, B3).

	Green biomass (t·ha ⁻¹)	Dead biomass (t·ha ⁻¹)	Total biomass (t·ha ⁻¹)
B1	2.51	13.19	15.70
B2	2.31	8.96	11.27
B3	3.54	14.85	18.39

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). Its 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).

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 more than 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. The 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 the statistical analyses were carried out using the sequence count for each OTU as an abundance value (Danzeisen et al., 2011) of non-singleton fungal communities. Data used for statistical analyses were transformed when needed to achieve the parametric criteria of normality and homoscedasticity. The observed richness and the Chao1 and ACE estimates of the fungal communities were calculated using the estimate R function of the vegan package 2 (Oksanen et al., 2017). 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 sampling time after burning was defined as a fixed factor. A Tukey test was subsequently performed to check significant differences ($p \leq 0.05$) 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 similarity in the fungal community structure between treatments was analysed using a permutational multivariate ANOVA (PERMANOVA) based on 999 permutations using the adonis function in the vegan package. A one-way crossed analysis of similarities (ANOSIMs) was also performed to assess the significance of differences among groups observed in non-metric multidimensional scaling (NMDS) plots. A similarity percentages (SIMPER) routine was run to identify the fungal species responsible for dissimilarities in community structures (Parravicini et al., 2010). The analysis was performed using PAST software (Hammer et al., 2001).

Effects of edaphic variables on soil fungal community composition were determined based on the Bray–Curtis dissimilarity after excluding singleton OTUs and were visualized using 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 (Oksanen et al., 2017; R Core Team, 2020). NMDS analyses were performed for total fungi, trophic groups and ECM fungi. Isolines of edaphic variables were also plotted on NMDS ordinations using the ordisurf function (Oksanen et al., 2017; R

Core Team, 2020).

3. Results

3.1. Taxonomic composition of fungal communities

A total of 79,499 high-quality sequences were grouped into 2017 OTUs. We obtained between 19,081 and 56,542 high-quality reads from each sample. The total OTUs were assigned to 16 fungal phyla (Fig. 3). Taxonomic classification revealed that the majority of OTUs belonged to Ascomycota (48.1%) or Basidiomycota (22.6%). In total, 947 OTUs (46.9%) were resolved to genus level and were assigned to 443 different genera. Of these, 945 OTUs were assigned to 21 trophic groups, of which 11% were ECM fungi. Unidentified fungi were classified down to kingdom level and represented about 325 OTUs (16.2% of the total).

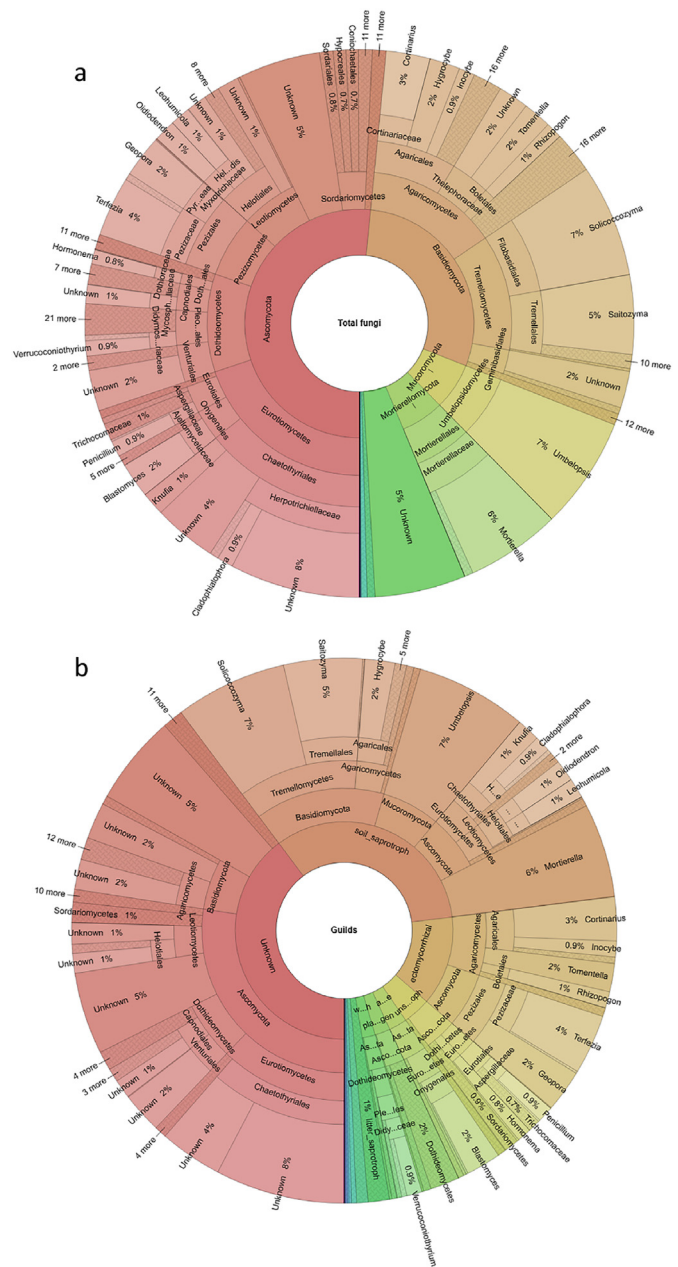


Fig. 3. Krona charts showing the relative abundance of (a) the total fungal taxa in each division, class, order and family and (b) in each fungal guild based on sequence abundance.

Fig. 3 shows the relative abundance of fungal taxa in each division, class, order and family and in each guild.

3.2. Effect of fire prevention treatments on fungal richness

Evolution of total fungal OTU richness prior to prescribed burning and at 1 day, 6 and 12 months after the PB treatment was not significantly different ($F = 0.616$; $p = 0.61$; Fig. 4), indicating that total fungal OTU richness in the short-to medium-term was not affected by PB. Furthermore, there were no significant differences in total fungal OTU abundance before PB and after treatment ($F = 0.078$; $p = 0.972$).

Analysis of specific guilds revealed that the richness of ECM fungi, mycoparasites, plant pathogens, and wood saprotrophs was significantly affected by prescribed burning ($p < 0.05$; Table 3; Fig. 5). Epiphytes, lichen parasites and pollen saprotrophs were also significantly affected; however, taxa belonging to these guilds were only present in very low numbers, therefore, we have focused on the most abundant and representative guilds in this study.

A slightly significant difference in time evolution of ECM fungal after prescribed burning richness was detected (Table 3). Although only marginally significant ($p = 0.062$), richness 6 months after treatment was higher than that prior to burning. However, 12 months after burning, richness levels had fallen with no significant differences with respect to pre-fire levels (Fig. 5). Mycoparasite richness before and after prescribed burning also differed significantly (Table 3). Although richness increased significantly in the short-term (1 day after treatment) 12 months after the PB treatment was performed, richness levels were not significant differences with respect to pre-fire levels, as in the case of ECM fungal (Fig. 5). Plant pathogen richness levels showed a significant decrease in richness 1 day ($p = 0.001$) and 6 months ($p = 0.000$) after the execution of prescribed burning that recovered to pre-burn levels 12 months post-fire (Fig. 5). Wood saprotroph richness levels had also decreased significantly 6 months after the PB treatment was performed ($p = 0.009$). Although richness levels showed a tendency to recover after 12 months to pre-burn levels (Fig. 5).

3.3. Soil fungal communities and edaphic variables

The pH level of the soil did not change significantly over time (Fig. 6). Although nitrogen (N) and potassium (K) had decreased 6 months after PB regarding to pre-burn levels ($p = 0.099$ and $p = 0.002$, respectively), tended to recover 12 months post-fire to pre-burn levels, and even significantly higher than those before the fire in the case of nitrogen ($p = 0.014$ and $p = 0.581$, respectively) (Fig. 6). As in the case of nitrogen, 12 months after prescribed burning, P levels were significantly higher than those before the fire ($p = 0.000$) (Fig. 6).

Table 3

Influence of time since the execution of prescribed burning on the richness of specific fungal guilds. Values in bold indicate significant differences ($p < 0.05$).

Guilds	Time	
	F	p-value
Animal parasites	0.364	0.780
Arbuscular mycorrhizae	0.560	0.645
Dung saprotrophs	2.148	0.115
Ectomycorrhizal fungi	5.131	0.005
Epiphytes	3.196	0.037
Lichen parasites	3.217	0.036
Lichenized fungi	1.084	0.371
Litter saprotrophs	1.826	0.164
Mycoparasites	4.592	0.009
Plant pathogens	17.34	0.000
Pollen saprotrophs	8.881	0.000
Root endophytes	0.675	0.574
Soil saprotrophs	1.629	0.203
Wood saprotrophs	3.914	0.018

3.4. Relationship between ecological factors and fungal community composition

The PERMANOVA analyses indicated that the total fungal composition detected at each of the four sampling times differed significantly ($F = 2.702$, $R^2 = 0.212$, $p = 0.001$; Fig. 7), which was also supported by ANOSIM ($R = 0.3794$, $p = 0.0001$). The SIMPER analysis identified fungal OTUs that were responsible for the differences in fungal composition at the different sampling times. The cumulative contribution of the most influential OTUs for the dissimilarity between sampling times is provided (Table S1). Edaphic parameters such as pH, N and K were significantly correlated with the total fungal OTU composition (Table 4).

NMDS of guilds followed by PERMANOVA also indicated that guild communities differed with sampling time ($F = 5.32$, $R^2 = 0.3473$, $p = 0.001$, Fig. 8) and this was also confirmed by ANOSIM ($R = 0.3542$, $p = 0.0001$). The SIMPER analysis identified the guilds responsible for differences between the four sampling times. ECM taxa are the most abundant guild detected at all four sampling times. The cumulative contribution of the most influential guilds for the dissimilarity is provided (Table S2). None of the explanatory edaphic variables had a significant influence on guild composition.

When considering ECM fungi specifically, the PERMANOVA indicated that ECM communities detected in the soil samples collected at the four sampling times differed significantly ($F = 3.859$, $R^2 = 0.278$, $p = 0.001$, Fig. 9), which was also supported by ANOSIM ($R = 0.4113$, $p = 0.0001$). The SIMPER analysis also identified influential ECM OTUs responsible for the differences between treatments; their cumulative contribution to the dissimilarity is shown in Table S3. Edaphic

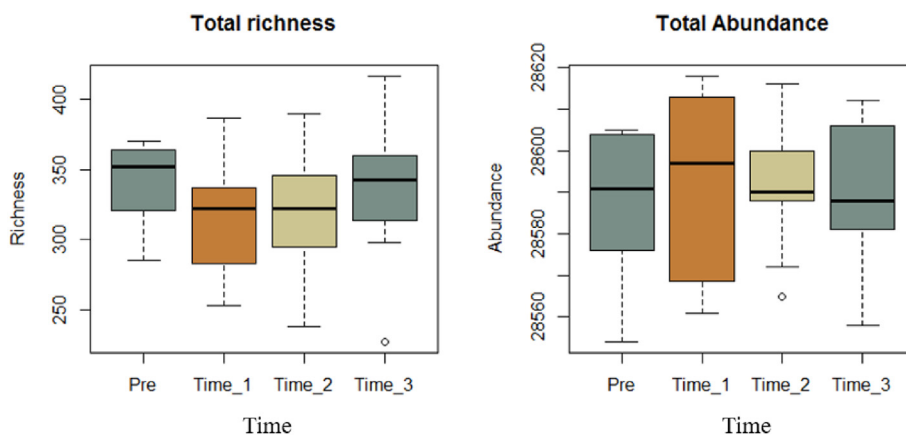


Fig. 4. Total richness (left) and total abundance (right) of OTUs collected before prescribed burning (Pre) and 1 day (Time_1), 6 months (Time_2) and 12 months (Time_3) after PB. The means and the interval distribution of the data are shown.

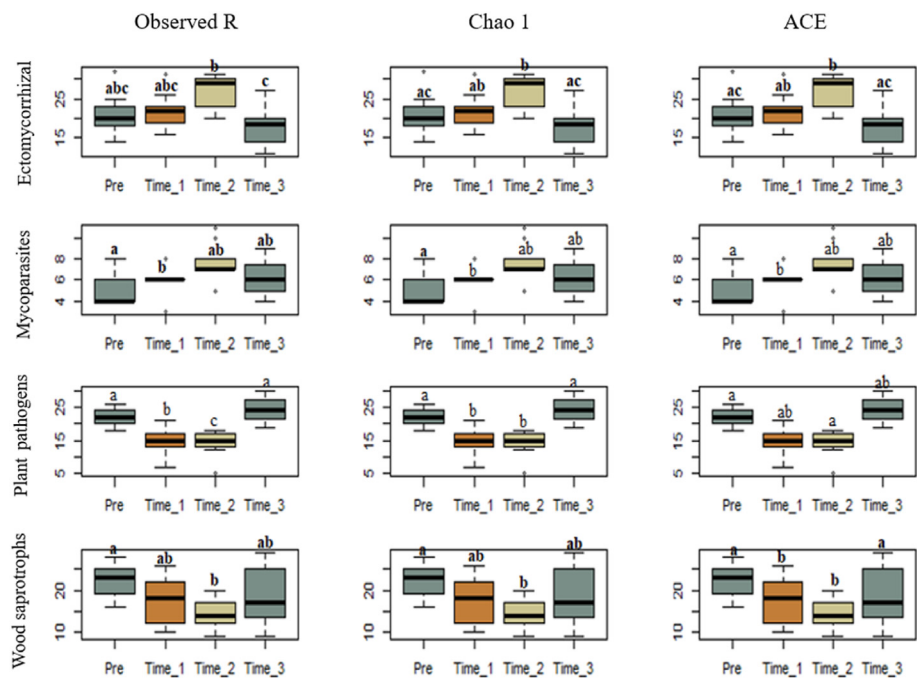


Fig. 5. Observed R and estimated (Chao1 and ACE) fungal richness across four treatments: Pre = before PB; Time_1 = 1 day after PB; Time_2 = 6 months after PB; and Time_3 = 12 months after PB. Data are presented using box plots for ECM fungi, mycoparasites, plant pathogens, and wood saprotrophs. Different letters above bars indicate significant differences between treatments ($p \leq 0.05$) based on a Tukey post-hoc pairwise comparison. The means and the interval distribution of the data are shown.

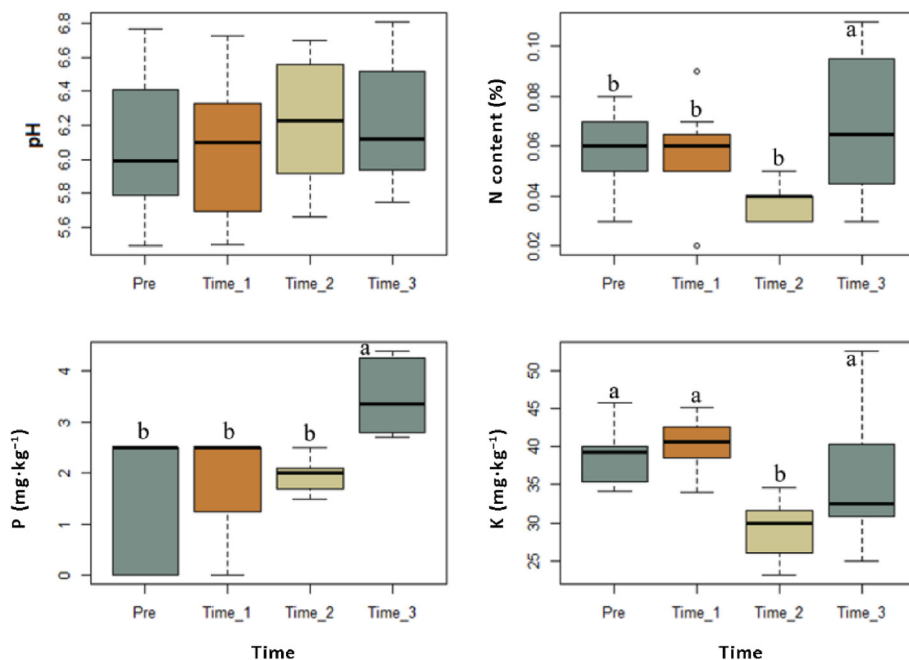


Fig. 6. Changes in edaphic variables over four time intervals (Pre = before PB; Time_1 = 1 day after PB; Time_2 = 6 months after PB; and Time_3 = 12 months after PB). Different letters above bars indicate significant differences between treatments ($p \leq 0.05$) based on a Tukey post-hoc pairwise comparison. The means and the interval distribution of the data are shown.

parameters such as pH and P were significantly correlated with the composition of ECM fungal OTUs.

4. Discussion

In this study, we analysed the impact of prescribed burning on soil fungal communities in mature shrubland ecosystems of Doñana Biological Reserve. Although there is a limitation regarding the control plots, the soil fungal communities were analysed at four sampling times (prior to prescribed burning and 1 day, 6 and 12 months after it was

conducted). The patterns of fungal communities along the time sequence following burn provided important clues about the implication of prescribed burning effect on the structure of fungi communities and the potential use of this management option to prevent highly severe uncontrolled wildfires in this type of emblematic ecosystems.

Previous studies have reported that fungal richness may be negatively impacted after moderate-to high-intensity fire events (Kutorga et al., 2012; Reazin et al., 2016; Pulido-Chavez et al., 2021). This might be because fire is likely to eradicate fungal species that cannot withstand intense heat (Dove and Hart, 2017). Furthermore, the physicochemical

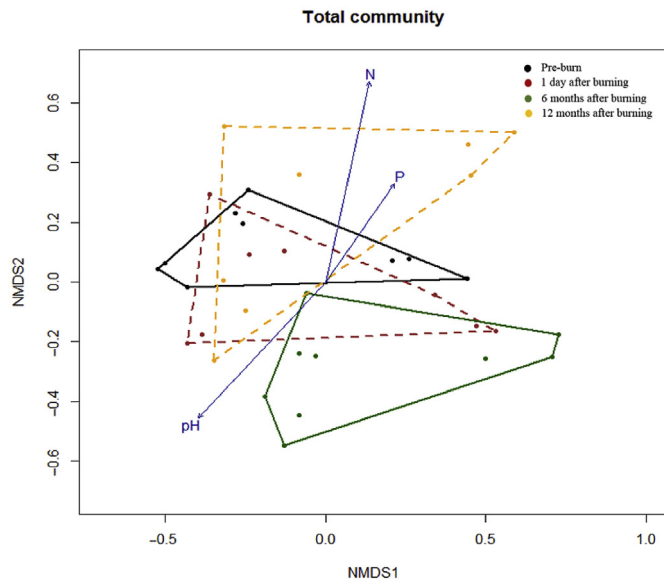


Fig. 7. Non-metric multidimensional scaling (NMDS-stress 0.0147) ordination graph of the four sampling times. The polygons indicate the soil fungal community composition at the different sampling times.

Table 4

Significance of the explanatory variables for the total OTU, guild and ECM soil fungal OTU community compositions. Values in bold indicate significant differences ($p < 0.05$).

Edaphic variables	Total OTUs		Guilds		ECM OTUs	
	R^2	p	R^2	p	R^2	p
pH	0.376	0.002	0.0102	0.847	0.3144	0.006
Nitrogen	0.485	0.001	0.1086	0.176	0.1413	0.105
Phosphorus	0.158	0.069	0.1539	0.075	0.1791	0.045
Potassium	0.220	0.018	0.0169	0.779	0.1205	0.133

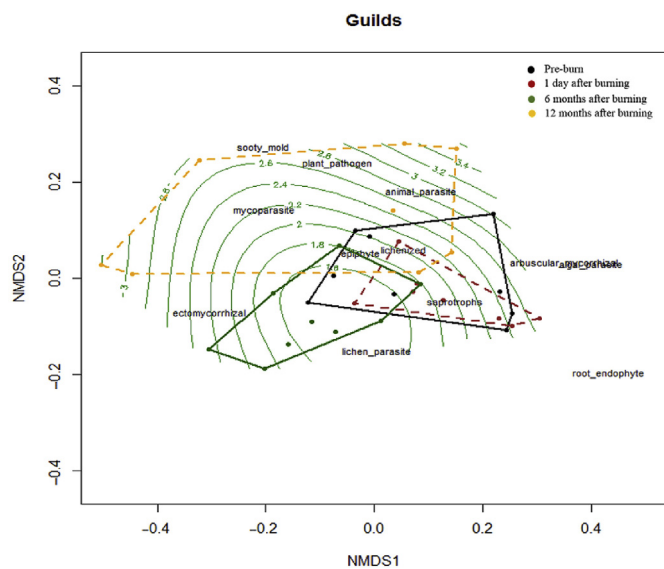


Fig. 8. Non-metric multidimensional scaling (NMDS stress 0.077) ordination graph of the four sampling times. The polygons indicate the soil fungal community composition at the different sampling times. Guild names are displayed. Isolines show P variations among plots.

changes in the soil environment and shifts in vegetation composition following fire likely select fungal species that can best compete under

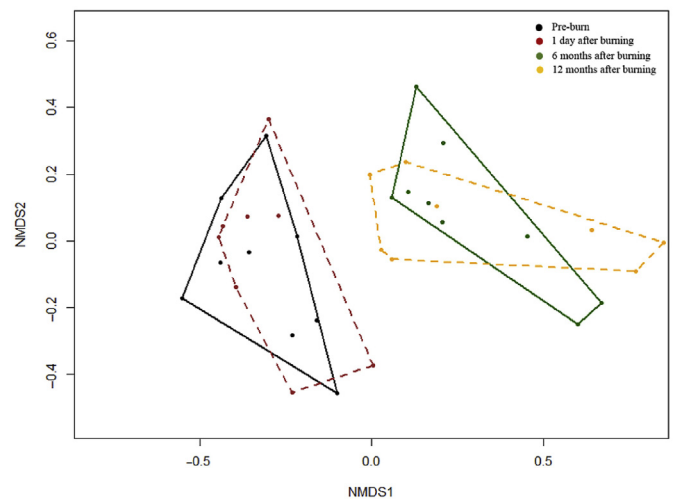


Fig. 9. Non-metric multidimensional scaling (NMDS stress 0.146) ordination graph of the four sampling times. The polygons indicate the composition of ECM fungi.

fire-altered conditions (Hart et al., 2005; Cairney and Bastias, 2007). However, our results showed no significant differences in total richness after PB at any of the time intervals considered. This could partly be explained by the rapid advancement of the fire front (a mean of $7.6 \pm 4.4 \text{ m} \cdot \text{min}^{-1}$), which prevented the soil from overheating and the excessive consumption of organic matter (Espinosa et al., 2021). The soil texture could also influence the results obtained and the sandy texture of the study area could have stimulated the development of fungi as compared to other textural characteristics of a soil (Zamora-Martínez and Nieto de Pascual-Pola, 1995). Thus, our findings indicate that PB had a non-destructive effect on most of the fungal populations in the study area, which may support the application of this treatment as a shrublands management tool. Our findings also agree with those of Oliver et al. (2015) who reported that low-intensity PB does not affect the richness of fungal communities in *Pinus taeda* L. stands. In addition, Vázquez-Veloso et al. (2022) reported that low-intensity prescribed burning had little effect on fungal communities in *Pinus nigra* Arn. stands. There was a non-significant decrease in total richness 1 day and 6 months after burning, probably because the fire destroyed the wood that fungi grow on and the fruiting bodies of the fungi themselves. However, fungal richness recovered, probably because fungal species in the soil were able to take advantage of the conditions created by the burning and flourish following the fire (Bean et al., 2009). Indeed, pioneer shrubs may facilitate the establishment of an ECM network after fire (Hernández-Rodríguez et al., 2013).

The prescribed burning treatment also had no significant effect on total abundance values, although a slight non-significant increase was detected just after PB. Smith et al. (2021) also reported that fire did not have an impact on fungal abundance in oak woodlands; however, they also showed the opposite response in mixed evergreen forests, so it is not possible to define a common response for all ecosystem types. Changes in fungal abundance may also be due to differences in fire severity. Although Gassibe et al. (2011) showed drastic changes in fungal community composition after stand-replacing fires, Hernández-Rodríguez et al. (2013) suggested that moderate-intensity fires may have lower impacts on fungal community composition. Overall, some authors show that fungal communities are resilient to heat (Kipfer et al., 2010; Peay et al., 2009), with fire adaptations in dominant taxa, which are therefore likely to be less affected by fire than other species. Moreover, it is probable that such fungal communities will be found where ecosystems burn more frequently. This confirms the use of a recurrent fire regimen in this area in the past, with shrubland vegetation types (*Halimium halimifolium* or Ericaceae family) that are adapted to an intense fire regime

(Jiménez-Morillo et al., 2020) progressively declining as a result of insufficient forest management (i.e., fire but also grazing).

When considering fungal trophic levels separately, the impact of the prescribed low-to moderate-intensity fire on ECM fungal richness in the study area was minimal. This may be because the heat generated by the prescribed burn was not high enough to cause drastic changes into the ECM fungal community. Our findings are consistent with previous studies, for example, Cowan et al. (2016) showed that there was no significant difference in ECM richness following low- or high-intensity PB in a *Pinus ponderosa* Douglas ex C. Lawson forest. Furthermore, Castaño et al. (2020) pointed out that after a low-to medium-intensity silvicultural fire-prevention treatment, there is likely to be sufficient host plant biomass and functional roots remaining to sustain the mycorrhizal community. Overall, the ECM fungal community that establishes after a fire reflects the fire-resistant structures in the soil (Hernández-Rodríguez et al., 2013): for example, the mycelium of a fungal species in the rhizosphere may persist in root tips, or as sclerotia or resistant spores (Cairney and Bastias, 2007). However, we did observe an increase in ECM richness at 6 months post-fire (not significant), probably because the nutrient content of the soil usually increases due to ash deposition, nutrient mineralization and the formation of stable forms such as black carbon, charcoal and apatite. However, the increase was followed by a significant fall in the 12-month post-fire samples, as plants grow and develop, nutrient availability decreases and, therefore, host plants tend to depend on mycorrhizal species for their nutrient acquisition (Castaño et al., 2019). This can sometimes lead to a decrease in the number and richness of mycorrhizal fungi after a fire as the host plant grows older (Alem et al., 2020).

In our study, we observed that prescribed burning had an immediate impact on the richness of plant pathogens. This might be because the fire destroyed the inoculum of most of the pathogenic fungi that sporulate on dead materials in the soil (Lygis et al., 2010). Even a slight rise in the temperature of the deeper soil layers following prescribed burning might have a profound impact, suggesting that pathogenic fungi are more sensitive to the effects of fire than some other guilds. Furthermore, after the fire, the area would have been exposed to direct sunshine and this could have had some additional effect on the viability of pathogenic fungi in the soil (Hood and Sandberg, 1989; Whitney and Irwin, 2005). However, a recovery to pre-burn levels was also observed 12 months post-fire. Although further studies are required to confirm these findings, prescribed burning could be used as a tool to control pathogenic fungi in forests at short-term (Lygis et al., 2010).

By contrast, the increased richness of mycoparasites immediately after burning could be because the increased temperatures caused by the fire reduced the amount of pathogenic fungal inocula (Froelich et al., 1978). This is because of the antagonistic nature of the two guilds: Reaves et al. (1990) reported that parasitic fungi obtained from burned soils were more antagonistic towards pathogenic fungi, although further studies are needed to confirm this claim.

We also found that saprotrophic taxa were significantly affected by PB. Unlike the ECM fungal community, the richness of saprotrophic taxa tended to be significantly lower in samples collected 6 months after PB than in pre-burn samples; however, a slight recovery trend is observed 12 months after burning. This could be due to the amount and type of substrate available in the forest soil. A reduction in substrate richness has been found to influence the diversity and richness of saprophytic species in forest systems (Smith et al., 2008; Reverchon et al., 2010) as they depend on available substrates. This could also be due to the immediate effect of the PB on organic matter deposited in the soil, depending on the fire intensity, leading to an indirect effect on these fungal growth and perpetuation (Kennedy et al., 2015). The temporary loss of topsoil by erosion after a fire could also reduce the infectivity of fungal propagules (Rashid et al., 1997) and, thereby, reduce saprotrophic taxa richness following a fire. The recovery of saprotroph richness levels 12 months after the fire could be due to the high soil humification rate and because the litter layer is relatively developed in these forest systems, which are

particularly relevant for the occurrence of saprophytic fungi. Overall, saprotrophic taxa are expected to recover relatively quickly after a fire compared with other trophic groups (Santos-Silva and Louro, 2016). In addition, the increased availability of dead material (Franco-Manchón et al., 2019) might explain the rapid recovery after PB. The SIMPER analysis identified saprotrophic species as the most influential guild responsible for differences in richness levels between sampling times. This might be because the mycelium of saprotrophic fungal species is affected by temperature changes (Salerni et al., 2002) due to PB. An increase in the soil temperature due to PB could also facilitate the decomposition of organic matter in the soil and accelerate the availability of nutrients. Thus, saprophytic species are likely to respond to post-fire soil conditions (Nicolás et al., 2019).

We also assessed changes in pH, N, P and K levels after the prescribed burning treatment and their relationship with the composition of the total soil fungal community, guilds and ECM soil fungal community. Overall, we expected that prescribed burning would have some effect on soil C and nutrient content levels, soil texture, and pH, although, the effects are strongly dependent upon burning intensity and frequency (Fontúrbel et al., 2021). Accordingly, shifts in the structure of fungal communities were also expected owing to changes in soil nutrient availability (Lauber et al., 2008).

Our findings show that the composition of soil fungal communities, particularly the composition of ECM fungi, is strongly correlated with soil pH (Table 4). We had assumed that pH would increase after burning owing to the release of calcium (Ca), magnesium (Mg) and K cations (Sun et al., 2015). In addition, rainfall and other soil characteristics may also regulate the soil pH response in the medium-term (Fontúrbel et al., 2021). However, although pH levels in our study plots showed an upward trend after burning, this effect was not significant. Thus, a suitable pH is crucial for the mycelial growth of ECM fungi (Yamanaka, 2003) and small changes in pH can induce changes in ECM fungal composition. Most likely because pH is considered to be one of the main soil variables that links soil organic matter recycling, plant nutrition and plant-microbial interactions in soils (Husson, 2013).

If the soil temperature remains low during the fire, as normally happens when a PB is performed, the N levels may be unaffected, or may even increase due to the deposition of N-rich materials from the partial combustion of vegetation and the incorporation of ash into the soil (Fontúrbel et al., 2021). Although a decrease in N content levels was observed 6 months post-fire, which may be directly related to fuel consumption (Fontúrbel et al., 2021), they had recovered 12 months post-fire ($p = 0.014$). Nitrogen availability after burning could have influenced the fungal community composition, particularly the composition of the mycorrhizal fungal community (Zhao et al., 2018). This is because when the N availability in the soil is high, the host plant's dependence on mycorrhizal fungi decreases. This could reduce the amount of carbon allocated to ECM fungi (Liu et al., 2019), which eventually could cause competition among ECM fungal species, leading to changes in their composition (Zhao et al., 2018; Wang and Wang, 2008). In addition to N, P is also considered one of the most limiting nutrients in many forest ecosystems (Fontúrbel et al., 2021). In this study, we observed a significant increase in P 12 months post-fire, which has been related to the duration of heating of the organic horizon, addition of ash, and thermal mineralization of organic P (Quinto et al., 2001; Wan et al., 2001). The amount of K lost following a PB is expected to be small (Fontúrbel et al., 2021), partly due to the high volatilization temperature (774 °C), together with the short duration of the flame phase during PB. However, a significant decrease in the soil K content was observed 6 months after PB. The edaphic cation element of K was also correlated with the total fungal community, which indicates that soil cation concentrations could influence the composition of the fungal community (Song et al., 2019). Cations in general play an important part in many physicochemical processes, such as photosynthesis (He et al., 2017) and, thus, can affect plant photosynthesis and, hence, the amount of carbon that is available to soil fungi (Shi et al., 2013). Thus, K is considered to be

one of the main edaphic factors that influence the structure of soil fungal communities worldwide (Alem et al., 2020).

Among the different genera, *Cortinarius* (OTU_4), and *Rhizopogon* (OTU_75) were identified as the dominant genera that were generally influential across the pairwise comparisons of the treatments. Of these two genera, *Cortinarius* spp. have been reported at different levels of stand development after fire (Hernández-Rodríguez et al., 2013), indicating that these genera are also multi-stage species that might be able to survive under different ecological conditions. Furthermore, the mycelial network of these kinds of species could also play a role in reducing soil erosion in forests, which could potentially occur when the first rain falls after a wildfire (Martín-Pinto et al., 2022). Thus, management policies that help to conserve a diverse community of fungal species that play important environmental roles as well as facilitating the production of some marketable edible species at different stages of forest development is imperative, while preventing the occurrence of fires by reducing fuel loads.

5. Conclusions

This study was carried out in the emblematic area of Doñana Biological Reserve, where conservation strategies have been based on non-intervention. However, this policy is leading to an risk of uncontrolled wildfires. Thus, measures to reduce the impact of potential wildfires on forests and their biodiversity, including fungal flora, are urgently required. Among the different measures, the use of prescribed burning can be a tool that favours the fauna and flora and reduces the risk of wildfire. The findings of this study should provide valuable scientific insights that can be used to promote the conservation and management of this fire-prone national park. Furthermore, given that there has been little investigation of the fungal diversity in this national park, the information obtained in this study could be used to map the soil fungal diversity in this protected park.

Our findings support the view that prescribed burning is a potentially valuable management tool for reducing fire hazards in shrublands that has little effect on the total richness and abundance of the fungal community. The ECM fungal community in the study area appears to be resilient to the effects of low-to moderate-intensity fires. In addition, prescribed burning could be used as a tool to control pathogenic fungi in forests at short-term. The findings also showed that parasitic fungi obtained from burned soils were more antagonistic towards pathogenic fungi. Saprotrophic taxa may benefit from the increased availability of dead material after prescribed burning, showing only a very short-term perturbation (6 months post-fire). Fire effects on the chemical composition of the soil, particularly those that change the pH and the N and K content, can affect the composition of the fungal community. In addition, small changes in pH and P can induce changes in ECM fungi, given that P is a limiting nutrient. Despite the positive response of the fungal community to prescribed burning, a long-term study is needed to understand the duration of the prescribed burning effect on fungal communities.

Authors' contributions

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

Funding

This research was funded by: Spanish R&D projects MYCOINFOR (Mycosilviculture Applied to Forest Fire Prevention in Mediterranean Systems; PID2019-105188RB-I00); VIS4FIRE (Comprehensive vulnerability of forest systems to fire: implications for forest management tools; RTA2017-00042-C05-01); and Interreg-POCTEP CILIFO (Iberian Centre for Research and Forest Firefighting; 0753-CILIFO-5-E). This study was also financed by European Social Fund "NextGenerationEU" through a grant "Margarita Salas" awarded to Juncal Espinosa into the project GFIRE.

Availability of data and materials

The datasets used during the current study are available from the corresponding author upon reasonable request.

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

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.

Acknowledgments

We are grateful to everyone that was involved in the fieldwork. Logistic and technical support at DBR were provided by ICTS-RBD-CSIC, Ministry of Science and Innovation, Spain and co-financed by FEDER Funds.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.fecs.2023.100110>.

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