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Soil mycobiome and forest endophytic fungi: Is there a relationship between them?

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ABSTRACT

Fungi are important ecological agents in forests that contribute to increase the resilience of the whole ecosystem against environmental challenges. Mediterranean forests rank among the habitats most threatened by climate change and the spread of pests and diseases, which ultimately lead them into a spiral of decline. As such, changes in the composition of soil and trees' mycobiota might correlate with health status of the forest and has been scarcely addressed in Mediterranean tree species. In this work, rhizosphere and bark-wood samples from declining Spanish forests of *Castanea sativa* Mill. (chestnut), *Quercus ilex* L. (holm oak), *Q. suber* L. (cork oak) and *Q. pyrenaica* Willd. (Pyrenean oak) were compared. Fungal communities were characterised by means of ITS metabarcoding. Higher diversity in terms of richness was found in soil, with 674 genera belonging to 15 phyla in soil vs 420 genera and 6 phyla in trees. Fungal genera exclusive to declining forests' soils and trees didn't include pathogenic organisms, thus preventing the association of certain genera with forest decline. Alpha diversity didn't correlate with health status or sample type either, as it only increased in soils of asymptomatic chestnuts and not in any of the other analysed tree species. Some differentially abundant genera found in asymptomatic trees, such as *Metarhizium*, *Aspergillus*, *Russula*, *Chaetomium*, *Mortierella* or *Cladophialophora*, may be related to the biological control of decline-contributing pathogens. Finally, no relationship was found between health status and the primary lifestyles of fungi in soil and bark, which can be interpreted as a sign of resilience against adversities following cross-talk between soil and plant fungal communities.

1. Introduction

Mediterranean forests are ecosystems of great ecological importance, as they sport wide biodiversity with high genetic variability, prevent soil erosion and favour water purification (Scarascia-Mugnozza et al. 2000; Morán-Ordóñez et al. 2020). Humans have been taking advantage of Mediterranean forests' resources for millennia, mainly timber, mushrooms and cork (Morán-Ordóñez et al. 2020; Roces-Díaz et al. 2021); however, human activity in this ecosystem has decreased in the last decades (Roces-Díaz et al. 2021).

Mediterranean climate is characterized by the existence of a dry season, the duration and severity of which varies greatly from region to region (Ramírez-Valiente et al., 2022). In particular, the Mediterranean Basin is facing a situation of increasing aridity, reduced precipitation and rising temperatures in the coming decades (Peñuelas and Sardans, 2021). More severe drought conditions, together with the spread of pests and diseases, fires and soil degradation, put the survival of the Mediterranean forest at serious risk (Peñuelas and Sardans, 2021), as it is one of the ecosystems most vulnerable to abiotic and biotic stresses (Pinheiro et al. 2014).

Fungi are important ecological agents in forest ecosystems, playing a key role in the movement of nutrients between different trophic levels. In recent years, high-throughput sequencing (HTS) studies of fungal diversity (mycobiota) have made it possible to relate fungal

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communities in ecosystems to their functioning and stability (Nilsson et al. 2019). Such studies are of special interest for forests under abiotic or biotic stresses, both at the level of soil and tree mycobiota.

Many studies have shown how abiotic stresses strongly modify the diversity and activity of forest trees' mycobiota (Kasanen, 2021). Trees' mycobiota consists of pathogenic fungi and fungi that are highly beneficial to trees and the ecosystem, such as endophytic, saprophytic or mycorrhizal fungi (only present in root tissues) (Poteri et al. 2021). As such, trees can themselves be considered as holobionts (tree + mycobiota) (Lloyd and Wade, 2019). The role of endophytic fungi in tolerance under abiotic stresses and resistance against biotic stresses is widely known (Terhonen et al. 2019). In this regard, mycobiota present in bark and wood of Mediterranean tree species have been identified as an important focus of study to assess changes in response to multifactorial forest decline (Zamora et al. 2008; Botella et al. 2010; Botella and Diez, 2011; Diez-Hermano et al. 2022).

As far as soil mycobiota is concerned, fungi play a fundamental role in the maintenance of basic processes, being the major decomposers of organic matter or in plant-fungi interaction (as mutualists or pathogens) (Fernandes et al. 2022). Given the importance of studying soil fungal diversity, the Global Soil Mycobiome consortium (GSMc) was created in 2021. GSMc is a global soil fungal dataset with more than 700 thousand operational taxonomic units (OTUs) obtained from more than 100 different countries, allowing a biogeographical and macroecological study of fungal diversity (Tedersoo et al. 2021). The microbiota of forests' soils is strongly affected by different disturbances, such as climate change, pests, pathogens, wildfire, logging, drought and anthropogenic disturbances (Martínez-Arias et al. 2020; Bowd et al. 2022). In Mediterranean forests, several studies have been carried out on soil fungal diversity (Habiyaremye et al. 2020; Adamo et al. 2022; Costa et al. 2022; Diez-Hermano et al. 2023). In oak declining 'dehesas', a metabarcoding study revealed that the structure of fungal and oomycete communities in the soil was clearly influenced by tree health status (Ruiz-Gómez et al. 2019). Similarly, metabarcoding has identified how the mycobiota present in chestnut soils affected by the oomycete pathogen *Phytophthora cambivora* are particularly resilient to the pathogen (Venice et al. 2021).

To our knowledge, no study correlating soil and tree mycobiota in Mediterranean forests has been carried out so far. Therefore, the aim of this work is to correlate forest health status with plant and soil mycobiota diversity in Mediterranean forests affected by decline. Key tree species for the ecosystem and human activity, such as chestnut, cork oak, holm oak, and Pyrenean oak, were used to obtain samples of soil, wood and bark from asymptomatic and declining specimens, analysing mycobiota composition by metabarcoding.

2. Materials and methods

2.1. Sampling sites and procedure

Analysed data correspond to rhizosphere and bark-wood samples of asymptomatic and declining trees of *Castanea sativa* (chestnut), *Quercus suber* (cork oak), *Quercus ilex* (holm oak) and *Quercus pyrenaica* (pyrenean oak) from forests in Salamanca (Castile and Leon, Spain), collected in June and July 2020. Each sampling site corresponded to a single tree species. Total number of collected samples was 48 (24 from trees and 24 from soil: 4 tree species x 2 health conditions x 3 plots per sampling site). See Supplementary Material 1 (Table S1 and Fig. S1) for details on sampling sites and locations.

Declining patches were defined as areas with high percentage of declining trees (presence of canker wounds or stem bleeds, >70 % of trees with severe dieback and foliage wilting). Health condition was assessed visually from the ground following guidelines from the ICP Forests Manual Part IV "Visual Assessment of Crown Condition and Damaging Agents". Stands of asymptomatic trees were primarily composed of trees free of dieback or crown transparency. Three circular plots of asymptomatic trees and three with high degree of decline were selected in each site. Distance between sampled trees ranged between 10 and 50 m. Material from five live trees (North orientation) was sampled and pooled per plot. After removing the external bark, one sample was taken per tree from the main trunk at the height of 50 cm over the collar, to a depth of 2–3 cm. Only xylem and the internal bark layer (phloem) were considered in the analysis. Regarding rhizosphere samples, soil under the canopy of the same five live trees was sampled in and pooled per plot. Surface debris was removed and four cores (100 cm3 each at opposite N, S, W, E cardinal points) of topsoil from underneath the litter layer were collected, around one meter from each tree trunk. Coarse roots and stones were removed. All soil cores from each plot were pooled, resulting in a composite soil sample per plot. Samples were stored at −20 ºC prior to processing.

2.2. Sample processing and sequencing

Wood-bark samples were sent for molecular analysis to Biome Makers Inc. (West Sacramento, CA, USA). Region 1 of fungal Internal Transcribed Spacer 1 (ITS1) gene was amplified using WineSeq® custom primers according to Patent WO2017096385 (Becares and Fernández, 2017). After quality control by gel electrophoresis, each library was pooled in equimolar amount and subsequently sequenced on an Illumina MiSeq V2 instrument (Illumina, San Diego, CA, USA) using 2 × 300 paired-end reads.

Soil samples were sent for molecular analysis to Base Clear B.V (Leiden, Netherlands). DNA extraction was performed using the DNeasy PowerLyzer PowerSoil kit (Qiagen). Region 2 of fungal Internal Transcribed Spacer (ITS2) gene was amplified using the following primers: ITS7-F: 5'-GTG ART CAT CGA RTC TTT G-3', ITS4-R: 5'-TCC TCC GCT TAT TGA TAT GC-3' (Fujita et al., 2001; Ihrmark et al., 2012). Paired-end sequence reads (2×300 bp) were generated using an Illumina MiSeq V2 system.

2.3. Bioinformatic analysis

Illumina adapters and chimeras were removed (Edgar et al., 2011) and reads were quality-trimmed. Wood-bark sequencing data were analysed through a QIIME-based custom and inhouse (Biome Makers Inc.) bioinformatics pipeline (Becares and Fernández, 2017; Caporaso et al., 2010). Soil sequencing data were processed following the DADA2 pipeline (Callahan et al., 2016). Parameters' values were as follows: filtering and trimming (maxN = 0, maxEE = 2, truncQ = 2, minLen = 50, rm.phix = TRUE, compress = TRUE), learning error rates (nbases = 1e+08, nreads = NULL, errorEstimationFunction = loessErrfun, MAX_CONSIST = 10, OMEGA_C = 0), merging paired reads (errorEstimationFunction = loessErrfun, selfConsist = FALSE, pool = FALSE) and removing chimeras (method = "consensus").

In order to obtain amplicon sequence variants (ASVs), no clustering based on similarity percentages was applied. Taxonomy assignment and abundance estimation were performed comparing ASVs against UNITE database version 9.0 (Abarenkov et al., 2022). Rarefaction curves were used to evaluate the relationship between sequencing depth and the number of ASVs.

Sequencing of wood-bark samples yielded 38421 (25817–66879) reads on average (median and P25–75), whereas soil samples yielded 32042 (29590–33305) reads on average (median and P25–75), following quality control (see Supplementary Material, Table S2).

2.4. Statistical analysis

Differences between mycobiome communities were evaluated in terms of alpha and beta diversity. Alpha diversity was assessed using Hill diversity indexes, characterised by their exponent l, which determines the rarity scale and corresponds to richness ($l = 1$) or equivalence-corrected versions of Shannon ($l = 0$) and Simpson indexes ($l = -1$)

(Roswell et al. 2021). Differences between health conditions per tree species at $l = [-1, 0, 1]$ were contrasted using Wilcoxon's rank test.

Beta diversity was evaluated in terms of differential abundance by taking into account that high-throughput sequencing counts should be considered compositional data (Gloor et al. 2017). Analyses followed the ZicoSeq procedure, which has been shown to be overall more robust and powerful than other existing methods in recent benchmarks (Yang and Chen, 2022). Compositional effects were addressed by adopting a reference-based approach (selecting close-to-invariant taxa as baseline abundances) and association testing was conducted by linear model-based Smith permutation testing (LDM and DACOMP methods in Brill et al. 2022 and Hu and Satten 2020, respectively). Reference taxa were adjusted for health status (factor with two levels: asymptomatic, declining) and type of sample (factor with two levels: soil, trees) as covariates. Taxa were filtered if their prevalence was less than 20 % and their mean relative abundance was less than 0.2 %. Percentage of top outliers replaced by winsorization was 10 %. Abundances were square root transformed. Multiple test correction of p-values was based on 500 permutation tests.

All fungal genera were included in the functional analyses. Each genus was assigned a functional guild according to the "primary lifestyle" column obtained from FungalTraits database V1.2 (Põlme et al. 2020). Raw read numbers of each guild were summed per tree species, health condition and type of sample and expressed as $\log_2$(guild abundance/total abundance).

All analyses were performed in R environment 4.1.3 (R Core Team, 2022). Analysis of sequencing data and ASV identification were performed using the packages *Biostrings* (Pagès et al. 2022), *dada2* (Callahan et al. 2016) and *ShortRead* (Morgan et al., 2009). Hill diversity analysis was carried out using the package *MeanRarity* (Roswell and Dushoff, 2022). For compositional analysis the package *GUniFrac* (Chen et al. 2022) was used. Taxonomic information was handled and plotted with the package *metacoder* (Foster et al. 2017).

3. Results

3.1. Tree and soil-fungal community description

The analysis of fungal communities showed that soil had higher diversity in terms of richness than tree bark (674 genera belonging to 15 phyla in soil vs 420 genera and 6 phyla in trees) (Fig. 1). Both niches shared the two major phyla (Ascomycota and Basidiomycota), however, the remaining phyla differed. In trees, the main phyla were Ascomycota (~72 %), Basidiomycota (~21 %) and Mucoromycota (~5 %), while in soil they were Ascomycota (~66 %), Basidiomycota (~26 %), Glomeromycota (~2 %), Chytridiomycota (~2 %) and Mucoromycota (~2 %).

In order to find commonalities associated with health status, presence/absence of fungal genera was analysed independently of tree species. In this sense, only those genera that were present in at least 80 % of the samples were taken into account. Five genera exclusive to soil (~9 %) and six exclusive to trees (~10.9 %) were found in asymptomatic samples, with no genera common to both and not present in declining samples (Fig. 2 and Table 1). Less number of exclusive genera were found in declining samples: three in soil (~5.4 %) and two in trees (~3.6 %), again with no common genera that were absent in asymptomatic samples. Five genera were reported in all samples, identified as *Mortierella*, *Penicillium*, *Saitozyma*, *Solicoccozyma* and *Talaromyces*.

3.2. Biodiversity analysis

Alpha diversity and differential abundance (DA) were assessed by health status and sample type, per tree species. In chestnut, a higher alpha diversity was reported in soil than in tree, being significantly higher in asymptomatic forest soils than in declining forest soils. However, alpha diversity between declining and asymptomatic chestnuts was comparable (overlapping curves at Hill = 1 and −1) (Fig. 3). In cork oak, significantly higher alpha diversity of non-dominant genera (Hill = 1) was reported in soil, compared to trees. There were significant differences between asymptomatic and declining forest soils, with more dominant genera found in the latter (Hill = −1). Alpha diversity between asymptomatic and declining trees was similar (similar Hill = 1 and −1). In the case of holm oak and Pyrenean oak, no significant differences in terms of fungal alpha diversity were reported.

Regarding DA, in asymptomatic chestnuts two fungal genera were more abundant in soil (*Metarhizium* and *Cloheyomyces*) and two in tree (*Plectosphaerella* and *Aspergillus*) (Fig. 4). No differences were found in declining chestnuts. In asymptomatic cork oaks, DA fungi included two genera in soil (*Russula* and *Tomentella*) and one in tree (*Chaetomium*). No

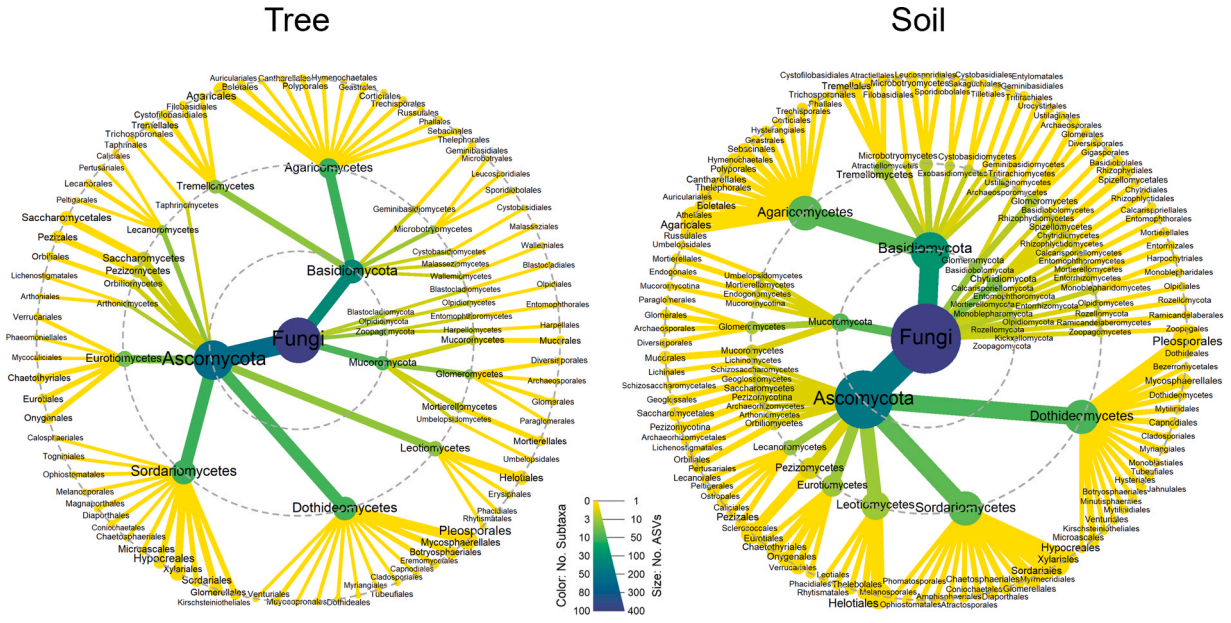

Fig. 1. Taxonomic heat tree. Node size represents the number of ASVs and colour scale represents the number of subtaxa. Dashed grey circles indicate the following taxonomic levels: phylum (inner), class (middle), order (outer). NA: Not Assigned.

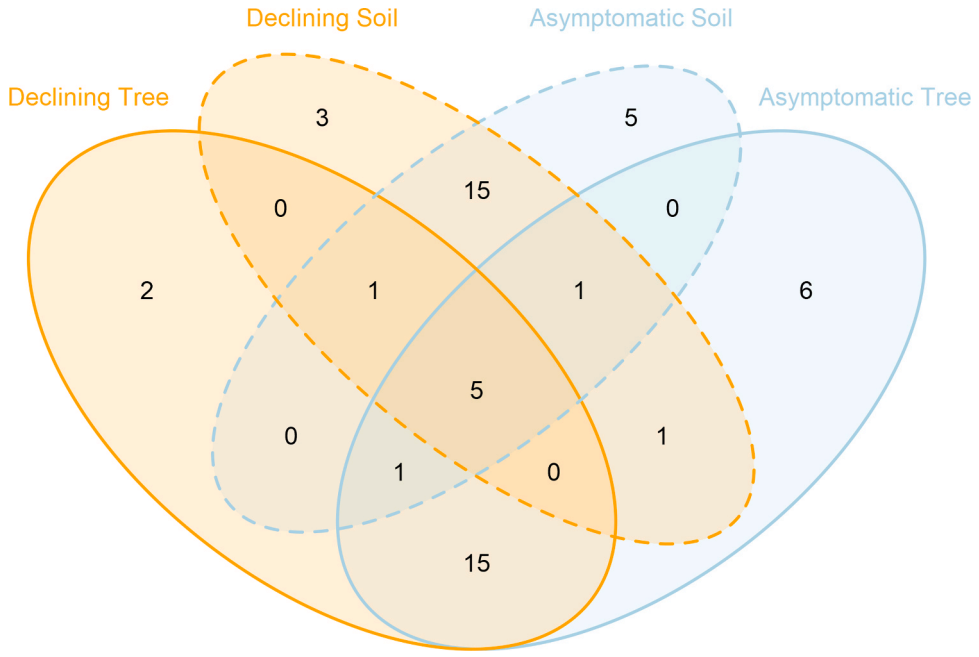

Fig. 2. Combined effect of health status and type of sample in mycobiota. Venn's diagram showing the number of common and exclusive genera between asymptomatic and declining samples. Only genera present in 80 % of samples per condition were included, regardless of tree species. Identity of genera for every intersection can be found in Supplementary Material 2.

Table 1
Fungal genera exclusive to soil or trees by health status.

Asymptomatic		Declining	
Soil	**Trees**	**Soil**	**Trees**
Coleophoma	*Periconia*	*Meliniomyces*	*Preussia*
Geomyces	*Phoma*	*Pleurotus*	*Tausonia*
Sagenomella	*Podospora*	*Polyphilus*	
Scytalidium	*Purpureocillium*		
Varicellaria	*Stachybotrys*		
	Zopfiella		

differences were found in declining cork oaks. With respect to asymptomatic holm oaks, two fungal genera were reported as differentially abundant in soil (*Umbelopsis* and *Cladophialophora*) and seven in trees (*Fusarium*, *Solicoccozyma*, *Mortierella*, *Alternaria*, *Cladosporium*, *Aspergillus* and *Penicillium*). In declining holm oaks, four differential genera (*Solicoccozyma*, *Linnemannia*, *Mortierella* and *Preussia*) were found only in trees. Finally, in asymptomatic Pyrenean oaks, four fungal genera were reported as more abundant in soil (*Cortinarius*, *Inosperma*, *Geminibasidium* and *Cladophialophora*) and two in trees (*Solicoccozyma* and *Mortierella*). On the other hand, in declining Pyrenean oaks, five fungal genera were found to be differentially abundant in soil (*Russula*, *Tomentella*, *Geminibasidium*, *Exophiala* and *Cladophialophora*) and two genera in tree (*Fusarium* and *Solicoccozyma*).

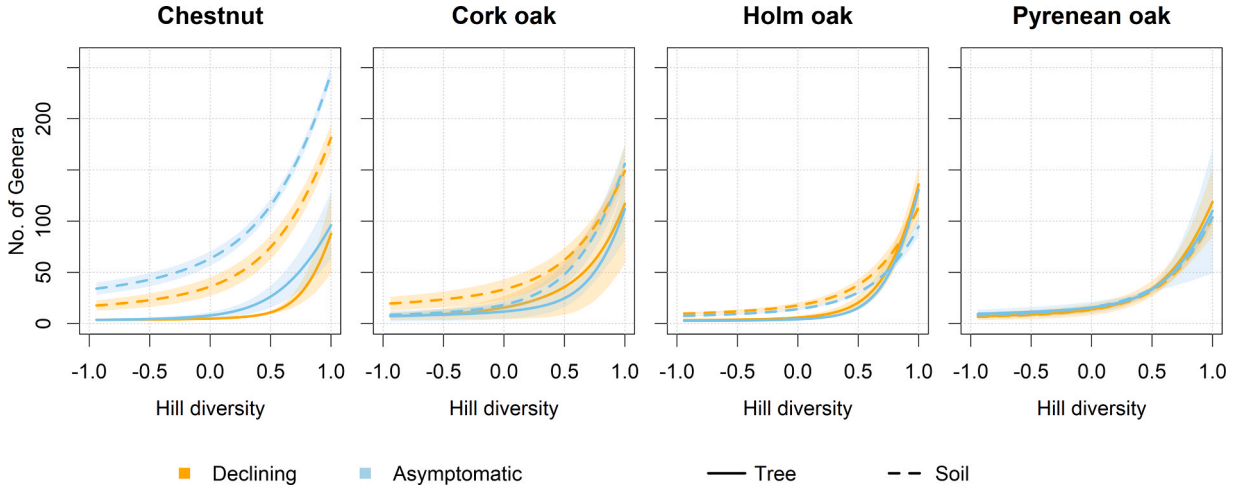

Fig. 3. Diversity profiles per tree species, health status and type of sample. Curves represent the average diversity in samples from asymptomatic and declined trees in terms of an imaginary assemblage with that same diversity, but in which all species are equally abundant (Roswell et al. 2021). The horizontal axis represents the exponent l of Hill diversity, which can be interpreted as equivalence-corrected versions for richness (l = 1), Shannon (l = 0) and Simpson (l = −1) diversity estimators. Shadowed intervals correspond to standard error. Significant differences were found at l = [1, 0,−1] between declining and asymptomatic chestnut soils, between chestnut soils and bark samples, and at l = −1 for declining cork oak soils (Wilcoxon test, n = 3 per tree species, health condition and sample type, $p > 0.05$). Raw curves prior to averaging can be found in Supplementary Material 1 (Fig. S2).

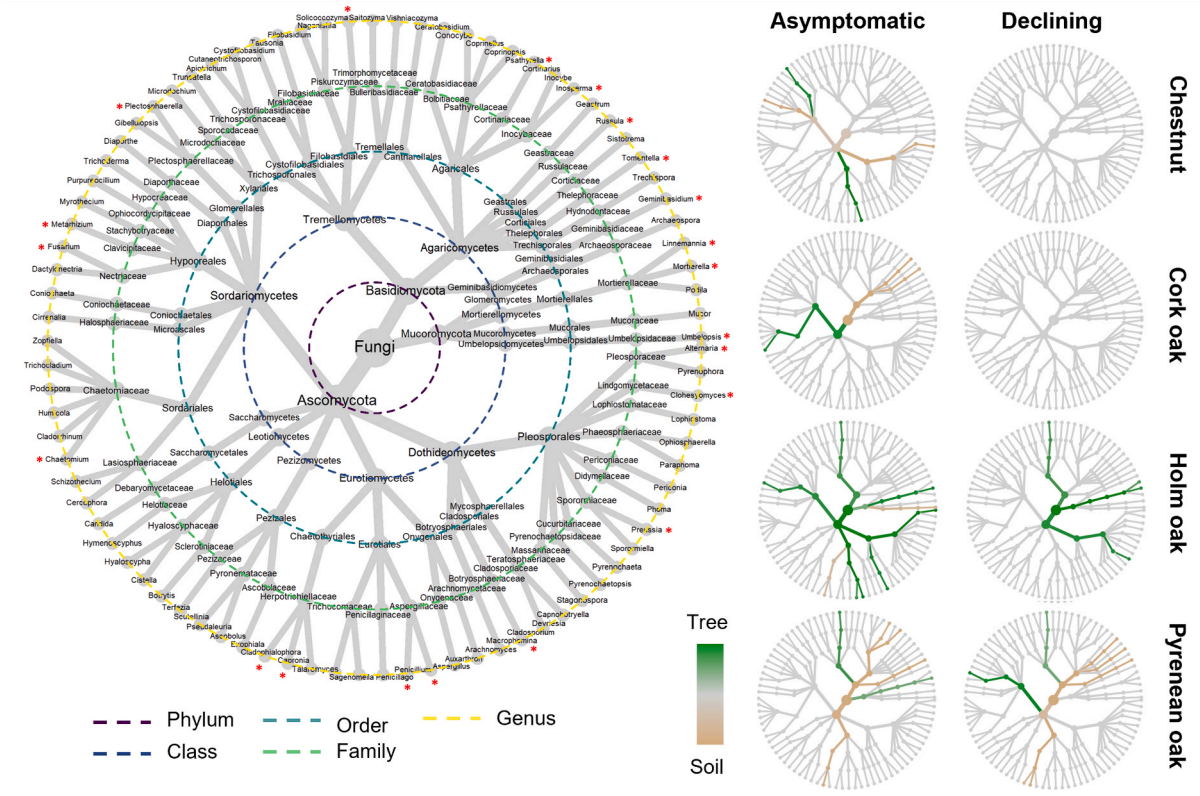

Fig. 4. Differentially abundant genera found by ZicoSeq analysis. Coloured branches in small taxonomic trees to the right indicate genera found to be significantly more abundant in soil (brown) or in trees (green) according to ZicoSeq method (p-val < 0.1 and absolute value of R2 > 0.1). Empty, large taxonomic tree to the left is meant to be used as a reference for identity of genera. Zoomed in versions of the small trees with named branches can be found in Supplementary Material 1 (Figs. S3 to S10).

3.3. Functional profiles

Primary lifestyles according to FungalTraits database were assigned to each of the fungal genera reported in soil and trees of asymptomatic (Fig. 5) and declining (Fig. 6) samples. This functional assessment is mainly predictive, based on species-specific predictions. Not all fungal species have predicted functions in the database. Therefore, generalization was performed at the genus level. Main functional guilds found in asymptomatic samples were ectomycorrhizae, root endophytes, mycoparasites and lichens, which were consistently more abundant in soil for all tree species, as well as plant pathogens, saprotrophs and algal parasites, which were more abundant in trees. A similar pattern was found in declining samples. Abundance of animal parasites was also comparable in all samples, whereas other lifestyles such as moss symbionts and animal endosymbionts were totally absent.

4. Discussion

Imbalances in the holobiont microbiome may compromise its essential functions and thus its ability to adapt to different biotic and abiotic stresses existing in the ecosystem. It is clear that microbial diversity plays a key role as a buffer against forest decline, making them more resilient when facing adversities (Bettenfeld et al. 2020). In this sense, metabarcoding studies provide relevant information on the relationship between microbial diversity of plants and soils and the health status of forests.

In the present work we show that there is more fungal diversity in soils than in trees regardless of trees' health status, an aspect widely confirmed for different plant species and ecosystems (Pagano et al. 2017). When considering the sanitary condition, some fungal genera were reported only in soils (such as *Meliniomyces, Pleorotus* and *Polyphilus*) and trees (*Preussia* and *Tausonia*) of declining samples. However, none of these genera has been previously described as a plant pathogen. The genus *Meliniomyces* has been described as an endophyte or ericoid mycorrhiza (Ohtaka and Narisawa, 2008; Vohnik et al. 2013). The genus *Pleorotus* is widely known as an edible saprophytic fungus (Suwannarach et al. 2020; Doroški et al. 2022) and even as a biological control agent against nematodes (Singh et al. 2019). *Polyphilus* is a recently created fungal genus, which includes nematophagous fungi of eggs and cysts of plant-parasitic nematodes (Ashrafi et al. 2018). In trees, the genus *Preussia*, widely described as endophyte (Mapperson et al. 2014; Tane et al. 2019) and the genus *Tausonia*, which include yeasts present in very different niches and producing important enzymes of biotechnological applications (Trochine et al. 2022), were reported. Therefore, in our analysis we did not find a relationship between the genera exclusive to soil and tree of declining forests with behaviours known to be pathogenic to plants.

With respect to alpha diversity, we found greater diversity in chestnuts' soil than in bark. Previous studies have pointed out the great microbial diversity present in chestnuts' soils, being even higher than that of other forest species (Kelly et al. 2021). We also found more diversity in soils from asymptomatic samples than in declining soils, which might be related to the absence of decline. However, alpha diversity in asymptomatic and declining chestnut bark was similar, contrary to other authors who identified how bleeding canker or yellow crinkle diseases significantly modify the microbiota of bark (Koskella et al. 2017), twigs and leaves (Ren et al. 2021). Similarly, we also observed higher alpha diversity in cork oaks' soils than in bark. However, contrary to chesnuts, declining cork oaks' soils had higher fungal diversity than asymptomatic ones, which does not allow to relate higher diversity to the asymptomatic status of the tree, as other authors reported before (Gómez-Aparicio et al. 2022). As in chesnuts, no correlation was found between alpha fungal diversity and health status of cork oak trees. Finally, we found no differences in alpha diversity for holm oaks and Pyrenean oaks, neither

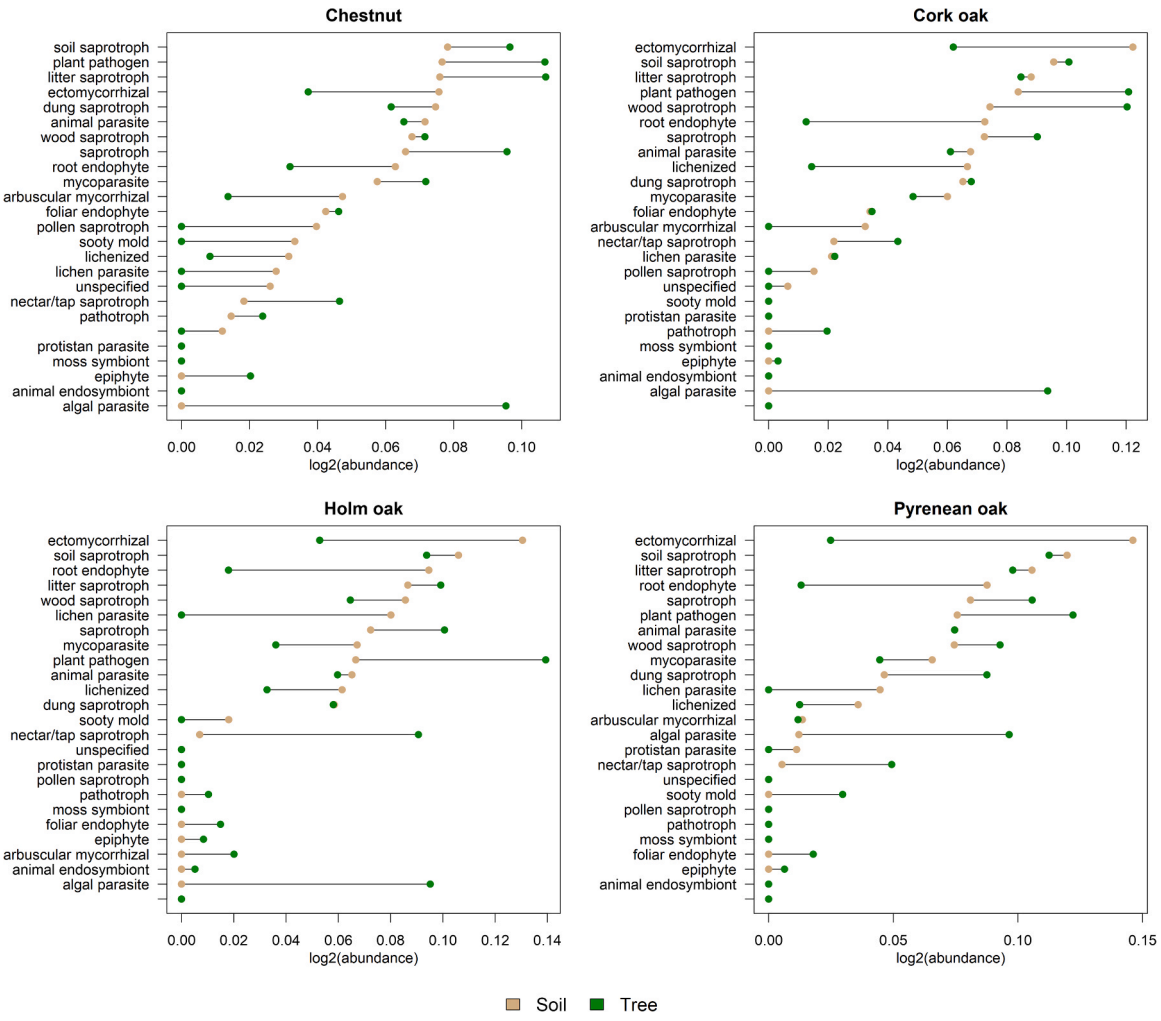

Fig. 5. Comparison of functional guilds between soil and bark of asymptomatic trees. Horizontal axis represents sum of abundances expressed as $\log_2$ (guild abundance/total abundance). Connecting lines between two dots correspond to the difference between soil and trees. Single dots indicate overlapping.

between soil and trees, nor due to health status. Forest decline has been associated previously with significant changes in microbial diversity in holm oak, nonetheless (Català et al. 2017; Ruíz-Gómez et al., 2019).

Some genera with known activity as biological control agents were found to be differentially abundant (DA) between bark and soil of asymptomatic chestnuts and cork oaks, such as *Metarhizium* (Stone and Bidochka, 2020), *Aspergillus* (Choi and Ahsan, 2022), *Russula* (Osaki-Oka et al. 2019) and *Chaetomium* (Madbouly and Abdel-Wareth, 2020). Holm oaks and Pyrenean oaks had several DA fungi in common. In asymptomatic samples, *Mortierella* was found in bark and *Cladophialophora* in soil, both being genera that include several species used as biological control of nematodes (DiLegge et al. 2019) and pathogenic fungi (Harsonowati et al. 2020), respectively. In declining samples, more abundance of the genus *Solicoccozyma* was found in bark than in soil although so far it has only been described as a promoter of plant growth (Carvajal et al. 2023).

Analysis of primary lifestyles showed a homogeneous functional profile across tree species, health status and sample type. Predominant lifestyles were ectomycorrhizae, saprotrophs, root endophytes and plant pathogens, widespread functional niches among fungi that make up the mycobiota of all forest soils (Li et al. 2022). This might be reflecting a resilient behaviour of the functional characteristics of fungal communities against forest decline, and could be explained by a continuous exchange of soil-tree mycobiota, and to a lesser extent from the tree to the soil, specially of those fungi whose dispersal is limited to a way in particular (wind, insects, rain, etc.) (Asiegbu, 2022).

The present study has some limitations that should be taken into account. First, different ITS regions were sequenced in wood-bark (ITS1) and soil (ITS2) samples. Mixed results can be found in studies comparing both: in some of them, ITS1 and ITS2 yielded comparable diversity and taxonomic resolution (Bazzicalupo et al., 2013; Blaalid et al., 2013); whereas others favour ITS1 (Mbareche et al., 2020; Wang et al., 2015) or ITS2 Yang et al., 2018). Second, wood-bark samples were processed using a QIIME-based pipeline, whereas soil samples were analysed by means of DADA2. Although using the same genetic markers and bioinformatic pipelines would have been preferable, we still believe that the results shown here hold interpretability and add value to existing comparisons between soil and plant mycobiome diversity.

5. Conclusion

As conclusions, soils had more diverse mycobiota than trees in the ecosystems studied, overall. Fungal genera exclusive to declining forests' soils and trees didn't include pathogenic organisms, thus preventing the association of certain genera with forest decline. Alpha diversity didn't correlate with health status or sample type either, as it only increased in soils of asymptomatic chestnuts and not in any of the other analysed tree species. Some differentially abundant genera found in asymptomatic trees, such as *Metarhizium*, *Aspergillus*, *Russula*, *Chaetomium*, *Mortierella* or *Cladophialophora*, may be related to the biological control of decline-contributing pathogens. Finally, no relationship was found between health status and the primary lifestyles of fungi in soil

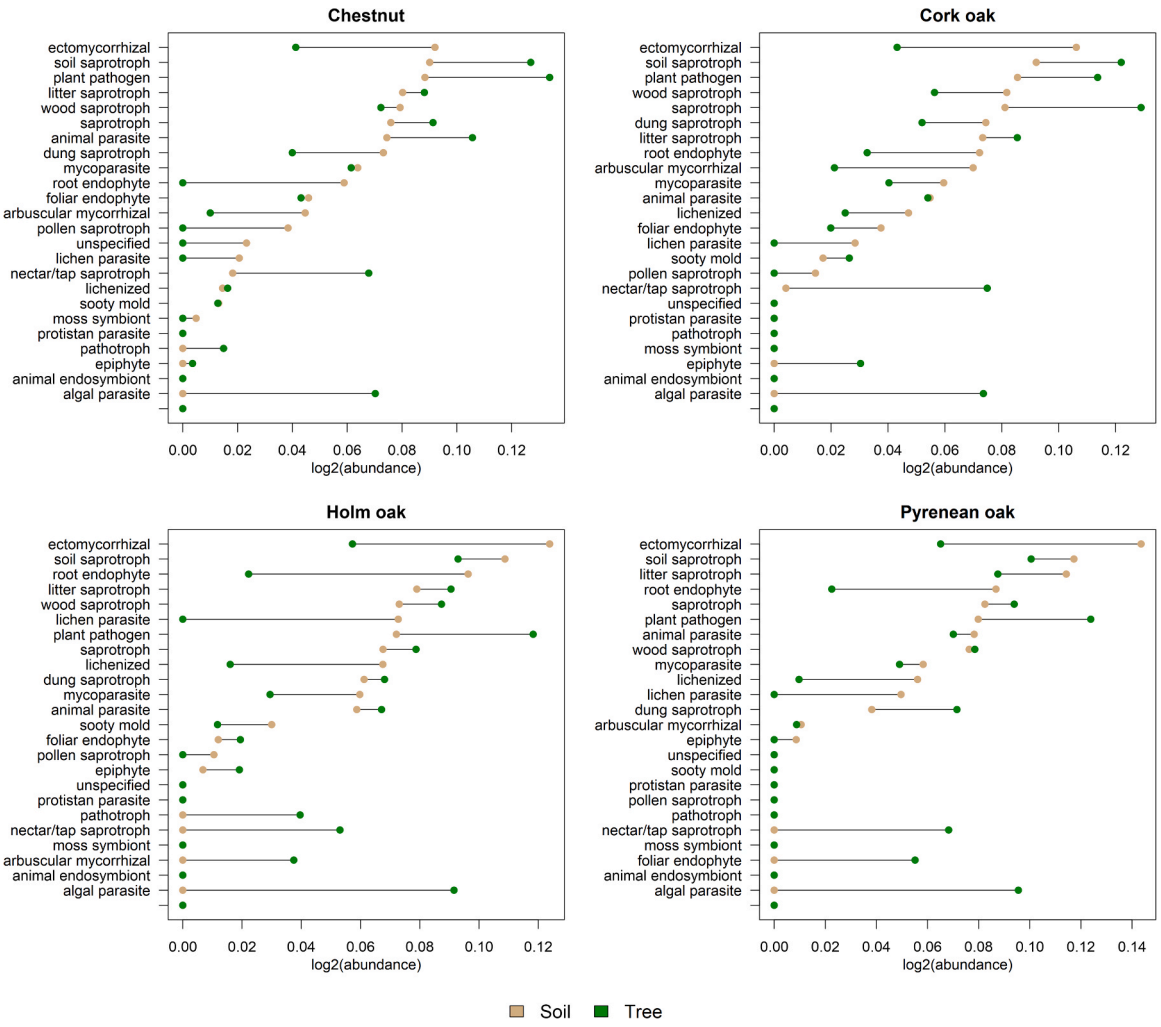

Fig. 6. Comparison of functional guilds between soil and bark of declining trees. Horizontal axis represents sum of abundances expressed as $\log_2$ (guild abundance/total abundance). Connecting lines between two dots correspond to the difference between soil and trees. Single dots indicate overlapping.

and bark, which can be interpreted as a sign of resilience against adversities following cross-talk between soil and plant fungal communities.

CRediT authorship contribution statement

Sergio Diez-Hermano: Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Investigation, Formal analysis, Data curation. **Álvaro Benito:** Writing – review & editing, Project administration, Methodology, Investigation. **Jorge Poveda:** Writing – original draft, Formal analysis. **Pablo Martín-Pinto:** Writing – review & editing, Supervision, Resources, Project administration, Funding acquisition, Conceptualization. **Álvaro Peix:** Writing – review & editing, Supervision, Resources, Project administration, Funding acquisition, Conceptualization. **Julio Javier Diez:** Writing – review & editing, Supervision, Resources, Project administration, Funding acquisition, Conceptualization.

Declaration of Competing Interest

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

Data Availability

Data and scripts used in this study are available in the following GitHub repository: https://github.com/serbiodh/2024_ForEcolMan_SoilvTrees. Raw sequencing data are available at NCBI SRA under BioProjects PRJNA953856 (soil) and PRJNA885270 (trees).

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the

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