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Tree traits drive phylogenetic and functional responses of soil fungal communities in Mediterranean forests subjected to recurrent fires

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Abstract

Wildfires are a natural disturbance in Mediterranean ecosystems, where plant species have usually developed fire-adaptive traits. In these fire-dependent ecosystems, fire-resistant fungal communities might co-evolve with fire-adapted plant communities, and long-term ecosystem stability may be a matter, not only of plants but also of associated soil fungi, particularly mycorrhizal species.

In this study, we investigated the soil fungal phylogenetic diversity and structure (ITS1-MiSeq, Net Relatedness, and phylogenetic structure indices) and functioning (soil enzymatic activities) in Mediterranean *Pinus halepensis* Mill. forests from two zones with contrasting fire regimes. We further aimed to differentiate the effects of tree genotypes (single nucleotide polymorphism assay for *Pinus* spp. fire-adaptive candidate genes) and phenotypes from those of environmental factors such as climate and soil conditions on fungal phylogenetic assembly and community.

Under high fire recurrence regime, the phylogenetic diversity of soil fungal communities decreased. Their phylogenetic structure also changed with fire regime, and pointed to a clustered community within the Basidiomycota clade. Fungal phylogenetic indices and higher abundances of ectomycorrhizal fungi under high fire recurrence were significantly related to higher activities of soil enzymes involved in nitrogen and phosphorus mobilization. The phylogenetic diversity and structure of soil fungal communities was primarily regulated by the phenotype of trees, and to a lesser extent by their genotype, while neither local climatic and soil conditions appeared to play a role. Our results suggest that long-term fire-induced changes in plant community occur with changes in phylogenetic and compositional shifts in soil fungal community with potential consequences for nutrient cycling. We propose that the adaptation of *P. halepensis* to recurrent fires may partly depend on the association with soil symbiotic fungi.

Keywords Fire recurrence, *Pinus halepensis*, Serotiny, Phylodiversity, Soil fungi, Soil enzymatic activity, Tree phenotype, Tree genotype

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Introduction

Wildfires are a natural disturbance in many ecosystems, including the Mediterranean ones, where fire occurrence is tightly linked to climate. As a consequence, many plant species have developed traits that allow them to resist fire and enhance their fitness in areas historically affected by fires (Keeley et al. 2011; Pausas 2015). *Pinus halepensis* Mill. is a widespread species across the Mediterranean basin and a clear example of a tree species adapted to fire. Some of the traits presented by this species that conferred advantage to fire are the existence of canopy seed bank (i.e., serotinous cones), sexual precocity (i.e., the ability to reproduce at a young age), or accumulation of lower branches to favor the onset of fire (Guiote & Pausas 2022; Pausas 2015). Generally, plant fitness is also determined by the interactions with a vast number of soil microorganisms to the point of being considered the extended phenotype (Jiang et al. 2024; Vandenkoornhuyse et al. 2015). Thus, relationships between *P. halepensis* and soil fungi might contribute to its persistence in fire-prone Mediterranean ecosystems.

Soil fungal communities represent a significant fraction of forest ecosystems and they are directly involved in the biogeochemical cycling of nutrients and the productivity of trees (Pérez-Izquierdo et al. 2021; Smith & Read 2008). Through the production of a wide set of extracellular enzymes, soil microbes, and fungi in particular, are able to decay biopolymers contained in the organic matter and mobilize nutrients (Baldrian 2014; Sinsabaugh 2010). Especially in nutrient-poor ecosystems as Mediterranean forests, fungi can determine plant productivity and fitness by enhancing the supply of growth-limiting nutrients such as nitrogen (N) and phosphorus (P) (Smith & Read 2008; Van Der Heijden et al. 2008). In such circumstances, it is estimated that up to 90% of P and N is provided by symbiotic mycorrhizal fungi and N-fixing bacteria (Van Der Heijden et al. 2008). Symbiotic fungi therefore represent a particularly important fungal guild in plant-soil interactions, to the extent that, for instance, the invasion success of pines seems to depend on a coupled plant-ectomycorrhizal fungal co-invasion (Policelli et al. 2023).

In fire-dependent ecosystems, fire-resistant fungal communities might co-occur with fire-adapted plant communities (Smith et al. 2021). Fungi have also developed different evolutionary adaptations to fire, such as ability to degrade aromatic carbon, production of heat-resistant spores or sclerotia, heat-stimulated spore production and even stimulation of growth (Fox et al. 2022; Glassman et al. 2016; Nguyen et al. 2013; Sari 2026). Since fire can kill certain fungi directly, recurrent fires can exert a strong selective pressure for fungal community evolution (Fox et al. 2022; Rincón et al. 2014). Since

fungi are key players in the plant–soil–microbial feedbacks, recovery of ecosystem structure and function after fire and long-term ecosystem stability may be a matter not only of plant but also fungal communities.

Phenotypic differences or similarities among species within a community are based in their evolutionary history, and it is commonly accepted that phylogenetically closely related species tend to be ecologically more similar than distantly related ones (Webb et al. 2002) and respond similarly to disturbance (Verdú & Pausas 2007). In that respect, recurrent fires are an important driving force in assembling phylogenetic plant community structure inducing a phylogenetic clustering of aboveground plant communities in Mediterranean ecosystems (Pausas & Verdú, 2008; Verdú & Pausas 2007). Following these aboveground vegetation patterns we analysed in the same set-up as Verdú & Pausas (2007), the influence of fire recurrence on soil fungal phylogenetic assembly, focusing on separating the relative effects of tree genotypes and phenotypes from those of environmental factors such as climate and soil conditions. In a previous study in the same study area, we have already observed that the taxonomic diversity of ectomycorrhizal fungi from root tips decreased in areas subjected to recurrent fires and it was related to climate and to the tree trait serotiny (Pérez-Izquierdo et al. 2020).

Here, we hypothesized that (i) as evidence suggests that fungal functional traits tend to be phylogenetically conserved (Goberna & Verdú, 2016; Kia et al. 2017; Maillard et al. 2018; Martiny et al. 2013), recurrent fires modulate the phylogenetic structure of soil fungal communities. We expected a decrease in fungal phylogenetic diversity in areas subjected to recurrent fires because of environmental filtering, by selecting competitive fungal clades with high relative fitness. We also envisaged that (ii) the high relative fitness of competitive fungal clades in fire-prone environments is associated with specific functions, i.e., enzymatic activities. Moreover, because the fire regime is strongly associated with climatic conditions and does directly affect the plant community (Pausas & Verdú, 2008; Verdú & Pausas 2007) and because different tree genotypes and/or phenotypes can directly influence their associated fungal communities and their phylogenetic structure (Gehring & Whitham 1991; Pérez-Izquierdo et al. 2017, 2019), we expected (iii) climate and tree phenotypes and genotypes of the dominant tree species, which in turn are modulated by the fire, to be determinant in structuring soil fungal communities.

To test these hypotheses, we determined the phylogenetic diversity and structure of soil fungal communities and the potential soil enzymatic activity in *P. halepensis* forests from two zones with contrasting fire regime. The tree genotypes were determined by a single nucleotide

polymorphism (SNP) assay enriched for well-known candidate genes for adaptive traits in Mediterranean pines (Budde et al. 2014). Our experimental setting allowed us to disentangle the effects of tree genotypes, phenotypes, climate and soil on fungal phylogenetic assembly and community structure in *P. halepensis* Mediterranean forests.

Material and methods

Study area and sampling

Natural populations of *P. halepensis* were selected in locations with different fire regimes in eastern Spain subjected to Mediterranean climate (Hernández-Serrano et al. 2013). Five pine populations were located in areas with historically frequent crown fires (hereafter HiFi populations), while three pine populations were located in zones with low fire recurrence (hereafter LoFi populations). Briefly, in the study area, fire is tightly linked to Mediterranean climatic conditions such as drought (Pausas 2004) and fire history information (Pausas 2004; Pausas & Fernández-Muñoz 2012) shows that more than 50% of the study area at HiFi conditions burned at least once during the period 1978–2001, while for LoFi conditions, the proportion was about 15% (Abdel Malak & Pausas 2006). Recurrent fires refer, hence, to multiple fire events occurring within the natural fire regime of Mediterranean ecosystems, where fire is a long-standing ecological and evolutionary driver rather than an exceptional disturbance. In these systems, fire-return intervals are highly variable (Eugenio & Lloret 2004). The mean fire-return interval in our study area decreased dramatically from 397 years during 1873–1972 to 49 years during 1973–2006 (Pausas & Fernández-Muñoz 2012). More recent studies in the Valencian Community indicate that fire recurrence remains high, with short fire-return intervals (< 10 years) occurring alongside much longer intervals (> 45 years) (Moghli et al. 2022). Moreover, in these areas distinct fire recurrence has induced a sharp serotiny divergence and genetic expression within the HiFi and LoFi populations, suggesting fire-related selection at the regional scale (Budde et al. 2017; Hernández-Serrano et al. 2014; Pinosio et al. 2014). All the stands were mature pine populations (i.e., more than 40 years old). More details about the study area and characteristics of the pine populations (i.e., temperature, precipitation, altitude and edaphic properties) can be found in Pérez-Izquierdo et al. (2020). Five trees separated by more than 10 m were selected within each population for a total of 40 trees ($n=25$ trees in HiFi+15 trees in LoFi). These trees had been previously geo-referenced and characterized for productivity (diameter at breast height (DBH)) and fire-adaptation traits, i.e., bark thickness and serotiny degree (Hernández-Serrano et al. 2013). Briefly, serotiny

was estimated by the number of closed cones (i.e., those remaining closed after maturation) with respect to the total fully ripe (open and closed) cones (see Hernández-Serrano et al. 2013, for details). Among tree phenotypic traits, trees in HiFi were 76% significantly more serotinous and had 12% higher DBH than LoFi populations (Table S1). Local climate conditions significantly varied between HiFi and LoFi sites with hotter and wetter conditions, as well as lower altitude in HiFi than LoFi plots (Table S1).

In May 2013, four soil samples were collected ~1 m from each tree trunk at the four orientations (north, south, east and west), by digging 10×10×20 cm soil holes after removing the litter layer. The four samples per tree were pooled into a composited sample and kept at 4 °C in plastic bags until processing ($n=40$). Tools were cleaned with ethanol between samples. Once in the lab, the soil samples were processed within 72 h. Soil was sieved (2 mm) and stored at – 20 °C for molecular analyses. Two aliquots of the remaining bulk soil were collected, one to perform enzymatic assays (on fresh soil) and a second aliquot that was air-dried for physico-chemical analyses. Data on gravimetric soil moisture, pH, electrical conductivity (EC), soil organic matter (SOM), total carbon (C), total nitrogen (N), and extractable phosphorus (P) and potassium (K) were previously collected by Pérez-Izquierdo et al. (2020). Soils, in general, had very low fertility (Table S1).

Molecular analysis and bioinformatics of fungal communities

Genomic DNA of soil samples (500 mg) was extracted with the PowerSoil DNA Isolation Kit (MOBIO Laboratories, Carlsbad, CA, USA). The internal transcribed spacer region ITS-1 of the fungal nuclear ribosomal DNA was amplified with the primer pair ITS1F-ITS2 (Gardes & Bruns 1993) adapted for Illumina-MiSeq. Samples were amplified in three independent 20- μ l PCRs (polymerase chain reactions), each containing 2 μ l of 10×polymerase buffer, 2.4 μ l of 25 mM MgCl₂, 1.12 μ l of 10 mg/ml bovine serum albumin, 0.4 μ l of 10 mM Nucleotide Mix, 0.4 μ l of 10 mM forward/reverse primers and 0.2 μ l of AmpliTaq Gold DNA polymerase (5 U/ μ l) (Applied Biosystems). Negative controls without DNA were included in all runs to detect possible contaminations. The PCR conditions were as follows: 3 min at 94 °C, 30 cycles of 1 min at 94 °C, 30 s at 53 °C and 45 s at 72 °C, with a final step of 10 min at 72 °C. Independent reactions were combined per sample, purified (UltraClean PCR clean-up Qiagen kit), quantified (PicoGreen, Life Technologies), and finally pooled in an equimolar library containing 40 samples tagged during the PCR amplification. The tagging, pooling and sequencing, carried out on an Illumina

MiSeq sequencer (2×300-bp paired-end reads), were performed in an external service (Parque Científico de Madrid, Spain).

Sequences were demultiplexed according to their tags, filtered and trimmed using the `fastq_filter` command and `fastq_truncqual` option of `usearch` version 7.0.1001 (Edgar 2013) for eliminating quality scores ≤ 10 . We used `flash` to merge reads with a minimum overlap of 110 bp, resulting in 62% of retained sequences (2,717,288 out of the initial set of 4,354,472 sequences). Then, sequences were dereplicated with the `derep_fulllength` `usearch` command. Dereplicated sequences were sorted by decreasing abundance, and singletons were discarded with the `sortbysize` `usearch` command. Finally, 2,672,346 sequences (61% out of the initial set) were retained.

Operational taxonomic units (OTUs) were generated from abundance-sorted sequences using the `cluster_otus` `usearch` command with a 97% similarity threshold. Extracted ITS sequences were then mapped against OTU representative sequences using the `usearch_global` `usearch` command. Taxonomic assignation of representative sequences for each OTU was done according to the 9.0 UNITE database (Abarenkov et al. 2022). Fungal taxonomic assignment served to identify those OTUs closely related to recognized fungal functional guilds (i.e., ectomycorrhizal, mold, yeast, saprotrophic, endophyte, lichenized, pathogen and parasite). To do that, we used FUNGuild (the assignments classified as “highly probable” were retained) and complemented manually from literature (Nguyen et al. 2016; Tedersoo et al. 2014; Tedersoo & Smith 2013).

Phylogenetic reconstruction and fungal community phylogenetic metrics

From the total OTU community, fungal phylogeny from 3102 fungal OTUs was approximated with the software *Phylomatic* as implemented in *Phylocom* v.4.2 (Webb et al. 2008) and *BEAST* v.1.5.4 (Drummond & Rambaut 2007). First, we constructed a genus-level tree from the literature and then, OTUs were inserted into this tree according to their taxonomic information (Pérez-Izquierdo et al. 2019; Pérez-Valera et al. 2018). Tree branch lengths were estimated from 43 dated nodes obtained from the literature (Pérez-Izquierdo et al. 2019; Pérez-Valera et al. 2018; Tedersoo et al. 2018). In order to resolve the polytomies, trees were generated with *BEAST* after running the *PolytomyResolver* script. Five phylogenetic trees were randomly selected after applying 25% of burn-in and were used for subsequent analyses.

The phylogenetic diversity and structure of the fungal community were defined by two phylogeny-weighted metrics on the constructed trees: the Net Relatedness Index (NRI) and the phylogenetic fuzzy-weighting

index PCPS. The NRI was calculated with the *picante* R package (Kembel et al. 2010). This computes $NRI = - (MPD_{obs} - MPD_{rand}) / sd_MPD_{rand}$, where MPD_{obs} is the mean pairwise phylogenetic distances of OTUs in the community, MPD_{rand} is the mean of MPD calculated after randomly shuffling the distance matrix labels of all OTUs and sd_MPD_{rand} is the standard deviation of MPD_{rand} (Webb et al. 2002). This allows examining whether co-occurring taxa are more (positive NRI) or less (negative NRI) closely related than expected by chance. The phylogenetic fuzzy-weighting method PCPS summarizes phylogenetic structuring continuously across the whole tree, from deep evolutionary splits to more recent lineage differentiation. PCPS defines the phylogenetic community structure by calculating a matrix (matrix P) (Pillar & Duarte 2010), where each OTU has a value per sample that increases as the phylogenetic distance between neighboring OTUs decreases. This matrix P was calculated with the *PCPS* R-package (Debastiani et al. 2015), and its dimensionality reduced by performing Principal Coordinate Analysis (PCoA) with Euclidean distances. Sample scores along the first principal component of the phylogenetic structure (PCPS1-Axe), which captures the deepest phylogenetic divergences among lineages (Duarte et al. 2012), were extracted and used in further statistical analyses as a single variable describing the community phylogenetic structure (Pérez-Izquierdo et al. 2019). The contribution of each fungal phylum (mean $\pm$ SE) was calculated as the loadings of each taxon to the respective PCPS1. To check for the reliability of our results regarding the phylogenetic tree used, we performed Pearson correlations between NRI and PCPS1 calculated with both the *Phylocom* and *BEAST* methods. The correlation values were 0.999, confirming the robustness of the analysis. For the sake of simplicity, we used a single tree for further analyses in each fungal community.

Enzymatic assays

Seven hydrolytic enzymes involved in C, P, and N cycling and commonly associated with fungal-mediated decomposition and nutrient mobilization in forest soils were selected. The enzymatic assays were performed on fresh soils using the method of Mathieu et al. (2013) with modifications (Pérez-Izquierdo et al. 2018). Briefly, the seven enzymatic tests were based on fluorogenic substrate release, methylumbelliferone (MU) or methylcoumarine (AMC), upon cleavage by the following enzymes. Enzymes involved in C degradation: MU- β -D-glucopyranoside (MU-G) for β -glucosidase (EC 3.2.1.3), MU- β -D-cellobioside (MU-C) for cellobiohydrolase (EC 3.2.1.91), MU- β -D-xylopyranoside (MU-X) for β -xylosidase (EC 3.2.1.37), 4-MU- β -D-glucuronide hydrate (MU-GU) for β -glucuronidase (EC 3.2.1.31).

Enzyme involved in P mobilization: MU-phosphate free acid (MU-P) for acid phosphatase (EC 3.1.3.2). Enzymes involved in N mobilization: MU-N-acetyl- β -glucosaminide (MU-Q) for chitinase (EC 3.2.1.14) and L-leucine-7-AMC (AMC-L) for leucine aminopeptidase (3.4.11.1) (Sigma-Aldrich Chemicals, Madrid, Spain). All enzymatic assays were done in 96-well microplates including controls performed by heating soil suspensions at 100 °C for 10 min. Reactions were performed at room temperature in the dark with different stirring incubation times depending on the enzyme. Measurements were carried out with a Victor microplate reader (Perkin-Elmer Life Sciences, MA, USA), with 355/460 nm excitation/emission wavelengths. Each experimental series included calibration wells of known MU or AMC concentrations and auto-fluorescence blanks.

SNP genotyping of *Pinus halepensis* trees

Each tree ($n=35$, five samples were missing) was genotyped using Illumina VeraCode® technology for a 384-plex Sngle nucleotide polymorphism (SNP) Oligo Pool Assay (OPA) (251 successfully scored and polymorphic SNPs) enriched for well-known candidate genes for adaptive traits in forest trees (Budde et al. 2014). This OPA includes polymorphic SNPs associated with climate variables in Mediterranean pines (*P. halepensis* and *Pinus pinaster* Ait.) (Grivet et al. 2011) and a wide representation of functional candidate genes for biotic and abiotic stress responses, serotiny, physical and chemical wood properties, phenology and growth (Budde et al. 2014; Eveno et al. 2008; Grivet et al. 2011; Lepoittevin et al. 2012; Pot et al. 2005). Tree genetic dissimilarity matrices derived from SNP analysis were obtained with the function *dist.gene* in ape R package (Paradis & Schliep 2019). Tree genetic distances were different between HiFi and LoFi populations (PERMANOVA; $F=1.32$; $R^2=0.04$; $P=0.050$) (Fig. S1).

Statistical analyses

All statistical analyses have been performed with R version 4.5.0 (R Core Team 2021). In order to determine if recurrent fires modulate the phylogenetic structure of soil fungal communities (*Hypothesis 1*), fungal phylogenetic indices NRI and PCPS1 were modeled by general linear mixed models (GLMMs) with the fire regime as fixed factor and the site as random factor ($p<0.05$). Residuals were checked for normality in all cases. The association of fire recurrence with fungal phylogenetic structure was tested by PERMANOVA analyses using the function *adonis* from vegan R package (Oksanen et al. 2013) on the matrixP (from PCPS), respectively. Results were drawn by Principal Coordinate Analysis (PCoA). Additionally, fire recurrence association with edaphic

properties, soil enzymatic activity, fungal richness and relative abundance of different fungal guilds was tested by GLMMs with the same syntax. Fungal richness (OTUs richness) was calculated after rarefying the abundance matrix to an equal sequencing depth across all samples. Differential abundance analysis of OTUs was performed using the R package DESeq2 (Love et al. 2014). False discovery rates were controlled using the Benjamini–Hochberg method, with OTUs considered statistically significant if they had an adjusted p -value (FDR) less than 0.05. We showed these results for the top 10 fungal OTUs under HiFi and LoFi. To evaluate the relationships of soil functioning with soil fungal phylogenetic structure (*Hypothesis 2*), separated GLMMs were run with enzymatic activities as response variables and NRI, PCPS1 and the relative abundance of different fungal guilds as explanatory variables, and the site as random factor. We also performed a sensitivity analysis based on repeated subsampling to assess whether the unbalanced sampling design (five HiFi vs. three LoFi populations) influenced model inference. In each iteration (total 100 iterations), three HiFi populations were randomly selected to match the number of LoFi populations. The linear mixed-effects models were then refitted using the balanced subset, including site as a random factor. The results of these analyses confirmed that our results were robust.

To separate the effects of tree genotypes and phenotypes, and climate and edaphic properties, on fungal phylogenetic diversity and community structure (*Hypothesis 3*), different analyses were performed. First, to reduce the dimensionality of each data set i.e., edaphic variables (pH, SOM, EC, N, P, K, C:N), climatic variables (mean annual temperature, mean annual precipitation, altitude) and tree phenotypic traits (DBH, bark thickness, serotiny), independent Principal Component Analyses (PCAs) were run for each data set and the first two axes (explaining the maximum amount of variance) of respective PCAs were used as edaphic, climatic and tree phenotypic trait indices to include as explanatory variables in models (Fig. S1). In the case of tree SNP genotypes, the first two Principal Coordinate Analysis (PCoA) axes representing the genetic dissimilarity matrix were used as explanatory variables for the models. To explore the relationships among edaphic variables, climatic variables, tree genotypes and phenotypic traits, Mantel tests were performed with the function *mantel.rtest* (9,999 permutations) in the ade4 R package (Dray & Dufour 2007). The Euclidean dissimilarity matrices of tree genotypes and phenotypic traits, and climatic and edaphic properties, were used for these analyses and all were calculated with the function *vegdist* in vegan R, except the tree genetic dissimilarity matrix that was obtained with the function *dist.gene*. Further, to determine if these variables (edaphic, climatic,

tree phenotype, tree genotype) explained the phylogenetic diversity (NRI) and structure (PCPS1) of their associated soil fungal communities, the relative abundances of the different fungal guilds and the enzymatic activities we ran GLMMs, with the site as random factor. In the models where we checked for the effect of the tree genotypes five sampling points were missing.

Results

We obtained a total of 2,672,346 sequences that were clustered into 6967 fungal OTUs. The mean $\pm$ SD number of sequences per sample was $65,577 \pm 7859$ in HiFi and $68,859 \pm 7303$ sequences in LoFi. After rarefaction, we observed 824 ± 185 OTUs in HiFi and 711 ± 143 in LoFi, which were not significantly different ($t = -2.13$; $P\text{-value} = 0.077$). Basidiomycetes were the dominant phylum (44% of total sequences), followed by Ascomycetes (38% of total sequences). Among the 10 most abundant fungi in HiFi, 5 species were ectomycorrhizal being 3 of them significantly indicative of this fire regime: *Tricholoma batschii* Gulden ex Mort. Chr. & Noordel. (96% more abundant in HiFi than LoFi), *Suillus collinitus* (Fr.) Kuntze (99.9%) and *Amphinema* sp. (91%) (Fig. 1). The 10 most representative fungal species in LoFi were saprophytic fungi. Among them, *Cryptococcus podzolicus* (Babeva & Reshetova) Golubev, *Penicillium restrictum* Thom, *Archaeorhizomyces* sp. and *Umbelopsis* sp. were significantly more abundant in LoFi than HiFi (Fig. 1).

Phylogenetic structure of soil fungal communities in HiFi and LoFi populations

Fungal phylogenetic community structure (matrix P) significantly differed between HiFi and LoFi (Fig. 2a). Soil fungal community was less phylodiverse (higher NRI index) in HiFi compared with LoFi, and PCPS1 results pointed to an overrepresentation and clustering of the phylum Basidiomycota in HiFi soils (Fig. 2b, c). The PCPS1, which captures deep phylogenetic differences among fungal lineages, explained 34.6% of the total variance of soil fungal communities, with similar contribution of Ascomycetes and Basidiomycetes (Fig. S2).

Relationship of soil fungal phylogenetic structure and soil functioning

Fungal community phylogenetic diversity (NRI) and structure (PCPS1) were significantly and positively related with potential soil chitinase (N cycling) and phosphatase (P cycling) activities, while no relation was observed with C cycling enzymes (Fig. 3; Table S2). This likely indicated the existence of a cluster of soil fungal communities, probably within the Basidiomycetes clade and more specifically of ectomycorrhizal fungi, explaining the high activities of enzymes related to nutrient

acquisition (Table 1). In fact, activities of hydrolytic enzymes that mobilize N (chitinase) and P (phosphatase) from organic matter were 40% and 37% significantly higher in HiFi compared with LoFi, while carbon hydrolyzing enzymes, i.e., glucosidase, cellobiohydrolase, xylosidase and glucuronidase, did not differ between HiFi and LoFi (Fig. 3; Fig. S3).

Potential soil enzymatic activities were not explained by tree genotypes, tree phenotypic traits, edaphic properties or climate, with the exception of chitinase that was related to climate (Table S3). When checking for cumulative effects of climate and fungal community phylogenetic indices on chitinase activity (i.e., GLMMs with climate and phylogenetic indices as explanatory variables in the same model, and the site as random factor), only the fungal phylogenetic indices were significantly related with chitinase (NRI: $F = 17.4$ $P < 0.001$; climate1 $F = 3.1$ $P = 0.087$; climate2: $F = 3.5$, $P = 0.072$; PCPS1: $F = 9.9$ $P = 0.004$; climate1: $F = 3.5$ $P = 0.070$; climate2: $F = 2.0$, $P = 0.168$).

Effect of tree genotypes, phenotypes, climate and edaphic properties on fungal phylogenetic diversity and community structure

Both soil fungal community phylogenetic indices NRI and PCPS1 were significantly related to tree phenotypic traits, and PCPS1 was also with the tree genotypes (Table 2). Neither climate nor edaphic properties significantly explained the phylogenetic structure of soil fungal communities (Table 2). When analysed by fungal guilds, we found significantly higher relative abundances of ectomycorrhizal fungi ($t = 3.75$; $p = 0.010$) and pathogen-parasites (marginal $t = 2.26$; $p = 0.064$) in HiFi, while molds prevailed in LoFi ($t = 4.08$; $p = 0.007$). The relative abundances of yeasts ($t = -1.47$; $p = 0.192$) and saprotrophs ($t = -1.52$; $p = 0.179$) did not change with the fire regime. Particularly, the relative abundance of ectomycorrhizal fungi and molds was significantly explained by *P. halepensis* phenotypes, while that of pathogens and parasitic fungi was significantly related to climate and edaphic properties (Table 3). The tree genotypes did significantly explain the abundance of soil fungal saprotrophs (Table 3).

Discussion

Our results show that fire recurrence is an important factor driving soil fungal communities in *Pinus halepensis* forests. We observed different phylogenetic and fungal guild community patterns between high and low fire recurrences, highly linked to the tree phenotypes. This entailed increased activities of enzymes involved in nutrient mobilization in high fire recurrence pine populations. We discuss the mechanisms underlying the relationship

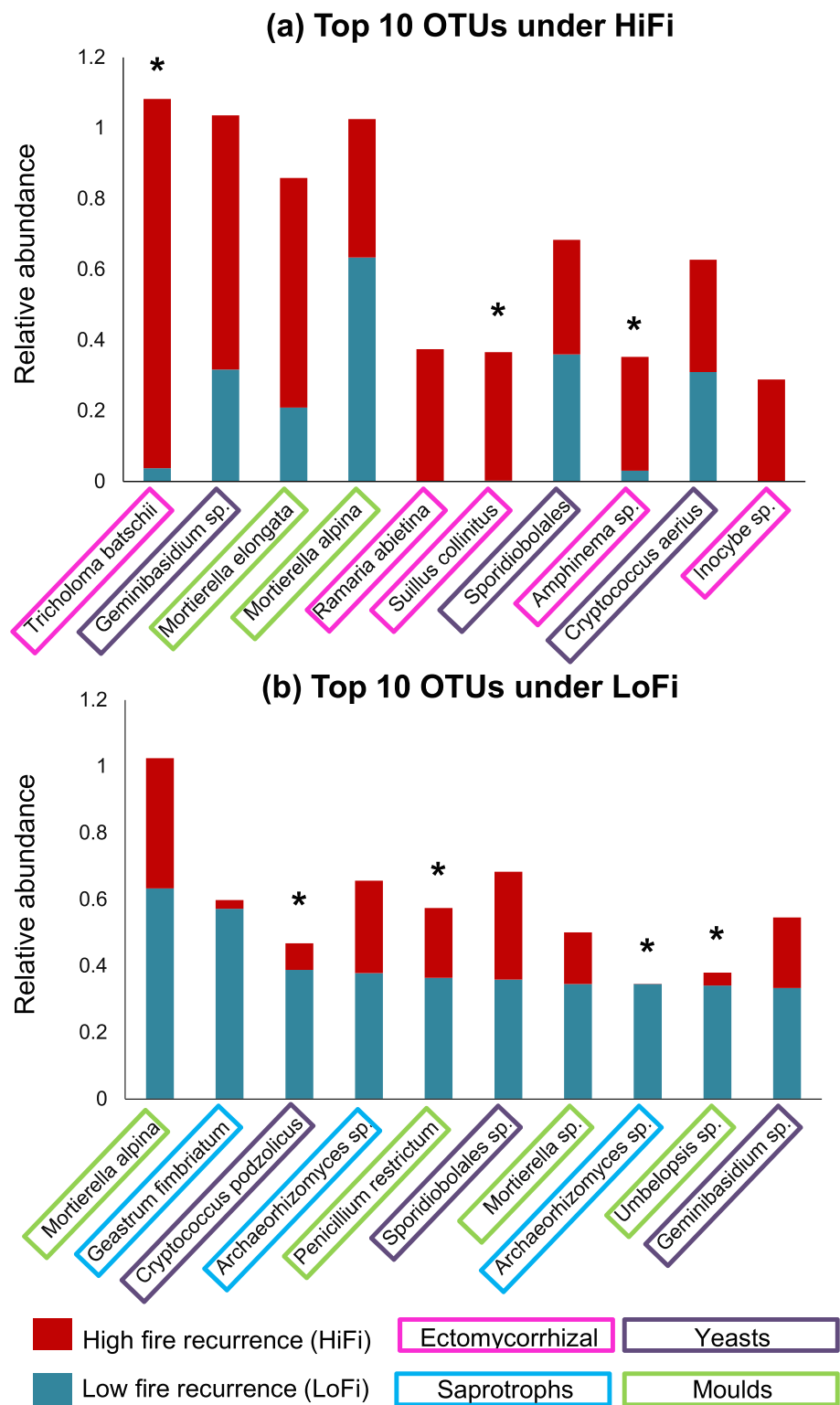


Fig. 1 The 10 most abundant OTUs under **a** high fire recurrence and **b** low fire recurrence. The bars represent the relative abundance of the sequencing reads per OTU in each treatment (high fire recurrence (HiFi) = red, low fire recurrence (LoFi) = blue). Colored rectangles in the x-axis represent different fungal guilds. Asterisks indicate significant differences in fungal abundances between treatments analyzed by DESeq (adjusted p -value (FDR, Benjamini-Hochberg) < 0.05 and $|\log_2\text{Fold Change}| > 1$)

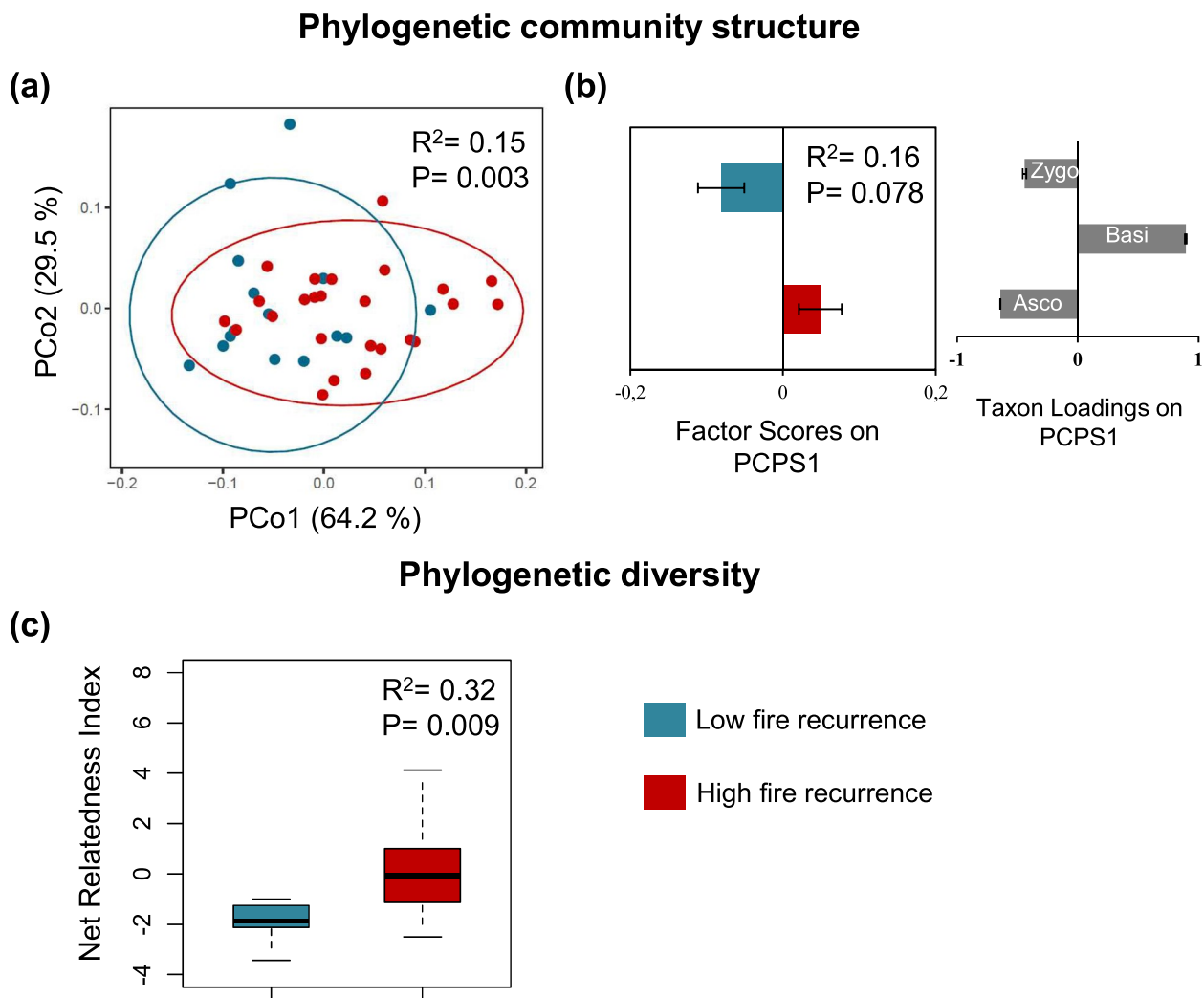


Fig. 2 Phylogenetic fungal community structure visualized by **a** Principal Coordinate Analysis (PCoA) and **b** factor scores and taxon loadings from the first principal component of the phylogenetic structure (PCPS1), and **c** fungal phylogenetic diversity visualized by boxplots. The phylogenetic fungal community structure was analyzed by the fuzzy-weighting method (PCPS) that calculates a phylogenetic matrix (matrix P). The phylogenetic diversity was expressed by the Net Relatedness Index (NRI) where higher NRI values indicate lower phylodiverse fungal communities. The P -values indicate effect of the fire regime (blue = low and red = high fire recurrence) on **a** matrix P analyzed by PERMANOVA and on **b** PCPS1 and **c** NRI by general linear mixed models (GLMMs). The marginal R^2 is also shown in the graph

between fungi and enzymes, proposing that the long-term fire-mediated adaptations in tree host partly determine these mechanisms.

According to our *first hypothesis*, the fungal phylogenetic diversity in areas recurrently affected by fire decreased. Fungal communities under high fire recurrence were clustered, which means that co-occurring taxa were more closely related than expected by chance. Across a 20-year fire chronosequence in Mediterranean areas near to our study site, Pérez-Valera et al. (2018) did not observe a big change in phylogenetic diversity with time since fire. Given that all our study sites are older than 40-year, this gives support to our hypothesis that

is the fire recurrence, and not so much the recent fire, which is responsible for the fungal clustering, and that long-stabilized community states are rather revealed in our study. Moreover, the phylogenetic structure of soil fungal communities did greatly differ depending on the fire regime. Our results specifically revealed a clustering within the Basidiomycota clade, which efficiently use organic matter of different recalcitrance (Kohler et al. 2015) and may outcompete distantly related fungal lineages, tending to coexist instead with phylogenetically close relatives. The number of taxa coexisting within the same niche may be limited not only by mechanisms such as competitive exclusion, but also by the availability of

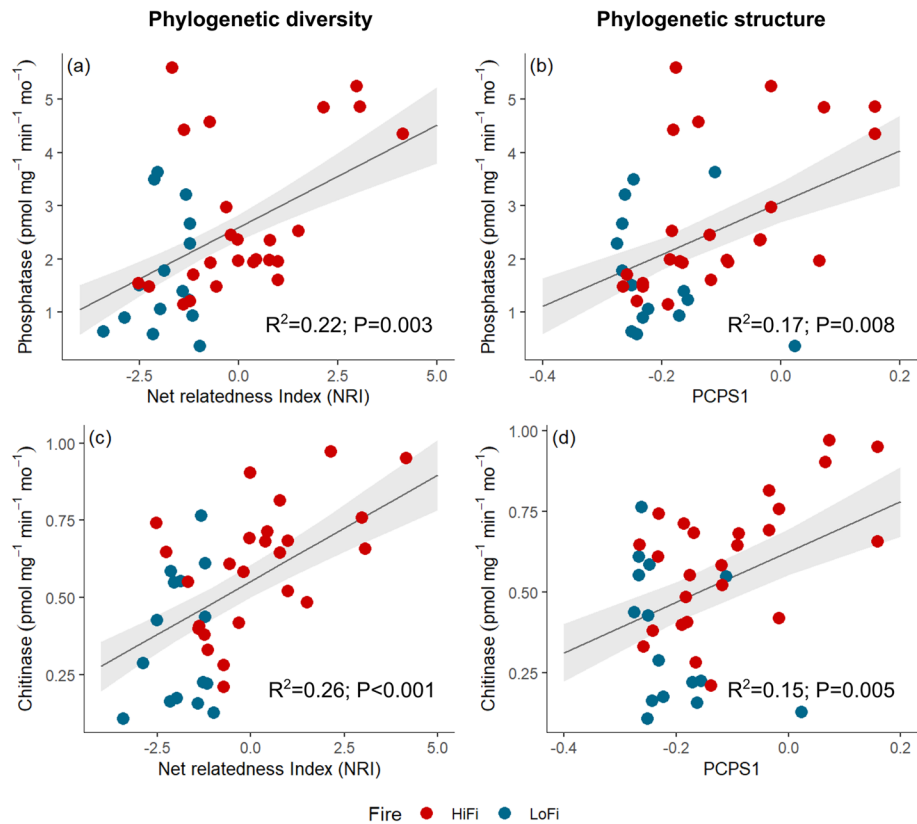


Fig. 3 Relationships between the phylogenetic diversity with **a** phosphatase and **c** chitinase activity and fungal phylogenetic community structure (PCPS1) with **b** phosphatase and **d** chitinase activity analyzed by general linear mixed model (GLMM) with the site as random factor. Black lines show the best linear trend fits at 95% confidence intervals (shaded area). The Phylogenetic diversity was expressed by the Net Relatedness Index (NRI) where higher NRI values indicate lower phylo diverse fungal communities. The phylogenetic fungal community structure was analyzed by the fuzzy-weighting method (PCPS) that calculates a phylogenetic matrix (matrix *P*). PCPS1 represents the first principal component of the phylogenetic structure (PCPS1). Different colored dots represent different treatments: high fire recurrence (HiFi) = red; low fire recurrence (LoFi) = blue. Results of the models are in Table S2. In the graph, the marginal *R*² and *P*-value are shown

Table 1 Relationships between the relative abundances of different fungal guilds with potential soil enzymatic activities involved in different nutrient cycles (C=carbon; P=phosphorous; N=nitrogen) analysed by general linear mixed models (GLMMs) with the site as random factor. The table shows *t* and *p*-value in parenthesis. Significant values are highlighted in bold

	Cycle	Ectomycorrhizal	Molds	Yeasts	Saprotrophs	Pathogen-parasites
Glucosidase (BG)	C	−0.50 (0.623)	0.11 (0.911)	−0.20 (0.839)	0.21 (0.837)	0.79 (0.433)
Cellobiohydrolase (CBH)	C	−0.43 (0.671)	−0.78 (0.439)	0.55 (0.585)	0.27 (0.792)	0.21 (0.833)
Glucuronidase (GUS)	C	−0.34 (0.736)	−1.71 (0.097)	−0.77 (0.446)	2.03 (0.052)	−0.03 (0.978)
Xylosidase (BXD)	C	−0.15 (0.881)	−1.37 (0.180)	−1.13 (0.265)	1.43 (0.164)	1.02 (0.315)
Phosphatase (aP)	P	3.36 (0.002)	−1.51 (0.142)	0.46 (0.648)	−1.66 (0.108)	−0.78 (0.441)
Chitinase (NAG)	N	3.18 (0.003)	−3.00 (0.005)	−0.47 (0.638)	−0.95 (0.349)	−0.85 (0.400)
Leucine (LAP)	N	−0.48 (0.635)	−0.42 (0.677)	1.06 (0.298)	−1.47 (0.151)	0.85 (0.402)

shared resources (Kennedy et al. 2009; Roy-Bolduc et al. 2016). The primary production of Mediterranean forests is highly constrained by the availability of water and nutrients, as it is probably the case of our study given the low values of N and P in soil. The calcareous nature of the

studied soils likely contributes to P deficiency, resulting from phosphate immobilization through precipitation with Ca²⁺ (Mayor & Roda 1994; Sardans et al. 2004). In this context of high competition for soil resources (Vilà & Sardans 1999), these ecosystems have evolved strong

Table 2 Effect of tree genotypic and phenotypic traits, climate and edaphic properties on the phylogenetic Net Relatedness Index (NRI) and the phylogenetic structure (PCPS) of soil fungal communities, separately analysed by general linear mixed models with the site as random factor (*t* and *P*-value shown). The first two axes of the multivariate analyses (PCoAs or PCAs) performed with each of the corresponding multivariate matrices (i.e., genotypic, phenotypic, climatic, and edaphic; Fig. S1) were extracted and used as explanatory variables in models (i.e., Axis 1 and Axis 2)

		NRI (<i>t</i> , <i>p</i> -value)	PCPS (<i>t</i> , <i>p</i> -value)
Genotypic traits	Axis1	−1.03 (0.315)	−2.68 (0.013)
	Axis2	−0.20 (0.839)	−0.40 (0.693)
Phenotypic traits	Axis1	2.67 (0.012)	2.10 (0.044)
	Axis2	1.86 (0.077)	1.75 (0.090)
Climate	Axis1	1.38 (0.178)	0.93 (0.358)
	Axis2	0.23 (0.818)	0.91 (0.371)
Edaphic properties	Axis1	0.50 (0.618)	−1.24 (0.223)
	Axis2	0.13 (0.895)	0.51 (0.611)

soil–plant interdependencies that enhance water and nutrient availability and improve resilience to environmental stressors (Prieto-Rubio et al. 2023; Pugnaire et al. 2019; Sardans & Peñuelas 2013), such as recurrent fires. In fact, in line with Fox et al. (2022), our results suggest that the effects of frequent fires on fungal communities are largely indirect, through fire-induced habitat modifications and vegetation changes, with the plant host emerging as key driver of fungal responses. Our phylogenetic approach may have, however, some limitations that should be acknowledged. First, as is the case for other fungal markers, the taxonomic resolution of ITS1 amplicon sequencing limited the phylogenetic reconstruction to the genus level, preventing us from capturing evolutionary relationships and ecological differences among congeneric species. In fact, the combination of

different DNA barcodes is presently recommended to study phylogeny and evaluate classification of fungi (Kausserud 2023; Tekpinar & Kalmer 2019). Second, since the phylogenetic relationships were reconstructed from published taxonomic and phylogenetic information rather than inferred directly from sequences of phylogenetic markers, we probably included the uncertainty due to the availability and resolution of previously established relationships among fungal lineages. Nevertheless, our approach allows to incorporate evolutionary information into the analysis of fungal communities and the resulting phylogenetic structure should be interpreted as an approximation of the evolutionary relationships among the detected taxa.

Regarding the fungal taxonomic community structure, the relative abundance of ectomycorrhizal fungi, highly represented by Basidiomycota species, was higher in HiFi populations and very correlated with phylogenetic indices. In a previous study, we have shown that root tip ectomycorrhizal taxonomic diversity decreased in *Pinus* spp. HiFi populations (Pérez-Izquierdo et al. 2020). All these results suggest a fire-induced filtering of the ectomycorrhizal community. Some ectomycorrhizal fungi (*vs* saprotrophic fungi) may use the host root system as an ecological niche for fire resistance, particularly in HiFi ecosystems where they are highly associated with fire-tolerant pine phenotypes. This strong correlation is particularly interesting for this fungal functional guild, which lives in symbiosis with the host tree and could contribute to the extended phenotype of *P. halepensis* (Fernandez et al. 2022). Within the ectomycorrhizal fungi in soil, the most abundant species by far were the basidiomycetes *T. batschii* and *S. collinitus*, and they were disproportionally more abundant in high fire recurrence, 96% and 99%, respectively. Both species present long-medium distance exploration types and grow with pines in dry calcareous soils (Agerer 2001; Christensen &

Table 3 Relations among tree genotypic traits, tree phenotypic traits, climate and edaphic properties with relative abundances of different fungal guilds analysed by general linear mixed models (GLMMs) with the site as random factor (*t*, *p*-value are shown). The first two axes of the multivariate analyses (PCoAs or PCAs) performed with each multivariate matrix (genotypic, phenotypic, climatic, edaphic; Fig. S1) were extracted and used as explanatory variables in models (i.e., Axis 1 and Axis 2). Significant values are highlighted in bold

		Ectomycorrhizal	Molds	Yeasts	Saprotrophs	Pathogen-parasites
Tree genotypic traits	Axis1	−1.11 (0.275)	0.25 (0.800)	0.66 (0.517)	2.37 (0.026)	0.78 (0.442)
	Axis2	0.24 (0.812)	0.41 (0.685)	0.79 (0.440)	−0.12 (0.909)	0.89 (0.381)
Tree phenotypic traits	Axis1	4.09 (<0.001)	−3.33 (0.002)	−1.16 (0.256)	−0.80 (0.432)	−2.43 (0.021)
	Axis2	3.21 (0.003)	−2.28 (0.029)	−1.50 (0.145)	−1.89 (0.068)	−1.31 (0.200)
Climate	Axis1	1.25 (0.221)	−1.83 (0.076)	−0.71 (0.482)	−0.45 (0.658)	2.69 (0.012)
	Axis2	0.94 (0.356)	0.11 (0.913)	0.11 (0.915)	−1.95 (0.060)	0.85 (0.405)
Edaphic properties	Axis1	−1.33 (0.192)	0.63 (0.535)	0.84 (0.406)	−0.36 (0.719)	2.18 (0.038)
	Axis2	−1.63 (0.114)	0.44 (0.664)	1.15 (0.259)	1.35 (0.188)	0.33 (0.746)

Heilmann-Clausen 2013). *Suillus collinitus* seems to be a strong vegetative competitor against other ectomycorrhizal fungi after fire not only by surviving in the spore bank (Glassman et al. 2015), but by propagating via mycelial spread (Karkouri et al. 2004). This species had probably resisted and survived successive fires outcompeting other fungi directly or indirectly, because these fungi were associated with phenotypes that are more tolerant to fire. The higher abundance of *T. batschii* is more likely related to indirect fire effects, probably on the trees, rather than post-fire colonization from resistant spores. The indirect fire effects may also explain the observed increase, although less pronounced, of *Amphinema* sp. under high fire recurrence, since *Amphinema* is considered a ruderal fungus that can be favored by disturbances and be maintained in mature forests (Jones et al. 2003; Ren et al. 2022; Rianhard et al. 2025).

On the other hand, ectomycorrhizal fungi with medium- and long-distance soil exploration types are considered to be more efficient in water, P and N mobilization due to their extended colonization of soil and capacity for enzymatic production (Khalfallah et al. 2024; Lilleskov et al. 2011). In fact, and according to our *second hypothesis*, we observed a relationship of ectomycorrhizal fungi, dominated by these previous fungal species, and phylogenetic indices with higher activities of enzymes that mobilize N and P. In our previous study, we did not observe differences in enzymes measured at the root-tips of *P. halepensis* (Pérez-Izquierdo et al. 2020). Thus, our results suggest that other ectomycorrhizal traits such as the capacity to produce extramatrical fungal mycelia and/or mine organic matter to acquire N and P might be relevant, as well for successful pine growth under recurrent fires (Talbot et al. 2008; Zak et al. 2019; Zanne et al. 2020). Recent findings have demonstrated evolutionary trade-offs related with the breakdown of recalcitrant pyrogenic organic matter and fungal growth, indicating specialization among fire-prone fungal lineages (Sari 2026). Observed variations of enzymatic activities under different tree genotypes have been proposed to be partly explained by effects on soil physico-chemical properties and substrate quality (Pérez-Izquierdo et al. 2018; Purahong et al. 2016). Here our result additionally suggests that the enzymatic activity variation is indirectly mediated by the tree-host influence on fungal communities. However, another possibility to not rule out is that the strong limitation exerted by climate and fire could have driven to an independent co-selection of tree and fungal traits that increase their fitness under these conditions. In fact, together with fire-adaptive traits, other tree traits related to climate could have been additionally selected that could have favored the clustering of the soil fungal community, or of certain ectomycorrhizal

species. For example, the trees under HiFi conditions might have developed the capacity to better lift water to ectomycorrhizal fungi, and then in return these fungi use the energy from the allocated tree C to secrete enzymes able to decompose organic matter (Querejeta et al. 2007). Further studies are needed to shed light on these mechanisms.

We further probed that the phylogenetic structure of bulk soil fungal communities was primarily regulated by the phenotypes of trees—and to a lesser extent by their genotypes—while neither local climatic nor soil conditions appeared to play a role (partly according to our *third hypothesis*). In our study, the factor fire recurrence is intimately linked to climate and both probably drive the phenotypes and genotypes of trees. Although serotiny was previously demonstrated as a tree trait structured by recurrent fires (Budde et al. 2014; Castellanos et al. 2015; Hernández-Serrano et al. 2014), other tree traits could have been co-selected by climate. Still, tree phenotypes were the main drivers of soil fungal community, reinforcing the hypothesis of Hart et al. (2005) proposing that fire-mediated shifts in vegetation, rather than direct fire effects, largely determine fungal community responses. Other authors have observed a pronounced influence of phenotypic tree traits on needle-inhabiting fungi (Würth et al. 2019), or direct relationships of host genotypic distances with their phyllosphere fungal communities (Cordier et al. 2012; Qian et al. 2018). Specific plant trait loci have been identified associated with certain rhizosperic fungi in Sorghum (Deng et al. 2021) and phyllosphere fungi in Norway spruce buds (Elfstrand et al. 2020). Brachi et al. (2022) even found important microbial hubs selected by the genotype that, in turn, contributed to plant fitness. In previous works, we have demonstrated variations in fungal taxonomic and phylo-diversity community structure related to different pine genotypes in common gardens (i.e., controlled edaphic and climatic variables), although not direct effects of genotypic and phenotypic traits were evaluated (Pérez-Izquierdo et al. 2017, 2019). The phenotypic characteristics of the plant are controlled, at least in part, by the genetic background (Buchanan et al. 2015). In our study, tree genotypes differed between HiFi and LoFi, but significance was borderline. We have to emphasize here that SNP samples from 5 trees were missing, probably decreasing the statistical signal. Moreover, although some SNPs have been identified to be under selection in *P. halepensis* and have been proposed to play a role in the expression of fire-related traits (Budde et al. 2017), further studies including a larger number of molecular markers to calculate the tree genetic distance, could provide more robust data on the effect of the tree genotypes on associated soil fungal communities.

Taken together, the adaptation of tree host and soil fungi to recurrent fires may arise from multiple non-exclusive mechanisms. Recurrent fires can act as a selective pressure favoring tree phenotypes with enhanced post-fire fitness (e.g., more serotinous, stress tolerant, higher capacity for belowground resource acquisition or deeper root system). Simultaneously, recurrent fires may promote fungal taxa, especially ectomycorrhizal species, with resistant propagules, persistent mycelium, or high extraradical exploration capacity, traits that enable rapid recolonization and foraging of resources. These processes may generate positive plant–fungal feedbacks, whereby fire-adapted hosts preferentially associate with fungi that enhance nutrient acquisition and soil exploration, ultimately promoting persistence under recurrent fire regimes.

Our results provide evidence that long-term fire-induced changes in dominant tree community co-occur with changes in phylogenetic and compositional shifts in soil fungal community with potential consequences for nutrient cycling. We then propose that the survival and adaptation of pines growing in Mediterranean areas, where climate and recurrent fires are major ecosystem drivers, may be partly due to the association with symbiotic soil fungi. These plant-fungal feedbacks might be key to better understand the fire ecology of Mediterranean forests and then to promote a sustainable management of these ecosystems or to apply in future restoration programs after fire disturbances.

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s42408-026-00577-2>.

Supplementary Material 1. Figure S1. (a) Principal coordinate analysis (PCoA) performed with the tree genetic SNPs and Principal component analyses (PCA) performed with (b) phenotypic tree traits serotiny, DBH and bark thickness, (c) climate-related variables altitude, mean temperature (Tm) and mean precipitation (Pm), and (d) the edaphic variables pH, electric conductivity (EC), carbon (C), potassium (K), nitrogen (N), phosphorus (P), carbon to nitrogen ratio (CN) and organic matter (OM). The first two axes of each ordination analysis explaining the maximum of variance (in parenthesis) were used as genotypic, phenotypic, climatic and edaphic indexes in further modelling. Colours indicate the two contrasted fire regimes (blue = Low and red = High fire recurrence). Genotypic data are extracted from Budde et al. (2014), phenotypic and climate data from Hernández-Serrano et al. (2013) and soil data from Pérez-Izquierdo et al. (2020). Figure S2. Scores of main fungal phyla in matrix P. Values are means $\pm$ SD. In matrix P, each OTU has a value per sample that increases as the phylogenetic distance between neighbouring OTUs decreases. Figure S3. Soil enzymatic activities under two contrasted fire regimes (blue = Low and red = High fire recurrence). Boxes represent the interquartile range (IQR) between first and third quartiles and the horizontal line inside is the median. Whiskers denote the lowest and highest values within 1.5 $\times$ IQR from the first and third quartiles, respectively. Asterisks denote significant differences between the two fire regimes ($p < 0.05$) analysed by General Linear Mixed Models with site as random factor. Table S1. Effect of the fire regime (fix factor) on (a) edaphic properties, (b) phenotypic traits of trees and (c) climatic variables in *Pinus halepensis* forest analysed for

each variable by General Linear Mixed Models with the site as random factor. Significant effects are indicated in bold ($p < 0.05$). Means $\pm$ SE of HiFi and Lofi edaphic properties, phenotypic traits and climate. EC=electric conductivity; SOM=soil organic matter; CN=carbon to nitrogen ratio; DBH=diameter at breast height. Table S2. Relationships between the fungal Phylogenetic Net Relatedness Index (NRI) and the fungal phylogenetic structure (PCPS1) with the enzymatic activities involved in different nutrient cycles (C=carbon; P=phosphorous; N=nitrogen) analysed by General Linear Mixed Model (GLMM) with the site as random factor. Table S3. Relations among tree genotypic traits, tree phenotypic traits, climate and edaphic properties and soil enzymatic activities involved in different nutrient cycles (C=carbon; P=phosphorous; N=nitrogen) analysed by General Linear Mixed Models (GLMMs) with the site as random factor (t, p -value are shown). The first two axes of the multivariate analyses performed with each multivariate matrix (genotypic, phenotypic, climatic, edaphic) were extracted and used as explanatory variables (i.e., Axis 1 and Axis 2). Glucosidase (BG), Cellobiohydrolase (CBH), Chitinase (NAG), Phosphatase (aP), Glucuronidase (GUS), Xylosidase (BXD), Leucine (LAP).

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Authors' contributions

AR, MV and SCG-M designed the experiment; LPI, MZA and AR collected the data; LPI and MB performed the bioinformatics analysis; LPI performed the statistical analyses; LPI wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

Data availability

Sequencing data were deposited in the Sequence Read Archive (<http://www.ncbi.nlm.nih.gov/sra>) as PRJNA324526.

Declarations

Competing interests

The authors declare no competing interests.

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References

- Abarenkov, Kessy, Zirk, Allan, Piirmann, Timo, Pöhönen, Raivo, Ivanov, Filipp, Nilsson, R. Henrik, Kõljalg, U. 2022. Full UNITE+INSD dataset for Fungi. Version 16.10.2022. UNITE Community. <https://doi.org/10.15156/BIO/2483925>.
- Abdel Malak, D., and J. G. Pausas. 2006. Fire regime and post-fire normalized difference vegetation index changes in the eastern Iberian peninsula (Mediterranean basin). *International Journal of Wildland Fire* 15 (3): 407–413. <https://doi.org/10.1071/WF05052>.

- Agerer, R. 2001. Exploration types of ectomycorrhizae: A proposal to classify ectomycorrhizal mycelial systems according to their patterns of differentiation and putative ecological importance. *Mycorrhiza* 11 (2): 107–114. <https://doi.org/10.1007/s005720100108>.
- Baldrian, P. 2014. Distribution of extracellular enzymes in soils: Spatial heterogeneity and determining factors at various scales. *Soil Science Society of America Journal* 78 (1): 11–18. <https://doi.org/10.2136/sssaj2013.04.0155dgs>.
- Brachi, B., D. Filiault, H. Whitehurst, P. Darpe, P. Le Gars, M. Le Mentec, T. C. Morton, E. Kerdaffrec, F. Rabanal, A. Anastasio, M. S. Box, S. Duncan, F. Huang, R. Leff, P. Novikova, M. Perisin, T. Tsuchimatsu, R. Woolley, C. Dean, Magnus Nordborg, Svante Holm, and J. Bergelson. 2022. Plant genetic effects on microbial hubs impact host fitness in repeated field trials. *Proceedings of the National Academy of Sciences of the United States of America*. <https://doi.org/10.1073/pnas.2201285119>.
- Buchanan, B. B., W. Grissem, and R. L. Jones. 2015. *Biochemistry and molecular biology of plants*. In , ed. B. B. Buchanan, W. Grissem, and R. L. Jones. John Wiley & Sons.
- Budde, K. B., M. Heuertz, A. Hernández-Serrano, J. G. Pausas, G. G. Vendramin, M. Verdú, and S. C. González-Martínez. 2014. In situ genetic association for serotiny, a fire-related trait, in Mediterranean maritime pine (*Pinus pinaster*). *New Phytologist* 201 (1): 230–241. <https://doi.org/10.1111/nph.12483>.
- Budde, K. B., S. C. González-Martínez, M. Navascués, C. Burgarella, E. Mosca, Z. Lorenzo, M. Zabal-Aguirre, G. G. Vendramin, M. Verdú, J. G. Pausas, and M. Heuertz. 2017. Increased fire frequency promotes stronger spatial genetic structure and natural selection at regional and local scales in *Pinus halepensis* Mill. *Annals of Botany* 119 (6): 1061–1072. <https://doi.org/10.1093/aob/mcw286>.
- Castellanos, M. C., S. C. González-Martínez, and J. G. Pausas. 2015. Field heritability of a plant adaptation to fire in heterogeneous landscapes. *Molecular Ecology* 24 (22): 5633–5642. <https://doi.org/10.1111/mec.13421>.
- Christensen, M., & Heilmann-Clausen, J. 2013. *The genus Tricholoma. Fungi of Northern Europe, vol 4. Svampetryk, Denmark*. The Danish Mycological Society.
- Cordier, T., C. Robin, X. Capdevielle, M. L. Desprez-Loustau, and C. Vacher. 2012. Spatial variability of phyllosphere fungal assemblages: Genetic distance predominates over geographic distance in a European beech stand (*Fagus sylvatica*). *Fungal Ecology* 5 (5): 509–520. <https://doi.org/10.1016/j.funeco.2011.12.004>.
- Debastiani, V. J., S. C. Muller, J. M. Oliveira, F. S. Rocha, M. C. Sestren-Bastos, and L. D. S. Duarte. 2015. Recurrent patterns of phylogenetic habitat filtering in woody plant communities across phytogeographically distinct grassland-forest ecotones. *Community Ecology* 16 (1): 1–9. <https://doi.org/10.1556/168.2015.16.1>.
- Deng, S., D. F. Caddell, G. Xu, L. Dahlen, L. Washington, J. Yang, and D. Coleman-Derr. 2021. Genome wide association study reveals plant loci controlling heritability of the rhizosphere microbiome. *ISME Journal* 15 (11): 3181–3194. <https://doi.org/10.1038/s41396-021-00993-z>.
- Dray, S., and A. B. Dufour. 2007. The ade4 package: Implementing the duality diagram for ecologists. *Journal of Statistical Software* 22 (4): 1–20. <https://doi.org/10.18637/jss.v022.i04>.
- Drummond, A. J., and A. Rambaut. 2007. BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evolutionary Biology* 7 (1): 214. <https://doi.org/10.1186/1471-2148-7-214>.
- Duarte, L. D. S., P. V. Prieto, and V. D. Pillar. 2012. Assessing spatial and environmental drivers of phylogenetic structure in Brazilian Araucaria forests. *Ecography* 35 (10): 952–960. <https://doi.org/10.1111/j.1600-0587.2011.07193.x>.
- Edgar, R. C. 2013. UPARSE: Highly accurate OTU sequences from microbial amplicon reads. *Nature Methods* 10 (10): 996–998. <https://doi.org/10.1038/nmeth.2604>.
- Elfstrand, M., L. Zhou, J. Baisson, Å. Olson, K. Lundén, B. Karlsson, H. X. Wu, J. Stenlid, and M. R. García-Gil. 2020. Genotypic variation in Norway spruce correlates to fungal communities in vegetative buds. *Molecular Ecology* 29 (1): 199–213. <https://doi.org/10.1111/mec.15314>.
- Eugenio, M., and F. Lloret. 2004. Fire recurrence effects on the structure and composition of Mediterranean *Pinus halepensis* communities in Catalonia (northeast Iberian Peninsula). *Ecoscience* 11 (4): 446–454. <https://doi.org/10.1080/11956860.2004.11682854>.
- Eveno, E., C. Collada, M. A. Guevara, V. Léger, A. Soto, L. Díaz, P. Léger, S. C. González-Martínez, M. T. Cervera, C. Plomion, and P. H. Garnier-Géré. 2008. Contrasting patterns of selection at *Pinus pinaster* Ait. drought stress candidate genes as revealed by genetic differentiation analyses. *Molecular Biology and Evolution* 25 (2): 417–437. <https://doi.org/10.1093/molbev/msm272>.
- Fernandez, M., A. Vernay, L. Henneron, L. Adamik, P. Malagoli, and P. Balandier. 2022. Plant N economics and the extended phenotype: Integrating the functional traits of plants and associated soil biota into plant–plant interactions. *Journal of Ecology* 110 (9): 2015–2032. <https://doi.org/10.1111/1365-2745.13934>.
- Fox, S., B. A. Sikes, S. P. Brown, C. L. Cripps, S. I. Glassman, K. Hughes, T. Semenova-Nelsen, and A. Jumpponen. 2022. Fire as a driver of fungal diversity — A synthesis of current knowledge. *Mycologia* 114 (2): 215–241. <https://doi.org/10.1080/00275514.2021.2024422>.
- Gardes, M., & Bruns, T. 1993. ITS primers with enhanced specificity for basidiomycetes - application to the identification of mycorrhizae and rusts. *Molecular Ecology* 2:113–118. <https://doi.org/10.1111/j.1365-294X.1993.tb00005.x>.
- Gehring, C. A., and T. G. Whitham. 1991. Herbivore-driven mycorrhizal mutualism in insect-susceptible pinyon pine. *Nature* 353 (6344): 556–557. <https://doi.org/10.1038/353556a0>.
- Glassman, S. I., K. G. Peay, J. M. Talbot, D. P. Smith, J. A. Chung, J. W. Taylor, R. Vilgalys, and T. D. Bruns. 2015. A continental view of pine-associated ectomycorrhizal fungal spore banks: A quiescent functional guild with a strong biogeographic pattern. *New Phytologist* 205:1619–1631. <https://doi.org/10.1111/nph.13240>.
- Glassman, S. I., C. R. Levine, A. M. Dirocco, J. J. Battles, and T. D. Bruns. 2016. Ectomycorrhizal fungal spore bank recovery after a severe forest fire: Some like it hot. *The ISME Journal* 10:1228–1239. <https://doi.org/10.1038/ismej.2015.182>.
- Goberna, M., and M. Verdú. 2016. Predicting microbial traits with phylogenies. *The ISME Journal* 10 (4): 959–967. <https://doi.org/10.1038/ismej.2015.171>.
- Grivet, D., F. Sebastiani, R. Alía, T. Bataillon, S. Torre, M. Zabal-Aguirre, G. G. Vendramin, and S. C. González-Martínez. 2011. Molecular footprints of local adaptation in two mediterranean conifers. *Molecular Biology and Evolution* 28 (1): 101–116. <https://doi.org/10.1093/molbev/msq190>.
- Guiote, C., and J. G. Pausas. 2022. Fire favors sexual precocity in a Mediterranean pine. *Oikos* e093731. <https://doi.org/10.1111/oik.09373>.
- Hart, S. C., T. H. DeLuca, G. S. Newman, M. D. MacKenzie, and S. I. Boyle. 2005. Post-fire vegetative dynamics as drivers of microbial community structure and function in forest soils. *Forest Ecology and Management* 220 (1–3): 166–184. <https://doi.org/10.1016/j.foreco.2005.08.012>.
- Hernández-Serrano, A., M. Verdú, S. C. González-Martínez, and J. G. Pausas. 2013. Fire structures pine serotiny at different scales. *American Journal of Botany* 100 (12): 2349–2356. <https://doi.org/10.3733/ajb.1300182>.
- Hernández-Serrano, A., M. Verdú, L. Santos-Del-Blanco, J. Climent, S. C. González-Martínez, and J. G. Pausas. 2014. Heritability and quantitative genetic divergence of serotiny, a fire-persistence plant trait. *Annals of Botany* 114 (3): 571–577. <https://doi.org/10.1093/aob/mcu142>.
- Jiang, F., J. A. Bennett, K. M. Crawford, J. Heinze, X. Pu, A. Luo, and Z. Wang. 2024. Global patterns and drivers of plant–soil microbe interactions. *Ecology Letters* 27 (1): 1–12. <https://doi.org/10.1111/ele.14364>.
- Jones, M. D., M. D. Jones, D. M. Durall, and J. W. G. Cairney. 2003. Ectomycorrhizal fungal communities in young forest stands regenerating after clearcut logging. *New Phytologist* 157:399–422. <https://doi.org/10.1046/j.1469-8137.2003.00698.x>.
- Karkouri, K., F. Martin, and D. Mousain. 2004. Diversity of ectomycorrhizal symbionts in a disturbed *Pinus halepensis* plantation in the Mediterranean region. *Annals of Forest Science* 61:705–710. <https://doi.org/10.1051/forest>.
- Kausserud, H. 2023. ITS alchemy: On the use of ITS as a DNA marker in fungal ecology. *Fungal Ecology* 65:101274. <https://doi.org/10.1016/j.funeco.2023.101274>.
- Keeley, J. E., W. J. Bond, R. A. Bradstock, J. G. Pausas, and P. W. Rundel. 2011. *Fire in Mediterranean ecosystems: Ecology, evolution and management*. Cambridge University Press.
- Kembel, S. W., P. D. Cowan, M. R. Helmus, W. K. Cornwell, H. Morlon, D. D. Ackerly, S. P. Blomberg, and C. O. Webb. 2010. Picante: R tools for integrating phylogenies and ecology. *Bioinformatics* 26 (11): 1463–1464. <https://doi.org/10.1093/bioinformatics/btq1166>.

- Kennedy, P. G., K. G. Peay, and T. D. Bruns. 2009. Root tip competition among ectomycorrhizal fungi: Are priority effects a rule or an exception? *Ecology* 90 (8): 2098–2107. <https://doi.org/10.1890/08-1291.1>.
- Khalfallah, F., Bon, L., El Mazlouzi, M., Bakker, M. R., Fanin, N., Bellanger, R., Bernier, F., De Schrijver, A., Ducatillon, C., Fotelli, M. N., Gateble, G., Gundale, M. J., Larsson, M., Legout, A., Mason, W. L., Nordin, A., Smolander, A., Spyrogliou, G., Vangelova, E. I., et al. 2024. "Ectomycorrhizal exploration type" could be a functional trait explaining the spatial distribution of tree symbiotic fungi as a function of forest humus forms. *Mycorrhiza* 34 (3), 203–216. <https://doi.org/10.1007/s00572-024-01146-8>
- Kia, S. H., K. Glynou, T. Nau, M. Thines, M. Piepenbring, and J. G. Maciá-Vicente. 2017. Influence of phylogenetic conservatism and trait convergence on the interactions between fungal root endophytes and plants. *ISME Journal* 11 (3): 777–790. <https://doi.org/10.1038/ismej.2016.140>.
- Kohler, A., A. Kuo, L. G. Nagy, E. Morin, K. W. Barry, F. Buscot, B. Canbäck, C. Choi, N. Cichocki, A. Clum, J. Colpaert, A. Copeland, M. D. Costa, J. Doré, D. Floudas, G. Gay, M. Girlanda, B. Henrissat, S. Herrmann, Jaqueline Hess, Nils Högberg, Tomas Johansson, Hassine-Radhouane. Khouja, Kurt LaButti, Urs Lahrmann, Anthony Levasseur, Erika A. Lindquist, Anna Lipzen, Roland Marmeisse, Elena Martino, Claude Murat, Chew Y. Ngan, Uwe Nehls, Jonathan M. Plett, Anne Pringle, Robin A. Ohm, Silvia Perotto, Martina Peter, Robert Riley, Francois Rineau, Joske Ruytinx, Asaf Salamov, Firoz Shah, Hui Sun, Mika Tarkka, Andrew Tritt, Claire Veneault-Fourrey, Alga Zuccaro, Anders Tunlid, Igor V. Grigoriev, David S. Hobbett, and F. Martin. 2015. Convergent losses of decay mechanisms and rapid turnover of symbiosis genes in mycorrhizal mutualists. *Nature Genetics* 47 (4): 410–415. <https://doi.org/10.1038/ng.3223>.
- Lepointevin, C., L. Harvengt, C. Plomion, and P. Garnier-Géré. 2012. Association mapping for growth, straightness and wood chemistry traits in the *Pinus pinaster* Aquitaine breeding population. *Tree Genetics & Genomes* 8 (1): 113–126. <https://doi.org/10.1007/s11295-011-0426-y>.
- Lilleskov, E. A., E. A. Hobbie, and T. R. Horton. 2011. Conservation of ectomycorrhizal fungi: Exploring the linkages between functional and taxonomic responses to anthropogenic N deposition. *Fungal Ecology* 4 (2): 174–183. <https://doi.org/10.1016/j.funeco.2010.09.008>.
- Love, M. I., W. Huber, and S. Anders. 2014. Moderated estimation of fold change and dispersion for RNA-seq data with DESeq2. *Genome Biology* 15 (12): 550. <https://doi.org/10.1186/s13059-014-0550-8>.
- Maillard, F., M. Didion, L. Fauchery, C. Bach, and M. Buée. 2018. N-Acetylglucosaminidase activity, a functional trait of chitin degradation, is regulated differentially within two orders of ectomycorrhizal fungi: Boletales and Agaricales. *Mycorrhiza* 28:391–397. <https://doi.org/10.1007/s00572-018-0833-0>
- Martiny, A. C., K. Treseder, and G. Pusch. 2013. Phylogenetic conservatism of functional traits in microorganisms. *ISME Journal* 7 (4): 830–838. <https://doi.org/10.1038/ismej.2012.160>.
- Mathieu, Y., Galhaye, E., Dumargay, S., Gérardin, P., Harvengt, L., & Buée, M. 2013. Selection and validation of enzymatic activities as functional markers in wood biotechnology and fungal ecology. *Journal of Microbiological Methods* 92:157–163. <https://doi.org/10.1016/j.mimet.2012.11.017>.
- Mayor, X., and F. Roda. 1994. Effects of irrigation and fertilization on stem diameter growth in a Mediterranean helm oak forest. *Forest Ecology and Management* 68 (1): 119–126. [https://doi.org/10.1016/0378-1127\(94\)90143-0](https://doi.org/10.1016/0378-1127(94)90143-0).
- Moghli, A., V. M. Santana, M. J. Baeza, E. Pastor, and S. Soliveres. 2022. Fire recurrence and time since last fire interact to determine the supply of multiple ecosystem services by Mediterranean forests. *Ecosystems* 25 (6): 1358–1370. <https://doi.org/10.1007/s10021-021-00720-x>.
- Nguyen, H., N. L. Nickerson, and K. A. Seifert. 2013. Basidiomycetes and Geminibasidium: A new lineage of heat-resistant and xerotolerant basidiomycetes. *Mycologia* 105 (5): 1231–1250. <https://doi.org/10.3852/12-351>.
- Nguyen, N. H., Z. Song, S. T. Bates, S. Branco, L. Tedersoo, J. Menke, J. S. Schilling, and P. G. Kennedy. 2016. FUNGuild: An open annotation tool for parsing fungal community datasets by ecological guild. *Fungal Ecology* 20:241–248. <https://doi.org/10.1016/j.funeco.2015.06.006>.
- Oksanen, J., Blanchet, F., & Kindt, R. 2013. Package "vegan". *R Packag. ...* http://watson.nci.nih.gov/cran_mirror/web/packages/vegan/vegan.pdf.
- Paradis, E., and K. Schliep. 2019. Ape 5.0: An environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics* 35 (3): 526–528. <https://doi.org/10.1093/bioinformatics/bty633>.
- Pausas, J.G. 2004. Changes in fire and climate in the eastern Iberian Peninsula (Mediterranean basin). *Climatic Change* 63:337–350. <https://doi.org/10.1023/B:CLIM.0000018508.94901.9c>
- Pausas, J. G. 2015. Evolutionary fire ecology: Lessons learned from pines. *Trends in Plant Science* 20 (5): 318–324. <https://doi.org/10.1016/j.tplants.2015.03.001>.
- Pausas, J. G., and S. Fernández-Muñoz. 2012. Fire regime changes in the Western Mediterranean Basin: From fuel-limited to drought-driven fire regime. *Climatic Change* 110 (1–2): 215–226. <https://doi.org/10.1007/s10584-011-0060-6>.
- Pausas, J. G., and M. Verdú. 2008. Fire reduces morphospace occupation in plant communities. *Ecology* 89 (8): 2181–2186. <https://doi.org/10.1890/07-1737.1>.
- Pérez-Izquierdo, L., M. Zabal-Aguirre, D. Flores-Rentería, S. González-Martínez, M. Buée, and A. Rincón. 2017. Functional outcomes of fungal community shifts driven by tree genotype and spatial-temporal factors in Mediterranean pine forests. *Environmental Microbiology* 19 (4): 1639–1652. <https://doi.org/10.1111/1462-2920.13690>.
- Pérez-Izquierdo, L., L. Saint-André, P. Santennoise, M. Buée, and A. Rincón. 2018. Tree genotype and seasonal effects on soil properties and biogeochemical functioning in Mediterranean pine forests. *European Journal of Soil Science* 69 (6): 1087–1097. <https://doi.org/10.1111/ejss.12712>.
- Pérez-Izquierdo, L., M. Zabal-Aguirre, S. C. González-Martínez, M. Buée, M. Verdú, A. Rincón, and M. Goberna. 2019. Plant intraspecific variation modulates nutrient cycling through its below-ground rhizospheric microbiome. *Journal of Ecology* 107:1594–1605. <https://doi.org/10.1111/1365-2745.13202>.
- Pérez-Izquierdo, L., M. Zabal-Aguirre, M. Verdú, M. Buée, and A. Rincón. 2020. Ectomycorrhizal fungal diversity decreases in Mediterranean pine forests adapted to recurrent fires. *Molecular Ecology* 29 (13): 2463–2476. <https://doi.org/10.1111/mec.15493>.
- Pérez-Izquierdo, L., A. Rincón, L. Db, and B. M. 2021. Fungal community of forest soil: Diversity, functions and services. In *Forest microbiology vol 1: Tree microbiome: Phyllosphere, endosphere and rhizosphere*, ed. Fred O. Asiegbu and Andriy Kovalchuk, 231–256. Elsevier.
- Pérez-Valera, E., M. Verdú, J. A. Navarro-Cano, and M. Goberna. 2018. Resilience to fire of phylogenetic diversity across biological domains. *Molecular Ecology* 27 (13): 2896–2908. <https://doi.org/10.1111/mec.14729>.
- Pillar, V. D., and Ld. S. Duarte. 2010. A framework for metacommunity analysis of phylogenetic structure. *Ecology Letters* 13 (5): 587–596. <https://doi.org/10.1111/j.1461-0248.2010.01456.x>.
- Pinoso, S., S. C. González-Martínez, F. Bagnoli, F. Cattonaro, D. Grivet, F. Marroni, Z. Lorenzo, J. G. Pausas, M. Verdú, and G. G. Vendramin. 2014. First insights into the transcriptome and development of new genomic tools of a widespread circum-Mediterranean tree species, *Pinus halepensis* Mill. *Molecular Ecology Resources* 14 (4): 846–856. <https://doi.org/10.1111/1755-0998.12232>.
- Policelli, N., J. D. Hoeksema, J. Moyano, R. Vilgalys, S. Véliz, and J. M. Bhatnagar. 2023. Global pine tree invasions are linked to invasive root symbionts. *New Phytologist* 237 (1): 16–21. <https://doi.org/10.1111/nph.18527>.
- Pot, D., Vid, McMillan, L., Echt, C., Le Provost, G., Garnier-Géré, P., Cato, S., & Plomion, C. 2005. Nucleotide variation in genes involved in wood formation in two pine species. *New Phytologist* 167 (1): 101–112. <https://doi.org/10.1111/j.1469-8137.2005.01417.x>.
- Prieto-Rubio, J., A. Perea, J. L. Garrido, J. M. Alcántara, C. Azcón-Aguilar, A. López-García, and A. Rincón. 2023. Plant traits and phylogeny predict soil carbon and nutrient cycling in Mediterranean mixed forests. *Ecosystems* 26 (5): 1047–1060. <https://doi.org/10.1007/s10021-022-00815-z>.
- Pugnaire, F. I., J. A. Morillo, J. Peñuelas, P. B. Reich, R. D. Bardgett, A. Gaxiola, D. A. Wardle, and W. H. Van Der Putten. 2019. Climate change effects on plant-soil feedbacks and consequences for biodiversity and functioning of terrestrial ecosystems. *Science Advances* 5 (11): 1–11. <https://doi.org/10.1126/sciadv.aaz1834>.
- Purahong, W., W. Durka, M. Fischer, S. Dommert, R. Schöps, F. Buscot, and T. Wubet. 2016. Tree species, tree genotypes and tree genotypic diversity levels affect microbe-mediated soil ecosystem functions in a subtropical forest. *Scientific Reports* 6 (1): 36672. <https://doi.org/10.1038/srep36672>.
- Qian, X., T. Duan, X. Sun, Y. Zheng, Y. Wang, M. Hu, H. Yao, N. Ji, P. Lv, L. Chen, M. Shi, L. Guo, and D. Zhang. 2018. Host genotype strongly influences phyllosphere fungal communities associated with *Mussaenda pubescens* var.

- alba (Rubiaceae). *Fungal Ecology* 36:141–151. <https://doi.org/10.1016/j.funeco.2018.10.001>.
- Querejeta, J. I., L. M. Egerton-Warburton, and M. F. Allen. 2007. Hydraulic lift may buffer rhizosphere hyphae against the negative effects of severe soil drying in a California Oak savanna. *Soil Biology and Biochemistry* 39 (2): 409–417. <https://doi.org/10.1016/j.soilbio.2006.08.008>.
- R Core Team. 2021. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Ren, Y., M. Guo, G. Ding, and Y. Wang. 2022. Ectomycorrhizal fungi associated with *Pinus sylvestris* var. *mongolica* were altered by soil environments with aging plantation in a semi-arid desert. *Frontiers in Environmental Science* 10: 858452. <https://doi.org/10.3389/fenvs.2022.858452>.
- Rianhard, O. M., J. M. Kranabetter, D. M. Durall, and M. D. Jones. 2025. Ectomycorrhizal fungal community succession and fragmentation across forest edges nearly three decades postharvest. *Lants, People, Planet* 7 (5): 1510–1523. <https://doi.org/10.1002/ppp3.70008>.
- Rincón, A., B. Santamaría-Pérez, L. Ocaña, and M. Verdú. 2014. Structure and phylogenetic diversity of post-fire ectomycorrhizal communities of maritime pine. *Mycorrhiza* 24:131–141. <https://doi.org/10.1007/s00572-013-0520-0>.
- Roy-Bolduc, A., E. Laliberté, and M. Hijri. 2016. High richness of ectomycorrhizal fungi and low host specificity in a coastal sand dune ecosystem revealed by network analysis. *Ecology and Evolution* 6 (1): 349–362. <https://doi.org/10.1002/ece3.1881>.
- Sardans, J., and J. Peñuelas. 2013. Plant-soil interactions in Mediterranean forest and shrublands: Impacts of climatic change. *Plant and Soil* 365 (1–2): 1–33. <https://doi.org/10.1007/s11104-013-1591-6>.
- Sardans, J., F. Rodà, and J. Peñuelas. 2004. Phosphorus limitation and competitive capacities of *Pinus halepensis* and *Quercus ilex* subsp. *rotundifolia* on different soils. *Plant Ecology* 174 (2): 305–317. <https://doi.org/10.1023/B:VEGE.0000049110.88127.a0>.
- Sari, E. 2026. *Gene duplication, horizontal gene transfer, and trait trade-offs drive evolution of postfire resource acquisition in pyrophilous fungi*. 123 (1): e2519152123. <https://doi.org/10.1073/pnas.2519152123/-DCSupplemental.Published>.
- Sinsabaugh, R. L. 2010. Phenol oxidase, peroxidase and organic matter dynamics of soil. *Soil Biology and Biochemistry* 42 (3): 391–404. <https://doi.org/10.1016/j.soilbio.2009.10.014>.
- Smith, S., and D. Read, eds. 2008. *Mycorrhizal symbiosis*. London: Academic Press.
- Smith, G. R., L. C. Edy, and K. G. Peay. 2021. Contrasting fungal responses to wildfire across different ecosystem types. *Molecular Ecology* 30 (3): 844–854. <https://doi.org/10.1111/mec.15767>.
- Talbot, J. M., S. D. Allison, and K. K. Treseder. 2008. Decomposers in disguise: Mycorrhizal fungi as regulators of soil C dynamics in ecosystems under global change. *Functional Ecology* 22 (6): 955–963. <https://doi.org/10.1111/j.1365-2435.2008.01402.x>.
- Tedersoo, L., and M. E. Smith. 2013. Lineages of ectomycorrhizal fungi revisited: Foraging strategies and novel lineages revealed by sequences from belowground. *Fungal Biology Reviews* 27 (3–4): 83–99. <https://doi.org/10.1016/j.fbr.2013.09.001>.
- Tedersoo, L., M. Bahram, S. Polme, U. Koljalg, N. S. Yorou, R. Wijesundera, L. V. Ruiz, aM. Vasco-Palacios, P. Q. Thu, A. Suija, M. E. Smith, C. Sharp, E. Saluveer, A. Saitta, M. Rosas, T. Riit, D. Ratkowsky, K. Pritsch, K. Poldmaa, Meike Piepenbring, Cherdchai Phosri, Marko Peterson, Kaarin Parts, Kadri Pärtel, Eveli Otsing, Eduardo Nouhra, André L. Njouonkou, R. Henrik Nilsson, Luis N. Morgado, Jordan Mayor, Tom W. May, Luiza Majuakim, D. Jean. Lodge, Su See Lee, Karl-Henrik Larsson, Petr Kohout, Kentaro Hosaka, Indrek Hiiesalu, Terry W. Henkel, Helery Harend, Liang-dong Guo, Alina Greslebin, Gwen Grelet, Jozsef Geml, Genevieve Gates, William Dunstan, Chris Dunk, Rein Drenkhan, John Dearnaley, André De Kesel, Tan Dang, Xin Chen, Franz Buegger, Francis Q. Brearley, Gregory Bonito, Sten Anslan, Sandra Abell, and K. Abarenkov. 2014. Global diversity and geography of soil fungi. *Science* 346 (6213): 1256688. <https://doi.org/10.1126/science.1256688>.
- Tedersoo, L., S. Sánchez-Ramírez, U. Kõljalg, M. Bahram, M. Döring, D. Schigel, T. May, M. Ryberg, and K. Abarenkov. 2018. High-level classification of the fungi and a tool for evolutionary ecological analyses. *Fungal Diversity* 90 (1): 135–159. <https://doi.org/10.1007/s13225-018-0401-0>.
- Tekpinar, A. D., and A. Kalmer. 2019. Utility of various molecular markers in fungal identification and phylogeny. *Nova Hedwigia* 109 (1–2): 187–224. https://doi.org/10.1127/nova_hedwigia/2019/0528.
- Van Der Heijden, M. G. A., R. D. Bardgett, and N. M. Van Straalen. 2008. The unseen majority: Soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems. *Ecology Letters* 11 (3): 296–310. <https://doi.org/10.1111/j.1461-0248.2007.01139.x>.
- Vandenkoornhuise, P., A. Quaiser, M. Duhamel, A. Le Van, and A. Dufresne. 2015. The importance of the microbiome of the plant holobiont. *New Phytologist* 206 (4): 1196–1206. <https://doi.org/10.1111/nph.13312>.
- Verdú, M., and J. G. Pausas. 2007. Fire drives phylogenetic clustering in Mediterranean Basin woody plant communities. *Journal of Ecology* 95 (6): 1316–1323. <https://doi.org/10.1111/j.1365-2745.2007.01300.x>.
- Vilà, M., and J. Sardans. 1999. Plant competition in Mediterranean-type vegetation. *Journal of Vegetation Science* 10 (2): 281–294. <https://doi.org/10.2307/3237150>.
- Webb, C. O., D. D. Ackerly, M. A. McPeck, and M. J. Donoghue. 2002. Phylogenies and community. *Annual Review of Ecology and Systematics* 33 (May): 475–505. <https://doi.org/10.1146/annurev.ecolsys.33.010802.150448>.
- Webb, C. O., D. D. Ackerly, and S. W. Kembel. 2008. Phylocom: Software for the analysis of phylogenetic community structure and trait evolution. *Bioinformatics* 24 (18): 2098–2100. <https://doi.org/10.1093/bioinformatics/btn358>.
- Würth, D. G., M. B. Dahl, M. Trouillier, M. Wilmking, M. Unterseher, M. Scholler, S. Sørensen, M. Mortensen, and M. Schnittler. 2019. The needle mycobiome of *Picea glauca* – A dynamic system reflecting surrounding environment and tree phenological traits. *Fungal Ecology* 41:177–186. <https://doi.org/10.1016/j.funeco.2019.05.006>.
- Zak, D. R., P. T. P. Argiroff, W. A. Castillo, B. James, T. Y. Nave, L. E., Averill, C., Beidler, Kaitlyn V. Jennifer Bhatnagar, J., Blesh, J., Classen, A. T., Matthew, C., Fernandez, C. W., Gundersen, P., Johansen, R., Koide, R. T., Lilleskov, E. A., Lindahl, B. D., Nadelhoffer, K. J., Richard P., P., and Tunlid, A. 2019. Exploring the role of ectomycorrhizal fungi in soil carbon dynamics. *New Phytologist* 223:33–39. <https://doi.org/10.1111/nph.15679>.
- Zanne, A. E., K. Abarenkov, M. E. Afkhami, C. A. Aguilar-Trigueros, S. Bates, J. M. Bhatnagar, P. E. Busby, N. Christian, W. K. Cornwell, T. W. Crowther, H. Flores-Moreno, D. Floudas, R. Gazis, D. Hobbett, P. Kennedy, D. L. Lindner, D. S. Maynard, A. M. Milo, R. H. Nilsson, Jeff Powell, Mark Schildhauer, Jonathan Schilling, and K. K. Treseder. 2020. Fungal functional ecology: Bringing a trait-based approach to plant-associated fungi. *Biological Reviews* 95 (2): 409–433. <https://doi.org/10.1111/bvr.12570>.

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