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Co-responses of bacterial and fungal communities to fire management treatments in Mediterranean pyrophytic ecosystems



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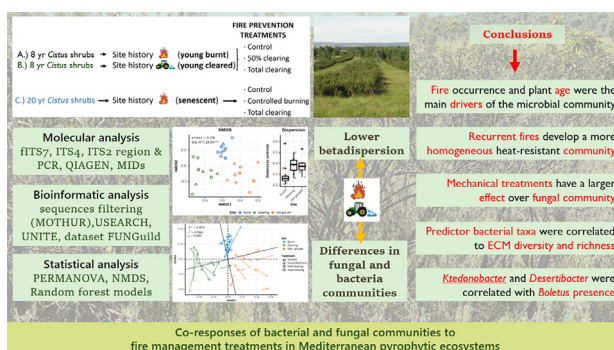
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HIGHLIGHTS

- Fire occurrence and plant age were the main drivers of the microbial communities.
- Recurrent burned areas develop more homogeneous heat-resistant communities.
- Clearing treatments have a larger effect on fungal communities than bacterial communities.
- Predictor bacterial taxa related to total fungal and ectomycorrhizal diversity and richness were identified.
- The bacteria *Ktedonobacter* and *Desertibacter* correlated with *Boletus* species.

GRAPHICAL ABSTRACT



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ABSTRACT

Cistus scrublands are pyrophytic ecosystems and occur widely across Mediterranean regions. Management of these scrublands is critical to prevent major disturbances, such as recurring wildfires. This is because management appears to compromise the synergies necessary for forest health and the provision of ecosystem services. Furthermore, it supports high microbial diversity, opening questions of how forest management practices impact belowground associated diversity as research related to this issue is scarce. This study aims to investigate the effects of different fire prevention treatments and site history on bacterial and fungi co-response and co-occurrence patterns over a fire-risky scrubland ecosystem. Two different site histories were studied by applying three different fire prevention treatments and samples were analyzed by amplification and sequencing of ITS2 and 16S rDNA for fungi and bacteria, respectively. The data revealed that site history, especially regarding fire occurrence, strongly influenced the microbial community. Young burnt areas tended to have a more homogeneous and lower microbial diversity, suggesting environmental filtering to a heat-resistant community. In comparison, young clearing history also showed a significant impact on the fungal community but not on the bacteria. Some bacteria genera were efficient predictors of fungal diversity and richness.

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For instance, *Ktedonobacter* and *Desertibacter* were a predictor of the presence of the edible mycorrhizal bolete *Boletus edulis*. These results demonstrate fungal and bacterial community co-response to fire prevention treatments and provide new tools for forecasting forest management impacts on microbial communities.

1. Introduction

Microorganisms can co-evolve in communities including microbial species from a broad diversity of fungal and bacterial families (Peleg et al., 2010; Scherlach et al., 2013). Synergies between fungi and bacteria are essential for forest ecosystems, and mediate several important ecosystem services, such as nutrient cycling, organic matter decomposition, and energy flow (Courty et al., 2010; Felsmann et al., 2015). Interactions between fungi and bacteria contribute significantly to the balance between plant health and diseases (Deveau et al., 2018; Frey-Klett et al., 2011; Whitman et al., 2019). Furthermore, bacteria can directly feed on fungal mycelia and they can act as commensalisms by consuming fungal exudates and products of decomposition. Similarly, fungi have mutualistic interactions where fungi gain protection against fungicides by the bacteria. However, forest disturbances influence multiple factors that can affect the composition of fungal and bacterial communities through the alteration of the composition of tree species, and the proportions of biomass contributed to the soil (Whitman et al., 2019), as well as several soil physical and chemical properties. Such forest disturbances also influence many components of the ecosystem including, for example, the availability and quality of resources for microbial development regarding leaf litter, pH, or the presence/absence of ECM hosts, which leads to structural and successional alterations of the fungal and bacterial communities (Goldman et al., 2015; Purahong et al., 2015).

Scrublands dominated by *Cistus ladanifer* L. are distributed throughout the Mediterranean basin (Hernández-Rodríguez et al., 2013; Martín-Pinto et al., 2006) owing to their historical adaptation to recurrent fires in this region (Hernández-Rodríguez et al., 2013). Studies have demonstrated that microbial diversity is high in *Cistus* scrublands (Comandini et al., 2006; Hernández-Rodríguez et al., 2015; Martín-Pinto et al., 2006). *Cistus* are obligate pyrophytic shrubs, which frequently colonize highly degraded areas after fire. High temperatures generated by a fire in the top soil layers trigger its seed germination (Bastida and Talavera, 2002). Thus, fire plays a key role in structuring plant communities and affecting the microbial communities drastically (Castaño et al., 2019; Oria-de-Rueda et al., 2008). For instance, in the northwest of the Iberian Peninsula, it is very common to use fire controlling shrub encroachment (Hernández-Rodríguez et al., 2015). Such management could modify not only the vegetation but may also alter soil properties, which may have a direct effect on the below-ground microbial communities including bacterial and fungal species (Mediavilla et al., 2020; Savoie and Largeteau, 2011). Shrub clearing is effective in terms of wildfire risk reduction and improving the water status of trees (Lecomte et al., 2022). As with prescribed burning, clearing generates new niches that have been observed to improve production and diversity for both fungal and bacterial communities (Bonet et al., 2004; Hernández-Rodríguez et al., 2015; Mediavilla et al., 2019). However, clearing treatments should not drastically affect the soil's chemical properties (Castaño et al., 2018), but may impact environmental conditions such as solar incidence, moisture, or even biomass available to decompose (Sanz-Benito et al., 2022). In this context, forest fire prevention treatments are needed to reduce the risk of altering belowground communities, and their pivotal roles in these ecosystems derived from wildfires.

Knowledge of soil microbial communities' response to fire disturbance and the development of fire prevention mechanisms is vital, particularly in *C. ladanifer*-dominated shrubland where forest wildfire is a common phenomenon (Martín-Pinto et al., 2006). However, studies investigating soil microbial diversity in this ecosystem are still scarce. Although our previous studies suggest that soil fungal and bacterial community shifts in response to fire are likely to occur and showed similar trends (Castaño et al., 2020;

Mediavilla et al., 2020), no studies have fully characterized the co-occurrence and co-responses of fungi and bacteria communities to different fire prevention treatments in *C. ladanifer* dominated ecosystem. Interestingly, given their ectomycorrhizal ecology, *C. ladanifer* ecosystems can sustain a high diversity of valuable edible mushroom species, including *Boletus edulis* (Oria-de-Rueda et al., 2008). In this regard, the interactions between fungi and bacteria in the soil are likely to affect sporocarp development and production (Antony-Babu et al., 2014). Thus, understanding whether fungal and bacterial communities respond to different fire prevention options such as clearing or prescribed burnings to reduce fuel accumulations in a similar way is essential because these microorganisms are the vital components of the plant–fungus–bacteria tripartite symbioses (Barbieri et al., 2005; Bonfante and Anca, 2009; Deveau et al., 2018). For example, the symbiotic development of fungi on plant roots is influenced by the bacteria present in the mycorrhizosphere (Barbieri et al., 2005). Specific bacterial–fungal associations are well documented, such as that of *Burkholderia* spp. that protect fungal symbionts in *Lyophyllum* from antagonistic agents (Marupakula et al., 2016; Nazir et al., 2014), or specific ecological roles of mycorrhizal helper bacteria that mediate symbioses between plants and fungi (Frey-Klett et al., 2007; Meade et al., 2020). Additionally, studying bacteria and fungi independently may overlook co-occurrence resulting from habitat sharing or interactive associations. In addition, understanding bacterial and fungal relationships is critical for predicting ecosystem functioning and for using bacteria as predictors of fungal diversity and abundance. Therefore, studying the relationship between fungal and bacterial communities can provide information for management practices and the technical use of microbes to improve forest function.

In order to test the effects of site history and forest management on bacterial and fungal communities, we studied three areas with different site histories to assess if bacterial and fungal communities under different management treatments respond similarly to the same treatments. Our specific objectives were: (1) to test the co-responses of fungi and bacteria to different fire prevention treatments and site histories in terms of fungal richness, abundance, and composition, and (2) to evaluate the co-occurrence patterns of fungal and bacterial communities. We hypothesized that the application of different management treatments (prescribed burning, total and partial clearings) would differentially affect the soil fungal and bacterial communities and that this effect would be more pronounced in fungal than bacterial diversity. This is expected as the mycorrhizal component of the microbiome depends directly on living plants to survive. Furthermore, we expected that the effect of fire treatments would have the greatest impact on both communities, given fires directly affect soil processes and microbial viability. To address these hypotheses, we characterized soil bacterial and fungal communities from *C. ladanifer*-dominated scrublands in a long-term experiment where fire prevention treatments have been applied in North-western Spain.

2. Materials and methods

2.1. Description of the study area

This study was conducted in Zamora province, in the areas dominated exclusively by *C. ladanifer*, with ca. 80 % canopy coverage, located in North-western Spain. Zamora province is located at 41.692260/41.696931 N, –6.212323/–6.224103 W, with an altitudinal range between 750 and 780 m above sea level (m.a.s.l.) (Hernández-Rodríguez et al., 2015; Mediavilla et al., 2017). The study area is characterized by a sub-Mediterranean climate, with cool winters and warm to hot summers. The rainfall is mainly recorded during two seasons, spring and autumn,

with summer characterized by droughts. The annual rainfall in the study area ranges from 450 to 700 mm while the mean temperatures of the study area range from 14.5 to 15.8 °C. Climatic data were provided by the closest meteorological station (Alcañices, 0724617 Longitude-UTM, 4618218 Latitude-UTM, 29 T Grid and 806 m (a.s.l.), Spanish Meteorological Agency). According to the soil taxonomy (Soil Survey Staff, 2010), the soil was classified as Inceptisol suborder Xerept and characterized by stoniness, acidity (pH 5.0–5.5), and lack of calcium and phosphorus. Nitrogen and potassium availability was variable, with a good level of humification (García Rodríguez et al., 1964; Forteza et al., 1980).

2.2. Fuel reduction treatments

We established our study plots in *C. ladanifer* stands in 2010, taking into consideration the similarity of the stands in terms of ecological conditions such as climate, altitude, and soil. The plots were comprised of three areas with different ages and site histories: a) an eight-years-old stand regenerating from a wildfire, from now on “young burnt stands”; b) an eight-years-old stand following the total clearing of the previous stand, from now on “young cleared stands”; c) a 20-year-old stand following a wildfire, from now on “senescent stands”. Given the short cycle life of *C. ladanifer*, a stand of 20 years of age is considered senescent or declining (Oria-de-Rueda et al., 2008). Then after the establishment of the plots, the forest fire prevention treatments were applied depending on their feasibility following the age and vegetation characteristics of the stands. In the 8-year-old stand plots, the fuel reduction treatments were: 1) uncleared i.e., control; 2) 50 % cleared; and 3) total clearing. *C. ladanifer* mean height in the middle-aged stands (a and b) was 1.30 m when the treatments were carried out. Mechanized cutting practices (clearing) are used to control shrub density in these stands. In the 20-year-old stand plots (c), the treatments were: 1) uncleared i.e., control; 2) total clearing; and 3) prescribed burning. In the senescent stand, *C. ladanifer* mean height was 2 m. It is a senescent stand with characteristics (high density, presence of dead plants and branches and lichens –*Evernia prunastri*-covering the stems) that are optimal for the ignition and spread of fire. All were followed following the methods used in Hernández-Rodríguez et al. (2015). In summary, we studied three different areas with three treatments per area, and three plots per treatment, resulting in a total of twenty-seven plots sampled. The total clearing was carried out in the spring of 2010 with a New Holland TS115 tractor with a brush thrasher mower, whereas 50 % clearing was performed by two operators manually removing half of the plants with a brush cutter. Prescribed burning was performed with the help of Zamora EPRIF (Integral Fire Prevention Team) (Ministry of Agriculture, Food, and Environment) in October 2010 under favorable weather conditions that allowed ignition without the risk of any fire getting out of control. Treatments were performed in strips and boundaries were marked with wooden stakes. Perimeter security areas were established around the prescribed burning plots.

2.3. Sampling and molecular work

2.3.1. Sampling

Soils were sampled in April 2014, four years after the implementation of the fire prevention treatments. A total of twenty-seven sampling plots, in three different areas with three treatments per area, and three plots per treatment were established. Each plot covered an area of 100 m², with a rectangular shape (2 m × 50 m), and was established in accordance with previous studies (Luoma et al., 1991; Smith et al., 2002). At each site, five soil cores, 3.5 cm diameter and 26 cm deep, were taken 5 m apart from each other along the longitudinal axis of the plot (Taylor, 2002). The soil was dried at room temperature and coarse elements were discarded. The five cores were pooled resulting in a composite soil sample per site (Castaño et al., 2020).

2.3.2. Molecular methods

DNA was extracted from 0.25 g of dry soil per sample using PowerSoil® DNA Isolation Kit (MoBio Laboratories Inc., Carlsbad, CA, USA) following the manufacturer's instructions.

To characterize the fungal communities, the primer pair fITS7 (Ihrmark et al., 2012) and ITS4 (White et al., 1990) containing Ion Torrent adapters were used to amplify the ITS2 region (approximately 250 bp) of the nuclear ribosomal rDNA repeat. Regarding bacterial community, the primers 515F and 806R-trP1 (Caporaso et al., 2011; Caporaso et al., 2012) were used to amplify a ~ 255 bp portion of bacterial 16S rDNA. The ITS4 and the primers 515F primers were labeled with sample-specific multiplex identification DNA tags (MIDs). Triplicate PCR reactions for each sample were performed with an initial denaturation step at 95 °C (5 min); then 37 cycles of 95 °C (20 s), 56 °C (30 s), and 72 °C (1.5 min); a final extension at 72 °C (7 min). A negative control consisting of sterile water was included in each PCR being amplicon free on an agarose gel.

PCR products were quantified using QIAxcel Advanced System (QIAGEN). Samples were pooled in equimolecular amounts and sequenced using an Ion Torrent sequencer at the Naturalis Biodiversity Center (Leiden, The Netherlands). The sequencing Ion 318TMChip was used to allow the highest possible sequencing coverage.

2.4. Bioinformatic analysis

We used the online platform Galaxy (<https://main.g2.bx.psu.edu/root>) to demultiplex sequences according to samples and to remove sample-specific barcodes. Poor-quality ends were trimmed off based on the 0.02 error probability limit in Geneious Pro 5.6.1 (BioMatters, Auckland, New Zealand).

For fungal communities, sequences were filtered using MOTHUR based on the following settings: no ambiguous bases (maxambig = 0), homopolymers no longer than 10 nucleotides (maxhomop = 10), and length range from 150 bp to 400 bp (minlength = 150; maxlength = 400). Sequences were then collapsed into unique sequence types, while preserving their original read counts, and global singletons and putative chimeric sequences were removed with USEARCH v.8.0 (Edgar, 2010). The curated UNITE dataset of fungal ITS sequences (Abarenkov et al., 2010) was used as a reference dataset. The remaining sequences were grouped into operational taxonomic units (OTUs) at 97 % sequence similarity using USEARCH. We assigned OTU representative sequences to taxonomic groups using CONSTAX (Gdanetz et al., 2018) against the eukaryotic UNITE database version 8.2 (Abarenkov et al., 2020). We excluded OTUs with <70 % similarity or <150 bp pairwise alignment length to a fungal sequence. Finally, we performed a functional identification of the taxa using FUNGuild (Nguyen et al., 2016) with a cut-off for assigning the OTUs to functional guilds of 90 %. Sequencing raw data, together with post-clustered fungal community data and the environmental data is stored in the Mendeley dataset, DOI: 10.17632/gd22y3664f.1

For bacterial communities, sequences were filtered using USEARCH v.8.0 (Edgar, 2010) based on the following settings: all sequences were truncated to 200 bp, and sequences with expected error > 1 were discarded. For each sample, sequences were collapsed into unique sequence types, while preserving their counts and excluding singletons. The quality-filtered sequences from all samples were grouped into operational taxonomic units (OTUs) at 97 % sequence similarity and putative chimeric sequences were removed using USEARCH. We assigned sequences to taxonomic groups of bacteria based on pairwise similarity searches against the curated Gold database of the Ribosomal Database Project (Cole et al., 2014). Representative sequences of bacterial OTUs were submitted to GenBank with the accession numbers MK323080 – MK325185.

2.5. Statistical analysis

To test the effects of site history and fire prevention treatments on microbial communities' composition, we performed PERMANOVA using the

adonis function in the R package “vegan” (Oksanen et al., 2015). Considering the sequential nature of the *adonis* implementation of PERMANOVA we tested 3 different models: \sim Treatment * Site, \sim Site * Treatment and \sim Treatment, strata = Site. Also, to verify the results of the tests, we, therefore, tested for differences in dispersion around centroids using the *betadisper* function from the package “vegan” (Oksanen et al., 2017). We used non-metric multidimensional scaling ordination (NMDS) plots to investigate how samples clustered according to site history and management treatment and PERMANOVA to test for dissimilarity in fungus and bacteria community composition among a priori-defined sample group (Anderson, 2001). These were performed on the Bray-Curtis dissimilarities on previously rarefied data sets. Rarefaction thresholds were set to the number of sequences of the sample with the fewest number of sequence counts in each dataset.

To investigate the concordance between the composition of fungal and bacterial communities, Procrustes analysis was performed using the *protest* function with 9999 permutations (Munck et al., 2015) in the R software package “vegan” (Oksanen et al., 2017). Concordance represents similarity in β -diversity between two communities across samples or sample groups and can indicate co-occurrence or similar responses of both communities to environmental factors or treatments. A significant correlation between the fungi and bacteria community profile was confirmed if $p < 0.05$ (Forsberg et al., 2014).

Random forest models were used to estimate the amount of variation in fungal diversity attributed (e.g., explained) by bacterial relative abundances. Random forest models were generated using the *random Forest* function in the “randomForest” R package (Liaw and Wiener, 2002) on OTUs abundances normalized into z-scores. To remove redundant features (i.e., OTUs) and avoid overfitting, we performed feature selection with the *Boruta* function in the package “Boruta” (Kursa and Rudnicki, 2010). The method performs a top-down search for relevant features by comparing original attributes' importance with importance achievable at random, estimated using their permuted copies, and progressively eliminating irrelevant features to stabilize that test. Models were tuned to achieve the lowest and most stable out-of-bag (OOB) error estimate possible, and the best mtry value (number of OTUs sampled at random in the entire pool for each tree at each split) selected using the *tuneRF* function in the “randomForest” R package.

3. Results

3.1. Sequencing output

A total of 1,065,416 fungal sequencing reads, with a minimum of 19,705 reads per sample, passed quality filtering, representing 1688 fungal OTUs. A total of 63,199 bacteria 16S raw reads, with a minimum of 2337 reads per sample, passed quality filtering, representing 2165 bacteria OTUs. Graphical representations of the overall distribution of sample libraries (Fig. S1) of the fungi and bacteria are provided. Both figures indicated that the fungal and bacterial datasets are rarefied to minimum sequencing depth after separating the data from the entire sub-datasets.

3.2. Influence of treatments on the microbial diversity

Non-metric multidimensional scaling (NMDS) analysis showed that soil fungal and bacterial communities clustered according to site history (Fig. 1A and C). Site history explained about 28 % and 23.6 % of the variability in fungal and bacterial communities, respectively. Shepard diagram of non-metric fit illustrated that observed dissimilarities and the ordination distances were highly correlated (non-metric fit was 0.976 in fungi, and 0.968 in bacteria, respectively) (Fig. S2), which suggested that the ordination accurately represented the dissimilarity between samples. The dispersion component of beta diversity of the fungi and bacteria communities in each site was examined by measuring the average distance between group centroids. In both communities, a significantly lower beta dispersion was found in the young burnt sites ($p < 0.05$, Fig. 1B and D), indicating a more homogeneous composition due to a low turnover rate. The highest

beta dispersion of fungi and bacteria communities was found in young clearing and old-growth sites, indicating greater heterogeneity in their composition. However, no significant variation was observed between the young clearing and old-growth sites' beta dispersion regarding fungal and bacteria communities ($p > 0.05$) (Fig. 1B and D).

3.3. Co-occurrence of fungi and bacteria communities

Procrustes analysis showed that co-response patterns of fungal and bacterial communities regarding the treatments carried out over the studied area were quite correlated. The configuration for the Procrustes rotation of the NMDS plots (Fig. 2) exhibited a good-fit correlation between the two community structures based on Bray-Curtis dissimilarity metrics ($R = 0.7866$, $M2 = 0.3812$, $p: 1e-04$, Permutations: 9999). Longer arrows were mostly found in the young clearing sites indicating that young clearing sites contributed to greater differences in fungal and bacterial communities compared to other treatments.

3.4. Bacterial taxa predictive of fungal diversity

Through random forest modeling we identified bacterial taxa that were predictive of fungal diversity in our dataset. Four bacteria taxa were found significantly ($p = 0.003$) influencing the ectomycorrhizal (ECM) Shannon diversity, with the explained variation amount of 28.3 % (Fig. 3A). *Naxibacter* was the most informative bacterial taxa with a higher percentage of mean squared error (>0.02). Similarly, selected eight bacterial taxa were able to significantly influence ($p = 0.001$) the entire fungal diversity, with the explained variation amount of 51.39 % (Fig. 3B). *Duganella*, *Burkholderia*, and Gp2 are the most informative bacteria taxon with a higher percentage of mean squared error (>0.02).

Regarding the richness, seven bacterial taxa were found to significantly influence ($p = 0.003$) the total fungal richness, with an explained variation of 53.5 % (Fig. 4A). *Spartobacteria* and *Haliangium* were the most informative taxa in this case, with a higher percentage of mean squared error (>200). In addition, eight bacterial taxa significantly ($p = 0.001$) influenced ECM richness with an explained variation of 49.6 % (Fig. 4B). In this case, *Favisolibacter* and *Gemmata* were the most informative bacterial taxa with a mean squared error over 7.5.

Five bacteria were found significantly influencing ($p = 0.001$) the presence of *Boletus* in the studied areas, with an explained variation of 49.5 % (Fig. 5). The most informative bacteria were *Ktedonobacter* and *Desertibacter* with the higher percentage of mean squared error (>0.02).

4. Discussion

4.1. Influence of treatments on the microbial diversity

In this study, we examined variation in the responses of fungal and bacteria communities to fire management treatments in *Cistus ladanifer*-dominated scrublands, where forest fires are a common phenomenon (Hernández-Rodríguez et al., 2013). Despite the differences in fire prevention treatments applied to the study plots, analysis of fungal and bacterial community structure revealed a clear differentiation between site histories, as demonstrated by beta-diversity analysis (Fig. 1). Beta diversity in young burnt site communities for the fungi and bacteria was particularly low, showing a low turnover rate in time, in comparison to those observed in those historically young cleared or the old-growth sites.

The NMDS plots showed that each community clustered separately and young burnt plots were characterized by low levels of species dispersion as compared to that of the old growth and young cleared sites. This might be an indication of a more homogenous species composition in fire-affected areas. Thus, the effect of the fire may be significant in limiting the number and type of microbial species (Anderson et al., 2006). This result highlights the selective effects that fire has on the belowground microbial communities, maintaining only those able to resist or adapt to the new post-burning conditions (Greeshma et al., 2016). In

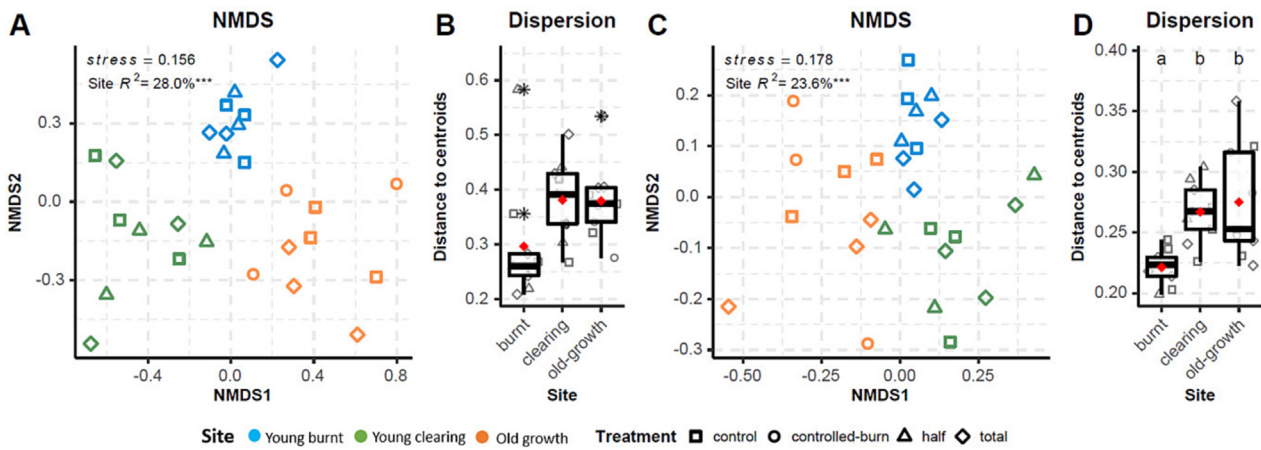


Fig. 1. Non-metric multidimensional scaling (NMDS) ordination of soil fungal (A) and bacterial (C) communities and box plots illustrating the beta dispersion of fungal (B) and bacterial (D) communities from centroids regarding site history and fire prevention treatments.

most cases, fire severity appeared to favor microbial taxa that are resilient to heat stress and able to rapidly colonize and take advantage of increased nutrients in the young burnt area. For example, studies that evaluated the responses of fungi to fire (Chen and Cairney, 2002; Hansen et al., 2019) indicate that fungi have developed a variety of evolutionary adaptations to fire, including heat-resistant spores, where species with such adaptations might be less compositionally altered by fire (Smith et al., 2021) and thus shows a high level of species similarity (Anderson et al., 2006). Indeed, some evidence indicates that pyrogenic ecosystems might host distinct soil fungal communities that can resist fire-related change (Hansen et al., 2019; Oliver et al., 2015). Others have also observed significant short-term rearrangement of fungal community structure after a fire, including within the same ecosystem types that were studied here (Semenova-Nelsen et al., 2019).

On the other hand, soil microorganisms also differ in their sensitivity to fire effects (Bárceñas-Moreno et al., 2009), and thus their respective community structure differs based on fire severity (Li et al., 2019). It has been

reported that bacteria are generally more resistant to heat disruption than fungi, and tend to recover more rapidly after a fire (Mabuhay et al., 2006). In this study, we observed an effect of prescribed fire on the structure of the bacterial community a few years after the disturbance. The lowest significant beta diversity of the bacteria community was found for the young burnt area as compared to the young clearing and old growth sites as we have seen for the fungal community. However, when compared to fungi, the beta dispersion of the bacterial community was much lower, indicating the higher homogeneity of the bacteria community composition in the young burnt sites of the study area than fungi. This shows that bacterial communities in young burnt areas are characterized by low species richness and diversity. Also, the vulnerability of bacteria to the immediate impacts of prescribed fire results in a lower degree of variation in the community structure. This result is in line with Mediavilla et al. (2019) and Ferrenberg et al. (2013) who observed a significant reduction of soil bacteria after the occurrence of fire, as the low-intensity fires may affect them through heat-induced mortality (Cairney and Bastias, 2007; Dooley and

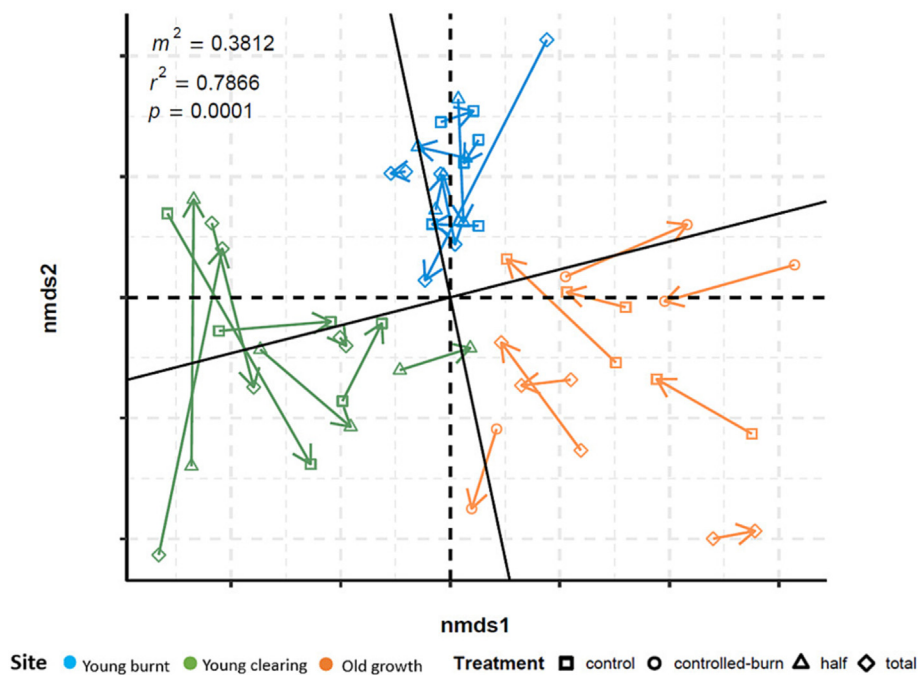


Fig. 2. Procrustes analysis showing the correlation between fungal and bacterial community structure based on NMDS (Bray-Curtis dissimilarity metrics) results ($m^2 = 0.3812$, $R = 0.7866$, $p = 0.0001$, 9999 permutations). Arrows connect the points (e.g. samples) of the fungal NMDS (start ordination) to points of the bacterial NMDS (end ordination). The length of the arrows represents the difference in distance between the samples in the ordination space.

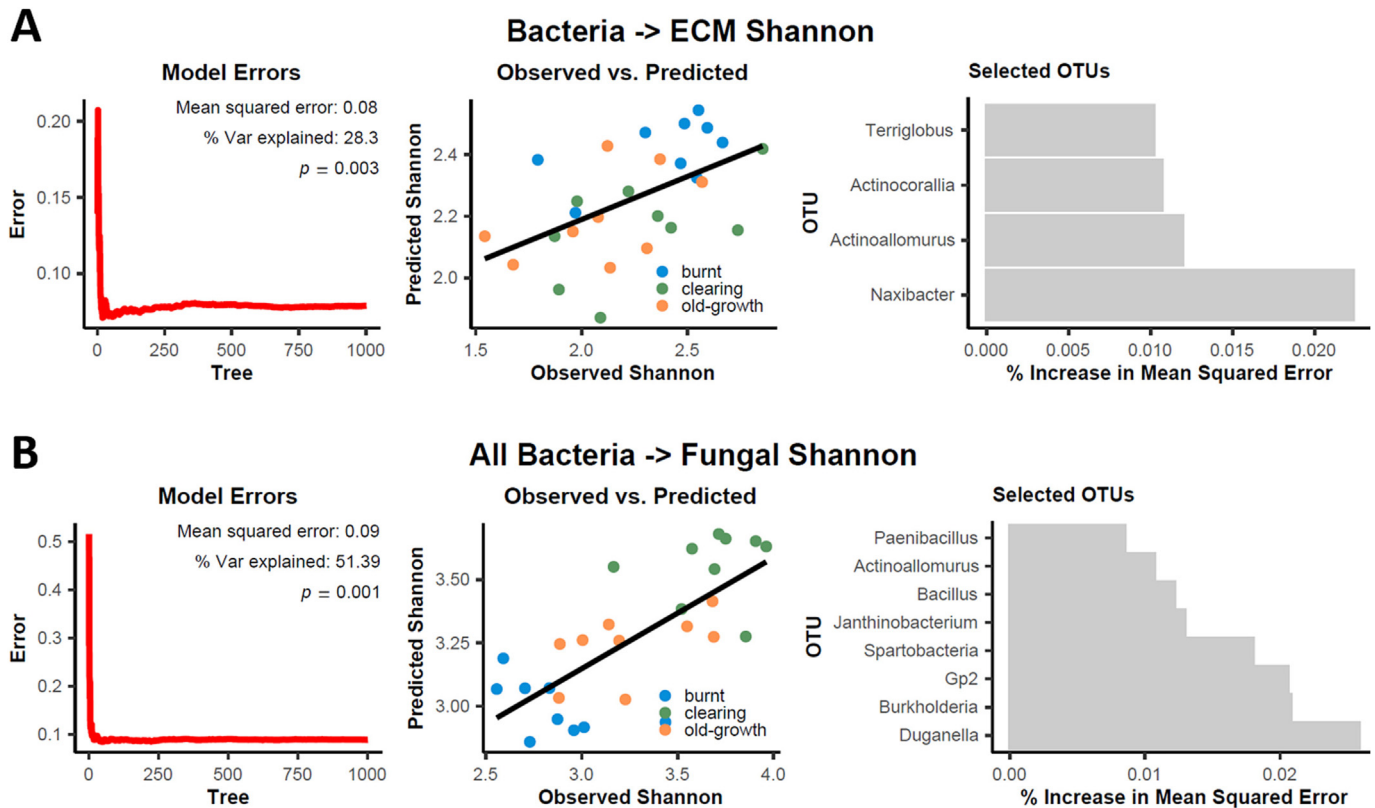


Fig. 3. Random Forest regression models (ITS and bacterial 16S sequences) for the co-response of bacterial communities and fungal Shannon diversity under the application of different management treatments (A for ECM fungi, B for all fungi). The histogram shows the most informative OTUs for the prediction of the model. The red lines are random forest error curves (i.e., out-of-bag error). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Treseder, 2012). Although it has been mentioned that bacterial communities tend to recover more quickly than fungal communities, recovery in burned sites may be slower in comparison to other disturbances (Smith et al., 2008). In most cases, the responses to fire are likely to change throughout recovery after fire and may persist till the vegetation regenerates (Cairney and Bastias, 2007; Dooley and Treseder, 2012; Parks et al., 2016). Moreover, soil pH has been reported to be an important factor and bacterial diversity decreased with the lower soil pH and thus affecting bacteria community composition after the fire (Lauber et al., 2009; Rousk et al., 2010). Also, fire may affect edaphic properties (Certini, 2005), which may have consequences on bacteria community composition (Sun et al., 2016). Thus, more research is needed to determine how these factors impact soil bacterial communities to understand the nature of the relationship between these factors and bacterial communities.

4.2. Co-occurrence of fungal and bacterial communities

Procrustes analysis indicated that the understory young clearing generated the greater significant differences in co-occurrence in terms of bacterial-fungal community, compared to young burnt and old-growth treatments. It has been demonstrated that fire can reduce fungal diversity, and this impact can persist for long durations, and indirect effects of fire, such as through increasing soil pH, can lead to a reduction of bacterial diversity as well (Adkins et al., 2020; Mediavilla et al., 2020). It is proposed that the co-occurrence of fungal and bacterial communities in young burnt areas is characterized by pyrophytic organisms that tend to appear commonly together and a burning disturbance (Ammitzboll et al., 2021; Knelman et al., 2015; Mediavilla et al., 2014). The removal of understory vegetation led to differentiated results in terms of diversity but appears to drive the microbial community of soils (Deng et al., 2022). It is possible that a faster recovery of the bacterial community, in an ecosystem that is considered mature in a relatively short-term of 8 years, leads to higher

heterogeneity (Mediavilla et al., 2020), favoring taxa with a faster colonizing ability to dominate the soil (Ammitzboll et al., 2021). It has been seen that bacterial communities along a secondary succession of originally agricultural lands diverge strongly (Zhang et al., 2016). However, greater differences in co-occurrence may result from the profound impact of young clearing treatments on the fungal community (Parladé et al., 2019; Sanz-Benito et al., 2022), particularly mycorrhizal fungi which are directly and negatively impacted by hosts removal (Castaño et al., 2020). This can be summarized as the higher values of beta dispersion in young cleared sites (Fig. 1B), likely due to a guild turnover of the fungal community. Meanwhile, bacterial communities remain unaltered. It has been seen that in young cleared areas fungal communities shift from Basidiomycota to Ascomycota-dominated (Yan et al., 2018). *Cistus ladanifer* is a pyrophytic plant (Águeda et al., 2008), thus, after fire treatments, its germination should be boosted by the heat effect (Valbuena et al., 1992), recolonizing the area quickly. Thus, the population dynamics of *Cistus* are not predicted to influence the community composition through vegetation shifts in young Burnt areas. Taken together, these data provide new insight into the overall correlations between the fungi and bacteria community compositions in the study area. However, it cannot decouple direct and indirect effects. Thus, further studies could provide an effective complement to the mechanisms that drive correlations in fungal and bacteria shifts.

4.3. Bacteria taxa predictive of fungal diversity

Naxibacter was the most predictive taxon for fungal diversity and has previously been reported as associating with ectomycorrhizal fungi (Marupakula et al., 2016). Belonging to Oxalobacteraceae family, these bacteria have been shown to have a phytopathogen control activity, through phosphorus stabilization, and a preference for fungi-derived sugars (Ofek et al., 2012; Scheublin et al., 2010). This may improve plant health, benefitting ECM fungi. The other three bacterial taxa were the most

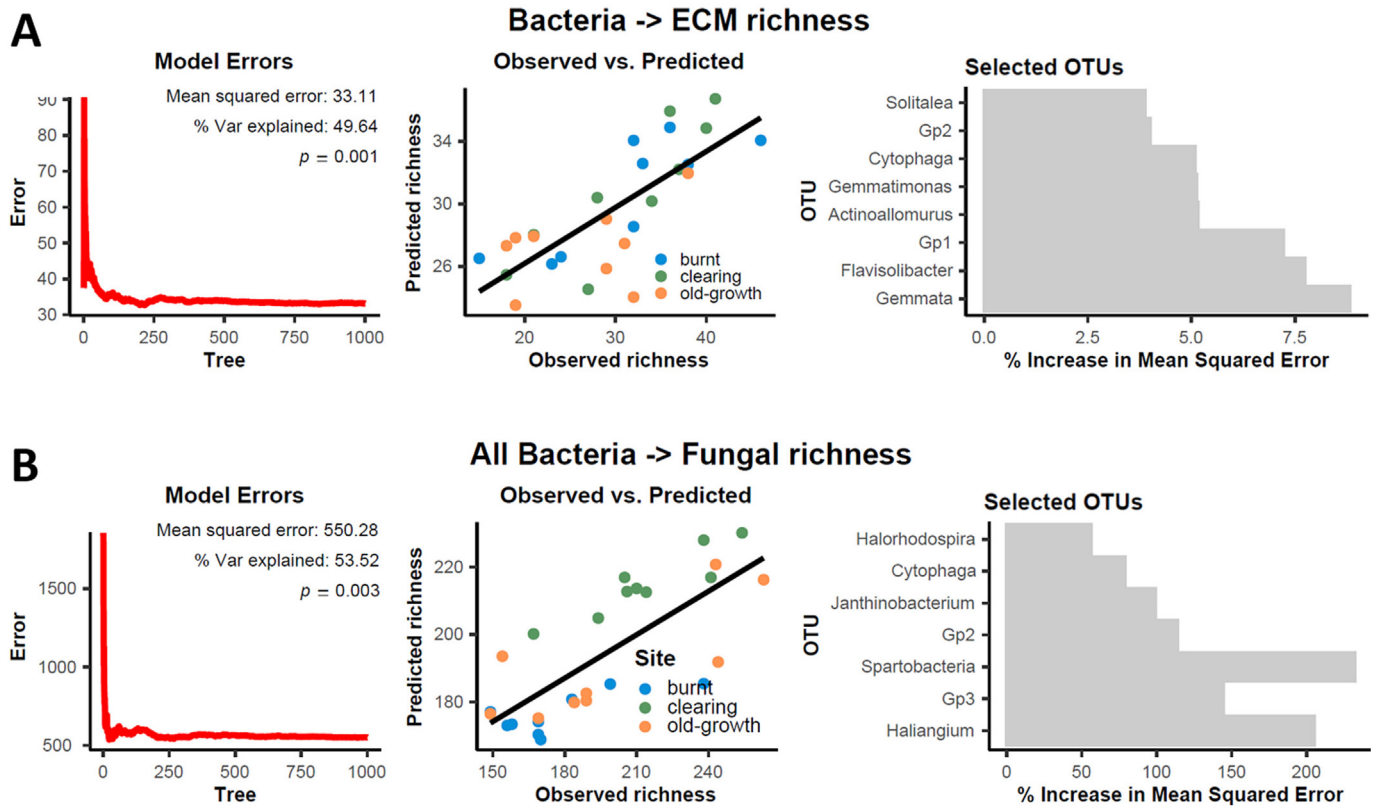


Fig. 4. Random Forest regression models (ITS and bacterial 16S sequences) for the co-response of bacterial communities and fungal richness under the application of different management treatments (A for ECM fungi, B for all fungi). The histogram shows the most informative OTUs for the prediction of the model. The red lines are random forest error curves (i.e. out-of-bag error). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

influential in total fungal diversity. *Duganella*, a member of Oxalobacteraceae, can help promote fungal diversity as described above, but also through N fixing and the production of indole-3-acetic acid (Meade et al., 2020). Furthermore, *Duganella* is a high producer of violacein, a pigment with antibacterial and anti-protazoal activity (Wang et al., 2009), as a proteolytic, lipolytic activity (Aranda et al., 2011) which can protect against fungal-attacking microorganisms. This bacterium can suppress *Fusarium graminearum* growth, a phytopathogen, but it also has an antifungal activity through chitinases (Haack et al., 2016). The order Burkholderiales is known as one of the most common fungal endobacteria groups, of a wide range of species, and it is a typical cellulose-degrading bacteria (Deveau et al., 2018). However, their

relationship with fungi can be either antagonist or complimentary depending on the edaphic environment (Eichorst and Kuske, 2012) as they can take profit from the fungal metabolites and overcome their defenses (Stopnisek et al., 2016). A higher density of this bacterial group has been seen in later-stage soils close to mature sporocarps than in bare soils, probably due to the degradation of the senescent mycelium of these mature fruit bodies (Orlofsky et al., 2021). This could relate the *Burkholderia* genus to a higher Shannon index for total fungal diversity observed in both cleared and old-growth stands due to the absence of bare soils. Moreover, *Burkholderia terrae* showed a protective activity of its host *Lyophyllum* sp. via shielding and detoxification against antifungal agents (Nazir et al., 2014) and an N₂ fixing activity (Estrada-De Los Santos et al., 2001), being

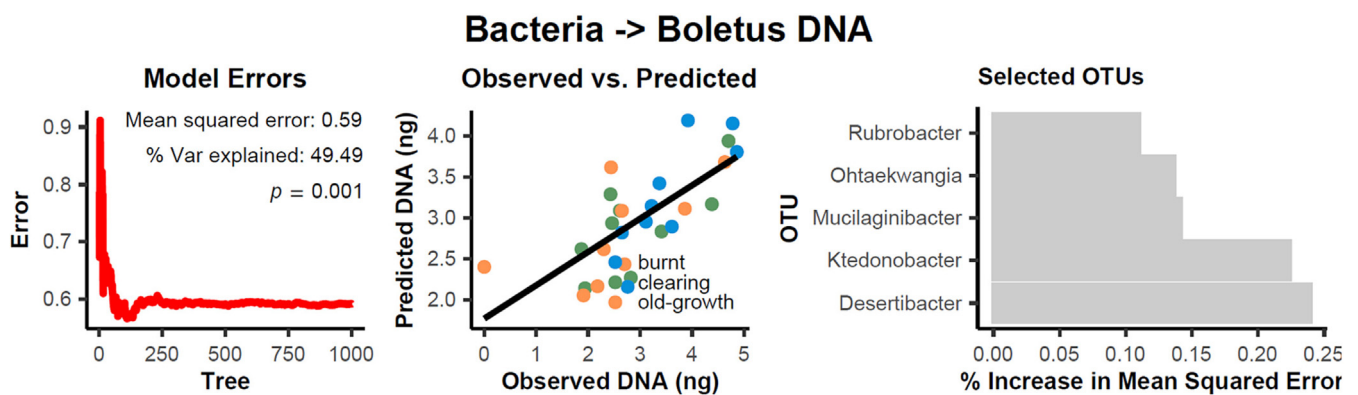


Fig. 5. Random Forest regression models (ITS and bacterial 16S sequences) for the co-response of bacterial communities and *Boletus* species under the application of different management treatments (A for ECM fungi, B for all fungi). The histogram shows the most informative OTUs for the prediction of the model. The red lines are random forest error curves (i.e. out-of-bag error). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

helpful in its acquisition in late stage stands with recalcitrant N. Gp2 it has been associated with late-stage forest soils and mycorrhizal fungi, with a positive response to N addition (Marupakula, 2016; Sui et al., 2019) but almost totally removed in soils with a high pH (Li et al., 2020; Praeg et al., 2020; Sui et al., 2019). It appears to be quite susceptible to fire, tending to disappear in burnt soils (Ammitzboll et al., 2021).

We found that *Spartobacteria* and *Haliangium* were among the most predictive taxa in terms of fungal richness. *Spartobacteria* is a class within the phylum Verrucomicrobia, which has been seen to be favored by acidic pH, correlating with an increase of C (Praeg et al., 2020). The abundance of *Spartobacteria* has been associated with roots colonized by *Paxillus involutus*, *Meliniomyces variabilis*, and *Russula* sp. (Marupakula, 2016; Marupakula et al., 2016) and correlates positively with tree growth (Cestaro et al., 2021). *Spartobacteria* is also linked to low C/N rate and low C inputs, which is associated with prairies or defoliated areas as could be the case of cleared stands (Ma et al., 2018; Maccherini et al., 2021). *Haliangium*, within the Myxococcales group, is a typical bacteria genus of oligotrophic areas (García-Carmona et al., 2021) and it has been described as a key component in vegetation restoration, especially in the biogeochemical processes (Hu et al., 2022). It produces haliangicin, a fungal growth inhibitor that can defend against pathogenic fungi (Gong et al., 2021; Kundim et al., 2003). Logically, it has a main role in the fungal richness and population in general.

Two genera of bacteria were particularly predictive concerning ECM fungal richness. The first was *Favisolibacter*, which has been found as one of the dominant bacterial taxa associated with some mycorrhizal species in *Pinus sylvestris* forests (Burke and Carrino-Kyker, 2021; Marupakula et al., 2016). Their abundance appears to decrease during dry periods (Bastida et al., 2019), and has been identified as an indicator of phosphorus-deficient soils (Khalid et al., 2021). Bacteroidetes, to which *Favisolibacter* belongs, are dominant in *Quercus* forests having high pH soils and are decomposers of cellulose (Lladó et al., 2017). Moreover, they are quite common in the rhizosphere of roots colonized by ECM (Burke and Carrino-Kyker, 2021).

Specifically related to *Boletus*, the abundance of *Ktedonobacter* and *Desertibacter* was positively associated with a higher presence of *Boletus* in these stands. *Ktedonobacter*, a Chloroflexi bacteria, has been associated with grasslands areas (Lin et al., 2021) and to low pH areas (Khalid et al., 2021), and dryer soils (Fulthorpe et al., 2020). This could be related to its influence in having a larger *Boletus* DNA in young burnt areas, as fire increases the pH of the soil through the liming effect and generates a hydrophobic layer in soil (Knicker, 2007), that promotes *Ktedonobacter* abundance and, then, *Boletus* DNA abundance. The other taxa that showed a high influence, *Desertibacter*, is known for being an extremely resistant bacterium, found in the desert of Taklamakan, with a high resistance to DNA-damaging agents (Ivo Baldani et al., 2013; Liu et al., 2011). Its higher influence could be related to being capable of resisting adverse situations, and thus fire effects, and being abundant after that disturbance and attaching it to the larger quantification of *Boletus* DNA. However, further research is needed regarding the functional role of *Desertibacter* in its relationship with *Boletus*.

5. Conclusion

This study revealed that regardless of the fire prevention treatments studied, site history drives the microbial communities. We observed that prescribed burning resulted in a homogeneous composition of microbial communities and lower beta-dispersion for both fungal and bacterial communities. The sharp reduction of microbial diversity and co-occurrence of bacterial and fungal communities in young burnt history plots indicates that fire is a strong selective agent. This selective effect results in a relatively homogeneous community of heat-resistant microbes and/or effective post-fire colonizers. Young clearing history also manifested a profound impact on the fungal community, but not on the bacteria. Our hypothesis of differential effects of treatments, with a larger impact on fungal community, was partly corroborated. However, fire did not differentially affect microbial

communities, and resulted in reduced diversity, homogeneous, and probably heat resistant and pyrophilus microbes. Meanwhile, the mechanical one did affect, differently, bacterial vs. fungal communities, the mycorrhizal community being more affected due to its hosting loss some bacteria were revealed as strong predictors of the fungal community. For example, *Duganella*, *Burkholderia*, and Gp2 (*Acidobacteria*) influence the total fungal diversity, *Naxibacter* was the most influential on ECM diversity, *Spartobacteria* and *Haliangium* were the most informative for fungal richness, and *Favisolibacter* and *Gemmata* for ECM richness. Finally, *Ktedonobacter* and *Desertibacter* were the best predictors of the *Boletus* presence. Overall, this study informs how fuel reduction treatments in forests can affect the microbial community, homogenizing in the case of fire or disturbing largely the fungal community regarding the young clearing effect. In addition, some bacteria genera are proposed as ecological indicators of fungal diversity, which may be a useful tool for mycosilviculture management systems.

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CRediT authorship contribution statement

Pablo Martín-Pinto: Conceptualization, Supervision, Methodology, Supervision, Writing – review & editing. **Tatek Dejene:** Writing – original draft, Writing – review & editing. **Gian Maria Niccolò Benucci:** Conceptualization, Formal analysis, Writing – review & editing. **Olaya Mediavilla:** Data curation, Formal analysis, Writing – review & editing. **María Hernández-Rodríguez:** Writing – review & editing. **József Geml:** Conceptualization, Methodology, Supervision, Writing – review & editing. **Petr Baldrian:** Supervision, Writing – review & editing. **Ignacio Sanz-Benito:** Writing – original draft, Writing – review & editing. **Jaime Olaizola:** Supervision, Writing – review & editing. **Gregory Bonito:** Supervision, Writing – review & editing. **Juan Andrés Oria-de-Rueda:** Supervision, Writing – review & editing.

Data availability

We have share the data of sequences for fungi and bacteria through the links in the M&M section

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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