Prescribed burning in spring or autumn did not affect the soil fungal community in Mediterranean *Pinus nigra* natural forests

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ABSTRACT

In the context of global change, wildfires are not only a threat but are also increasing in their severity in forest ecosystems worldwide, affecting and modifying vegetation, wildlife, and fungal dynamics. Mediterranean ecosystems are frequently affected by fire and prescribed burning is being increasingly used as a tool to reduce the risk and severity of wildfires. Although some of the effects of prescribed burning have been studied, the best moment to perform a prescribed burn to reduce the impact of fire on fungal communities has not been fully investigated. In this study, we analysed the effect of prescribed burning in two different seasons (spring and autumn) on soil fungi associated with natural *Pinus nigra* forests. Four years after prescribed burning was applied, our analyses showed that the total fungal richness and the composition of fungal communities in spring-burned, autumn-burned, and unburned control plots did not differ significantly. However, analyses of specific phyla and functional trophic groups did reveal some significant differences between spring- or autumn-burned plots and unburned control plots. Valuable edible fungi, which were not affected by the prescribed burning, were also found in the study area. Thus, our results suggest that prescribed burning is not only an interesting tool that could be used to reduce the risk of wildfire but also is compatible with the conservation of fungal communities, and could even promote specific valuable edible species, generating complementary incomes for the rural population. Although further studies are needed, our analyses suggest that the season (spring or autumn) in which prescribed burning is performed does not affect fungal conservation and, therefore, does not need to be one of the factors taken into consideration when selecting the most appropriate time to perform a prescribed burning.

1. Introduction

Fire is one of the most common and likely one of the most destructive disturbances that affect terrestrial ecosystems (Marlon et al., 2009). The effect of fire on ecosystem components greatly depends on its intensity, frequency, and extent (Eales et al., 2018; Penttilä et al., 2013). The combination of these factors determines whether the fire will either be beneficial or harmful (Penttilä et al., 2013). The existence of some ecosystems depends on recurrent fires, including Mediterranean ecosystems, owing to the extreme climate conditions and the accumulation of fuel (Vega et al., 2009). In this region, fire potentially affects the vegetation resources (Gassibe et al., 2011; Hernández-Rodríguez et al.,

2013), including the biodiversity constituting the ecosystem. In addition, stand-replacing fires can alter the physical, chemical, and biochemical properties of the soil, mainly due to the intense heating of the soil and ash deposition (Peay et al., 2009; Smith et al., 2021).

Fungal communities play a vital role in Mediterranean ecosystems, contributing to the restoration of the ecosystem after the disturbance (Mediavilla et al., 2014). After the fire, stress conditions affecting the vegetation can be mitigated by ectomycorrhizal (ECM) fungi because these fungi can facilitate the acquisition of the required resources for their host plant. Soil restoration processes, such as nutrient cycles and organic matter decomposition, are promoted by the action of saprotrophs (Hernández-Rodríguez et al., 2015), which are stimulated just

after a fire (Hernández-Rodríguez et al., 2013). However, fungi can also be influenced by fires owing to changes in soil and vegetation composition. Fire can alter fungal communities in the short term, promoting the colonization of new species. Existing populations of fungi can also be altered by changes in the types of ecological niche that are available after fire (Castaño et al., 2020; Hernández-Rodríguez et al., 2015; Mediavilla et al., 2014). Furthermore, fire can have a direct effect on fungal communities by affecting the below-ground microorganisms (Buscardo et al., 2012). Both decreases and increases in microbial biomass have been detected following fire; however, the extent of such changes appears to depend largely on fire intensity and the time elapsed between burning and sampling (Cairney and Bastias, 2007). Differences in the return interval of fires can also modify the structure, composition, and diversity of fungal communities (Buscardo et al., 2010). Thus, fires can affect the subsequent structure of fungal communities, mainly driven by the dynamics of post-fire plant communities (Cairney and Bastias, 2007). Fire could also provide competition-free resources to use for some fungi such as *Rhizopogon* spp., which increased in abundance after the fire (Glassman et al., 2016; Peay et al., 2009). Previous studies have evaluated the influence of fire on fungal succession in Mediterranean ecosystems. Notably, these studies have drawn attention to the effects of fire on above-ground fungal communities. Specifically, Fernández-Toirán et al. (2006) evaluated fungal sporocarps production in *Pinus pinaster* stands, reporting an increase of fungal richness with stand age. In addition, Gassibe et al. (2011) observed that sporocarp production followed different trends according to the fungal trophic group in *P. pinaster* stands in Mediterranean ecosystems. Furthermore, Hernández-Rodríguez et al. (2013) analysed post-fire fungal succession in a Mediterranean ecosystem dominated by *Cistus ladanifer*, which revealed a shift in the composition of the fungal community during *C. ladanifer* succession.

Exploring the effects of fire and developing mitigation mechanisms is a high priority, particularly given the increased risk of fire associated with global change. Forest management can play a key role in reducing the impact of fire. Indeed, fuel reduction is considered to be an important tool for preventing forest fires in Mediterranean scrublands (Hernández-Rodríguez et al., 2015; Martín-Pinto et al., 2006) and forest stands (Marino et al., 2014; Martín-Pinto et al., 2006; Valor et al., 2015). Although the use of prescribed burning has some controversial connotations (Moreira et al., 2020; Senra Rivero et al., 2007), it has been used as an important management tool to reduce fuel loads, to remove non-fire-adapted species, and to sustain fire-adapted taxa in many forest ecosystems (Oliver et al., 2015). In some places, prescribed fire is also viewed as an ecosystem restoration tool, producing an overall improvement in the ecosystem by removing unnecessary plant species (Smith et al., 2004). Compared with wildfires, the negative ecological impact of prescribed burning is low, with less smoke production or soil and root damage (Fernandes and Botelho, 2004). Furthermore, prescribed burning can increase the resilience of the forest to wildfire events (Espinosa et al., 2018; Valor et al., 2015). However, the ecological consequences of the use of prescribed burning as a management tool on below-ground fungal community composition have not been studied. We have only limited knowledge of the influence of prescribed burning on fungal communities in Mediterranean ecosystems and the severity when implemented at different times of the year. We, therefore, studied the soil fungal community under natural stands of *Pinus nigra* trees following the prescribed fire to examine the soil fungal spore bank, which is essential for post-fire restoration of the ecosystem.

Pinus nigra subsp. salzmanii is one of the most widely distributed species in Central and Eastern Spain, it is native to Spain and is the dominant tree species in 544,286 ha of Spanish forests (Tiscar and Linares, 2011). Historical documents indicate that timber from *P. nigra* trees has been used as a construction material in Spain for the past 100 s years. Timber from *P. nigra* is still a valuable resource and the species continues to be harvested despite economic and environmental constraints. However, owing to the low price of timber for the past two decades, about 21% of the forests occupied by *P. nigra* are currently within nature reserves (Tiscar and Linares, 2011). Indeed, some of these forests have been recognized as a priority habitat under the European Union Habitats Directive owing to their biological values (Espinosa et al., 2018; Lucas-Borja et al., 2016). However, in general, wildfires pose the greatest threat to the sustainability of pine ecosystems in the Mediterranean basin (Fulé et al., 2008). Recurrent large wildfires are threatening the permanence of *P. nigra* forests in this region because of the almost total lack of capacity of this non-serotinous pine to regenerate after the fire (Espinosa et al., 2018; Ordóñez et al., 2005). However, *P. nigra* is resistant to low-intensity surface fires owing to its thick bark (Fulé et al., 2008; Touchan et al., 2012). Thus, devising conservation strategies for fungal resources in *P. nigra* forest ecosystems from ecological, management, and social perspectives through understanding the impact of prescribed burning is imperative.

This study examined the effects of prescribed burning conducted in spring or autumn on soil fungal communities, four years after its application. Although prescribed burning could affect the soil environment by creating differences in humidity or temperature in the soil, our first hypothesis was that fungal community diversity in burned plots would be greatest under moderate disturbance (Chen et al., 2018; Rousk et al., 2010). We hypothesize that the disturbance made by the prescribed burning in this study would not be severe enough (Espinosa et al., 2018) to alter the environment substantially but would be sufficient to create space and opportunities for a wide range of fungal species. Forest fires usually occur during the summer season, when fuels are dry and fire-causing factors are prevalent (Jasinge et al., 2018). However, prescribed fires are conducted in spring or autumn when fuel and weather conditions permit burning with minimal risk of uncontrolled fires (Espinosa et al., 2019). Fuel moisture levels are higher when burns are performed in spring rather than in autumn. In addition, temperature levels are lower and, therefore, spring burns differ substantially from autumn burns. Thus, our second hypothesis was that the effects of prescribed burning on fungal communities would differ depending on the season of burning and that the fungal communities would be drive by the specific heat and moisture conditions under the different burning seasons (Smith et al., 2004). Although many factors influence the fungal community response to prescribed fire, site conditions seem to be a key factor (Cairney and Bastias, 2007; Dove and Hart, 2017). Despite the severity, natural stands are assumed to be more resistant and resilient to fire disturbance (Proença et al., 2010; Silvério et al., 2020). Thus, our third hypothesis was that site conditions, mainly edaphic variables, could influence the composition of soil fungal communities in the study area. Finally, given the short period of time (4 years) since the application of burning, our fourth hypothesis was that ECM fungal richness would not be restored owing to the removal of vegetation and hosts associated with them (Smith et al., 2004) and that the abundance of edible fungal species represented in the soil would be affected by prescribed burning. Our general goal was to determine whether prescribed burning in spring or autumn influenced fungal communities to identify when prescribed burning should be performed in the study area.

2. Material and methods

2.1. Study area

The study was conducted in Beteta (40° 33′ 06″ N/002° 06′ 32″ W), which is located in the Cuenca Mountains (Iberian System), in Castilla-La Mancha Autonomous Community (Spain). The mean altitude of the site is 1294 m a.s.l., with a mean slope of 10%. The Beteta *P. nigra* stands are forests that have naturally been established from the seed bank. Forest management in the study area has mainly focused on the conservation and promotion of environmental services since 1971. *Genista scorpius* Sibth. & Sm. ex Boiss. and *Rosa canina* L. are the most dominant shrub understory covering from 5 to 20% of the ground in each of the plots. *Pinus* regeneration results in an irregular distribution of seedlings

(from 78 to 11,611 seedlings ha^{-1}). The soil in the study area is an Inceptisol according to the Soil Taxonomy classification (USDA, 1987) used in the National Soil Atlas of Spain (1: 200,000). The climate is classified as humid Mediterranean (Espinosa et al., 2018). The mean annual temperature is 10.7 °C (the warmest month is July with an average temperature of 19.8 °C and the coldest month is December with an average temperature of 2.0 °C) and the mean annual precipitation is 537 mm, with 56 mm falling during the summer months. Further details about the study area are provided in Espinosa et al. (2018) and Espinosa et al. (2020a; 2020b).

2.2. Experimental design, prescribed burning, soil sampling, and molecular work

In total, nine blocks >500 m apart, one in each of the 50 × 50 m (2500 m^2) areas, running perpendicular to the slope, were established (Luoma et al., 1991; Smith et al., 2002). Blocks were established in burning and controlling *Pinus nigra* stands in 2016. In each block, in addition to the pure stands of *P. nigra*, *Genista scorpius* Sibth. & Sm. ex Boiss. and *Rosa canina* L. were also found as the main understory species. The mean density of trees is 1286 trees ha-^{1}, while the mean shrub cover in all plots was in a range of 5–20%. The blocks were laid out randomly in the forest to avoid confounding spatial effects inherent to such a plot-based design (Hiiesalu et al., 2017; Rudolph et al., 2018). Each of the nine blocks contained three plots (27 plots in total), each 2 × 50 m in size, about 10 m apart from each other and assigned to treatments. The prescribed burning was conducted by the Castilla-La Mancha Regional Forest Service in 2016 as a wildfire prevention treatment to reduce the vertical and horizontal continuity of fuel. The strip ignition technique was applied at a distance of 1–2 m downhill of the plots in a headwind. This was done to promote the rapid advancement of the fire front to reduce the residence time of the fire in the soil to prevent overheating, excessive consumption of organic matter, and high temperatures. The efficacy of the prescribed fires in spring and autumn was moderate to high (59–77% reduction in understory and litter biomass). Additional fire severity measurements are provided in Table 1, as described in Espinosa et al. (2020a, 2020b).

The spring and autumn burns were conducted in May and November 2016 respectively. The soil samples from all the plots were collected four years after, in spring 2020, to avoid effect of the environmental sampling season conditions. Plots were analysed as independent samples (Ruiz-Almenara et al., 2019). Within each plot, five soil cores, (n = 15 Autumn, n = 15 Spring, and n = 15 control) were extracted 5 m apart along the centreline of each plot using a cylindrical soil borer (2 cm radius, 20 cm deep, and 250 cm^3) (De la Varga et al., 2012) to collect samples with spatial variability while minimizing the likelihood of repeatedly sampling the same genet. Litter and twigs were removed from the surface before soil samples were taken (Voříšková and Baldrian, 2013). The five cores were pooled to produce a composite soil sample for each plot established in each *P. nigra* stand. The samples were transported to the laboratory in sterile plastic bags and stored at 4 °C. Next, the samples were air dried, sieved through a 1-mm^2 mesh, and then ground to a fine powder using a mortar and pestle. 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) contents (%) using a modified Kjeldahl methodology; and organic matter (%) using the relationship 1:0.5 between organic matter and C content (Bianchi et al., 2008) (Table 1). In addition, the ITS2 region (ca. 250 bp) of the nuclear ribosomal DNA repeat was PCR amplified using the forward primer fITS7 (GTGARTCATCGAATCTTTG) (Ihrmark et al., 2012) and the reverse primer ITS4 (TCCTCCGCTTATTGATATGC) (White et al., 1990). ITS amplification was performed using the following amplification programme: the first cycle of 95 °C for 5 min,

Table 1
Mean physicochemical properties of soil samples and variables measured during and after prescribed burning of *Pinus nigra* forests in different seasons.

Soil properties	Control	Autumn	Spring
pH	7.83a	7.98a	7.96a
N (g/100 g)	0.22b	0.24ab	0.31a
C (g/100 g)	3.74b	5.00b	8.41a
C/N	19.25b	21.67b	27.55a
Organic matter (%)	7.48b	10.00b	16.82a
P (mg/kg)	4.06a	5.16a	5.13a
K (mg/kg)	260.22a	296.44a	271.56a
Dry matter (%)	78.07a	77.36a	77.36a
T(°C)	–	12.0 (0.9)	20.4 (1.5)
RH	–	43.5 (0.8)	32.7 (2.3)
WS	–	0.1 (0.1)	0.8 (0.1)
RS	–	0.7 (0.0)	0.8 (0.1)
FLI	–	13.8 (10.7)	32.6 (13.3)
FH	–	26 (13)	43 (8)
FL	–	25 (9)	38 (8)
HSmMx	–	59 (26)	160 (16)
HSmMn	–	4 (3)	40 (18)
TmMxB	–	94 (108)	279 (208)
TmMxC	–	40 (13)	41 (45)
TMxB	–	702 (–)	755 (–)
tC40C	–	7 (15)	666 (545)
tC60C	–	2 (0)	251 (206)
Litterfall (needles fraction)	130.98ab	151.64a	174.24b

Note: Different lowercase letters indicate a significant difference in soil property between treatments ($p < 0.05$). T, mean air temperature; RH, mean relative humidity; WS, mean wind speed; RS, mean fire rate of spread; FLI, fire-line intensity; FH: flame height; FL: flame length; HSmMx, mean maximum scorch height; HSmMn: mean minimum scorch height; TmMxB, mean maximum bark temperature; TmMxC, mean maximum cambium temperature; TMxB, absolute maximum bark temperature; tC40C, mean time during which temperature is higher than 40 °C in cambium; tC60C, mean time during which temperature is higher than 60 °C in cambium.

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. Afterward, a second PCR was performed for barcoding amplicons for sequencing using the Illumina MiSeq platform at BaseClear B.V. company (The Netherlands) BaseClear (Naturalis).

2.3. Bioinformatic analysis

Raw sequence reads were obtained from the Illumina output, which comprised demultiplexed sample reads. We identified both senses of DNA strand sequence and used cutadapt (Martin, 2011) to remove poor-quality ends in both directions (3′ and 5′), with q = 15 as the quality criteria value. After that, we joined both sample sequences using USEARCH v.10.0.240 (Edgar, 2010) and cutadapt, with 200 bp as the minimum sequence length. We trimmed primers (ITS4 reverse and fITS7 forward) and removed sequences with errors > 1. Similar sequences were joined to form a single sample, and the count number of the joined sample was recorded to generate an operational taxonomic unit (OTU) map displaying the number of repetitions of the same OTU per sample. Sequences of taxonomic groups were assigned based on their similarity to the curated UNITE database (version v.8.2 released on February 2nd, 2020; Abarenkov et al., 2020), which contains identified and unidentified sequences assigned to species hypothesis (SH) groups that are defined taking into account dynamic sequence similarity thresholds (Kõljalg et al., 2013). OTUs were filtered, excluding those with < 70% similarity or < 200 bp length of pairwise alignment to a fungal sequence, resulting in 2331 OTUs. After discarding singleton sequence types, we obtained 212,256 high-quality sequences. Although only OTUs with identities of > 95% are considered in taxonomic studies, given that we were analysing fungal communities from an ecological point of view in this study, we considered all detected OTUs.

Each OTU was assigned a functional trophic group based on Põlme

et al. (2020). ECM OTUs were classified by exploration type based on criteria used in previous studies (Geml, 2019; Tedersoo & Smith, 2013). Finally, OTUs with 99.5% similarity to known edible fungi were considered to be edible fungi, assessing the importance of the selected species following Gerhardt et al. (2000) and Moreno and Manjón (2010).

2.4. Statistical analysis

Data were transformed when needed to achieve the parametric criteria of normality and homoscedasticity. Fungal data were normalized by rarefying abundance data to the smallest number per plot. In addition, data from soil variables were scaled using base R and used for subsequent statistical analyses. Fungal richness at phyla taxonomic levels, trophic group, the abundance, which was interpreted as semiquantitative (Amend et al., 2010), of edible fungi, and differences in soil variables among treatments were studied using linear mixed-effects models (LME, $p \leq 0.05$), which were developed using the package Nlme (Pinheiro et al., 2016) in R (R Core Team, 2019). A Tukey test was subsequently performed to check significant differences ($p \leq 0.05$) between treatments when needed.

Differences in fungal community species composition between the treatments were evaluated using permutational multivariate analysis of variance (PERMANOVA) (Anderson, 2001), implemented as 'Adonis' in the R Vegan package (Oksanen et al., 2015) using Bray–Curtis distance measurements. This difference was also tested using the *betadisper* function in the vegan package in R (Oksanen et al., 2017). ANOSIM was used to test differences between paired specific groups. The relationship between soil fungal composition and edaphic parameters was visualized using non-metric multidimensional scaling (NMDS) based on a Hellinger transformed OTU abundance data matrix and environmental scaled data. The correlation of NMDS axes scores with explanatory variables was assessed using *envfit* function in R (Oksanen et al., 2017; R Core Team, 2020). NMDS analyses were performed for total fungi, trophic groups, ECM exploration types, and edible fungi. For ECM fungal OTUs that were identified to species level in this study, fungal traits associated with foraging distance (exploration type) and ability to absorb water in
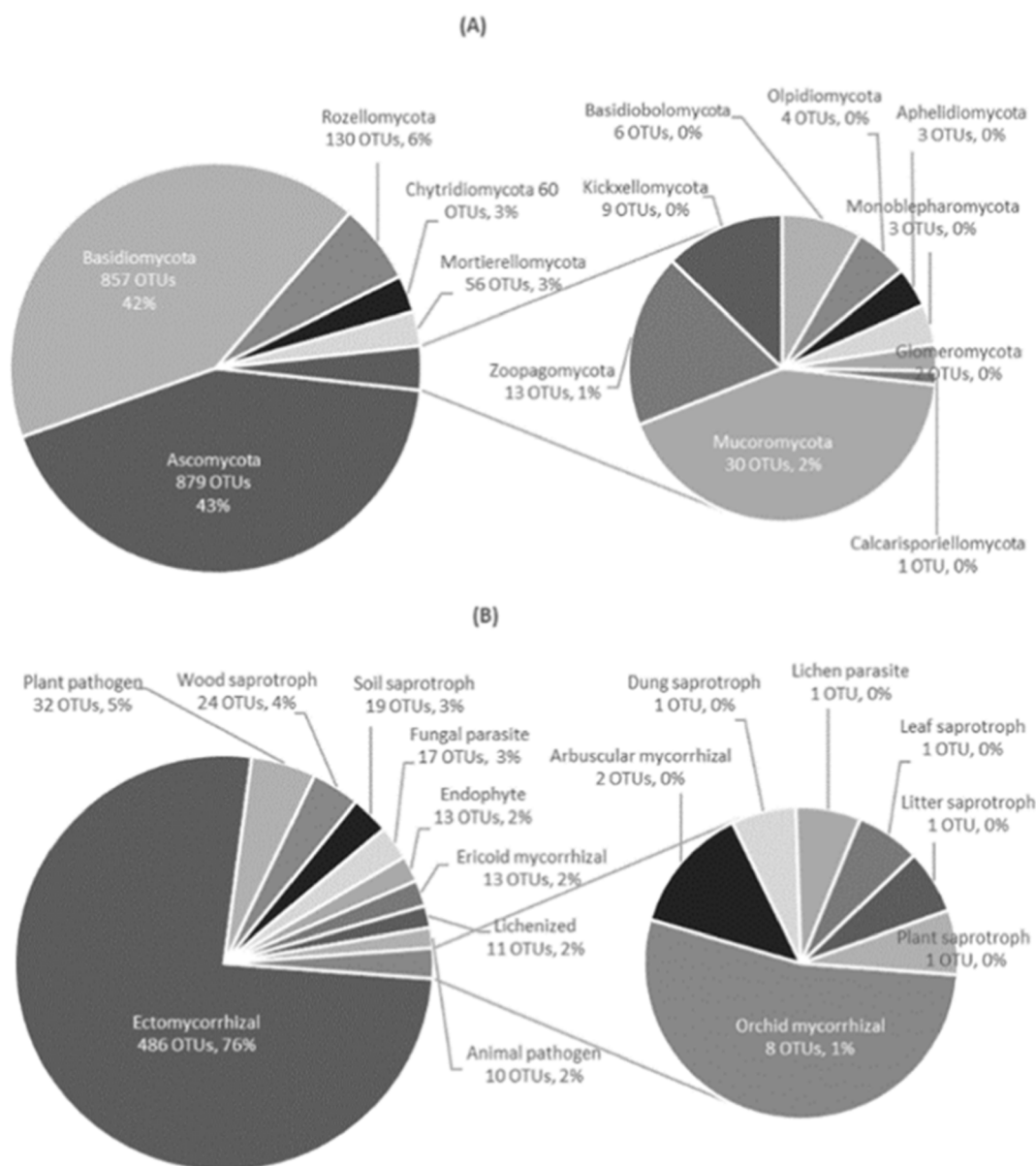
Fig. 1. Relative proportions of fungal operational taxonomic units (OTUs): (A) taxonomic classification at the phylum level (name of phylum; the number of OTUs; percentage); (B) classification of trophic groups (trophic group; the number of OTUs; percentage) based on the Fungal Traits database (Pölme et al., 2020) and manual checking of unrecognized groups.

<15 s (hydrophobicity) (Agerer, 2001; Unestam, 1991) were assigned using classification from Tedersoo and Smith (2013). Then, the ECM OTUs were differentiated based on their exploration distance at different stages of stand development. Thus, we classified ECM OTUs as contact/short-distance/medium-distance smooth with hydrophilic hyphae (C_SD_MDS) or medium-distance mat/medium-distance fringe/long-distance with hydrophobic hyphae (MDM_MDF_LD). In addition, abundance data (i.e., the number of OTUs per identified edible species) were recorded for each plot. Analyses were conducted in R (R Core Team, 2020).

3. Results

3.1. Sequencing output and taxonomic distribution

A total of 1,511,404 high-quality sequences were grouped into 2331 OTUs. We obtained between 32,032 and 97,058 high-quality reads from each sample. From these, 469,978 sequences were obtained in the unburned plots, and 475,540 and 565,886 were collected in spring and autumn plots respectively. In total, 2053 OTUs were assigned to 14 fungal phyla (Fig. 1A). The taxonomic classification revealed that the majority of OTUs belonged to Ascomycota (43%) or Basidiomycota (42%). About 64% (1313 OTUs) were resolved to genus level and were assigned to 328 different genera. Of these, 640 OTUs were assigned to 16 trophic groups, of which 76% were ECM fungi. Unidentified fungi were classified down to kingdom level and represented about 278 OTUs (12% of the total). The proportion of fungal OTUs at the genus level sharing the same ecological function is presented in Fig. 1B.

Although Ascomycota and Basidiomycota were considered the dominant phyla, no significant difference in their distribution was found among the treatments ($p > 0.05$). The Rozellomycota also did not significantly differ in their abundance between the three treatments. The abundance of Chytridiomycota was significantly higher in burned plots than in control plots ($p = 0.01$). However, the abundance in spring- and autumn-burned plots did not differ significantly ($p > 0.05$). Although there was a greater abundance of the phyla Rozellomycota in autumn-burned plots, the value, was not significantly different from that of spring-burned or control plots ($p > 0.05$). However, there was a significantly greater abundance of Zoopagomycota in autumn-burned plots than in spring-burned plots ($p = 0.03$).

3.2. Effect of prescribed burning on fungal richness and diversity

The total fungal OTU richness in burned and unburned plots was not significantly different ($F = 1.55$; $p = 0.234$), suggesting that total fungal OTU richness was not affected by prescribed burning (Fig. 2A). The highest richness value was observed in burned plots, whereas the lowest was observed in controlled stands. Autumn- and spring-burned plots also showed no significant differences in terms of their total fungal richness ($p = 0.947$; Fig. 2A).

The observed Shannon diversity indices were affected by prescribed burning ($F = 3.397$; $p = 0.05$; Fig. 2B). The highest mean Shannon diversity index value was found in spring-burned plots. However, this value was not significant when compared with the autumn-burned plots ($p = 0.802$; Fig. 2B), while it differed marginally with the control plots ($p = 0.048$). The same trend was observed for Simpson diversity index values. Higher values were obtained from spring-burned plots but were only significantly different from those of the control plots ($p < 0.05$; Fig. 2C).

ECM and saprotrophic fungi were the most dominant trophic modes in this study (Fig. 3). Although higher richness values for both of these trophic groups were found in spring-burned plots, the values obtained for the three treatments were not significantly different ($p > 0.05$; Fig. 3). In terms of exploration type, the highest richness value for C_SD_MDS was also obtained in spring-burned plots; however, richness values across treatments did not differ significantly ($p = 0.184$; Fig. 3). The richness values of the MDM_MDF_LD exploration type also did not differ between treatments ($p = 0.994$; Fig. 3). The most common ECM OTUs identified (99.5% similarity) as the C_SD_MDS exploration type were *Tomentella bryophila*, *Russula delica* and *Inocybe fraudans*. Species of *Cortinarius* predominantly belonged to the MDM_MDF_LD type.

In this study, we also identified important edible species, including *Tuber melanosporum*, *Suillus granulatus*, *Rhizopogon roseolus* and *Picoa juniperi*, based on 99.5% taxonomic similarity. Sporocarps of these species have been traditionally collected from these forests by local communities for decades. The abundance of total edible fungi did not differ significantly among treatments ($p = 0.81$). However, analysis of the most common species revealed that the abundance of *S. granulatus* was considerably lower in spring-burned plots than in autumn-burned plots ($p = 0.005$). The abundance of other important species such as *R. roseolus* ($p = 0.347$), *P. juniperi* ($p = 0.444$) and *T. melanosporum* ($p = 0.510$) did not differ significantly between treatments.

3.3. Ecological factors driving fungal community composition

Non-metric multidimensional scaling (NMDS) based on Bray–Curtis distance followed by a perMANOVA confirmed that the total soil fungal communities differed among treatments ($F = 1.335$, $R2 = 0.10$, $p =$
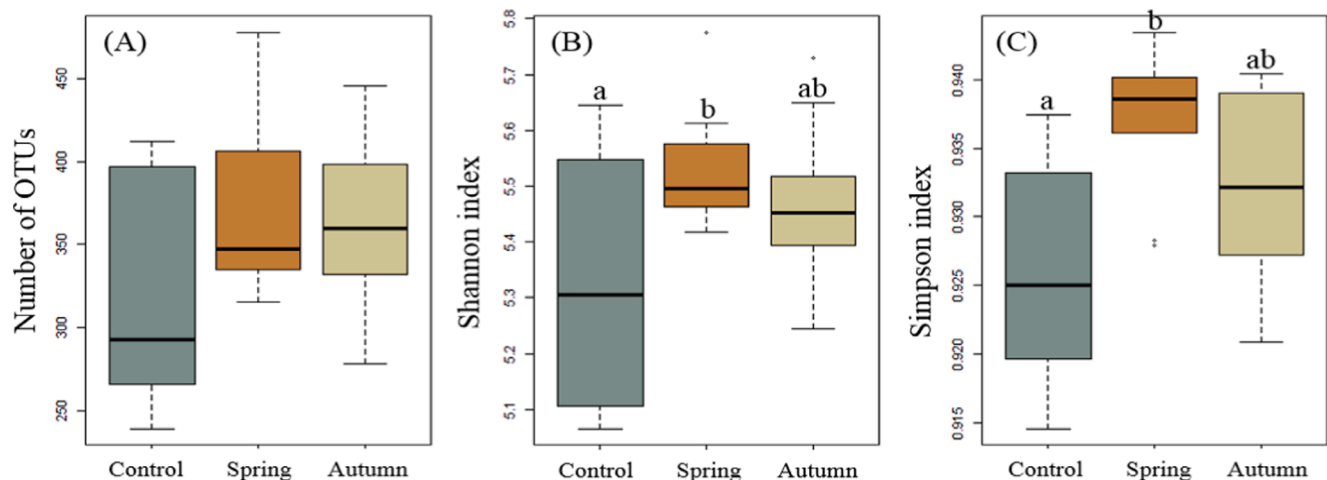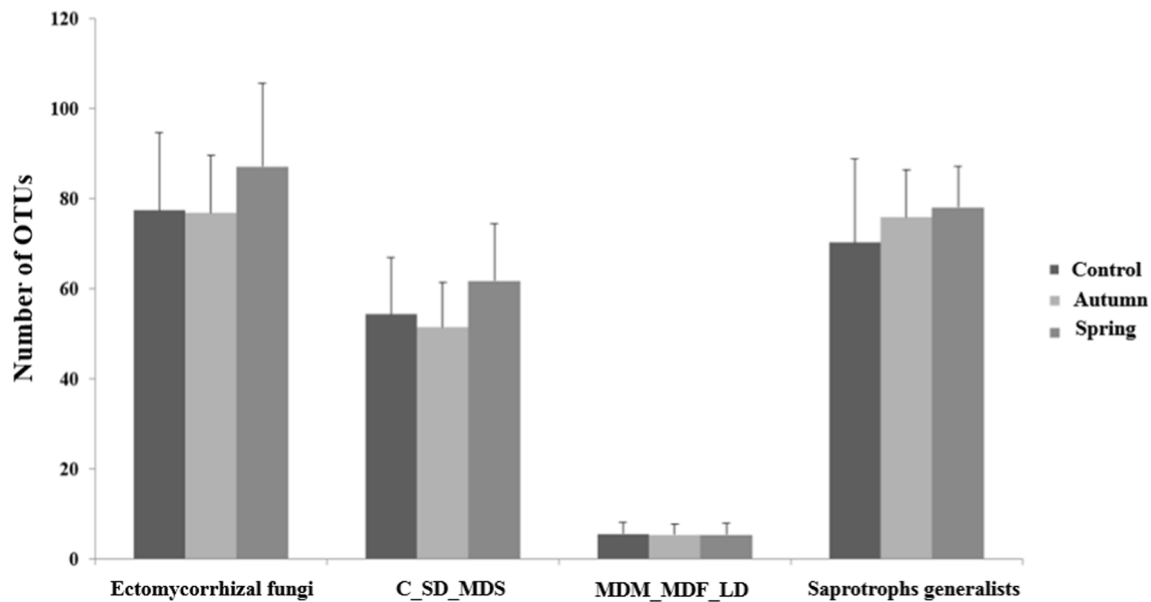

Fig. 2. Total richness (A), Shannon diversity index (B), and Simpson index (C) based on fungal OTUs in *Pinus nigra* stands four years after prescribed burning was performed in spring or autumn. Bars represent the standard error of the mean values. Different lowercase letters above the bars indicate a significant difference between treatments ($p < 0.05$). The absence of letters above the bars indicates that there is no significant difference between the data.

Fig. 3. Total richness of the most common trophic groups in the study area based on the number of fungal operational taxonomic units (OTUs) detected in the soil of *Pinus nigra* stands four years after prescribed burning was performed in spring or autumn. ECM genera were grouped based on their root exploration type into C_SD_MDS (contact/short-distance/medium-distance smooth with hydrophilic hyphae) and MDM_MDF_LD (medium-distance mat/medium-distance fringe/long-distance with hydrophobic hyphae). Bars represent the standard error of the mean values. The absence of letters above the bars indicates that there is no significant difference between the data.

0.048). The betadisper result also indicated that the treatments are compositionally different (F = 0.244; p = 0.785). However, the ANOSIM pair-wise analysis showed that this difference was marginal between the spring- and autumn-burned plots (p = 0.079) and that the strength of such differences was not high (R = 16.62). This was also supported by the ordination patterns, which showed some overlapping in terms of the composition of the fungal communities among the three treatments (Fig. 4A). Among the soil variables, pH and potassium (K) were significantly correlated with total fungal OTU composition ($p < 0.05$; Fig. 4A; Table 2).

When fungal trophic groups were analysed separately, perMANOVA analyses showed that the difference between treatments was not significant (F = 1.108, R2 = 0.08, p = 0.347). The ordination also revealed some overlapping of trophic group composition among treatments (Fig. 4B). However, soil fertility variables (Table 2), such as pH and the carbon to nitrogen ratio (C/N), significantly influenced the trophic modes composition in the study area (Table 2).

The NMDS ordination by exploration type showed a marginal difference between treatments in terms of their species composition (Fig. 5A). This was confirmed by Adonis analyses (F = 1.335, R2 = 0.10,
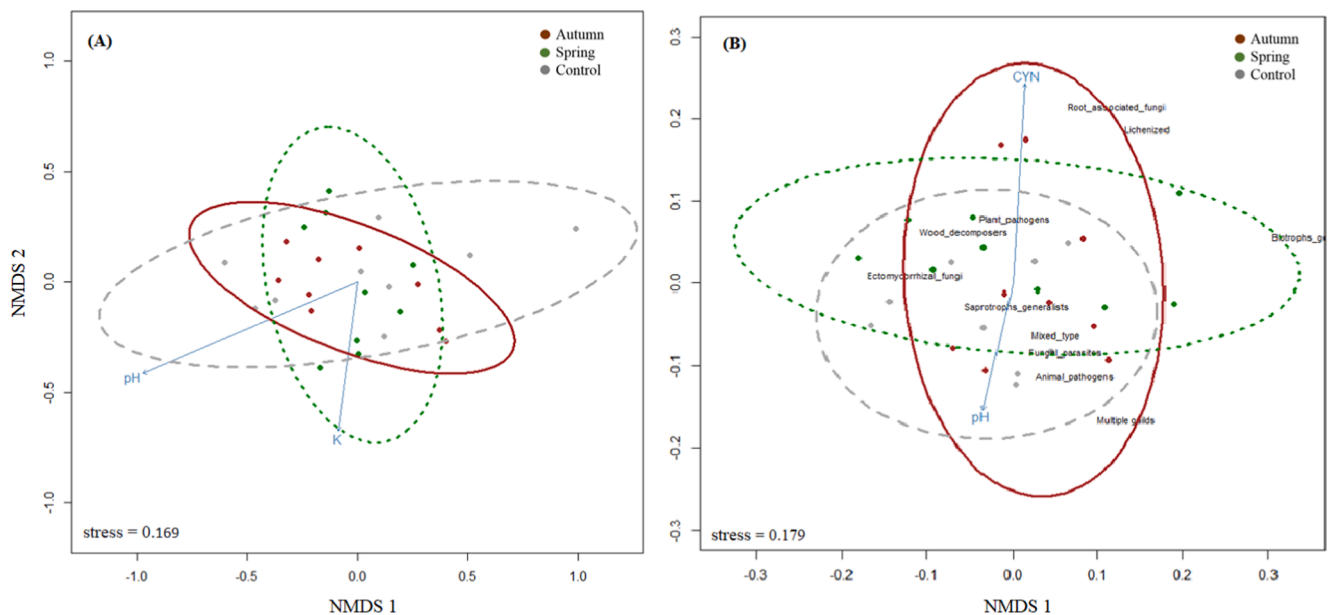
Fig. 4. Non-metric multidimensional scaling (NMDS) ordination graphs based on dissimilarities calculated using the Bray–Curtis index of soil fungal community composition by total OTUs (A) and trophic groups (B) across prescribed burning treatments in *Pinus nigra* stands, Spain. The ellipsoids indicate stands belonging to the same treatment group. Edaphic variables are shown in blue. CYN indicated the C/N ratio. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2

Significance of explanatory variables for soil fungal community composition based on Hellinger-transformed fungal and scaled soil data matrices. Numbers in bold indicate a highly significant effect ($p < 0.001$).

| Groups	Variables	pseudo-F	p
Total phyla	pH	0.907	**0.001*****
	K	0.376	**0.001*****
Trophic groups	pH	0.203	0.06·
	C/N	0.486	0.002**
Exploration types	N	0.271	0.02*
	C/N	0.201	0.063·
Edible species	pH	0.381	0.033*
	N	0.134	0.172
	C/N	0.072	0.407

Note: Significance codes: '***', $p < 0.001$; '**', $p < 0.01$; '*', $p < 0.05$; '·', $p < 0.1$.

$p = 0.048$). This marginal difference was observed between both burned treatments and the unburned control; however, it was not observed between the autumn and spring burnings ($p > 0.05$). By contrast, the NMDS ordination by edible species showed variation between treatments in terms of composition (Adonis, F = 2.9563, R2 = 19.76, $p = 0.015$; Fig. 5B). The ANOSIM also confirmed a significant difference in the composition of edible fungi between treatments (F = 0.095; $p = 0.02$). This difference was not significant between the control and spring-burned plots ($p = 0.919$).

The edaphic variables N and C/N significantly influenced the composition of the ECM species when analysed by the exploration type (Table 2; Fig. 5A). The MDM_MDF_LD species were positively correlated with N and C/N ratios while the C_SD_MDS were found at sites with lower levels of both N and C/N. Although the main edible fungi showed ordination towards some edaphic variables, only pH was significantly correlated with their composition (Table 2; Fig. 5B). Highly valued species such as *P. juniperi* and *T. melanosporum* were associated with pH levels at the higher end of the pH values when considering the NMDS2 axis. By contrast, *S. granulatus* and *R. roseolus* were found at pH levels at the lower end of the pH values.

4. Discussion

In this study, we analysed the influence of prescribed burning in spring or autumn on soil fungal richness four years after burns were conducted. Fires typically affect fungal communities, which could result in a reduction in richness (Pulido-Chavez et al., 2021; Kutorga et al., 2012; Oliver et al., 2015; Reazin et al., 2016). This might be because fire disturbs the environmental heterogeneity, which is likely to result in lower levels of species richness than before the fire (Waldrop et al., 2006). The results from our study partially demonstrate our initial hypotheses. Although we expected differences immediately after burning, the total richness of fungal communities in the entire plots was not significantly different four years later, which may be evidence that prescribed fire had a non-destructive effect on most of the fungal populations in the study area, which can have very interesting implications to support scientific based decision for the forest managers. This could be due to the fire behaviour given that the ignition pattern of the prescribed fire favoured rapid advancement of the front and, therefore, a short residence time in the soil, thus preventing overheating, excessive consumption of organic matter, or high temperatures being reached in the soil (Espinosa, et al., 2020b). The lesser effects of prescribed burning on the soil compared with wildfire are important factors for the survival and growth processes of soil fungi (Bean et al., 2009). Our findings agree with those of Oliver et al. (2015) who reported that low-intensity prescribed burning does not affect the richness of fungal communities. In the case of low-intensity fires, fungal species in the soil were able to take advantage of the conditions created by the burning (Bean et al., 2009) and flourish in abundance following the fire and, thus, fungal richness did not differ from unburned stands. However, we expected to find an influence of prescribed burning on the diversity estimators, which showed significant differences among treatments. This result might indicate that the fungal communities in the three forest stands do not share similar gene profiles, which might promote fungal communities with differing compositions (Mundra, 2015). This result might also be explained by the fact that fungal communities in burned areas undergo taxon re-ordering rather than loss of species in the community constituents and indicate that the fungal diversity of the community in the fire-
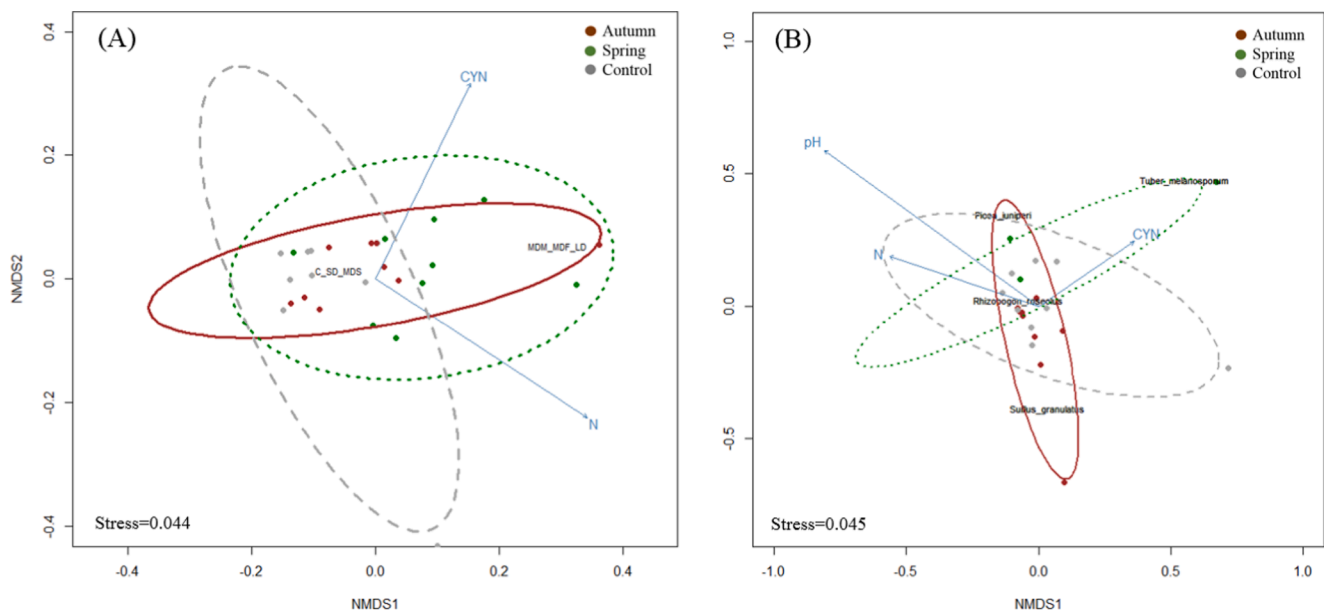
Fig. 5. Non-metric multidimensional scaling (NMDS) ordination graphs based on dissimilarities calculated using the Bray–Curtis index of soil fungal community composition by exploration types (A) and edible species (B) across prescribed burning treatments in *Pinus nigra* stands, Spain. The ellipsoids indicate stands belonging to the same treatment group. Edaphic variables are shown in blue. CYN indicated the C/N ratio. Abbreviations: C_SD_MDS, contact/short-distance/medium-distance smooth with hydrophilic hyphae; MDM_MDF_LD, medium-distance mat/medium-distance fringe/long-distance with hydrophobic hyphae. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

affected area would be distinct from that of others (Oliver et al., 2015). The high recovery rate of soil fungal communities after the occurrence of fire might also be one of the factors for such occurrences. This assumption is supported by Mediavilla et al. (2014) and Dejene et al. (2017) who reported rapid recovery of fungi in Mediterranean *P. nigra* stands five years after the occurrence of fire and in other forest systems only a year after the disturbance, respectively.

When analysing richness by phylum, the richness of Chytridiomycota was greater in burned plots than in unburned plots. The *Spizellomyces* and *Rhizophlyctis* were the largest genera of Chytridiomycota detected in this study (representing 50% of Chytridiomycota OTUs). Members of these genera are abundant in grassland ecosystems (Lozupone and Klein, 2002) owing to their particular nutritional requirements (Willoughby, 2001). In addition, species of *Rhizophlyctis* genera have been reported to grow saprophytically on damp-rich soils (Ward, 1939). In our plots, the burning treatments reduced the scrub and created an opportunity for new grass to cover the area, which may explain the abundance of Chytridiomycota in the study area (Loydi et al., 2020). The high number of Chytridiomycota species in the burned plots might also be due to their ability to accumulate nutrients either in the soil or to use other remnants of organic matter after the fire (Bonello et al., 1998). Another explanation for higher numbers of Chytridiomycota in spring-burned plots than in other plots might be the presence of fewer fungal competitors, which is linked to the slower recovery of scrublands and fungi. In this study, we also found higher levels of Zoopagomycota and Rozellomycota richness in autumn-burned plots than in spring-burned plots. Given that members of the Zoopagomycota and Rozellomycota are parasitic fungi (Cai et al., 2011), the less favourable climate conditions that followed the autumn burn could have given them opportunities to establish well in the area. After a fire, saprotrophic fungi play a role in the mineralization of nutrients and the stabilization of soil moisture (Dighton et al., 1986), which could also be the reason for their higher richness levels in these areas. The non-significant differences in Zoopagomycota richness in control plots could also be linked to shrub mortality owing to their senescence and higher density. Concerning the richest phyla, Ascomycota and Basidiomycota richness did not seem to be affected by any of the treatments, indicating that members of the Ascomycota and Basidiomycota were able to recover well after prescribed burning (Holden et al., 2016). This could be because the intensity of the prescribed burning in our study area was low (Espinosa et al., 2018; Espinosa et al., 2020a; Espinosa et al., 2020b).

When considering the fungal trophic level separately, we also found that saprotrophs were not affected by prescribed burning or by the season in which the prescribed burning was carried out. Saprotrophic taxa are expected to recover relatively quickly after a fire (Santos-Silva and Louro, 2016) compared with other trophic groups. This might be because of the attributes of the new ecological conditions that are created by fire, which may have supported the spore germination of several fungal species in the soil (Heino, 2012) following the fire in the investigated forests. In addition, the increase in the amount of dead material available (Franco-Manchón et al., 2019) might explain the rapid recovery of fungi after prescribed burning in spring or autumn. Generally, a disturbance, such as fire, has negative effects on ECM fungi; however, this does not apply to all types of fire (Salo et al., 2019; Salo and Kouki, 2018). In this study, ECM fungal richness did not differ significantly between treatments, possibly because the heat generated by the prescribed burning was not high enough (Espinosa et al., 2018; Espinosa et al., 2020b) to cause change (Dahlberg et al., 2001; Taudière et al., 2017). Hence, mycorrhizal fungi in the soil may have been able to escape the penetrating heat being associated with forests that have been affected by burning for generations (Dahlberg et al., 2001). In addition, the mycelium of fungal species in the rhizosphere may persist without being affected by fires (Cowan et al., 2016), or the ECM fungal community in the study forests may be resilient to the effects of fire to some extent (Cowan et al., 2016; Jennings et al., 2012). Thus, the responses of ECM fungi in the study area to prescribed low-intensity fire might also

appear to be minimal. However, further studies are needed to confirm such justifications for prescribed burning in the study areas.

With regard to the effect that season has on the outcome of prescribed burning, although the impact was not statistically significant, there was a tendency for higher ECM richness in spring-burned plots than in autumn-burned plots. This result is consistent with the ECM short-exploration type, which was the dominant type in this study and is typical of Mediterranean stands (Castaño et al., 2018). These results can be linked to the climate conditions after the prescribed burn treatments were performed, which influenced ECM resilience, as reported by Dove & Hart (2017). Because weather conditions can influence the growth of fungi (Talley et al., 2002), the moisture in Spring may favor the C_SD_MDS fungi, as these species are hydrophilic may predict their abundance and richness in this climatic condition. The other ecological implication could be the burns conditions which could favour a low allocation to belowground carbon are likely to favor the C_SD_MDS than the other exploration types in the area. Because the C_SD_MDS species form rhizomorphs that do not require as much carbon to construct than the other exploration types. Such conditions are likely to happen in areas where regularly affected by fire (Rúa, 2021), although the phenomenon needs further investigation to justify the case. However, the ECM long-exploration type did not differ significantly across treatments. This finding can be linked to the low abundance of this exploration type, in general terms, in the study area. Similarly, the availability of phosphorus could be one of the reasons, this is because long-distance explorers have enhanced capacity for soil exploration and may therefore exploit soil resources such as P more completely (Köhler et al., 2018; Kyaschenko et al., 2017). However, in our study, we found there is no difference in terms of P availability between the treatments, which might limit the availability of such kinds of ECM fungi and also which might be the reason for no significant difference in the ECM long-exploration species. The higher richness of the ECM short-exploration type compared with that of the ECM long-exploration type was expected given the higher root densities in mature stands (Geml, 2019) and the dry conditions of Mediterranean ecosystems (Castaño et al., 2018). Immediately after fire treatments, a reduction in ECM richness was expected (Hernández-Rodríguez, 2017) owing to the reduction or absence of host plants (Franco-Manchón et al., 2019), followed by a recovery phase (Hernández-Rodríguez, 2017). Holden et al. (2016) also noticed the sensitivity of mycorrhizal groups to fire severity, and also a greater reduction in soil C accumulation in more severe fires. In our study, mineral soil layers did not differ across treatments and were expected to have recovered 3–4 years after the fire (Fontúrbel et al., 2016). However, a higher N content was found in the spring-burned plots than in the control plots and a higher C/N ratio, C content, and organic matter content in spring-burned plots than in control or autumn-burned plots. This trend for higher ECM fungal richness in more organic soils is contrary to the findings of previous studies (Alem et al., 2020; Castaño et al., 2020).

NMDS of the composition of the total fungal community and edible fungal species indicated that the fungal communities detected differed among the treatments. The ANOSIM analysis distinguished that the dissimilarity was between the spring and autumn burning treatments, although the difference was marginal among treatments in terms of their fungal species composition. This result is in line with Oliver et al. (2015) who indicated that the prescribed burning season had minimal effects on fungal community compositions. In addition, if prescribed burning is undertaken frequently, the burn could shift the overall community structure and may select for fire-adapted and/or fire-tolerant fungi (Oliver et al., 2015). However, other studies (Cairney & Bastias, 2007; Dove & Hart, 2017) have indicated that site factors, including edaphic variables, are more important than fire characteristics when analysing the effects of fire on belowground fungal communities (Dahlberg, 2002). Furthermore, different fungal species are likely to respond to environmental drivers in different ways (Crowther et al., 2013). Thus, in turn, the composition of soil fungal communities is directly correlated with

edaphic variables (Cozzolino et al., 2016). In this study, edaphic variables such as pH and K were correlated with the overall fungal community. Of these, pH is an important driver of fungal communities in terms of diversity, richness, and composition (Day et al., 2019; Tedersoo et al., 2020). The pH was assumed to be increased in burned areas owing to the production of oxides and hydroxides (Hul et al., 2015). However, the absence of a significant alteration in these parameters between treatments can be a key factor in the homogeneity of the composition of fungal communities between treatments. Another factor supporting this argument is the lack of variation in the composition of the main phyla, Ascomycota and Basidiomycota. Zeng et al. (2020) reported strong links between pH and the composition of Ascomycota and Basidiomycota, supporting the homogeneity we found in their composition across treatments.

Although our analysis of trophic groups indicated greater levels of variability in community composition in spring-burned plots, no clear differences between treatments were found. Fire events are known to reduce or increase the strength of inter- or infra-specific competition between species and to promote the colonization of new host species in *P. nigra* stands (Mediavilla et al., 2014) with xerotolerant and heat-stimulated fungi still present in the field 4–6 years after the fire event (Robinson et al., 2008; Rutigliano et al., 2013). In this study, our analyses showed that the C/N ratio was one of the driving factors for the composition of fungal trophic groups. The C/N ratio of soil in autumn-burned plots and control plots was relatively low compared with that of the spring-burned plots (Table 1). The majority of the trophic group were clustered with values at the lower end of C/N ratios and only root-associated and lichenized fungi were associated with values at the higher end of C/N ratios. This result is inconsistent with Alem et al. (2020) who reported that a high C/N ratio negatively influenced fungal community structure, probably because a lower concentration of N restrains the expansion of fungi (Jarvis et al., 2013), which could also reduce the capacity of fungal communities to adapt to a warming climate in the long term. In addition, soil N enrichment has been shown to increase the richness and diversity of saprotrophic taxa, which could be a key factor in explaining our results (Morrison et al., 2016). Alem et al. (2020) noted that a reduction in the abundance and diversity of ECM was associated with an increase in soil N. Although this association was not observed in our study, it does suggest that perhaps the composition of this trophic group may alter after prescribed burning. In our study, ECM composition showed an increasing trend with increasing soil N content, which suggests that the composition of this trophic group is affected by soil fertility (Alem et al., 2020; Castaño et al., 2020, 2018).

Analysis of the ECM exploration type also revealed that the compositional difference was marginal between treatments. The ECM composition was marginally different in spring-burned plots to that detected in the control treatment, suggesting that this difference may be driven by the significantly higher N content in spring-burned plots. The variability in ECM composition was lower in control plots than in the burned plots, which could suggest that the fungal community in the control areas is more stable. This is because, if stability is defined at the species level, then less diverse assemblages can have higher species-level stability. This is because there is a limit to the number of individuals that can be packed into a particular community (Cleland, 2011). However, various aspects have to be dealt with before prescribed burning, such as seasonal changes (Castaño et al., 2018), fire severity (Castaño et al., 2018; Day et al., 2019), and the initial ECM biomass present in the soil before burning. These variables can modify ECM recovery after fire, and, hence, lead to variations in the ECM community composition.

In addition, fire can be used under controlled conditions in forest ecosystems to re-establish the whole suite of processes and conditions (Kalisz and Powell, 2000). Thus, some fungi are more sensitive to this kind of fire disturbance than others (Holden et al., 2016). Fungi reported responding positively after a fire including *Russula* sp. and Suillus (Oliver et al., 2015). We also found some interesting edible fungal OTUs, mainly belonging to suilloid genera (i.e., *Suillus* and *Rhizopogon*), as expected given their close relationship with their Pinaceae hosts (Glassman et al., 2016). These species are also pioneer species after the fire in *Pinus* and *Pseudotsuga* stands (Miyamoto et al., 2019). Interestingly, *Suillus* species found in both burned and unburned plots, particularly *S. granulatus*, were found abundantly. Although further studies are required to elucidate why these ECM fungi responded positively to fire in this study, we speculate that the low intensity of the prescribed burning might be the reason, particularly where soil physicochemical and biotic responses belowground are supposed to be minimal (Oliver et al., 2015; Southworth et al., 2011). However, the abundance of *Suillus* spp. was lower in spring-burned plots than in autumn-burned plots. This could be linked to competition from other fungal groups that are favored by the more rapid recovery of plants after spring burning than after autumn burning. About the *Russula* genus, we found no differences between burned and unburned areas. Miyamoto et al. (2021) noticed a greater prevalence of Russula in unburned areas than in burned areas due to their late-successional character. The presence of *T. melanosporum* in our study area was also an important finding, which is known to be collected nearby in areas of *Quercus* stands. Thus, the existence of *T. melanosporum* in our study plots might be associated with dispersion by animals from nearby *Quercus* stands (Ge et al., 2017). Although no differences in abundance were found across treatments, suggesting that the influence of prescribed burning 4 years earlier had not influenced their populations, the detection of this highly valued edible species in the study area is important because of its potential commercial use.

5. Conclusions

In the context of global warming and fuel accumulation in Mediterranean forests, new tools are needed to prevent wildfires. Although fungal communities are an important part of these ecosystems, their ecological and economic roles are frequently not taken into consideration when forest management plans are designed. Insights regarding the effect of prescribed burning on these communities could help managers to arrive at an optimal solution. Thus, this study describes, for the first time, the soil fungal community in Mediterranean natural forests of *P. nigra*, analysing how these fungi are affected by prescribed burning treatments carried out in different seasons. Four years after the treatments were applied, no differences in the richness or composition of fungal communities between control and burned areas or between spring-burned and autumn-burned areas were detected. However, specific differences at phyla and trophic levels were found. Chytridiomycota, Rozellomycota, and Zoopagomycota showed different tendencies due to their behavior. A trend for higher levels of the richness of ECM fungi in spring-burned plots was observed, and their composition was linked to less-fertile areas. Some interesting edible species were found in the study area, and no alterations in their abundance and composition were found after prescribed burning in spring or autumn. Our results suggest that prescribed burning, which is an interesting tool for reducing fuel accumulation under trees to minimize the spread and severity of wildfire, is compatible with maintaining the diversity of soil fungal communities and with the conservation of some valuable fungi, which can potentially generate additional income for rural populations. This can be especially important in poor rural areas. Given that this study was undertaken in natural forests where fungal communities can be more resilient, further studies in forest plantations are needed to get a better understanding of the potential use of prescribed burning as a management tool for reducing the impact of wildfire in other types of forest. Finally, special attention should be given when developing management plans involving prescribed burning to optimize its effectiveness as a wildfire prevention tool while at the same time reducing the impact of this management tool on the fungal community and also of other ecological parameters.

CRediT authorship contribution statement

Aitor Vázquez-Veloso: Data curation, Writing – original draft. **Tatek Dejene:** Data curation, Methodology, Writing – review & editing. **Juan Andrés Oria-de-Rueda:** Supervision. **Mercedes Guijarro:** Methodology, Writing – review & editing. **Carmen Hernando:** Supervision. **Juncal Espinosa:** Data curation, Writing – review & editing, Methodology. **Javier Madrigal:** Investigation, Methodology, Conceptualization, Supervision, Funding acquisition. **Pablo Martín-Pinto:** Conceptualization, Methodology, Investigation, Supervision, Writing – review & editing.

Declaration of Competing Interest

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

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