iVES OENO One vine & wine

DOI: https://doi.org/10.20870/oeno-one.2026.60.2.9619

OPEN ACCESS

VITICULTURE ORIGINAL RESEARCH ARTICLES

Decoding the mycobiome of grapevine organs in diverse Argentine regions

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Article number: 9619

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Associate editor:
Doris Rauhut

Received:
16 September 2025

Accepted:
10 May 2026

Published:
03 June 2026

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ABSTRACT

This study provides the first integrated analysis of fungal communities across soil, leaves, and must in *Vitis vinifera cv.* Malbec and *Vitis vinifera cv.* Cabernet-Sauvignon from four key Argentine wine regions: Mendoza, San Juan, Salta, and Río Negro. Using high-throughput ITS metabarcoding, we characterised compartment-specific fungal diversity and network structures, revealing that the rhizosphere harbours the most diverse and environmentally driven communities, while leaf and must-associated microbiomes exhibit more structured and centralised networks. Core fungal taxa, including *Cladosporiaceae, Pleosporaceae*, and *Lophiostomataceae*, were consistently found across compartments, suggesting potential microbial exchange between belowground and aerial tissues. Region- and altitude-specific patterns highlighted the influence of edaphic and climatic factors, particularly the abundance of *Metschnikowiaceae* and *Aureobasidium* in high-altitude sites. Antagonistic interactions between *Bacillus* and pathogenic fungi such as *Dactylonectria* were also identified, reinforcing the role of microbial networks in plant health and vineyard resilience. This work underscores the ecological relevance of fungal communities in viticulture and supports the integration of microbial data into the *terroir* concept. These findings lay the groundwork for future studies aimed at improving vineyard management and wine quality through microbiome-informed strategies.

KEYWORDS: *terroir*, fungi, grapevine, Argentina

INTRODUCTION

Ranked as the seventh-largest wine producer globally in 2022, Argentina boasts an extensive expanse of grapevine cultivation (International Organisation of Vine and Wine, 2024). Of the 23 provinces that make up the country's territory, 20 have cultivated vineyard areas: Mendoza (MZA) accounts for 71.4 % of the total, San Juan (SJ) accounts for 19.8 %, La Rioja accounts for 3.5 %, Salta (SAL) accounts for 1.9 %, Catamarca accounts for 1.3 %, Neuquén accounts for 0.6 %, and Río Negro (RN) accounts for 0.6 %, with smaller vineyard areas in other provinces such as La Pampa, Córdoba and Buenos Aires, among others.

The diversity of Argentine *terroirs* is shaped by regions that differ significantly in climate, topography, soil composition, altitude, and native flora and fauna. These factors collectively contribute to the distinctive characteristics of wines from various geographical locations and facilitate the adaptation of specific grapevine cultivars. The International Organisation of Vine and Wine (OIV) defines *terroir* as the interaction of identifiable physical and biological factors within a given area that, along with winemaking practices, imparts unique characteristics to the products of that region (Resolution OIV/Viti 333/2010). Argentina's iconic Malbec (MA) wines and its versatile Cabernet-Sauvignon (CS) varietals exemplify this concept. However, harsh climatic conditions in key wine-producing regions can have substantial economic repercussions due to reduced yields or diminished quality in certain seasons. This has prompted scientific research aimed at safeguarding and improving the future economic value of Argentina's wine industry.

Plants host diverse microbial communities. In grapevines, these communities form complex associations with plant tissues and play crucial roles in promoting crop health and productivity. Studies on grapevine cultivation have revealed that vine-associated microbial communities are influenced by topography, climate, soil physicochemical properties, and agricultural practices. These communities play crucial roles in enhancing plant productivity and resistance to pests and diseases (Villanueva-Llanes *et al*., 2025). Additionally, microbial interactions may release aromatic precursors, chemical compounds, and secondary metabolites, which affect the sensory attributes of wine (Minerdi & Sabbatini, 2025), further contributing to the *terroir*'s distinctive expression in the final product (Liu *et al*., 2019). The rhizosphere, the soil region influenced by root activity, serves as a hotspot of complex biological interactions and supports diverse microbial communities, including filamentous fungi, yeasts, protozoa, algae, and prokaryotes, which contribute to grapevine health and productivity (Xie *et al*., 2024).

The rhizosphere and endosphere microbial communities represent distinct subsets of the soil microbiome (Adeleke & Babalola, 2021). Classical studies on grapevine-associated microbial communities have focused on pathogens and endophytic bacteria. Soil acts as a key reservoir shaping grapevine-associated microbiota, with belowground communities influenced by edaphic parameters (*e.g.*, pH and C:N ratio) and sharing taxa with aboveground compartments (Zarraonaindia *et al*., 2015). Regarding the epiphytic counterpart, research has focused primarily on ecologically relevant microorganisms, particularly acetic acid and lactic acid bacteria, as well as yeast communities (Darriaut *et al*., 2022). Aboveground tissues can share a stable core mycobiome across organs and seasons, frequently dominated by *Aureobasidium pullulans* alongside *Cladosporium* and *Alternaria* (Knapp *et al*., 2021).

At the regional scale, soil and grape must microbiota show distinctive geographic patterns that correlate with wine metabolite profiles, underscoring a microbial component of terroir (Liu *et al*., 2020). Within a single terroir, epiphytic communities vary with tissue type and phenological stage and are modulated by cultivar genotype, while repeatedly retaining *Aureobasidium* among core/dominant fungal genera (Awad *et al*., 2022). Although many studies have characterised grapevine-associated microbial communities, little is known about the relationships between microbial communities associated with grapes and those associated with other plant tissues, such as leaves and roots, or about the impact of environmental, geographical, and vineyard management factors in Argentine vineyards.

Plant-microorganism associations, encompassing mutualistic, commensalistic, or host-pathogen interactions, are widespread phenomena (Orozco-Mosqueda & Santoyo, 2021). In vineyards, soil microbial populations significantly influence plant health, soil texture, nutrient cycling, and biodiversity (Wang *et al*., 2024), thereby affecting fruit quality and, ultimately, wine production (Rivas *et al*., 2021). Variations in microbial populations within the grapevine phyllosphere are shaped by the grapevine genotype, geographical area, and climatic conditions (Singh *et al*., 2018). Microbial communities in roots, root zones, and bulk soil differ from those associated with aboveground plant organs (Minerdi & Sabbatini, 2025). In contrast, numerous studies indicate that microbial community structure in grape berries and juice samples remains relatively stable under optimal conditions, aligning with those observed before fermentation (Aires *et al*., 2025).

Throughout their lifecycle, grapevines interact with a wide range of filamentous fungi and yeasts that colonise vegetative tissues and reproductive organs (Windholtz *et al*., 2021). Fungi associated with plants can influence fruit development and can also be responsible for driving fermentation, ultimately shaping the quality and style of the final product (Barata *et al*., 2012). Fungi are essential drivers of ecosystem processes and biodiversity in terrestrial environments. Fungi are best known for their degradative function, dominating the decomposition of plant material, particularly lignified cellulose (Shinde *et al*., 2022). Furthermore, they produce a wide range of extracellular enzymes capable of breaking down complex organic polymers into simpler forms, which are subsequently utilised by fungi themselves or other organisms. In the case of fungi, evidence suggests that their distribution can range from highly endemic to global (Op De Beeck *et al*., 2021).

Traditionally, fungal identification has been based on microscopic observation, isolation, and biochemical and genetic analysis. However, these techniques are only effective for fungi that can be cultured in the laboratory. Cultivation-independent studies have significantly expanded the knowledge of fungal diversity across different environments. Next-Generation Sequencing technologies (NGS) have facilitated significant advancements in the study of plant-microbe interactions in *Vitis vinifera* cultivars. By complementing classical microbial techniques, NGS enables the detection of non-culturable microbes within complex ecosystems, providing a comprehensive understanding of the grapevine microbiome (Burns *et al*., 2016).

In Argentina, recent NGS-based studies have shed light on vineyard-associated fungal communities. Oyuela Aguilar *et al*. (2020) analysed microbial compositions in MA and CS cultivars from two SJ vineyards. Taxonomic analysis of fungal communities associated with the rhizosphere revealed 12 phyla, with Ascomycota as the dominant group. Basidiomycota and Mortierellomycota were also prominent, whereas Glomeromycota (known for its role in mycorrhizal associations) was present in low but noticeable abundance. Vineyard and cultivar comparisons revealed variations in relative abundances, particularly higher Basidiomycota levels in the MA rhizosphere. Rivas *et al*. (2022) investigated microbial communities in MA vineyards in Southwest Buenos Aires. Fungal communities in vineyard soils and rhizospheres were dominated by *Pleosporales*, *Hypocreales*, and *Sordariales*, with a notable presence of *Ilyonectria* in Saldungaray, potentially linked to grapevine decline symptoms. In wine samples, *Saccharomyces* species dominated the fermentation process, likely due to their widespread use in winemaking. This dominance can result from direct inoculation or from winemakers fostering conditions that favour their growth (Lee *et al*., 2019). In some cases, these yeasts have even been found to persist in tanks and barrels despite standard cleaning procedures.

Paolinelli *et al*. (2023) studied fungal communities in MZA vineyards, highlighting location-specific taxonomic, ecological, and metabolic variations. Ascomycota was also the dominant fungal phylum across all soil samples, followed by Basidiomycota, with Zygomycota inc. sed. (currently referred to as phyla Mucoromycota and Zoopagomycota) and Chytridiomycota being more prevalent in specific sites. Genus-level comparisons revealed site-specific distributions, with *Mortierella*, *Alternaria*, and *Fusarium* predominating in Santa Rosa, whereas *Umbilicaria*, *Coniochaeta*, and *Aureobasidium* were more common in Gualtallary, in the Uco Valley zone (MZA). Mezzatesta *et al*. (2024) also investigated MZA vineyards, focusing on microbial diversity in a high-elevation MA vineyard with contrasting soil stoniness. These results indicate that soil type significantly influences fungal populations, whereas vintage is the primary driver of microbial variation. While depth affected fungal communities, bulk vs rhizosphere sampling had no significant impact. Key soil components, such as pH and calcareous content, shape microbial composition, highlighting the role of microbial diversity in soil-plant-environment interactions.

Research on grapevine microbial communities in Argentina remains limited. Existing studies have focused primarily on major wine-producing regions, including MZA and SJ, leaving other significant areas, such as Alto Valle del Río Negro, the Atlantic coast of Patagonia, and SAL, where vineyards are cultivated at altitudes exceeding 2000 m above sea level (masl), largely unexplored (National Institute of Viticulture, 2023). Despite the widespread use of NGS in wine-related microbial diversity studies, comparative analyses of how geography, altitude, soil, and grape cultivar influence the composition and diversity of vineyard microbiomes across major wine-producing regions in Argentina remain underexplored. This study addresses this gap by analysing fungal diversity in MA and CS vineyards across four key Argentine wine regions: RN, MZA, SJ, and SAL.

Here, we present the first standardised, multi-region comparison of grapevine-associated fungal communities across major Argentine wine regions, spanning strong gradients in altitude, climate, and soil composition, and including previously underexplored viticultural areas. We test the hypothesis that biogeophysical and climatological variables explain a larger fraction of fungal community variation across Argentina. Our results have direct implications for disease risk forecasting, biocontrol strategy deployment, and the microbial component of terroir, with potential downstream relevance for wine quality and vineyard management under climate change.

MATERIALS AND METHODS

1. Sampling

Samples were collected in 2016, one week before the harvest period, from ungrafted grapevines of the MA and CS cultivars. Fourteen vineyards were sampled across four wine-producing provinces of Argentina: the South region (RN, Patagonia), the Centre-West region (SJ and MZA), and the North-West region (SAL).

In SJ, part of the Centre-West wine region, samples were obtained from two vineyards located in the Ullum Valley, 6 km apart. In MZA (also in the Centre-West wine region), samples were taken from vineyards in Agrelo (Luján de Cuyo), cultivated using a vertical shoot positioning system on loamy-clay soils. Both SJ and MZA have arid climates. In RN, located in the South wine region, samples were collected from Mainque (RN1, only MA samples) in the Upper Valley of Río Negro and Viedma (RN2, samples of both CS and MA) near the Atlantic Ocean. Both zones have semi-arid climates. Annual rainfall in RN1 ranges from 120 to 180 mm, with temperatures between 30 and 34 °C in summer and 10 to 14 °C in winter. RN2's climate is influenced by its proximity to the Atlantic Ocean, where summer temperatures can reach 30 °C, and winter temperatures range from 2 to 12 °C. Samples were collected from two plots with loamy-sandy soils, situated 7 metres above sea level (masl).

In Salta Province, part of the North-West wine region, the climate is warm and dry. Samples from MA and CS vineyards were taken in the Calchaquí Valleys (southwest of the province) at three sites: Molinos (SAL1) and Cafayate (SAL2), while only MA samples were collected in Cachi (SAL3). The altitude of these sites ranged from 1700 masl at Molinos to 2500 masl at Cachi.

The study included nine vines sampled per plot within a 49 m^2 area, with sampling points located at least 7 m from the plot edge. The sampling design comprised nine vines spaced 2.5 m apart within a 14 m^2 quadrat. Samples were pooled to form three composite biological replicates. Samples were collected in sterile containers, transported on ice, and stored at −20 °C until analysis. A schematic of sample collection can be found in Figure S1 of Oyuela Aguilar *et al*. (2020). Further details regarding the locations, geographical characteristics, grapevine age, management type (organic or conventional), and inter-row management (bare ground or vegetation cover) can be found in our previous research (Oyuela Aguilar *et al*., 2021; Toscani *et al*., 2025).

Soil and rhizosphere samples were collected from each vineyard at a depth of 30 cm and 20–30 cm from the vine trunks. Sampling involved nine vines per plot, covering an area of 49 m^2, with each plot located at least 7 m from the vineyard edge to avoid border effects. The first layer of surface soil was discarded prior to collecting root-associated samples. Soil was gently detached from the roots and collected using a sterile metal spoon; adherent soil was further dislodged by carefully rubbing the root surface with sterile scalpels. Samples were subsequently sieved (0.5 mm mesh) to remove residual roots and plant debris. DNA was extracted from 0.4 g of rhizosphere soil using the FastDNA Spin Kit for Soil (MP Biomedicals, LLC, Solon, OH, USA) according to the manufacturer's instructions.

Leaves were washed with saline solution containing 0.01 % Tween 80 in 50 mL polypropylene tubes (2 or 3 samples). 3 or 4 leaves of each sample were maintained in a horizontal shaker for 1 h at 100 rpm. The resulting solution was centrifuged at 4000 × g, and the pellet was transferred to a 2 mL microtube for further analysis.

Grapes from different vineyards were hand-harvested and crushed under aseptic conditions in the laboratory. Only healthy grapes were used. A fraction of must derived from approximately 100 g of grapes was centrifuged at 16,000 rpm, and the pellet was washed twice with a 0.9 % saline solution. The pellet was transferred to a 2 mL microtube and stored.

Samples were stored at –20 °C until analysis. Nine samples from each location and cultivar were pooled to yield three biological replicates.

2. Determination of soil physicochemical characteristics

Soil samples were carefully collected from the root systems of grapevines in the vineyards. Adherent soil was gently removed into a sterile bag, using a scalpel when necessary. Detailed information on soil physicochemical characterisation is found in our previous publication (Toscani *et al*., 2025). In summary, SAL soils were distinguished from the others by their high sand content. SJ, MZA, and RN1 exhibited similar properties, whereas RN2 differed markedly from the other three regions, likely due to its proximity to the Atlantic Ocean coast (Toscani *et al*., 2025).

3. DNA extraction, library preparation, and sequencing

DNA extractions were conducted using the FastDNA Spin Kit for Soil (MP Biomedicals, LLC, Solon, OH, USA), following the manufacturer's instructions. Extracted DNA was quantified with a Qubit 2.0 Fluorometer (Thermo Fisher Scientific), and its purity was assessed by 260/280 nm and 260/230 nm absorbance ratios using a NanoDrop spectrophotometer.

The diversity of the fungal community in each sample was analysed by amplification of the eukaryotic ITS1 (Internal Transcribed Spacer) region, located between the 18S rRNA and 5.8S rRNA ribosomal genes, using the primers ITS1F (ACTTGGTCATTTAGAGGAAGTAA) and ITS2 (BGCTGCGTTCTTCATCGATGC) (White *et al*., 1990). A two-step PCR approach was employed for Illumina sequencing library preparation, as described by Gobbi *et al*. (2020). Sequencing was carried out on the Illumina MiSeq platform using the V2 500-cycle reagent kit.

The double PCR amplification was performed as follows. In the initial PCR, a final reaction volume of 25 µL included 12 µL of AccuPrime SuperMix II (Thermo Scientific), 0.5 µL of bovine serum albumin (BSA; final concentration, 0.025 mg/mL), 0.5 µL each of forward and reverse primers (10 µM stock), 1.5 µL of sterile water, and 5 µL of template DNA. The thermal cycling conditions were as follows: an initial denaturation at 95 °C for 2 minutes, followed by 33 cycles of 95 °C for 15 seconds, 55 °C for 15 seconds, and 68 °C for 40 seconds, with a final extension step at 68 °C for 4 minutes. The total DNA concentration was quantified using a Qubit 2.0 Fluorometer (Thermo Scientific). The second PCR added indices to the amplicons generated in the first PCR. This reaction, with a final volume of 28 µL, contained 12 µL of AccuPrime SuperMix II (Thermo Scientific), 2 µL of primers with index sequences and Illumina P7 (CAAGCAGAAGACGGCATACGAGAT) and P5 (AATGATACGGCGACCACCGA) adapters, 7 µL of sterile water, and 5 µL of the initial PCR amplicons. Both PCR steps were verified through 1.5 % agarose gel electrophoresis.

4. Bioinformatics and statistical analysis

Illumina reads were demultiplexed using bcl2fastq V.2.17.1.14 (Illumina). Adapters were trimmed with Trim Galore v0.4 (https://github.com/FelixKrueger/TrimGalore.git) running cutadapt v1.8.3 (Martin, 2011), and primer sequences were deleted from the 5' ends of each read using the custom script (https://github.com/padbr/asat/blob/master/strip_degen_primer.py). Raw sequencing data associated with this work were uploaded to the SRA under the BioProject accession number PRJNA1282061.

Data analysis was performed using the Shaman platform (https://shaman.pasteur.fr/), following the pipeline described by Volant and collaborators (Volant *et al*., 2020). Read and Operational Taxonomic Unit (OTU) processing parameters were set with stringent quality and annotation thresholds to ensure high-fidelity analyses. During read processing, a Phred quality score cutoff of 20 was applied to trim low-quality ends, with a requirement that at least 80 % of nucleotides per read were correctly called. A minimum read length of 50 nucleotides was enforced. For OTU processing, reads were dereplicated using a prefix setting, with no upper limit on OTU length (maximum length set to 0) and a minimum OTU length of 50 nucleotides. Only sequences with a minimum abundance of 4 were retained during dereplication. Clustering was performed on both strands with a similarity threshold of 0.97.

OTU annotation was performed using the UNITE+INSD database (Abarenkov *et al*., 2024). The taxonomic assignment of ITS1 sequences was performed using BLAST against the UNITE database. First, a local BLAST database was created from the UNITE public release (version 21.04.2024) in FASTA format using the *makeblastdb* command with the nucleotide database type option. The database files were generated and stored in a specified directory. Then, a custom Python script was developed to automate the BLAST search and extract the best hits for each query sequence (Supplementary script). The script utilised the NcbiblastnCommandline function from the Biopython library to execute BLAST searches in tabular format (outfmt=6) with an e-value threshold of 1e-5. The output file containing the BLAST results was subsequently parsed to identify the best match for each query based on the lowest e-value. Only OTUs belonging to the Fungi and Stramenopila kingdoms (Phylum Oomycota) were used for subsequent analyses.

A weighted non-null normalisation by site and a filtering step, requiring a minimum of eight samples and a total abundance threshold of 2.4 (in logarithmic scale), were performed prior to analysis. Richness, Shannon and Inverse Simpson indices, principal coordinate analysis (PCoA), rarefaction plots, scatterplots, family barplots, and heatmaps were generated and analysed using the online Shaman platform.

Canonical Correspondence Analysis (CCA) was conducted using the PAST software package. (Hammer *et al*., 2001). Data were normalised by standard score ($(X-\mu)/\sigma$) before analysis (Han *et al*., 2012).

Linear Discriminant Analysis Effect Size (LEfSe) (Chang *et al*., 2022) was employed to identify overrepresented OTUs in the analysed samples. An alpha value of 0.05 was applied for the factorial Kruskal-Wallis test among classes and the pairwise Wilcoxon test between subclasses. Taxonomic units with a logarithmic LDA score greater than 4 were considered overrepresented and visualised in the resulting figure. LEfSe analyses were conducted using the Galaxy Metabiome environment (http://mbac.gmu.edu/mbac_wp).

To assign ecological functions to the fungal OTUs identified, we employed the tool FungalTraits (Tanunchai *et al*., 2023). This database was used to assign lifestyle-related functional traits at the genus and species hypothesis level. This resource integrates expert-curated information from FUNGuild and FunFun (Nguyen *et al*., 2016; Krivonos *et al*., 2023), and allows for trait-based assignments across a wide range of fungal taxa.

Figures were created using the Inkscape software package (Inkscape Project, 2020, https://inkscape.org) and GIMP (The GIMP Development Team, 2019, https://www.gimp.org).

5. Networking analysis

Fungal networks were constructed using the SparCC algorithm (Friedman & Alm, 2012) in the Integrated Network Analysis Pipeline 2.0 (iNAP 2.0. https://inap.denglab.org.cn) (Peng *et al*., 2024), run on the Galaxy platform (v1.0.0). Network graphs were generated in Cytoscape v3.10.3 (Shannon *et al*., 2003). SparCC was utilised to infer microbial associations from compositional data. A SparCC correlation matrix was computed using FastSpar (Watts *et al*., 2019), averaging 20 inference iterations. An initial filter was applied, excluding OTUs present in less than 50 % of the samples. To stabilise estimates, we used 10 exclusion iterations with a correlation-strength exclusion threshold of 0.7. Two-sided SparCC pseudo *p*-values were estimated with 100 permutations. Edges were retained when $|r| \geq 0.6$ and $p \leq 0.05$. Networks were generated with the "Generate networks from SparCC" Galaxy tool (version 1.0.0) as a single-mode adjacency network and exported to Cytoscape. Network modularisation used the greedy modularity optimisation algorithm, and module roles were classified using *Z–P* scores.

The integrated soil prokaryotic and fungal network was generated by normalising the respective OTU count tables using Scaling with Ranked Subsampling (SRS) prior to merging the tables (Beule & Karlovsky, 2020). Prokaryotic OTUs were obtained by 16S rRNA gene amplicon sequencing and were reported in our previous publication (Toscani *et al*., 2025). The SRS method for normalising species count data minimises subsampling error while preserving the original community structure. The SparCC algorithm was employed to infer microbial associations from compositional data. Pseudo *p*-values were estimated using 100 permutations, and a correlation strength threshold of 0.6 was applied.

RESULTS

1. Sequencing results

Following ITS sequencing, 9,857,782 amplicon sequences were obtained, which were reduced to 1,398,814 after dereplication (Table S1). After removing singletons and chimeras, 98,259 sequences remained for classification into Operational Taxonomic Units (OTUs), yielding 4669 OTUs (Table S2). Since ITS metabarcoding can detect a wide range of eukaryotes, we excluded OTUs assigned to taxa

outside the phylum Fungi and the phylum Stramenopila, order Oomycota, leaving 4422 OTUs for further analysis (Table S3). Extended details on the sequenced samples are provided in Table S1. Although three replicates were collected per vine, 11 samples could not be successfully sequenced (Table 1). Furthermore, as the rarefaction curve did not reach saturation, six of the sequenced samples were excluded from further analysis (Figure S1), resulting in 39 rhizosphere, 34 leaf, and 38 must sequences. Samples were normalised per site prior to statistical analysis.

2. Analysis of grapevine organs

To gain insight into organ-specific diversity, three estimators were used: OTU richness, Shannon diversity index, and the inverse Simpson index. Since no significant differences were observed between the MA and CS indices (Figure S2–4), we opted to pool samples by site for subsequent analyses.

To assess differences in fungal composition among plant organs, diversity indices were plotted accordingly (Figure 1A–C). A Mann–Whitney test with Bonferroni adjustment identified significant differences and revealed that the rhizosphere was the most diverse sample. Must samples exhibited the lowest diversity, whereas leaf samples showed intermediate values. The rhizosphere was the most diverse compartment, leaf samples showed intermediate diversity, and must samples showed the lowest values. PCoA analysis showed that Axis 1 significantly separated rhizosphere samples, whereas must and leaf samples largely overlapped (Figure 1D). Greater fungal diversity in the soil, both bulk and that associated with the rhizosphere, has been previously reported by other authors (Swift *et al*., 2021). Environmental factors, such as solar UV radiation, to which aerial organs are more exposed, are key drivers of shifts in fungal communities worldwide, exerting their greatest influence on the presence of free-living fungi (Egidi *et al*., 2023). The selective pressure imposed by these abiotic factors may account for the lower diversity observed in more exposed plant organs, as only fungi tolerant of these conditions can proliferate in these tissues. The richness observed in the rhizosphere may be due to routine application of fungicides, which imposes stress on fungal growth on leaves and fruits, and to the fact that the rhizosphere is a richer, physicochemically less hostile environment than exposed organs. Additionally, rhizosphere microbes are fuelled by sustained inputs of labile carbon released by grapevine roots, as well as by carbon derived from the rapid turnover and decomposition of fine roots (Darriaut *et al*., 2024). In parallel, arbuscular mycorrhizal fungi channel substantial host-derived carbon into the soil through their hyphal networks, which also turn over rapidly, thereby supporting a diverse microbial food web and contributing to soil organic matter formation (Kakouridis *et al*., 2024). Collectively, these factors may contribute to the greater diversity that characterises the rhizosphere.

Taxonomic analysis also revealed a heterogeneous distribution of fungal families among compartments (rhizosphere, leaf, and grape must). When analysing OTU distribution, 2504 OTUs were found exclusively in rhizosphere samples, whereas 47 and 27 were unique to leaf and must, respectively (Figure 1E, Table S4). A total of 1112 OTUs were shared by all three organs, forming the fungal core mycobiome.

Given that taxonomic assignment using ITS1 barcoding offered limited resolution at the genus (38.9 %) and species (23.2 %) levels (Table S3), we conducted the taxonomic analysis at the family level, which encompassed a larger proportion of the identified OTUs (45.7 %) while also allowing differentiation of the ecological characteristics associated with the various taxa. Consistent with previous observations (Iorizzo *et al*., 2024; Knapp *et al*., 2021), the core fungal community was predominantly represented by the families *Cladosporiaceae* and *Pleosporaceae* (Figure 1F), suggesting a close association of these fungal groups with *Vitis vinifera*, regardless of cultivar or geographic location. This observation mirrors the pattern reported for other fruit crops, such as strawberries, tomatoes, eggplants, cucurbits, peppers, citrus, pome and stone fruits, among others (Kalkan, 2025).

Other taxa commonly observed across the three organs included families *Lophiostomataceae*, *Saccotheciaceae*, and *Didymellaceae*. Although these OTUs were common across all three organs, the *Cladosporiaceae* family was more frequently observed in leaf and must samples, whereas the rhizosphere was richer in *Lophiostomataceae* and *Nectriaceae* fungal families. The family *Nectriaceae* comprises several genera linked to trunk diseases originating in nurseries, including *Pleurostoma*, *Dactylonectria*, and *Fusarium* spp. (Garcia *et al*., 2025).

Linear Discriminant Analysis Effect Size (LEfSe) analysis was also used to investigate differentially abundant OTUs across the studied organs (Figure 1G). Strains belonging to the families *Lophiostomataceae* and *Nectriaceae*, and the orders Xylariales and Agaricales, were differentially present in the rhizosphere. In contrast, OTUs belonging to the class Tremellomycetes were specifically associated with leaves, while three OTUs assigned to the order Cladosporiales were uniquely detected in must samples.

Although a substantial number of unique OTUs were detected in each organ, the presence of a large and structured core mycobiome supports the idea that a significant proportion of fermentative diversity may be transferred from the soil to the aerial organs, and vice versa. Consequently, the consistent presence of rhizosphere-associated species in fermentations carries commercial significance, as the microbial composition of grape juice is known to substantially influence the sensory characteristics of wine (Morrison-Whittle & Goddard, 2018).

3. Fungal diversity in the rhizosphere of Argentine wine-producing regions

In contrast to the pattern observed for rhizospheric prokaryotic diversity, where RN1 was the least diverse environment (Toscani *et al*., 2025), the analysis of rhizospheric fungal diversity revealed that SAL2 and SAL3 exhibited the lowest richness values (Figure S5A–C).

TABLE 1. Vineyard location metadata, multi-compartment sampling and sequencing summary.

Region	Location	Grape variety	Acronym	Elevation (masl*)	Coordinates	Rhizosphere			Leaf			Must		
						Obtained	Sequenced	Analyzed	Obtained	Sequenced	Analyzed	Obtained	Sequenced	Analyzed
San Juan	Valle de Ullum, Finca Norte	Malbec	SJ1Ma	780	31° 27.114′ S, 068° 42.523′ W	3	3	3	5	5	5	3	3	3
		Cabernet-Sauvignon	SJ1CS	770	31° 27.002′ S, 068° 42.109′ W	3	3	3	3	3	3	3	3	3
	Valle de Ullum, Finca Arriba	Malbec	SJ2Ma	800	31° 28.407′ S, 068° 45.486′W	3	3	3	3	2	2	3	3	3
		Cabernet-Sauvignon	SJ2MCS	800	31° 28.407′ S, 068° 45.347′ W	3	3	3	3	3	3	3	3	3
Mendoza	Agrelo, Lujan de Cuyo	Malbec	MZAMa	930	33° 09.437′ S, 068° 53.702′ W	3	3	2	3	1	1	3	3	3
		Cabernet-Sauvignon	MZACS	940	33° 09.416′S 068° 53.657 W	3	3	3	3	3	3	3	3	3
Rio Negro	Mainque, Alto Valle del Rio Negro	Malbec	RN1Ma	402	39° 02.190′ S 067° 19.757′ W	3	3	3	3	3	3	3	3	3
	Viedma	Malbec	RN2Ma	7	40° 46.415′ S 063° 21.789′ W	3	3	3	3	3	3	3	3	3
		Cabernet-Sauvignon	RN2CS	7	40° 46.437′ S, 063° 21.831′ W	3	3	3	3	3	3	3	1	1
Salta	Molinos	Malbec	SAL1Ma	2200	26° 04.846′ S, 066° 00.022′ W	3	3	1	3	3	1	3	1	1
		Cabernet-Sauvignon	SAL1CS	2200	26° 04.815′ S, 066° 00.206′ W	3	3	3	3	2	2	3	3	3
	Cafayate	Malbec	SAL2Ma	1700	25° 30.696′ S, 066° 23.352′ W	3	3	3	3	2	2	3	3	3
		Cabernet-Sauvignon	SAL2CS	1700	25° 30.495′ S, 066° 23.360′ W	3	3	3	3	3	3	3	3	3
	Cachi	Malbec	SAL3Ma	2600	25° 02.669′S, 066° 04.460′ W	3	3	3	3	1	0	3	3	3

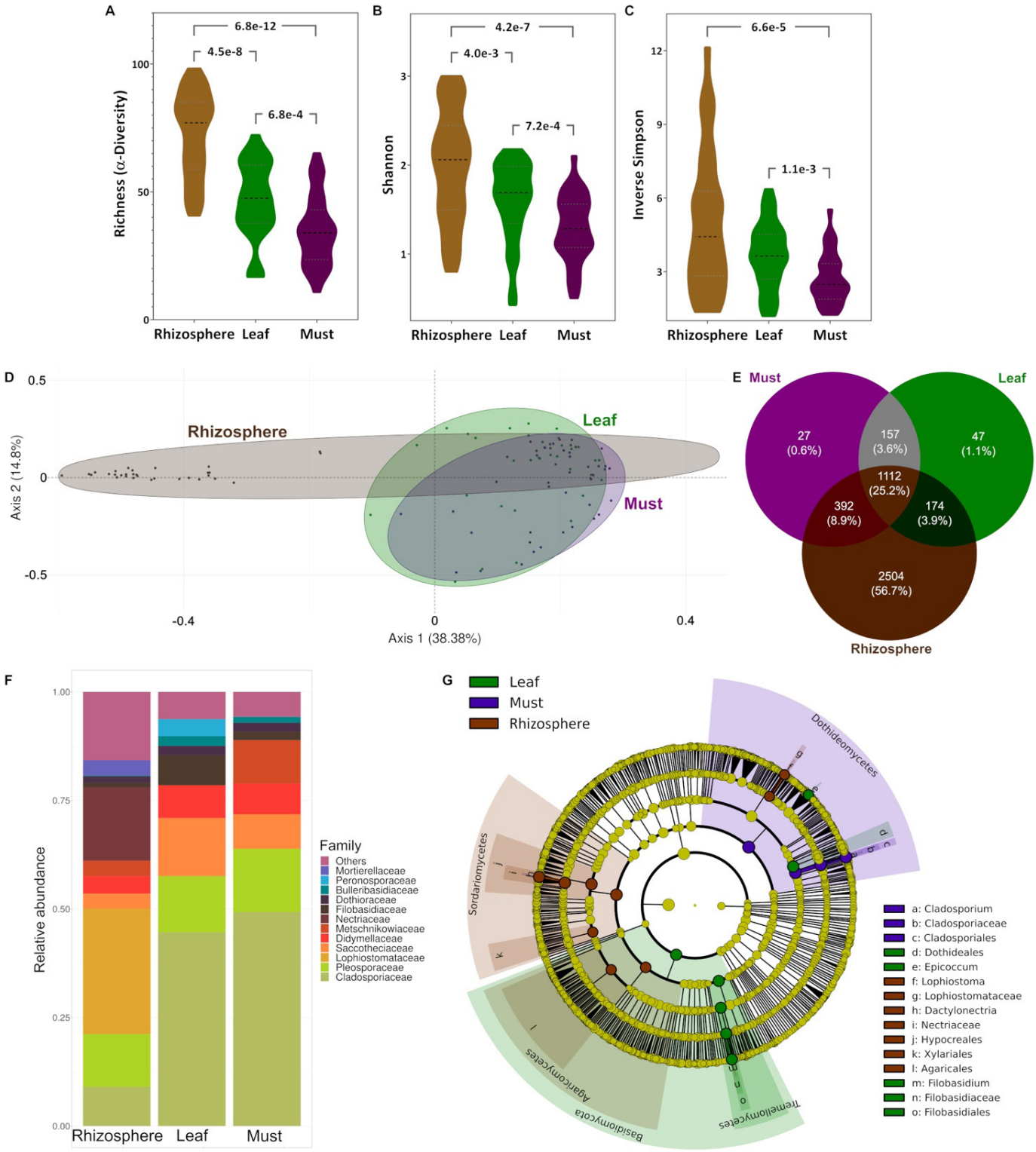


FIGURE 1. Analysis of fungal diversity in grapevine organs.

Violin plots illustrating: A. Richness, B. Shannon, and C. Inverse Simpson indices for fungal diversity. Statistical analysis was performed using the Kruskal–Wallis test, with pairwise comparisons identified through a post hoc Mann–Whitney test adjusted using the Bonferroni correction. D. PCoA summarising the differences in ITS rRNA gene sequences across various organs. The first two axes are displayed. A PERMANOVA test was used to assess variance based on distance matrices (p-value = 0.001). E. Venn diagram depicting fungal OTUs identified in Root (2716 total), Leaf (1405 total), and Must (1534 total) samples. F. Distribution of the fungal families identified in each organ. Families representing more than 1 % are shown individually. G. Cladogram plotted from LEfSe analysis showing the phylogenetic relationships of taxa significantly enriched across rhizosphere, leaf, and must samples. Each circle represents a taxonomic level, and colours indicate the group in which the taxon is significantly overrepresented. The coloured fan shapes represent all possible taxa to which the OTU.

Notably, only SJ1 showed significantly higher diversity, as indicated by both the Shannon and inverse Simpson indices. Furthermore, PCoA revealed that the fungal community at SAL3 was clearly distinct from those at the other sampling sites (Figure S5D). These findings suggest that fungal and prokaryotic communities in vineyard rhizospheres may be shaped by different environmental or edaphic factors, resulting in contrasting diversity patterns and site-specific community structures.

To further investigate fungal diversity in the rhizosphere of the sampled vines, OTUs were taxonomically annotated and integrated with physicochemical data and previously reported information on rhizospheric prokaryotic diversity (Toscani *et al*., 2025) (Table S5). *Lophiostomataceae, Nectriaceae, Pleosporaceae,* and *Cladosporiaceae* were the most frequently detected families, accounting for approximately 50 % of the annotated OTUs. *Lophiostomataceae* and *Nectriaceae* predominated in SJ1, SJ2, MZA, RN1, and RN2, whereas *Saccotheciaceae* and *Dothioraceae* were enriched in SAL (Figure 2A). *Pleosporaceae, Cladosporiaceae*, and *Metschnikowiaceae* were dominant in SAL2 and SAL3, whereas *Lophiostomataceae* was not detected. In contrast, SAL1 showed higher relative abundances of *Lophiostomataceae* and *Cladosporiaceae*. These families – *Saccotheciaceae, Dothioraceae, Pleosporaceae, Cladosporiaceae*, and *Metschnikowiaceae* – were associated with sandy soils, higher humidity, and increased precipitation, as observed in SAL (Figure 2C), supporting the fungal taxonomic distribution patterns reported herein.

To refine the characterisation of such fungal communities, a LEfSe analysis was conducted (Figure 2B). This analysis identified differential OTUs mainly associated with saprotrophic or pathogenic lifestyles (Table S6), including members of the *Nectriaceae* family in MZA and SJ1, where an OTU affiliated with the genus *Fusarium*, a genus of filamentous fungi that contains many agronomically important plant pathogens, mycotoxin producers, and opportunistic human pathogens (Ma *et al*., 2013), was overrepresented.

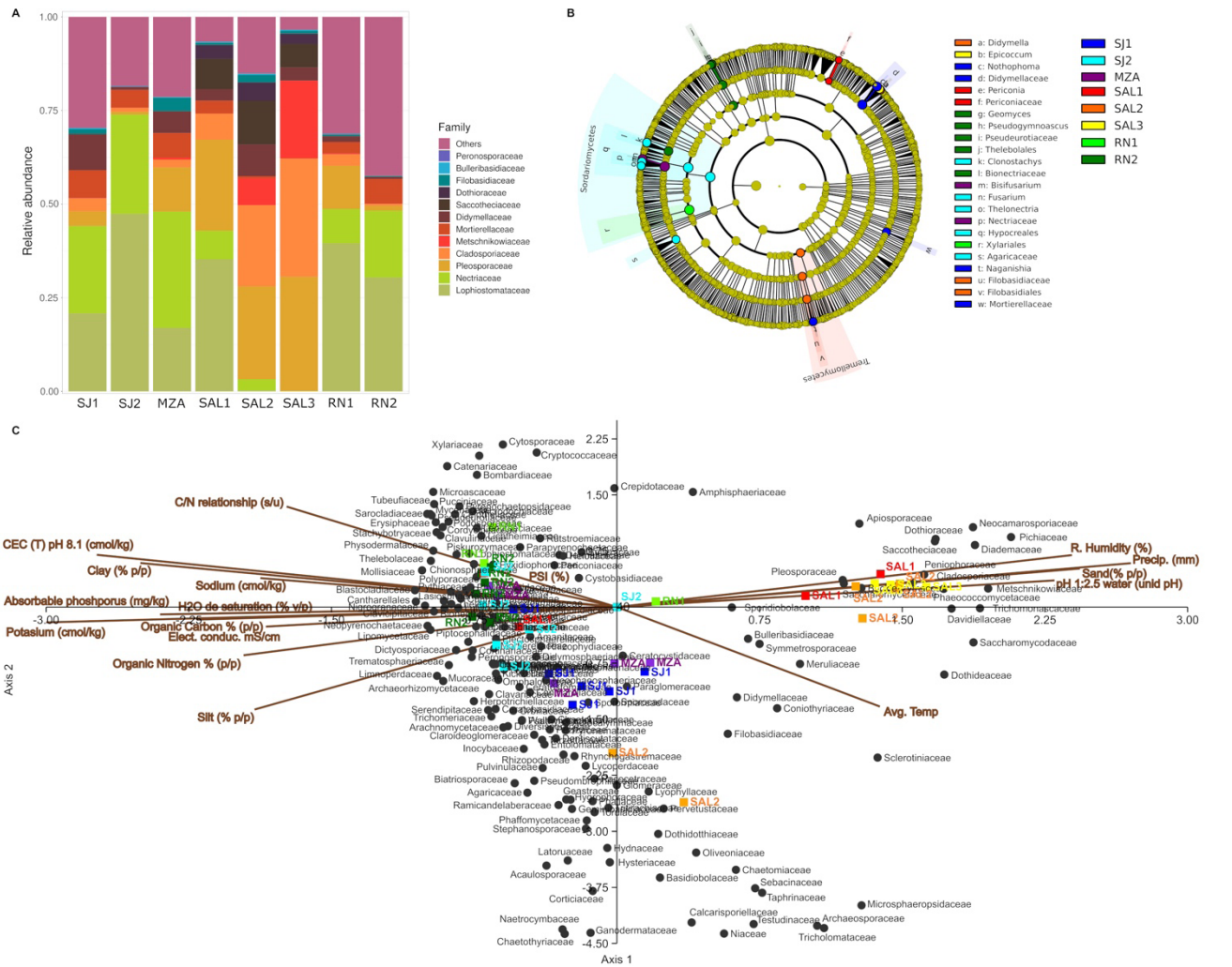


FIGURE 2. Fungal analysis in the rhizosphere of Argentine vines.

A. Distribution of the fungal families identified in rhizosphere samples. Families representing more than 1 % are shown individually. B. Taxonomic distribution of differential OTUs determined by LEfSe analysis. C. CCA plot of the most abundant fungal families and their relationship with the physicochemical features of soil. Perm (n = 999) Trace = 1.745, p = 0.012.

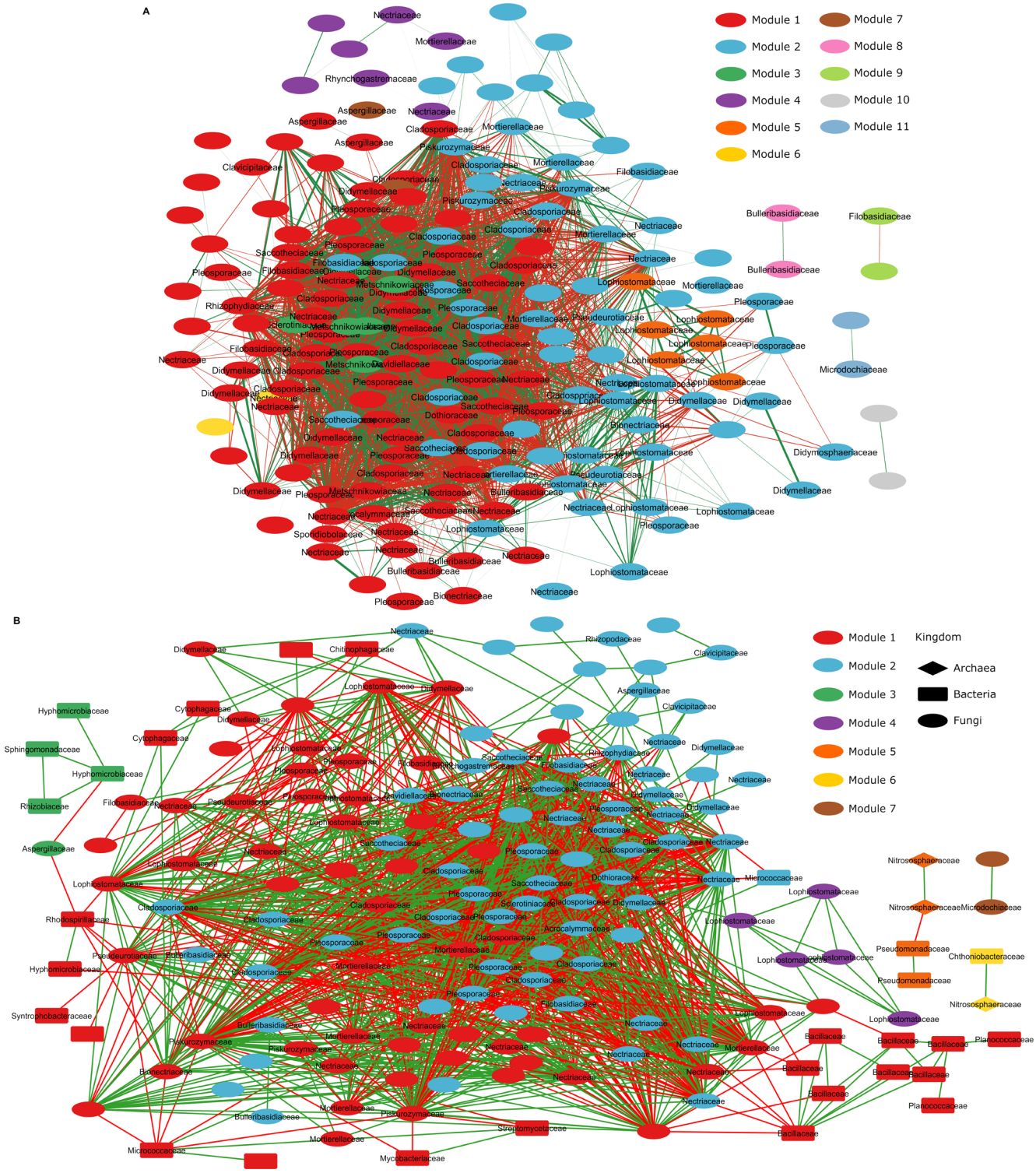


FIGURE 3. SparCC OTUs' network.

SparCC network for fungal (A) and fungal plus prokaryotic OTUs (B). Colours show modules that comprise the OTUs' network.

To gain insight into fungal interactions in the grapevine rhizosphere, we constructed a SparCC network that comprised 11 modules, with Modules 1 and 2 containing the majority of OTUs (Figure 3A). The topology is dominated by a densely connected core (Module 1, red), which concentrates most edges and contains several common vineyard families (*e.g.*, *Didymellaceae, Pleosporaceae, Cladosporiaceae,* and *Nectriaceae*). Surrounding this core, multiple satellite modules (notably the cyan, orange, and purple clusters) form smaller subgraphs with comparatively fewer between-module links. Positive correlations predominate within modules, whereas negative edges are rarer and tend to bridge modules, indicating niche partitioning among groups that otherwise exhibit strong intramodular co-selection.

The SparCC co-occurrence network shows a clear modular, visually core–periphery architecture. However, node-role analysis (Table S7) classified all taxa as peripherals, with no module hubs or connectors, suggesting low interdependence among microbial taxa. In the absence of hubs, interactions may be weaker or transient and more shaped by environmental heterogeneity than by stable ecological associations, consistent with strong niche partitioning or abiotic drivers overriding biotic interactions. From a management perspective, practices that minimise disturbance may favour more cohesive and resilient networks, potentially reducing interannual variability and helping to safeguard vintage quality.

Additionally, we constructed an inter-domain network between prokaryotes and fungi to trace ecological relationships in vineyard soil. Combining data from this study with previously published findings (Toscani *et al*., 2025) enabled the construction of a network consisting of seven modules (Figure 3B). Adding prokaryotic OTUs yielded a larger cross-kingdom network that retains a highly connected core (Module 1) but has fewer, larger modules overall, indicating increased connectivity after adding bacteria and archaea. Numerous positive, cross-kingdom associations link fungal families with bacterial groups typical of plant-associated soils (*e.g.*, *Rhizobiaceae, Sphingomonadaceae, Chitinophagaceae, Nitrosomonadaceae*), suggesting recurrent co-occurrence of bacterial–fungal consortia in the rhizosphere. By contrast, we also detected specific negative associations. In Module 1, *Bacillus* (family *Bacillaceae*; OTU_110 and OTU_1113) was negatively correlated with OTUs of *Dactylonectria* (family *Nectriaceae*; OTU_22988 [Module 1], OTU_21625 and OTU_23065 [Module 2]), *Mortierella* (family *Mortierellaceae*; OTU_21698 [Module 1]), and *Lophiostomataceae* (OTU_22525 [Module 1]). *Mortierellaceae* is under-represented in SAL2 and SAL3 (Figure 2A), where sandy soils are more likely to harbour *Bacillaceae* (Toscani *et al*., 2025). Thus, beyond potential inhibition, these patterns may reflect contrasting edaphic preferences that lead to spatial segregation.

Taken together, these patterns indicate that the rhizosphere harbours modular assemblies of taxa with strong within-module co-occurrence and relatively antagonistic or segregated relationships between modules. This architecture is consistent with microhabitat filtering and functional complementarity within modules, alongside inter-module niche differentiation across the vineyard rhizosphere.

4. Diversity patterns and taxonomic composition of foliar fungi in grapevines

When analysing the diversity of fungi present in grapevine leaves, it was observed that samples from RN1 exhibited high values for richness, Shannon index, and inverse Simpson index, whereas SAL1 and SAL2 showed the lowest values (Figure 4A–C). Additionally, PCoA revealed differences between Cuyo (SJ and MZA) and Patagonian (RN1) grapevine leaf samples (Figure S6A). Due to the low number of sequenced samples (Table 1), SAL3 was not included in the analysis.

Taxonomic analysis revealed that the most represented family was *Cladosporiaceae*, which was particularly abundant in SAL2 (Figure 4D). This family comprises melanised, airborne fungi with a worldwide distribution (Salgado-Castillo *et al*., 2023). Melanins enhance fungal tolerance to various environmental stresses, thereby improving survival by protecting fungal structures from UV radiation, extreme temperatures, and oxidising agents (Toledo *et al*., 2017). Their protective role against solar radiation may further contribute to fungal resilience, potentially conferring an adaptive advantage in high-altitude vineyards such as SAL2 (Figure 4E).

The second most represented family was *Saccotheciaceae*, which also showed a notable frequency in SAL1. The *Didymellaceae* family was prominently represented in MZA. In contrast, RN1 was characterised by a high frequency of OTUs affiliated with the *Dothioraceae* family, while RN2 exhibited an increased representation of *Peronosporaceae* and *Nectriaceae*.

The SparCC-inferred network revealed a structured microbial community, in which two connector hubs (OTU_22707, family *Filobasidiaceae,* and OTU_23256, family *Didymellaceae*), one module hub (OTU_22719, family *Symmetrosporaceae*), and several peripheral species were identified (Figure 5A–B, Table S7). Connector hubs indicate the presence of key taxa that may mediate interactions between otherwise distinct ecological modules, while the module hub likely represents a taxon with a dominant role in the internal stability and function of its specific sub-community. In contrast to what was observed in the rhizospheric network, this topological configuration suggests a non-random organisation that likely underpins functional complementarity and resilience within the leaf-associated fungal microbiome.

5. Fungal community structure in must samples and its potential impact on wine fermentation

Similarly to leaf samples, must from RN1 showed the highest values for species richness, Shannon, and inverse Simpson index, indicating a more diverse fungal community (Figure 6A–C). This consistency in the patterns observed across both aerial plant samples may be related to the fact that RN1 is the only organic vineyard sampled. This

distinctive production approach, which relies on alternative pest control methods, may account for the higher fungal diversity observed in RN1 compared to the other vineyards analysed. Furthermore, PCoA showed differences between must samples from SJ and RN (Figure S6B). In contrast to the pattern observed for leaves, must from MZA differed from that of SJ and clustered more closely with the RN samples.

In a similar manner, *Cladosporiaceae* was the most abundant family, although no association with high-altitude vineyards was observed (Figure 6D). Remarkably, the family *Metschnikowiaceae* was the most abundant in SAL3, and it was also present in SAL2, RN1, and less prominently in SAL1. Fungi of the *Metschnikowiaceae* family have been reported to be associated with environments characterised by high levels of precipitation and humidity (Jara *et al*., 2016). CCA revealed a close relationship between the presence of these fungi and climatic factors (Figure S6C). However, no such relationship was observed for the grape must samples from SAL2, SAL3, and RN1. Within the non-*Saccharomyces* wine yeasts, the genus *Metschnikowia* is among the best characterised, reflecting its wide distribution and recognised impact on winemaking (Vicente *et al*., 2020). Some species, including *M. pulcherrima*, *M. viticola*, and *M. fructicola*, exhibit moderate fermentative capacity and display enzymatic activities relevant to the release of aroma and colour precursors, thereby contributing to the organoleptic profile of wines from these regions.

The LEfSe analysis revealed the differential presence of yeast OTUs that may be involved in the wine fermentation process (Figure 6E). SAL3 was found to harbour an OTU corresponding to *Aureobasidium* spp., a group of ubiquitous black, yeast-like fungi commonly detected in both extreme and benign environments, where they may live as saprophytes, endophytes, or pathogens (Table S3). As producers of various bioactive compounds, these fungi play important roles in numerous food transformation processes and have several industrial applications (Di Francesco *et al*., 2023). Certain species within the genus *Aureobasidium*, such as *A. pullulans*, are used as biocontrol agents against fungal and bacterial diseases affecting grape, strawberry, and pome fruit. *A. pullulans* is consistently reported among the predominant endophytic (and occasionally saprobic) taxa, highlighting its recurrent association with grapevine wood and its potential relevance for the biological control of trunk disease pathogens (Perelló *et al*., 2025; Pizzi *et al*., 2025). Additionally, this genus may influence the early stages of

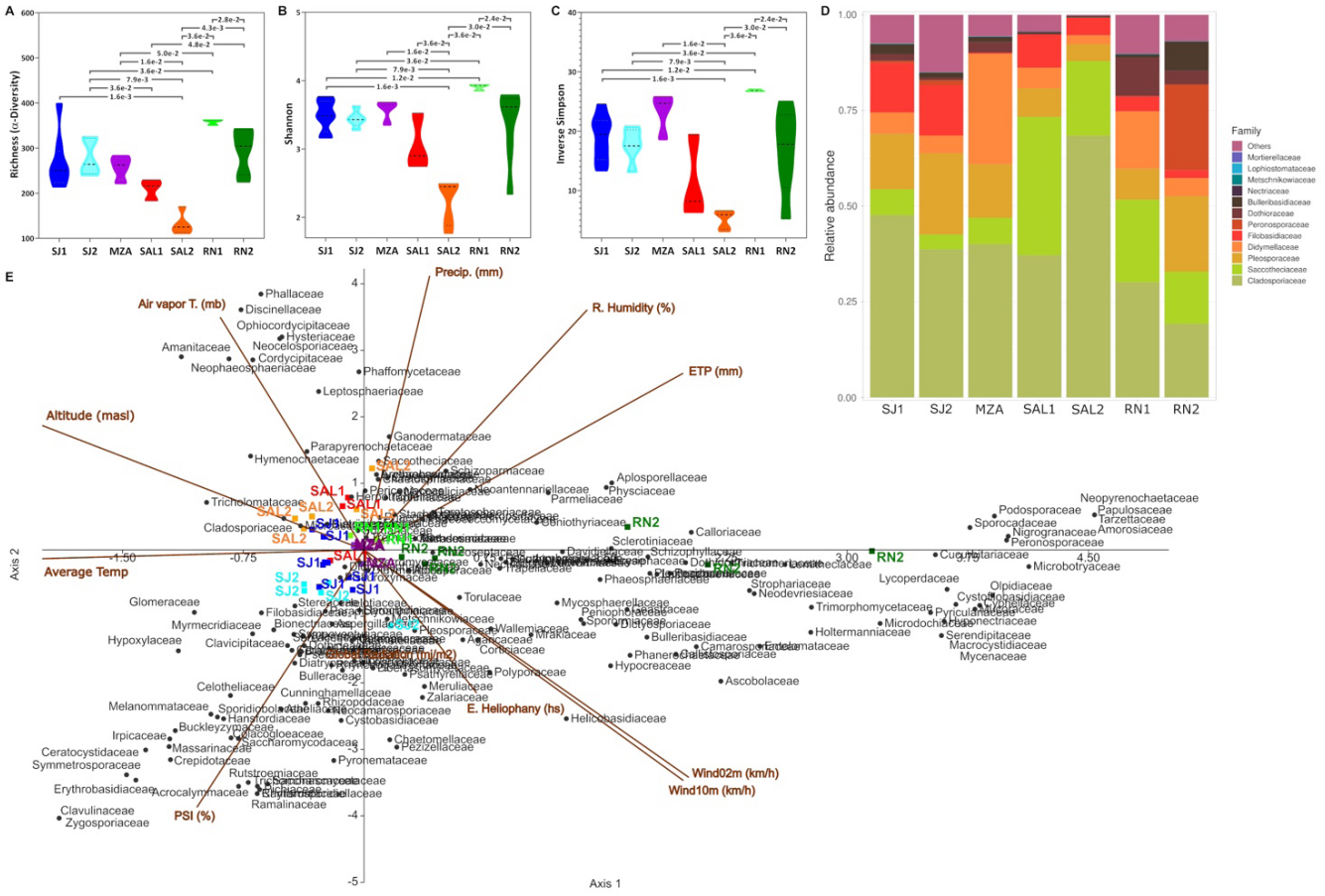


FIGURE 4. Fungal diversity and composition across grapevine leaves.

Violin plots depict: A. Species richness, B. Shannon diversity, and C. Inverse Simpson indices for fungal communities associated with Leaf samples. Statistical comparisons were conducted using the Kruskal–Wallis test, followed by pairwise Mann–Whitney tests with Bonferroni correction. D. Distribution of the fungal families identified in Leaf samples. Families representing more than 1 % are shown individually. E. CCA analysis of fungal families and their relationship with the climatological features. Perm (n = 999) Trace = 0.7496, p = 0.001.

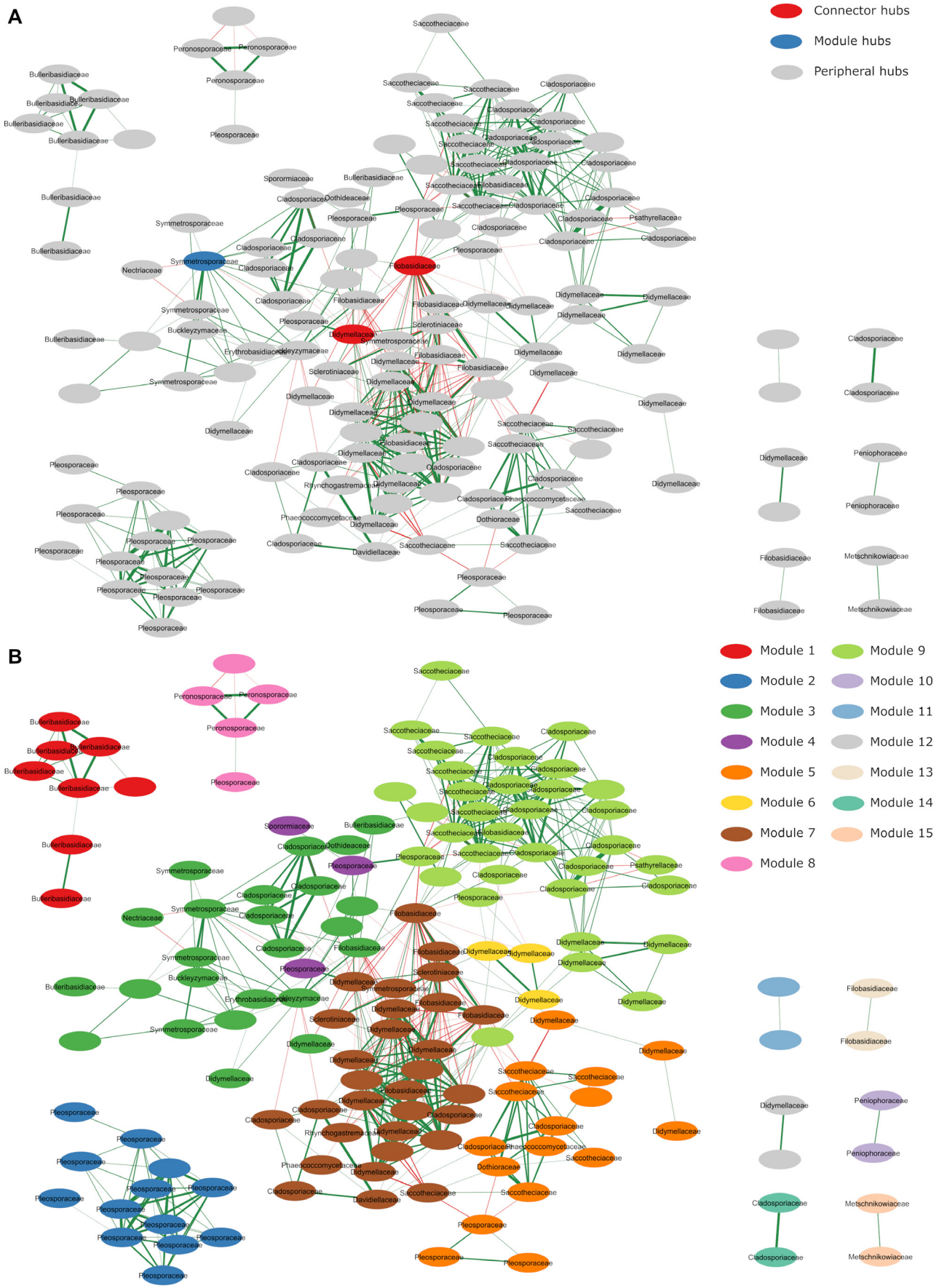


FIGURE 5. SparCC OTUs' network for leaf samples.

A. Colour code indicates the connector and peripheral hubs. B. Colours show modules that comprise the fungal OTUs' network in leaf samples.

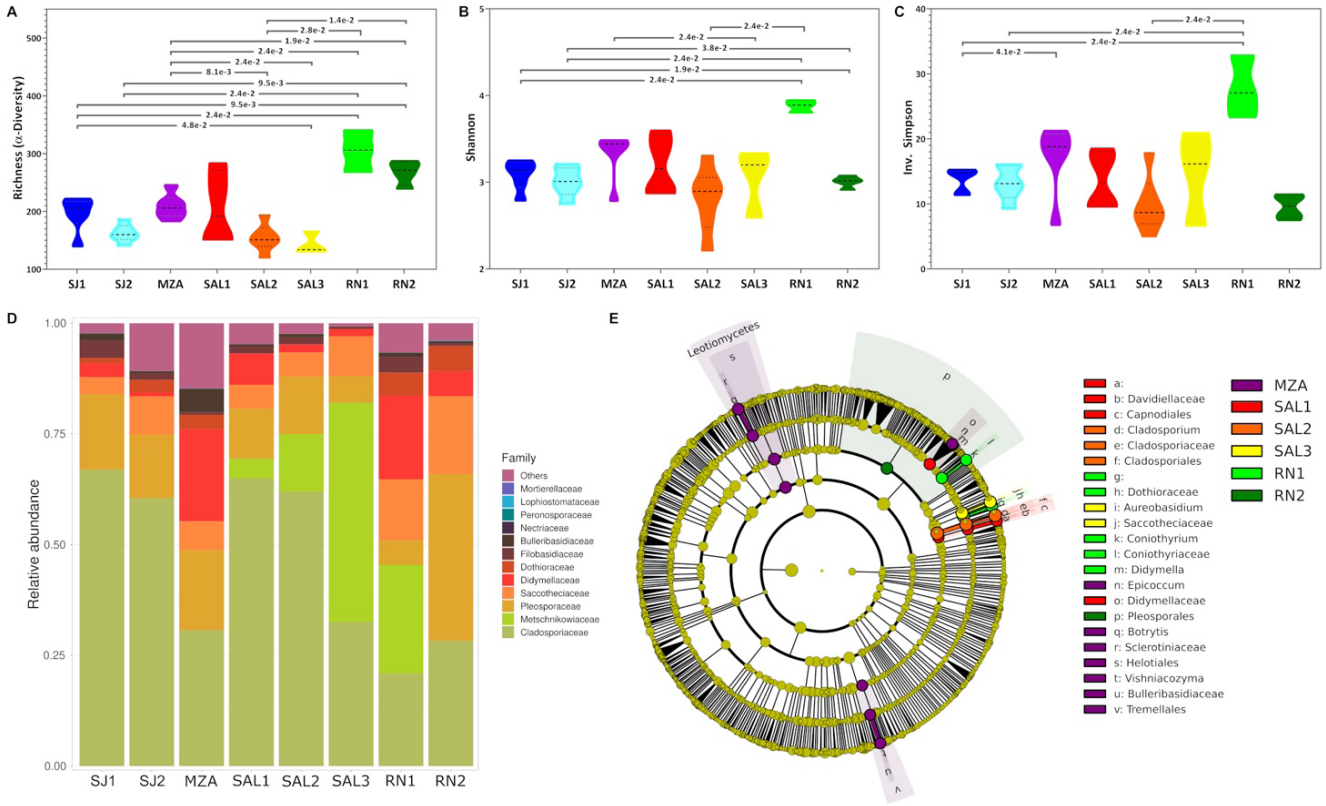


FIGURE 6. Taxonomic composition and fungal diversity in grape must samples.

A. Species richness, B. Shannon diversity, and C. Inverse Simpson indices for fungal communities associated with must samples. Statistical comparisons were performed using the Kruskal–Wallis test, followed by pairwise Mann–Whitney tests with Bonferroni correction. D. Taxonomic distribution of fungal families detected in must samples. Families contributing more than 1 % to the overall community are shown individually. E. Taxonomic distribution of differential OTUs determined by LEfSe.

wine fermentation as a member of the initial microbiota, modulating the aromatic profile through the release of volatile compounds and characteristic red wine flavour components such as 2-methylbutanoic acid, 3-methyl-1-butanol, and ethyl octanoate (Bozoudi & Tsaltas, 2018). RN1 also exhibited a differential OTU belonging to the *Dothioraceae* family, which includes *Aureobasidium* spp. along with other taxa not associated with wine fermentation. OTUs affiliated with the genera *Epicoccum* (MZA), *Botrytis* (MZA), and *Cladosporium* (SAL2) were also identified. Some species within these fungal families are commonly associated with grape rot and can synthesise bioactive compounds, including mycotoxins, that may alter the organoleptic properties of wine (Schueuermann *et al*., 2019). Despite not being among the differential OTUs identified by LEfSe, other species detected in grape must are associated with grape rot diseases. For instance, OTUs assigned to the family *Glomerellaceae*, which includes *Colletotrichum* spp., the causal agents of ripe rot (Crandall *et al*., 2022), were detected in SAL1, SAL2, MZA, SJ1, and RN2. In addition, several yeasts associated with sour rot (Hall *et al*., 2018) were present, including *Hanseniaspora uvarum* (commonly detected across must samples), *Hanseniaspora vineae* (SAL2 and the SJ samples), *Pichia terricola* (SJ2, RN1, and SAL3), and *Saccharomyces cerevisiae* (detected across all samples).

The SparCC network generated from must ITS-sequencing data exhibited a highly centralised topology, characterised by a single connector hub and multiple peripheral hubs (Figure 7A, Table S7). This pattern suggests the presence of a dominant taxon acting as a central node in microbial co-occurrence, with limited redundancy among key community members. The connector hub corresponds to OTU_21541 (family *Saccotheciaceae*) and is part of Module 1 (Figure 7B). This module comprises OTUs from the families *Saccotheciaceae* and *Metschnikowiaceae*, the latter being exclusive to Module 1. Module 1 is negatively associated with Module 4, which is primarily composed of OTUs of the family *Didymellaceae*. Module 2 includes OTUs mainly of the families *Saccotheciaceae, Dothioraceae, Buckleyzymaceae*, and *Didymellaceae*, while Module 3 includes OTUs of the family *Pleosporaceae*. The family *Cladosporiaceae* is widely distributed across Modules 1, 3, and 4, and is particularly well represented in Module 5.

DISCUSSION

This study offers a detailed characterisation of fungal community composition across different grapevine organs in the most important wine-producing regions of Argentina, thus enhancing current knowledge of the microbiota associated with *Vitis vinifera* cultivars in underexplored South American *terroirs*. Through high-throughput ITS metabarcoding, we identified distinct organ- and site-specific patterns of fungal diversity, with the rhizosphere exhibiting the highest

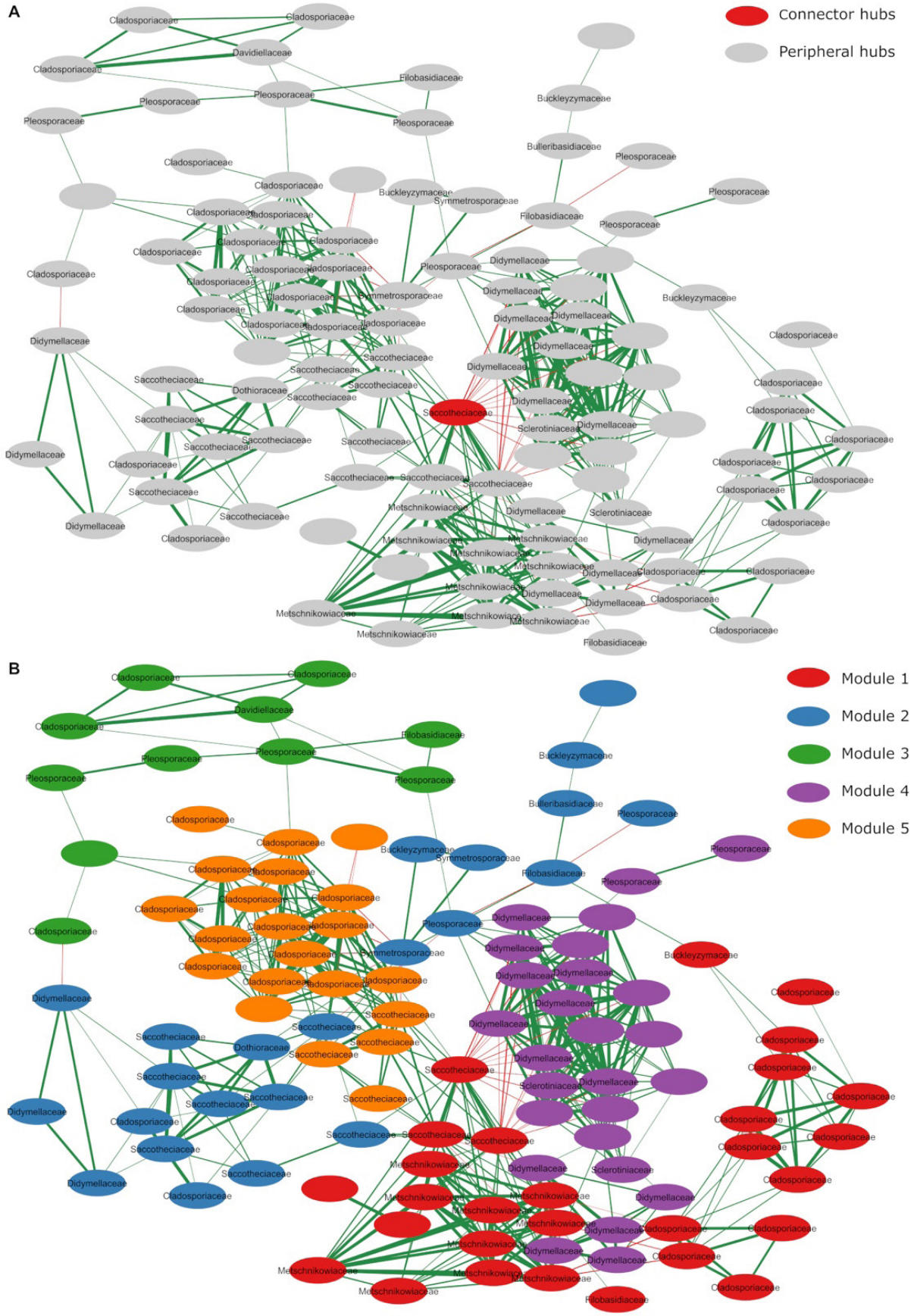


FIGURE 7. SparCC OTUs' network for grape must samples.

A. Colour code indicates connector and peripheral hubs. B. Colours show modules that comprise the fungal OTUs' network in must samples.

values, followed by leaves and must. These results support the observation that belowground plant compartments serve as important reservoirs of microbial diversity, contributing to the holobiont concept and highlighting the ecological relevance of the rhizosphere in viticultural ecosystems (Bill *et al*., 2021).

In mature vineyards, adult plants are particularly susceptible to infections via the root system, which represents the main route of colonisation for pathogens from genera such as *Dactylonectria*, associated with black-foot disease (Cobos *et al*., 2022). As shown in previous work from our group (Oyuela Aguilar *et al*. 2021), bacterial isolates identified as *Bacillus* spp. could inhibit the growth of phytopathogenic fungi like *Botrytis cinerea* or *Alternaria alternata*. Similarly, the OTUs annotated as *Bacillus* could interfere with the growth of *Dactylonectria* by synthesising inhibitory compounds such as lipopeptides and non-ribosomal peptides (Oyuela Aguilar *et al*., 2021). The identification of potentially antagonistic interactions between *Bacillus* spp. and phytopathogenic fungi such as *Dactylonectria* provides further evidence that fungal-bacterial relationships may be key to developing sustainable disease control strategies within vineyard ecosystems (Santos *et al*., 2016). The emerging picture of potential mutual exclusion and/or niche specialisation between microbial populations opens new avenues for the functional characterisation of soil and plant-associated microbes, with the potential to inform viticultural practices aimed at enhancing plant health and resilience under increasingly variable climatic conditions. Although these findings point to possible biocontrol interactions, they remain speculative in the absence of functional validation. Follow-up *in vitro* or greenhouse experiments would be crucial to verify these antagonistic effects and their consistency across different soil types or cultivars.

In addition to *Botrytis*, our must dataset captured a broader bunch-rot complex, including OTUs assigned to *Glomerellaceae* (*Colletotrichum* spp., ripe rot) and several taxa frequently reported in grape-rot contexts (*e.g.*, *Cladosporium*, *Epicoccum*). These organisms are typically favoured by wet or humid conditions and can contribute to berry deterioration and downstream changes in must chemistry, which may ultimately influence fermentation outcomes and wine sensory profiles. We also detected yeast genera commonly associated with sour rot and early fermentation stages, including *Hanseniaspora* and *Pichia*, alongside *Saccharomyces cerevisiae*. Notably, several of these rot- and fermentation-associated taxa occurred in sites characterised by higher humidity and precipitation (*e.g.*, SAL), consistent with the idea that climatic variability can modulate both disease-related communities and the initial microbial starting point of must fermentations.

Additionally, the observed spatial distribution of taxa such as the family *Metschnikowiaceae* and the genus *Aureobasidium* across high-altitude vineyards suggests that altitude and climate play a pivotal role in shaping grapevine-associated fungal assemblages, with potential implications for fermentation dynamics and wine sensory profiles (Zhu *et al*., 2021). These findings underscore the need to consider environmental gradients, such as altitude, when evaluating microbial *terroir* and its influence on viticultural and oenological outcomes.

Some strains of the genus *Mortierella* are classified as Plant Growth-Promoting Fungi (PGPF) and are commonly found in bulk soil, the rhizosphere, and plant tissues. These microorganisms are frequently present in extremely hostile environments and contribute to enhancing the availability of bioavailable forms of phosphorus and iron in the soil. They can also synthesise phytohormones and 1-aminocyclopropane-1-carboxylate (ACC) deaminase, and importantly, help protect agricultural crops from pathogens (Ozimek & Hanaka, 2020). Healthy vineyards are underpinned by diverse fungal and prokaryotic communities. Alterations in this microbial diversity can shift population dynamics and affect plant susceptibility to pathogens. Understanding these microbial patterns across grapevine organs is therefore critical for refining viticultural practices and promoting ecosystem resilience (Minerdi & Sabbatini, 2025).

The comparative network analysis across rhizosphere, leaf, and must compartments in grapevines revealed distinct topological configurations and potential ecological implications for fungal community assembly. The rhizospheric network, composed exclusively of peripheral taxa, lacked central or hub species, indicating limited interdependence and suggesting that community structure is primarily driven by environmental heterogeneity or abiotic filtering. In contrast, the leaf-associated network exhibited a modular and non-random topology, with defined connector and module hubs, pointing towards functional complementarity and internal resilience. Meanwhile, the must network was highly centralised, dominated by a single connector hub with minimal redundancy, reflecting a community potentially shaped by strong selective pressures and reduced ecological buffering. Such results suggest that the aerial ecosystems (leaves and grape must) are more structured than the rhizosphere. Collectively, these findings underscore the compartment-specific organisation of the grapevine mycobiome and highlight how niche-specific selective forces influence microbial network architecture and potential ecosystem functions. Our observations replicate and support patterns described by other authors, who identified two major groups: (1) microbial communities associated with grapes and leaves, and (2) those derived from the soil (Zhang *et al*., 2017). They also suggest a correlation between the microbial communities of belowground and aboveground grapevine tissues.

This work lays a critical foundation for advancing a microbial-*terroir* framework in Argentine viticulture, aligning with global efforts to decode how microbial communities influence crop quality. To deepen our understanding of the ecological mechanisms driving these patterns and assess their consistency across vintages, future research should incorporate functional omics approaches and multi-year datasets. Given the current limitations in interpreting the ecological roles of specific taxa, the application of functional inference tools or metatranscriptomic analyses will be particularly valuable

to better characterise their metabolic functions, assess the enological significance of microbial patterns, and clarify the ecological relevance of dominant fungal groups.

ACKNOWLEDGEMENTS

We would like to thank the wineries in Argentina for allowing us to collect samples from their vineyards. We would also like to thank the "MicroWine" team for their support and input. MO carried out her Marie-Curie ITN fellowship at the IBBM (Instituto de Biotecnología y Biología Molecular) CONICET-UNLP. AMT is a researcher at UNLP; CR and RRW are fellows of the Research Career of CONICET; MFDP and MP are members of the Research Career of CONICET; and LS is a Head Professor of the Universidad Nacional de Quilmes and a member of the Research Career of CIC-PBA.

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