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Exploring the soil microbiota of maritime pine (*Pinus pinaster*) groves, nearby woody crops (vineyards) and rainfed cereal crops, and its relation to tree decline

José Carlos Marcos-Romero · Jorge Poveda · Álvaro Benito-Delgado · Tamara Sánchez-Gómez · Jorge Martín-García · Julio Javier Díez

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Abstract Maritime pine (*Pinus pinaster*) is a conifer widely distributed in the western European Mediterranean Basin, which provides important resources, such as resin, pulpwood, wood, pellets and bark. These forests are seriously threatened by decline, which reduces the area of maritime pines in the Mediterranean Basin every year. Different crops, such as vineyards and rainfed cereals, are often established adjacent to these pine forests. The objective of this work is to explore for the first time the bacterial and fungal diversity of the soils of pine forests and surrounding crops, in order to establish a relationship with the presence or absence of tree decline. Soil samples were taken from three different areas in the south of the province of Burgos (Spain), where pine forests, vineyards and rainfed cereals were grown in the surrounding area, and the microbial diversity present was analyzed by metabarcoding (bacterial 16S and fungal ITS). The main bacterial phyla reported in pine forests were Proteobacteria and Actinobacteria, and the fungal phylum was Ascomycota. With regard to bacterial families and the different plant cover where they were found, the greatest co-occurrence was found in areas where there were diseased pine forests, unlike what occurred with fungal genera. The highest alpha diversity of bacterial families was reported in the soils of diseased pine forests and surrounding vineyards. While the highest alpha diversity for fungal genera was found in rainfed cereals associated with diseased pine forests. The bacterial families Hyphomonadaceae and Koribacteraceae and the fungal genus *Volutella*, found in the soils of diseased pine forests, include plant pathogens that could explain the presence of decline. In the soils of healthy pine forests was reported the presence of bacterial families such as Azospirillaceae and Bacillaceae, as well as the fungal genera *Amphinema, Emmonsiellopsis* and *Harmoniella,* possibly related to the absence of diseases in the trees. In the soils of diseased pine forests, ectomycorrhizal fungi were reported as the main functional niche, while in the surrounding crops, plant pathogenic and saprotrophic fungi were found. Therefore, the soil microbial diversity present in pine forests and surrounding crops could contribute to explain the presence or absence of tree decline, along with the study of other factors, such as abiotic conditions or pest infestations. The study of microbial diversity, along with other analyzes, could help prevent the onset of disease.

J. C. Marcos-Romero · J. Poveda (✉) ·
Á. Benito-Delgado · T. Sánchez-Gómez ·
J. Martín-García · J. J. Díez (✉)
Department of Plant Production and Forest Resources, Sustainable Forest Management Research Institute (iuFOR), Higher Technical School of Agricultural Engineering (ETSIIAA), University of Valladolid, Palencia, Spain
e-mail: jorge.poveda@uva.es

J. J. Díez
e-mail: juliojavier.diez@uva.es

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Introduction

Maritime pine (*Pinus pinaster* Ait.) is a conifer native to the western Mediterranean Basin, of great environmental importance. In south-western Europe, *P. pinaster* forests cover some 3 million hectares, with 0.7 million ha in Portugal, 0.8 million ha in Spain, 1 million ha in France and 0.4 million ha in Italy. In both the Iberian Peninsula and France, *P. pinaster* is the most abundant conifer (Ribeiro et al. 2022). Maritime pine has historically been exploited for the production of resin (until the first half of the twentieth century), and today it is an important resource for pulpwood for paper manufacturing, wood for packaging, furniture and construction, and pellets for firewood (Chevalier et al. 2024). In recent years, the bark has also been studied and utilized as an important source of bioactive compounds with applications in many different industries. Among the isolated and characterized compounds, phenolic compounds and terpenes stand out, being used in the pharmaceutical and nutraceutical industry for their anticancer, anti-inflammatory, antidiabetic or neuroprotective qualities (Mármol et al. 2019; Alonso-Esteban et al. 2022).

One of the main threats facing *P. pinaster* stands is forest decline, which year after year reduces the area of this conifer in the Mediterranean Basin. This forest decline is a complex process whose causes include biotic and abiotic factors that act synergistically, such as the climate (historical and extreme events, such as droughts, heatwaves or severe frosts), management, insect pests or phytopathogens, such as the nematode *Bursaphelenchus xylophilus* (Gea-Izquierdo et al. 2019; Calama et al. 2024).

Vineyard landscapes have been identified as important agroecosystems at the ecological (hotspots of biodiversity), economic (wine industry) and cultural (intangible benefits) levels (Candiago et al. 2023). Mediterranean viticulture produces more than 50% of all the wine produced in the world each year, and 55% of the world exports of this product. Nowadays, Mediterranean vineyards are greatly affected by climate change, due to an increase in warmer and drier periods each year (Costa et al. 2023). In certain regions in the southern Mediterranean Basin, maritime pine forests are found alongside vineyards of great commercial importance.

Other crops found alongside pine forests and vineyards in the southern Mediterranean Basin are rainfed cereals (Molénat et al. 2023). Worldwide, the demand for cereals by 2030 is expected to be 10 million tons and 15 million by 2050, in order to feed the entire population (Farooq et al. 2023). Obtaining these global cereal productions requires an increase in yields and in the areas dedicated to their cultivation. However, most cereals are produced using dry farming methods, which in recent years has led to a reduction in yield due to climate change. In North America, Europe and Australia, dry farming cereal production has fallen by 20% due to an increase in annual periods of drought (Whitworth-Hulse et al. 2023), an aspect of particular importance in the rainfed agricultural systems of the Mediterranean Basin (Molénat et al. 2023).

Forest systems represent an important focus of microbial diversity, with soil microorganisms playing a key role in maintaining ecosystem stability and alleviating the effects of climate change (Baldrian et al. 2023). These microorganisms interact closely with forest plants, continuously moving between soil and endophytic niches, with a direct impact on plant health (Diez-Hermano et al. 2024). The microbial communities associated with forest plant species are complex and dynamic, with mutualistic, commensal and pathogenic species. These microorganisms play a key role in the development of forest decline, because modifications or imbalances in these communities can lead to essential functions for holobiont fitness not being covered (Bettenfeld et al. 2020). The relationship between forest decline and soil microbiome has been studied for several forest species in the Mediterranean basin, such as chestnut (*Castanea sativa*) (Diez-Hermano et al. 2023), holm oak (*Quercus ilex*) (Diez-Hermano et al. 2023), cork oak (*Q. suber*) (Gómez-Aparicio et al. 2022; Diez-Hermano et al. 2023; Marcos-Romero et al. 2025) or Pyrenean oak (*Q. pyrenaica*) (Diez-Hermano et al. 2023). With regard to the pine decline, there is various work that has managed to relate a specific rhizospheric soil microbiota with the presence or absence of the disease (Lasa et al. 2024; Morales-Rodríguez et al. 2024), having been reported an absolute relationship between both factors (Gazol et al. 2024). Therefore, more research is required to obtain discernment of the true role of the rhizospheric and soil microbiota in the presence or absence of pine decline.

In the case of vineyards, the soil microbiome has been described as a fundamental pillar in the correct development of the grapevine, with microorganisms that protect the plant against pathogens and pests, that promote plant growth and that increase tolerance to abiotic stresses (Fournier et al. 2022). Even at the level of wine, the “terroir” (the characteristics that make up the soil in which the vineyards grow and that influence the quality and flavor of the wine) has been specifically linked to the soil microbiome (Franco et al. 2024). The health of vineyards is closely related to the microbiome of the soil in which they grow (Bettenfeld et al. 2022), also in relation to vineyard decline (Darriaut et al. 2023).

Finally, with regard to the microbiome of the soils of rainfed cereal crops, it is widely known that the communities of bacteria and fungi associated with soils of these crops are fundamental to the proper development of the plant and, therefore, to promoting world food security (Suman et al. 2022). For example, in the specific case of wheat, any change in crop management has been linked to a significant modification of the soil microbiome, which could imply significant changes in grain production (Rodgers et al. 2021).

The objective of this work is to analyze by metabarcoding the bacterial and fungal diversity of maritime pine soils and associated vineyards and rainfed cereal crops, together with their relationship with the presence or absence of diseased trees due to decline. Furthermore, as far as we know, this work would be the first to analyze the microbial diversity of vineyards and dryland cereal crops associated with pine forests, in addition to their relationship with forest decline.

Materials and methods

Characteristics of the study area and sampling

Soil samples were collected from three study areas within the municipalities of Gumiel de Mercado and La Horra, province of Burgos (Spain), during March 2021 (Fig. 1). The chosen areas were a mixture of pine forests, vineyards and fields of rainfed cereals (wheat, barley or rye). It is an area with a markedly oceanic climate, characterized by an average annual temperature of 11.9 °C and an average annual rainfall of 465 mm. In terms of soil, reddish silt and conglomerates are predominant, with luvisols and cambisols mainly found on top of them.

For the study, a total of 90 soil samples were taken, at the rate of 15 samples for each type of vegetation cover (pine forest, vineyard or rainfed cereal) and health status of the pine forest (healthy or diseased). Soil sampling was conducted to a depth of

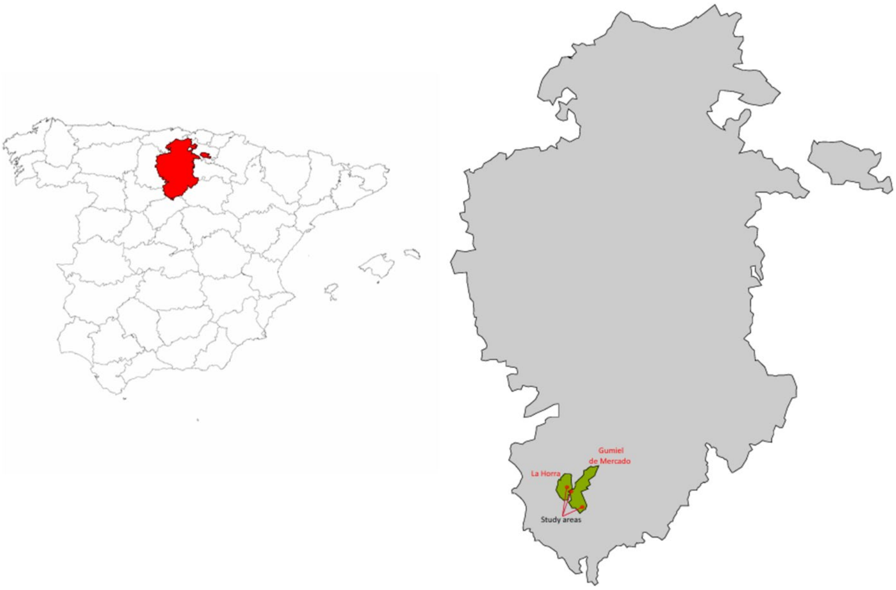


Fig. 1 Location of sampling sites. (Left) Map of Spanish provinces; the province of Burgos sampled are highlighted in red. (Right) Detail of the province of Burgos. The sampled municipalities are highlighted in red. The red dots correspond to the sampling sites

approximately 15 cm. Surface debris was removed prior to sampling to avoid contamination, and coarse roots and stones were discarded. After each extraction, sampling tools were disinfected with a 2% sodium hypochlorite solution. All soil cores from the same plot were combined into a single composite sample. In total, 18 composite samples were obtained (3 areas × 2 health conditions × 3 plant covers). Soil samples were labeled, placed in sterile containers, and stored at − 20 °C until laboratory processing.

Dasometric and health assessment of trees

The dasometric data have been obtained using a different methodology depending on the variable that was to be analyzed. The diameter at breast height of the trees has been measured with the help of a caliper at a height of 1.30 m from the ground, taking two measurements and subsequently obtaining the average as a representation of each tree. Regarding the height of the tree, it was obtained by measuring each tree's total height from the base to the tip of its crown using a clinometer. The level of defoliation has been visually assessed by comparing the leaf loss of each tree with the reference tree.

Sample processing and sequencing

Sample processing and sequencing of DNA fragments were performed using the methodology previously described by Morales-Rodríguez et al. (2024). DNA extraction was performed using the DNeasy PowerLyzer PowerSoil DNeasy kit (Qiagen, Germany). The V4 domain of bacterial 16S rRNA genes was amplified using primers F515 (5′-NNNNNNNNNNNGTGTGCCAGCCAGCMGCCGC GGTAA-3′) and R806 (5′-GGACTACHVGGG GGTWTCTAAT-3′), with the forward primer modified to contain a unique 8 nt barcode and a 2 nt Linker sequence at the 5′ end. Fungal internal transcribed spacer (ITS) loci 1 were amplified with primers BITS (5′-NNNNNNNNNNNNNNNNNNNNCTACCTGCG GARGGATCA-3′) and B58S3 (5′-GAGATCC RTT GYTRAAAGTT-3′), with a unique 8 nt barcode and linker sequence (bolded portion) incorporated into each forward primer. Samples were sent to Biome Makers Spain S.L. (Valladolid, Spain) for processing and sequencing using Illumina MiSeq 2 × 300.

Bioinformatic analysis

Bioinformatic analysis of the sequences obtained was performed using the methodology previously described by Diez-Hermano et al. (2024). Illumina adapters and chimeras were removed and the quality of the reads was trimmed. Sequencing data were processed following the DADA2 pipeline (Callahan et al. 2016). Parameter 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 of paired reads (errorEstimationFunction = loessErrfun, selfConsist = FALSE, pool = FALSE) and chimera elimination (method = "consensus").

To obtain amplicon sequence variants (ASVs), no clustering based on similarity percentages was applied. Taxonomic assignment and abundance estimation were performed by comparing the ASVs with the SILVA v138.1 database (Quast et al. 2012) for bacteria, and the UNITE database version 10.0 (https://unite.ut.ee) for fungi. Rarefaction curves were used to assess the relationship between sequencing depth and number of ASVs.

Statistical analysis

For the statistical analysis of the data obtained, the methodology previously described by Diez-Hermano et al. (2023) was followed. Prior to analysis, raw ASV readings were aggregated to genus level to have higher confidence and avoid misidentification of closely related species. Differences between mycobiome communities were assessed in terms of alpha and beta diversity. Alpha diversity was assessed using Hill's diversity indices (Roswell et al. 2021). Differences between pine health conditions were contrasted using the Wilcoxon rank test.

Beta diversity was assessed in terms of differential abundance, keeping in mind that high-throughput sequencing counts should be considered compositional data. Analyses followed the ZicoSeq procedure (Yang and Chen 2022), while compositional effects were addressed by adopting a reference-based approach (selecting taxa close to invariants as reference abundances). Association tests were conducted using Smith permutation tests based on the linear models of the LDM (Hu and Satten 2020) and DACOMP (Brill et al. 2022) methods. Reference taxa were adjusted for health status (factor with two levels: healthy, declining) as a covariate. Taxa were filtered out if their prevalence was less than 20% and their mean relative abundance was less than 0.2%. The percentage of top outliers replaced by winsorization was 10%. Abundances were square root transformed. Correction of p-values by multiple testing was based on 500 permutation tests.

All bacterial and fungal genera were included in the functional analyses based on the assignment of a functional guild using BactoTraits V2 (Cébron et al. 2021) and FungalTraits 1.2 (Põlme et al. 2020) databases. Only ASVs classified with a confidence level of "Probable" or "Highly probable" were used. The numbers of raw readings for each guild were summed by health condition and expressed as log2(guild abundance/total abundance).

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

Results

Characterization of tree decline

In the dendrometric and visual characterization of the sampled pines, an absence of significant differences was determined with respect to the diameter of the stem. The declining trees were significantly taller (over 12 m) than the healthy ones (under 10 m). With regard to the level of defoliation, the declining pines showed significantly higher levels of defoliation (over 60%) than the healthy trees (Fig. 2).

Description of bacterial communities

The analysis of the bacteria present in the pine soils sampled resulted in 15 phyla and 118 orders. As far as bacterial families are concerned, most of them correspond to the phyla Proteobacteria (27.43%) and Actinobacteria (14.35%) (Fig. 3).

The detailed analysis of the bacterial families present under healthy and diseased pines vineyards and rainfed cereal crops shows that there is more equality between the areas associated with diseased states (n = 51, 54.3%) as opposed to healthy ones (n = 35, 40.2%). Regarding the type of vegetation cover, was reported a significant equality of bacterial families between cereal crops and healthy pine forests (n = 16, 18.4%), compared with diseased trees (n = 1, 1.06%), where bacterial families reported less equality between crops and pine. There was more equality in

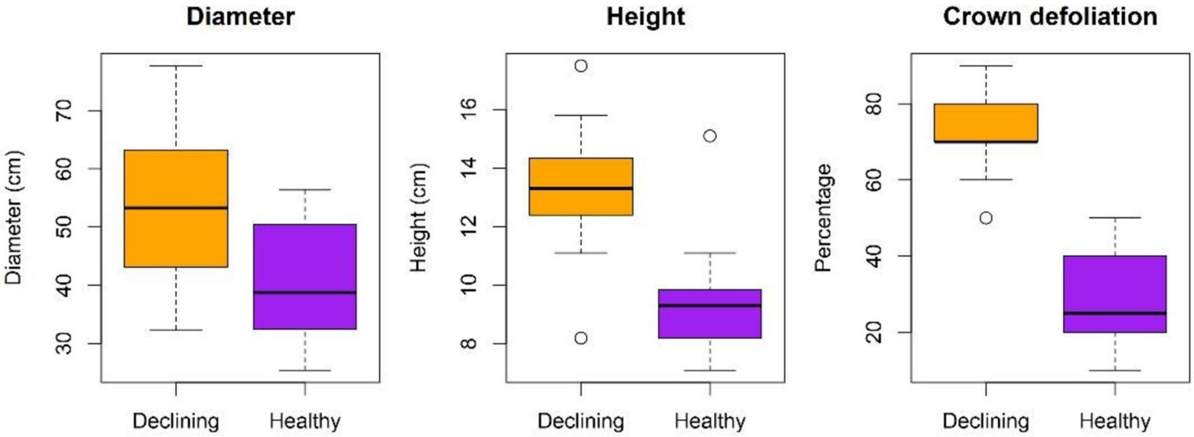


Fig. 2 Dendrometric measurements and level of defoliation and discoloration of trees. Boxplot corresponding to declining and healthy areas

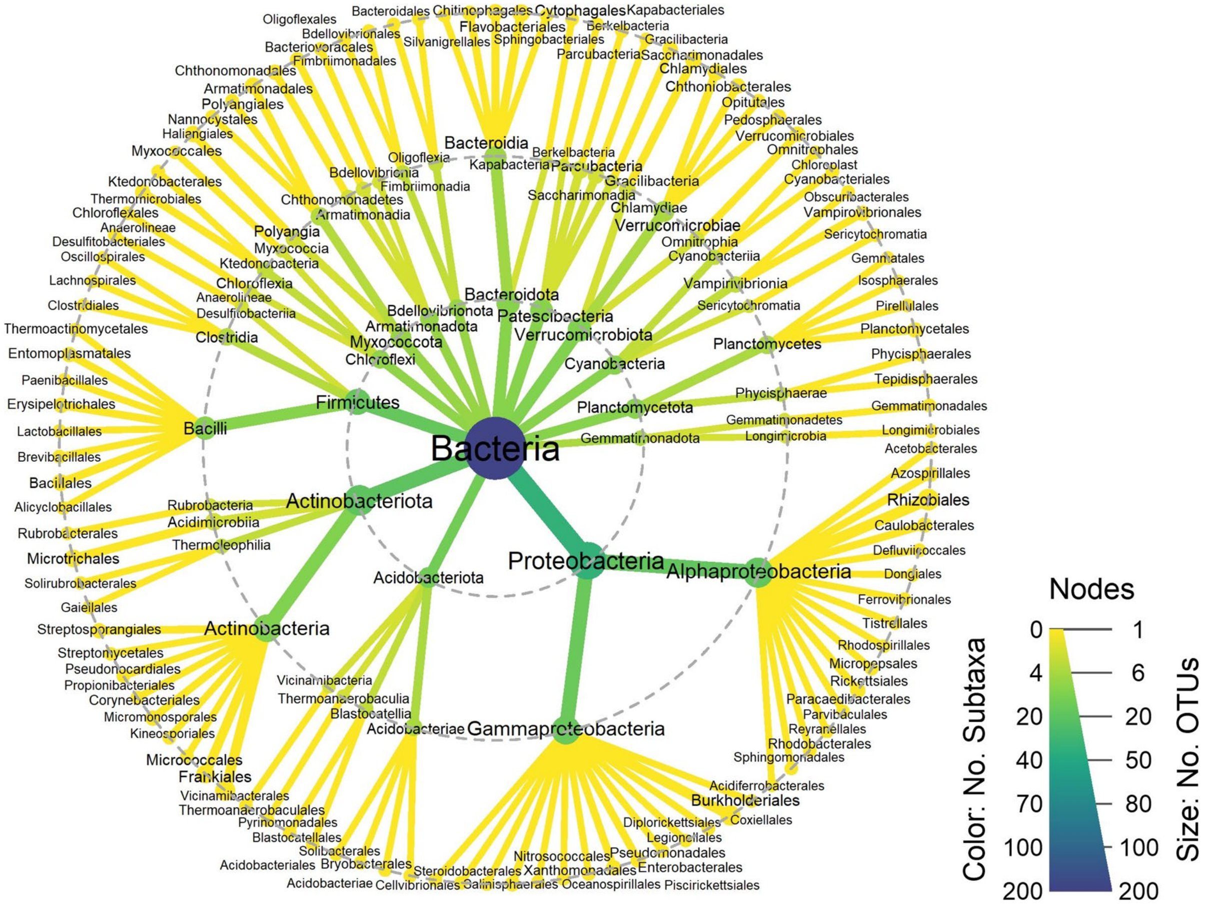


Fig. 3 Taxonomic tree of bacteria in maritime pine forest. The size of the node represents the number of taxonomic units and the color scale indicates the number of subtaxa. Concentric circles indicate taxonomic levels: phylum, class and order

bacterial families between vineyards and cereal crops surrounding diseased pine forests (n = 18, 19.1%), compared to healthy pine forests (n = 10, 11.5%). Finally, in healthy pine forests the presence of single genera is practically non-existent (n = 1, 1.15%), this value being higher in diseased pine forests (n = 12, 12.8%) (Fig. 4).

Description of fungal communities

The analysis of the fungal communities located under maritime pines resulted in 62 orders encompassed in 5 phyla. Most of the genera collected in the samples corresponded to the phyla Ascomycota, with a total of 412 genera (68.9%), and Basidiomycota, with a total of 174 genera (29.1%) (Fig. 5).

A more detailed analysis of the fungal genera reported that the number of matching genera in the three plant cover types analyzed was slightly higher in healthy pine forests (n = 25, 33.8%), compared to diseased ones (n = 12, 19.4%). As with the bacterial families, a significant equality in fungal genera was reported between vineyards and cereal crops associated with diseased pine forests (n = 16, 25.8%), compared to the same crops near healthy pine forests where fungal genera had less similarity (n = 11, 14.9%) (Fig. 6).

Microbial biodiversity analysis

The study of the microbial biodiversity of the soils was carried out separately, analyzing fungi and bacteria according to the health status of the predominant

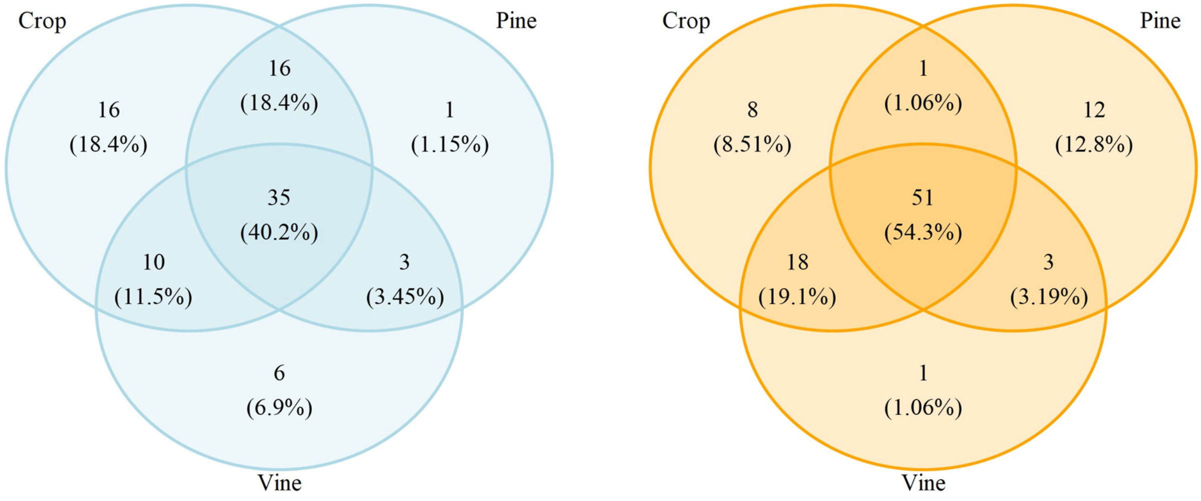


Fig. 4 Effect of plant cover type and health status on bacterial diversity. The Venn diagram indicates the coincidences and differences between bacterial families in at least 70% of the samples collected in healthy (in blue) and diseased (in orange) plots

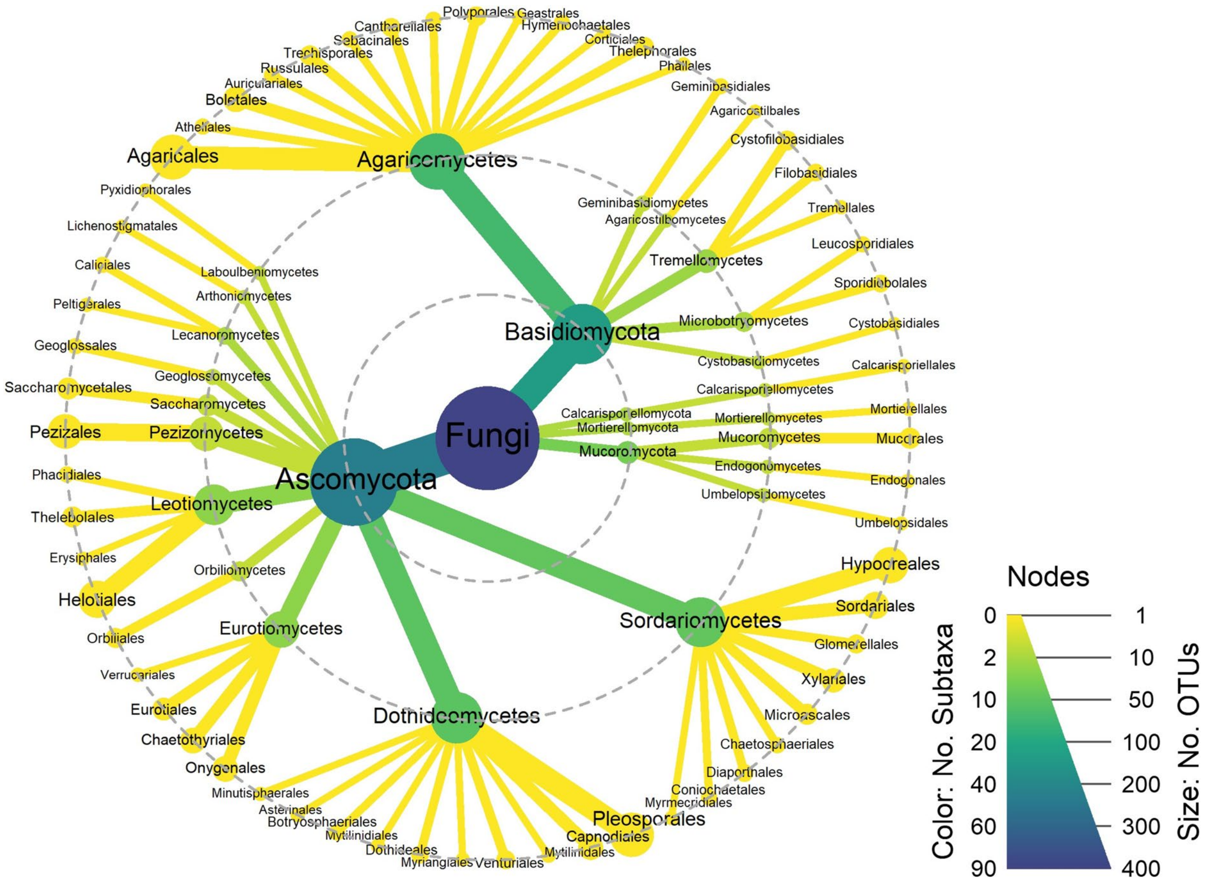


Fig. 5 Taxonomic tree of fungi in maritime pine forest. The size of the node represents the number of taxonomic units and the color scale indicates the number of subtaxa. Concentric circles indicate taxonomic levels: phylum, class and order

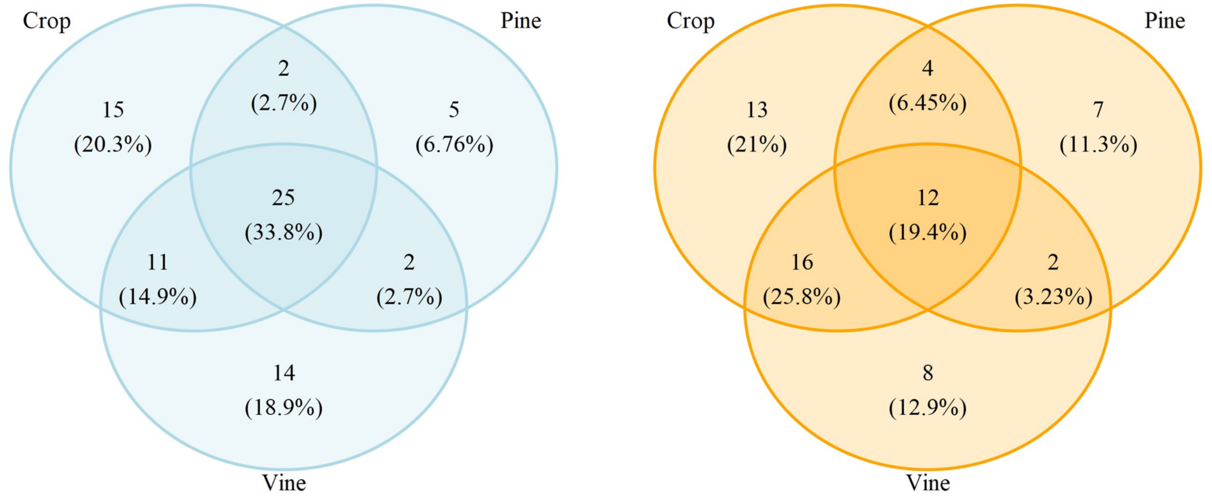


Fig. 6 Effect of plant cover type and health status on fungal diversity. The Venn diagram indicates the coincidences and differences between the fungal genera obtained for the samples collected in healthy plots (in blue) and diseased plots (in orange)

vegetation cover in each case. Regarding the alpha diversity of bacterial families, significantly greater diversity was reported in the soils of diseased pine trees, as well as in the vineyards associated with them. However, in rainfed cereal crops, the greatest bacterial alpha diversity was reported in crop soils associated with healthy pine forests (Fig. 7). Regarding alpha diversity of fungal genera, only rainfed cereal crops associated with healthy pine forests showed higher diversity, with no differences in pine forests or vineyards (Fig. 8). A comparison between the curves of bacteria and fungi under the three plant covers shows how bacterial communities have a higher proportion of dominant families ($\mathrm{Hill} = -1$), while there are fewer genera of fungi that act as dominant in the ecosystem.

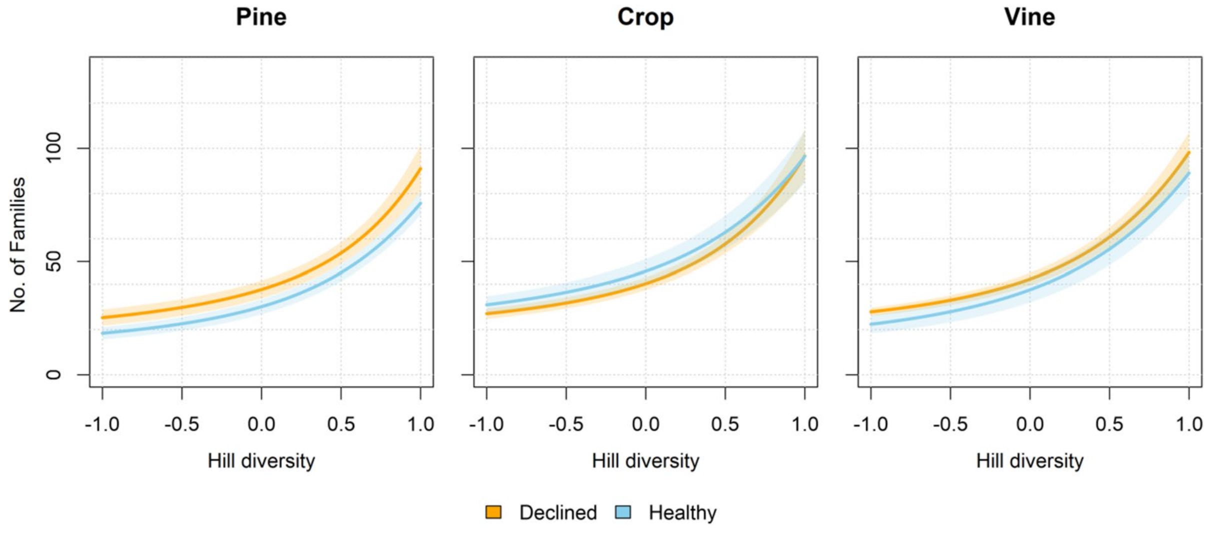


Fig. 7 Bacterial diversity according to sanitary status and vegetation cover. The horizontal axis represents the exponent l of Hill diversity, which can be interpreted as equivalence-corrected versions for richness ($l=1$), Shannon ($l=0$) and Simpson ($l=-1$) diversity estimators. Shadowed intervals correspond to standard error

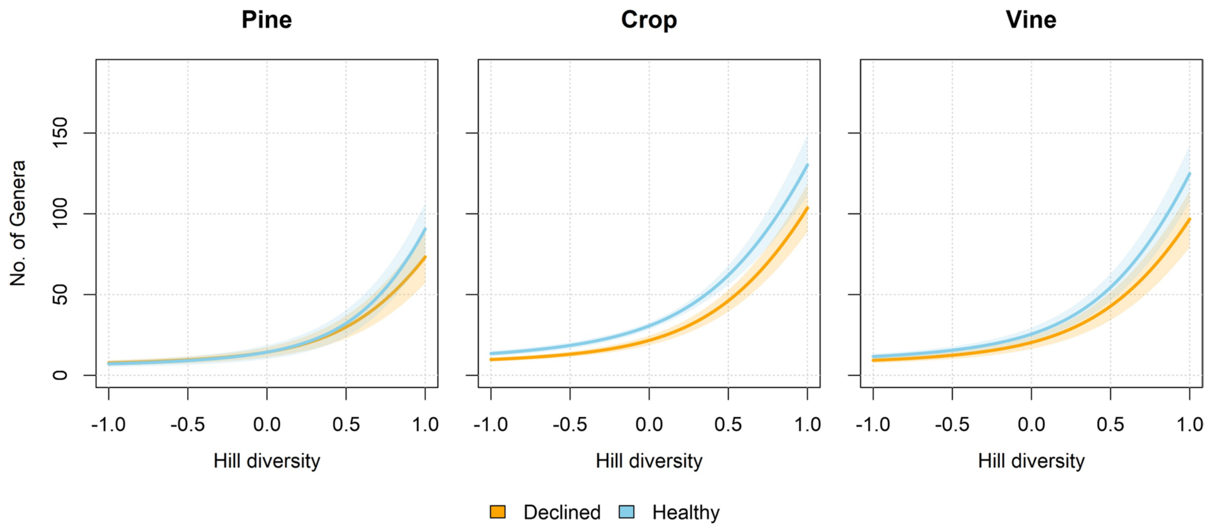


Fig. 8 Fungal diversity according to sanitary status and vegetation cover. The horizontal axis represents the exponent l of Hill diversity, which can be interpreted as equivalence-corrected versions for richness (l = 1), Shannon (l = 0) and Simpson (l = – 1) diversity estimators. Shadowed intervals correspond to standard error

Differential abundance analysis

A correlation analysis was carried out between the abundance of the different microbial family (bacteria) and genus (fungi) in healthy and diseased pines stands. The diversity under healthy cereal crops and vineyards was much higher in both cases compared to pine forests, where only two genera of fungi and one family of bacteria were reported (Fig. 9). In healthy pine forests, the presence of bacteria of the Azospirillaceae family and the fungal genera *Gymnascella* and *Wilcoxina* stands out. In cereal crops associated with healthy pine forests, the Fimbriimonadaceae family stands out among the bacteria, and the fungal genera *Lambertella*, *Harmoniella*, *Cladophialophora* and *Drechslera*. In vineyards close to healthy pine forests, bacteria from the Anaeromyxobacteraceae family and fungi from the *Ochroconis* and *Devriesia* genera were reported in the majority of cases (Fig. 9). On the other hand, in diseased pine forests, the presence of the bacterial families Hyphomonadaceae, Koribacteraceae, Frimbriimonadaceae and Ktenodobacteraceae stands out, in addition to the fungal genera *Volutella*, *Russula* and *Chaetomium* (Fig. 9).

Functional niche analysis

The most abundant functional niches in pine forests, and associated vineyards and cereal crops were the chemo-aerobic, hetero-aerobic and organo-aerobic niches, always being more present in plant cover associated with healthy than with diseased pine forests. On the other hand, the bacterial niches least present in all plant cover were photoautotrophic aerobes, facultative lithotrophs and facultative autotrophs, in all cases more present in associated soils and close to diseased pine forests (Fig. 10).

With regard to fungal functional niches, the most abundant in pine forests were ectomycorrhizal fungi, soil saprotrophs and saprotrophs. However, in cereal crops and vineyards the most abundant functional niches were soil saprotrophs, plant pathogens and saprotrophs (Fig. 11). Within these fungal functional niches, those most present in diseased pine forests (ectomycorrhizal) and in vineyards and cereal crops associated with diseased pine forests (plant pathogens and soil saprotrophs) stand out (Fig. 11). Finally, in terms of the less abundant fungal functional niches, neither lichen parasites nor epiphytes were present in

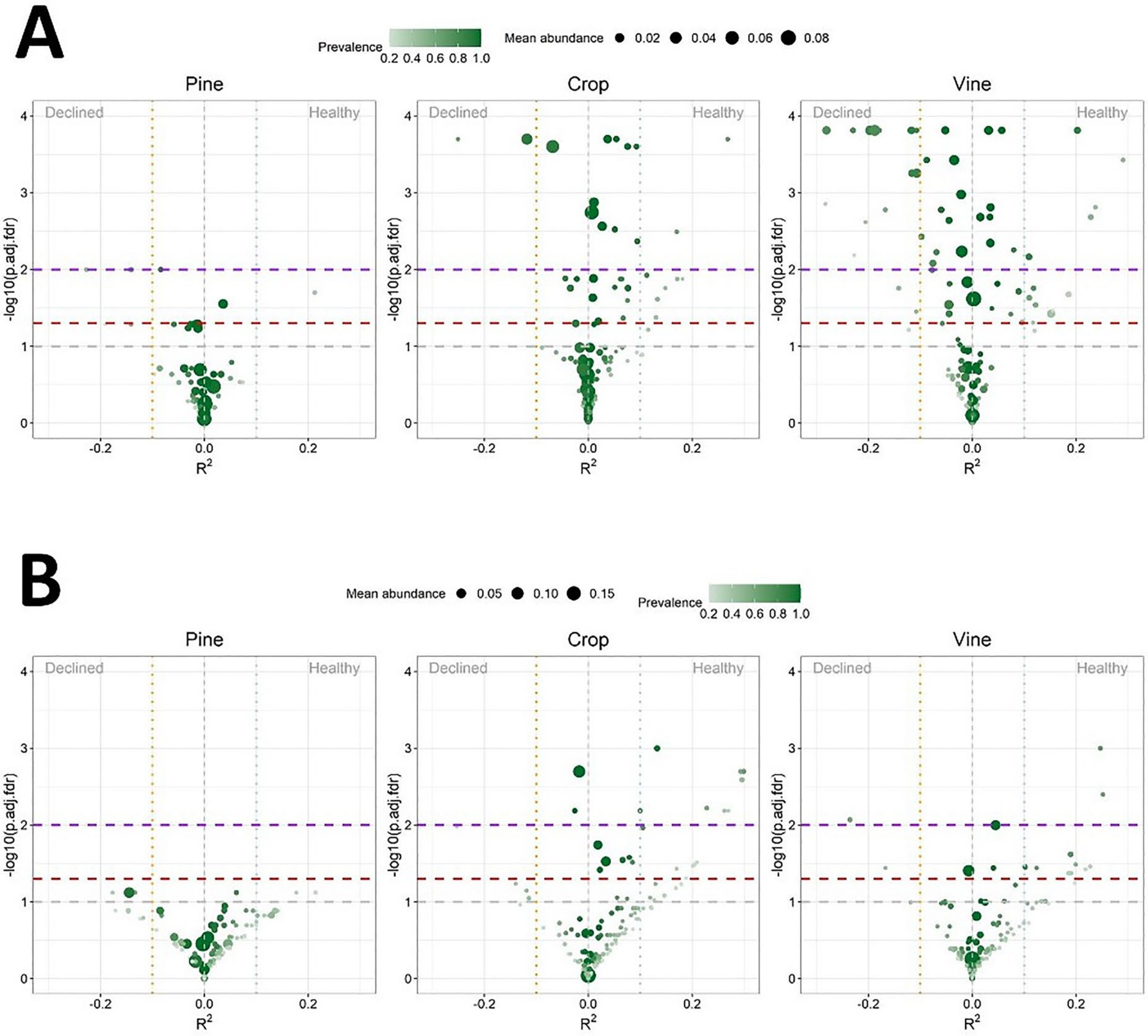


Fig. 9 Differential bacterial **A** and fungal **B** abundance. Volcano plot of differentially abundant families (bacteria) and genera (fungi) detected by ZicoSeq analysis. Each family is depicted by a dot. Dot size indicates the mean abundance across all samples and color indicates the proportion of samples in which the family or genus is present. Vertical axis represents value of p adjusted by false discovery rate (FDR) in logarithmic scale (1 = 0.1, 1.30 = 0.05, 2 = 0.01 and so on). Horizontal axis represents the strength of association between abundance and health condition, with the sign indicating the association direction (negative for declining, positive for healthy). Families and genera that surpass the horizontal dashed line are differentially abundant (p-value < 0.1)

either healthy or diseased pine samples, although these niches appeared infrequently in vineyards and cereal crops. In addition, pathotrophs, a niche present in cereal crops, do not appear in either pine forests or vineyards (Fig. 11).

Discussion

Microorganisms, such as soil bacteria and fungi, are crucial for the proper development of plant species. They contribute to essential soil functions, including

Fig. 10 Bacterial functional niche analysis. The X-axis corresponds to the abundance of bacterial functional traits on a logarithmic scale, and the Y-axis corresponds to a functional trait (oxygen utilization and feeding style). The distance of functional abundance between healthy and diseased samples is indicated by the line joining samples

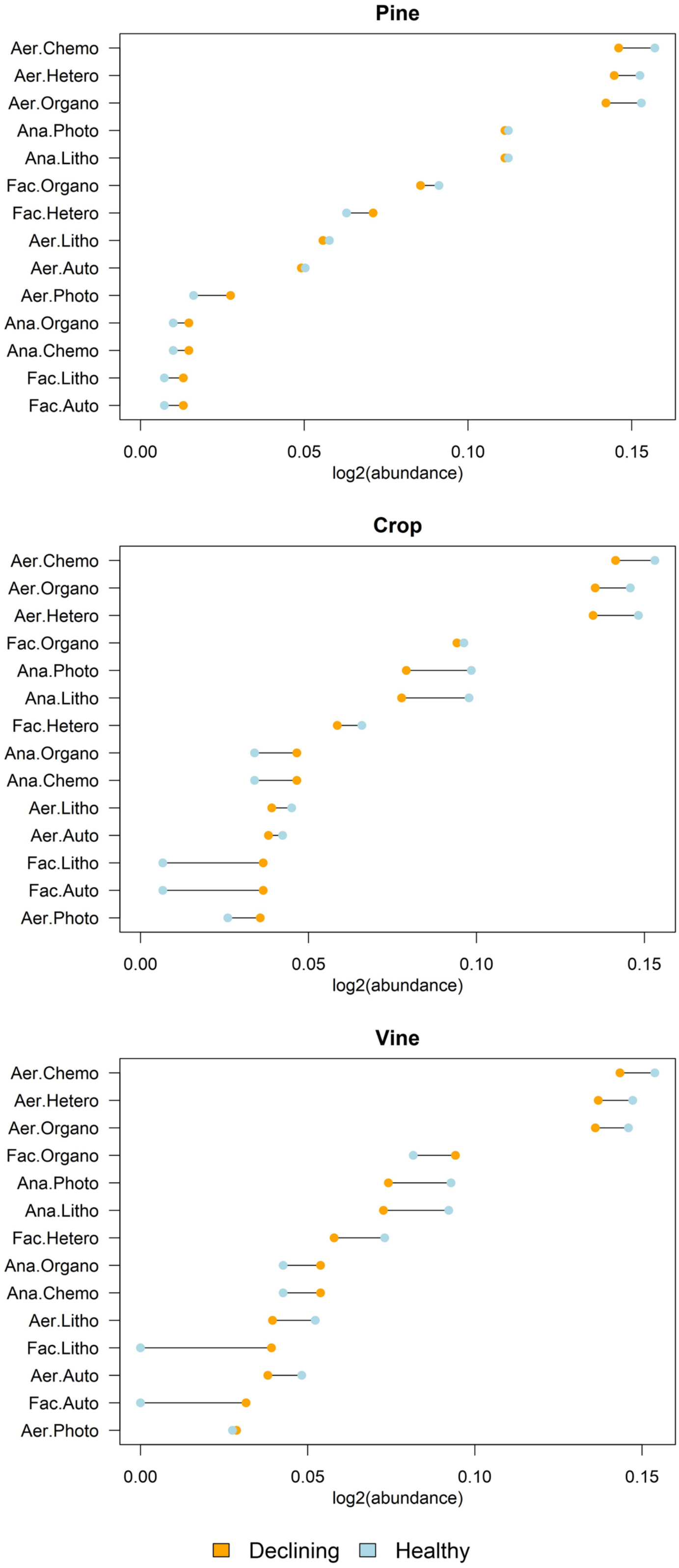
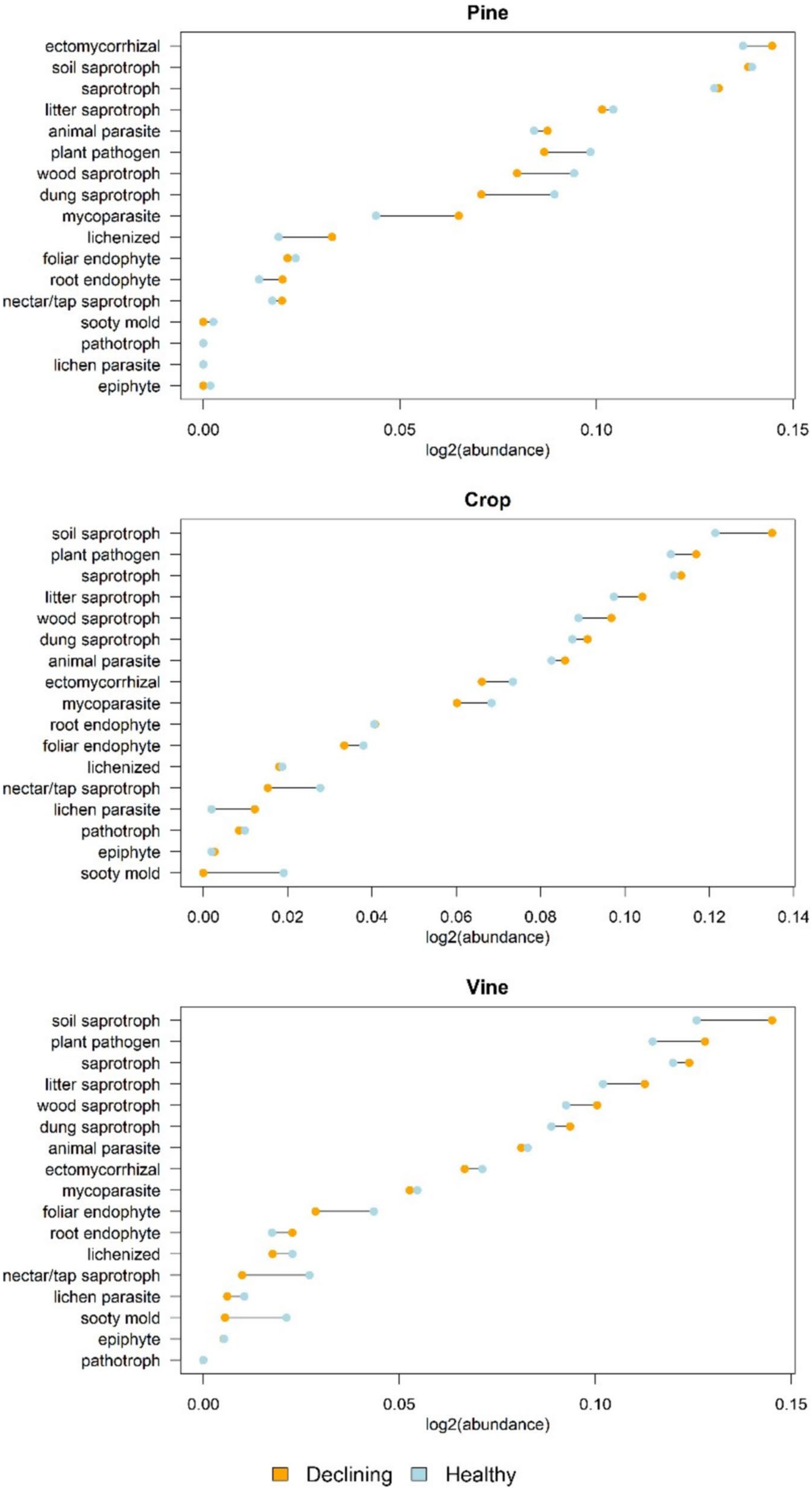


Fig. 11 Analysis of fungal functional niches. The X-axis corresponds to the abundance of fungal functional traits on a logarithmic scale, and the Y-axis corresponds to a functional trait. The distance of functional abundance between healthy and diseased samples is indicated by the line joining samples



the carbon, nitrogen, and phosphorus cycles (Lladó et al. 2018), influence the uptake of nutrients by plants (Oliverio et al. 2020), and can also act as pathogens affecting plant health (Mohammad-Razdari et al. 2022). In this regard, metabarcoding techniques offer a significant advancement, allowing for a better understanding of the microbial diversity in the soil environment and enabling the analysis of these microbial communities in relation to the health of trees (Diez-Hermano et al. 2023, 2024; Morales-Rodríguez et al. 2024; Marcos-Romero et al. 2025).

This work has described the bacterial and fungal diversity present in pine forests, vineyards and rain-fed cereal crops associated with these forests. Although this microbial diversity has been studied in maritime pines (Lasa et al. 2024; Morales-Rodríguez et al. 2024) and vineyards (Coller et al. 2019; Gobbi et al. 2022) and rainfed cereals (Hamel et al. 2018; Mavrodi et al. 2018), this work represents the first joint study of the microbiome present under the three plant covers and its relation with the presence/absence of forest decline.

In the analysis of microbial communities carried out in the soils of maritime pines, a greater presence of bacteria within the phyla Proteobacteria and Actinobacteria was reported, and fungi within the phylum Ascomycota. Previous works have described how these two bacterial phyla are the ones mostly present in the *P. pinaster* rhizosphere (Morales-Rodríguez et al. 2024; Lasa et al. 2025), both in spring (wet season) and in summer (dry season) (Lasa et al. 2022, 2023). Similarly, the fungal phylum Ascomycota has previously been described as the most abundant in the *P. pinaster* rhizosphere (Morales-Rodríguez et al. 2024).

With regard to the different plant covers, the bacterial families and fungal genera identified were the same in them, and in relation to the presence/absence of pine decline. Regarding the analysis of bacterial families, it was highlighted that more than half of the bacterial families were the same among the three vegetation covers when the pine forests were diseased, and this similarity decreased when the pine forests were healthy. This could be due to a reduction in bacterial diversity in soils where there are diseased pine forests, which would lead to a greater equality between all the plant cover. The presence of plant pathogens related to pine decline in the soil could lead to a standardization of bacterial families among all plant cover. However, alpha diversity analysis reported that diseased pine forests and their surrounding vineyards had the highest levels of diversity. Therefore, the greater coincidence of bacterial families that has been found in soils located in diseased pine forests could be related to the adaptation of bacterial microorganisms to forest declaim conditions, both for those microorganisms that promote decline and for those microorganisms that help combat the presence of diseases. This mechanism has been previously described for wheat plants when neighboring plants are attacked by a pathogen (Liu et al. 2021).

At the level of specific bacterial families, the diseased pine forests showed an abundance of families Hyphomonadaceae, Koribacteraceae, Frimbriimonadaceae and Ktenodobacteraceae. The family Hyphomonadaceae had previously been described as related to diseased plant tissues, for example, in the marine algae *Saccharina japonica* (Zhang et al. 2020). On the other hand, the bacterial family Koribacteraceae has been described as related to root rot-disease in gingseng (Wang et al. 2024). The families Frimbriimonadaceae and Ktenodobacteraceae have never previously been described as related to the absence/presence of plant diseases. In contrast, the soils of healthy pine forests presented differentially abundant bacteria within the family Azospirillaceae. This bacterial family has been widely described as a plant symbiont, mainly because of its ability to fix atmospheric nitrogen, but also to produce auxins and modulate systemic plant defense responses against biotic stresses and tolerance under abiotic stresses (reviewed by Fukami et al. 2018). Therefore, the family Azospirillaceae could play an important role in the ability of pine trees to successfully cope with decline.

Differentially abundant bacterial families were also found in the fields of vineyards and rainfed cereals surrounding the healthy pine forests. The Anaeromyxobacteraceae family present in vineyard soils includes species previously described as atmospheric nitrogen fixers (Masuda et al. 2024) and favoring the formation of nodules in legumes and their root development (Liang et al. 2023). On the other hand, the family Fimbriimonadaceae includes important ammonia-oxidizing bacteria, which are of great importance in the flow of nitrogen in ecosystems (Li et al. 2023). Therefore, these bacterial families could be related to the absence of decline in the pine forests surrounding the vineyards and dryland cereals by facilitating nitrogen uptake, a fundamental element for the growth and development of pines as it is an important component in chlorophyll, and therefore in the process of photosynthesis.

On the other hand, the opposite happened in the case of fungi, with a greater similarity of fungal genera (2 thirds) among all plant cover when the pine forests were healthy, this coincidence being reduced when the pine forests were sick. In this case, these common fungal genera could be related to microorganisms capable of preventing the presence of pine decline. For example, fungi that are antagonists of maritime pine pathogens, entomopathogens of insect pests or inducers of tolerance to abiotic stresses, activities widely described for soil fungi (Li et al. 2022). Furthermore, the soils of rainfed cereal crops were the ones with the greatest alpha diversity of fungal genera in their soils. This aspect represents an important advance in knowledge, as fungal diversity in these crops has only been addressed so far at the level of mycorrhizal fungi (Jerbi et al. 2021). Therefore, dryland cereal soils could represent a point of fungal diversity that is exchanged with the surrounding vegetation cover, positively or negatively affecting nearby vegetation depending on the type of species present, by influencing the nutrient cycle, or even participating in plant defense in the case of beneficial fungi.

With regard to the fungal genera present in differential abundance, *Volutella*, *Russula* and *Chaetomium* stood out for their abundance in soils of diseased pine forests. Of these three genera, only within *Volutella* have plant pathogens of sweet potatoes (Zhang et al. 2024) and legumes (Cannon et al. 2012) been previously described; however, species with nematicidal capacity have also been characterized (Zhang et al. 2021). On the other hand, different species with antifungal capacity have been described within the genera *Russula* (Osaki-Oka et al. 2019; Liu et al. 2024) and *Chaetomium* (Soytong et al. 2001; Ashwini 2019). Therefore, only the presence of the *Volutella* genus could have a direct relationship with the observed pine decline.

On the other hand, in healthy pine forest soils, the fungal genera *Gymnascella* and *Wilcoxina* were found to be differentially present, the former previously described as an endophyte with antifungal capacity against phytopathogens (El-Zayat et al. 2024), and the latter as an ammonium-supplying plant symbiont (Prabhu et al. 1996). In the surrounding vineyards, the genera *Ochroconis* and *Devriesia* were reported, including species described as endophytes in the former (Tazik et al. 2020) and plant pathogens in the latter (Li et al. 2013). In the soils of rain-fed cereal crops, *Lambertella*, *Harmoniella*, *Cladophialophora* and *Drechslera* were identified as the most abundant genera. Both *Lambertella* and *Drechslera* include species previously described as plant pathogens (Wiseman et al. 2015; Backes et al. 2020). However, the genus *Harmoniella* includes saprophytes of leaf litter (Masaki et al. 2023) and the genus *Cladophialophora* endophytes with the capacity to promote plant growth and act as a biological control agent for root pathogens (Harsonowati et al. 2020). Therefore, both in pine forest soils and in crop soils, fungal species with plant growth-promoting and pathogen-antagonizing capacities have been described in this work, which could be related to the absence of pine decline.

These results of differential abundance partially coincide with those reported with respect to the functional niches in the soils of diseased pine trees. In these soils, the genus of ectomycorrhizal fungi *Russula* was found to be differentially present, with ectomycorrhizae being the main functional niche reported. The presence of this group of beneficial fungi is expected to be related to an optimal sanitary state of the forest. However, as in our work, ectomycorrhizal fungi have been closely related to the presence of pine decline, because the abundance of these fungi is closely related to the older age of the trees, which are also more affected by the disease (Morales-Rodríguez et al. 2024).

Conclusion

In conclusion, the main microbial phyla present in maritime pine soils were Proteobacteria and Actinobacteria, for bacteria, and Ascomycota, for fungi. The presence of pine decline leads to a greater coincidence of bacterial families in the soils of pine forests and surrounding crops (vineyards and cereals). In diseased pine forests, the soil contains bacterial families (Hyphomonadaceae and Koribacteraceae) and fungal genera (*Volutella)* related to plant diseases, which could explain the presence of decline. Both in pine forest soils and in surrounding crop soils, there were beneficial microorganisms possibly related to the absence of tree disease. Therefore, although the health status of trees can be influenced by a significant number of stressors, such as soil moisture conditions or nutrient content, metagenomic analysis of soil microorganisms present in pine forests and surrounding crops, along with visual assessment of health status, could help differentiate the presence or absence of tree decline and could serve as a tool to prevent the onset of the disease.

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Data availability No datasets were generated or analysed during the current study.

Declarations

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

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