Seasonal drought surpasses the effects of irrigation regime in the microbial dynamics of grapevine rhizosphere and presents high impact in mycobiome

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Abstract

Background – Drought is expected to have a major impact for viticulture and other agriculture worldwide. The soil microbiome has been shown to be an important sustainable tool to mitigate the effects of climate change since its manipulation leads to increased plant resilience with little ecosystem disturbance and low cost. However, the identification of drought-induced shifts in bulk soil and rhizosphere microbiota associated with grapevine remains largely unexplored. We conducted a thorough analysis of this holobiont over two seasons in a Syrah vineyard submitted for six years to three irrigation strategies (absent, deficit and full irrigation). The study combined 16S rRNA and ITS1 based metabarcoding, physiological measurements, and edaphic and climate data.

Results – Leaf water potential and stomatal conductance agreed with the irrigation regime applied but one of the studied growth seasons presented more pronounced differences in microbiome diversity and structure than the other, highlighting the effect of climate. Prokaryotic members of the community may present growth promoting properties, but a wider array of putative functionalities were identified in the mycobiome ranging from pathogenicity and biofertilization to biocontrol. Fungal members also showed higher sensitivity to drought than prokaryotes. The mycobiome enrichment in Basidiomycota, the abundance of the basidiomycetous yeast Solicoccozyma aeria and the abundance of the bacterial family Chitinophagaceae have not been previously reported for grapevine associated microbiome.

Conclusions – This study highlighted the specificities of restructuring of grapevine rhizosphere microbiomes under drought stress where the irrigation strategy, climate, genotype, and soil parameters interact. The stability of the prokaryotic component may be eventually due to their functional redundancy while a lower ecological memory of fungi may be balanced by diverse functional attributes. Ultimately, our results suggest that members of the altered grapevine microbiota might contribute to grapevine survival under extreme environmental conditions, opening the door to more sustainable practices in viticulture.

Background

Portugal and other Mediterranean basin countries will be one of the most impacted regions in the globe by climate change (Pereira et al., 2021). The increase in drought periods has already been shown to have deep socio-economic implications in agricultural management (Schleypen et al., 2022). Viticulture and the wine-making industry are set to be one of the most affected agricultural sectors due to their high dependence on climate (Venios et al., 2020), ultimately resulting in a decrease in the wine's quality and productivity (Greer & Weston, 2010; van Leeuwen & Darriet, 2016).

The key strategy of the wine-making industry to tackle several viticultural issues, like prolonged drought periods, is selecting and breeding different adapted cultivars to a given stress (Nerva et al., 2022). The use of drought-tolerant grapevine varieties under drought conditions has been shown to be effective in improving productivity, yield, and overall crop quality (Vaz et al., 2016; Vink et al., 2021). Nevertheless, these practices are highly time-consuming when immediate answers are required. Due to the more frequent periods of drought, the implementation of irrigation regimes to vineyards has been growing in use (Zarrouk et al., 2016). And even though grapevines have been traditionally grown under rainfed conditions, it has been shown that deficit irrigation techniques are able to create a balance between reproductive and vegetative growth in the vineyard that maintains the crop's quality and productivity (Costa et al., 2016; Zarrouk et al., 2016). However, these techniques come at a cost, both economic and environmental, as water becomes a scarcer and ever more valuable resource (Azorín & García, 2020; van Leeuwen & Darriet, 2016). Hence, the development and application of more sustainable practices become imperative.

One aspect often overlooked when considering *Vitis vinifera*'s fitness to different environmental stresses is the inherent power of its indigenous soil and rhizosphere microbiota (Bettenfeld et al., 2022; Nerva et al., 2022). Several plants have been shown to harbor soil microbial communities with plant growth promoting (PGP) properties that enhance the crop's fitness to drought or induced water stress (Cherni et al., 2019; Liu et al., 2021; Marasco et al., 2012). For instance, the modulation of phytohormones (like auxins, ethylene, and/or abscisic acid), the production of exopolysaccharide matrices and antioxidant metabolites, as well as the increase of the water use efficiency and nutrient exchange, are a few known mechanisms in which microbes partake ameliorating the drought status

of a plant (Poudel et al., 2021). Although it has already been shown that the grapevine's microbiota showcases a vast array of these PGP traits (Rolli et al., 2015), there is still a knowledge gap in the exploitation of this microbiota for drought mitigation.

The soil is the main reservoir of microorganisms for plant-microbe associations (Darriaut et al., 2022b), and the selection of this microbiota is bound to plant mechanisms (Zarraonaindia et al., 2015) intrinsically connected to the plant genotype (Marasco et al., 2018). The grapevine scion cultivar Syrah has been shown to display high control of its stomatal conductance under water stress (Damásio et al., 2025). Additionally, the rootstock 1103 Paulsen (1103P) is characterized as drought-tolerant due to its growth plasticity to soil moisture and depth (Marín et al., 2021). However, studies on the correlation between grapevine physiological parameters and the rhizosphere and bulk soil microbiome have not been carried out, so far.

In the present work, we studied in two growth seasons the rhizosphere microbiome harbored by the *Vitis vinifera* cultivar Syrah grafted on the rootstock 1103P and grown in a commercial vineyard conducted under three different irrigation regimes for six years. By integrating plant physiology, soil, and climate data to our 16S rRNA and ITS1 meta-analysis, we observed differences and similarities in the microbial communities' diversity and structure among conditions, and defined core microbiota and rare taxa for each growing season.

Methods

Sample Collection - The study site was identified at the ampelographic collection vineyard of Herdade do Esporão (38°22'48.4"N; 7°33'38.6"W), located in Reguengos de Monsaraz, Portugal. The sample collection was carried out in July of 2022 and 2023, from grapevines of Syrah cultivar (*Vitis vinifera* L.) grafted on the rootstock 1103 Paulsen at *veraison* stage. The vineyard has been conducted, over the course of six years (2017-2023), under three different irrigation regimes: No Irrigation (NI – 0% ETc, corresponding to Rainfed Irrigation), Deficit Irrigation (DI – 50% ETc), and Full Irrigation (FI – 100% ETc). Five biological replicates were collected for each irrigation treatment, and 30 soil samples were analyzed (15 from each year of sampling). The samples were therefore divided

into six types corresponding to the three irrigation strategies and the two years of sampling. The actual soil samples were collected in a composite way from 2 to 4 cardinal directions very close to the grapevine trunk (15-20 cm) in order to catch the root-influence area across 10-20 cm depth. Rhizosphere samples were then homogenized and stored in ice before being moved to -80°C freezer and kept until analysis.

Analysis of Edaphoclimatic Conditions - The different climatic conditions associated with sampling were assessed through evaluation of atmospheric and edaphic variables. As for the climate, precipitation and temperature data were provided by the Instituto Português do Mar e da Atmosfera (IPMA) from their Reguengos de Monsaraz station (0840); this data was assessed in between the 1st of January and the 31st of June of 2022 and 2023.

As for the soil's physical and chemical properties, these were characterized in terms of dry bulk density (DBD), pH, water content (or humidity), grain size distribution, organic matter content (OMC), and other geochemical analyses for the quantification of metallic oxides and micronutrients. DBD was calculated as the dry sample weight (g) of the soil, after 48 hours in an oven at 60ºC, contained in vials of known volume (2.0 or 2.5 cm^3), and divided by the original wet sample volume (cm^3). The soil water content was calculated as the difference between net weight and dry weight and expressed as a percentage of the net weight. Soil pH was determined using the electrometric method (LNEC E203-1967) as proposed by the Portuguese Laboratório Nacional de Engenharia Civil (LNEC), where the soil samples were left in a pre-boiled and cooled distilled water solution for 24 hours at a ratio of 30g of soil for 75cm^3 of water; pH was measured with the InoLab WTW pH730 potentiometer using a WTW SenTix-41 electrode (Xylem Analytics, WTW GmbH, Germany) and calculated as a mean value of three measurements that did not differ more than 0.05 pH between them. For OMC, the adapted loss on ignition (LOI) method (Heiri et al., 2001) was used, where 2g of homogenized soil was incinerated at 500ºC for 2 hours in a Lenton Thermal Designs EF 11/88 chamber furnace (Lenton Laboratory & Scientific Equipment, South Africa). Particle size analysis was carried out on the fraction below 1mm, after sieving 1g of soil, by laser diffraction using a Malvern Mastersizer 2000 diffractometer (Malvern Panalytical, United Kingdom); the fraction above 1mm was weighed and combined with the Malvern results to characterize the grain size distribution.

For the geochemical analyses, 10g of homogenized soil was used for the quantification of total nitrogen, and whole rock composition (metallic oxides, and other trace elements) with ICP-OES following protocols 4F and 4B, respectively, by Activation Laboratories Ltd. (Ontario, Canada).

Assessment of Plant Physiological Parameters – The characterization of the grapevine water status was assessed through predawn water potential (Ψ_{pd}), and stomatal conductance (g_s) measurements. These parameters were assessed on the same day of sample collection for both years. For each parameter, five pre-selected homogenous grapevines from each irrigation strategy were randomly selected. Briefly, predawn water potential was performed at 05:00 am, using Scholander-type pressure chamber (Manofrigido, S. A., Lisboa, Portugal), using at least two leaves per plant. Fully expanded, healthy, and well-exposed leaves, from the third to fifth node of one of the main central shoots of the plant, were selected for the measurements. Leaves were removed using sharp scissors and immediately sealed in a plastic bag containing a damp paper towel to prevent water loss and wrapped with aluminum foil to avoid light during transport to the pressure chamber. Stomatal conductance measurements were performed with LI-600 porometer/fluorometer (LI-COR Inc., Lincoln, Nebraska, USA). Measurements were performed on sunny, cloud-free days between 11:00 am and 12:00 pm. Fully expanded, photosynthetic active, healthy and well-exposed to the sun leaves, from the third to fifth node of the main central shoots of the plant were selected for the measurements. Two leaves per grapevine from five plants per genotype and treatment were used. Additionally, the daily accumulated crop evapotranspiration (ETo) was measured corresponding to total crop measurements.

Soil DNA Extraction and Sequencing - Soil DNA was extracted with the DNeasy ® PowerSoil Pro Kit (QIAGEN, Germany), using an optimized protocol where two additional steps of enzymatic incubation were introduced prior to the application of the manufacturer's protocol. These were an incubation in a water bath with lysozyme (Carl Roth GmbH + Co. KG, Germany) for 1 hour at 37ºC, followed by another hour of incubation with proteinase K (Thermo Fisher Scientific, USA) at 55ºC. DNA yield and quality were assessed with Qubit 4 Fluorometer with the Qubit™ 1X dsDNA High Sensitivity Assay kit (ThermoFisher™ Scientific, USA) and with NanoDrop ND-1000 (NanoDrop Technologies, Inc., USA). A negative control was also processed for verification of the method. The

extracted environmental DNA was sequenced with Illumina MiSeq, following the manufacturer's guidelines, in a commercial sequencing service (MR DNA – Molecular Research LP, Shallowater, TX, United States of America), targeting the V4-V5 hypervariable regions of the 16S rRNA gene and ITS1 region, for archaea/bacteria and fungi, respectively. The primer pairs used were 515f/926r (5'-GTGCCAGCMGCCGCGGTAA-3', 5'-CCGYCAATTYMTTTRAGTTT-3') for the 16S rRNA gene, and ITS1f-ITS2 (5'-CTTGGTCATTTAGAGGAAGTAA-3', 5'-GCTGCGTTCTTCATCGATGC-3') for the ITS1 region (Walters et al. 2016). For both regions, a PCR using the HotStarTaq Plus Master Mix Kit (QIAGEN, Germany) was performed under the following conditions: 95ºC for 5mins, followed by 30-35 cycles of 95ºC for 30secs, 53ºC for 40secs, and 72ºC for 60secs, with a final elongation step at 72ºC for 10mins. After the amplification, the PCR products were checked in a 2% agarose gel and purified using calibrated AMPure XP beads (Beckman Coulter Life Sciences, USA). With the purified PCR products, an Illumina DNA library was prepared. Sequences with under 150bps and ambiguous base calls were removed. Afterwards, the sequences were quality filtered, dereplicated, denoised, and chimeras were removed.

Metagenomic Data Processing - Raw reads were processed using QIIME 2 v.2023.2.0 (Bolyen et al., 2019) with its DADA2 tool allowing for the inference of Amplicon Sequence Variants (ASVs), merging forward and reverse reads with the default parameters, and eliminating reads smaller than 243/251 nts for the prokaryotic dataset, and 248/268 nts for the eukaryotic dataset. The taxonomic classification of our ASVs was obtained by using a sckit-learn Naïve-Bayes machine-learning classifier trained on the Greengenes2 v.2023.03 database (McDonald et al., 2023) for the prokaryotes, and the UNITE v.9.0 database (Abarenkov et al., 2022) for the eukaryotes. ASVs corresponding to unknown sequences were filtered out from both datasets, and eukaryotic ASVs that were classified to any kingdom other than Fungi were also removed. ASVs with relative abundance below 0.005% were filtered out, as suggested by Bokulich and colleagues (Bokulich et al., 2013). ASVs present in the negative control were also filtered out from the remaining samples.

Microbial Diversity Analyses - Sequences were aligned using MAFFT-FastTree algorithm (using Jukes-Cantor + CAT models) and the phylogenetic distances were calculated between the obtained ASVs. Followingly, indices of alpha diversity (Observed ASVs – richness, and Shannon) and beta

diversity (Bray-Curtis Dissimilarity) were calculated using the sampling depth that retained the highest amount of ASVs in 100% of the samples. Statistical tests were computed through QIIME2, including the Kruskal-Wallis' test to compare the α-diversity indices between groups, and Permutational Multivariate Analysis of Variance (PERMANOVA) for β-diversity metrics. In addition, the correlation of both alpha and beta indices to the soil's edaphic parameters was calculated.

Microbial Relationships and Structure - The taxonomic composition and structure of the microbiome was assessed with the aid of MicrobiomeAnalyst 2.0 (Lu et al., 2023), using the Marker Data Profiling workflow. With this tool, the taxonomic pattern of the samples was uncovered, followed by the prediction of a core microbiome. The core microbiome for the prokaryotic dataset was calculated at the Family level, while the core of the fungal dataset was calculated at the Species level; for both these cores, only taxa present in 75% of the samples and with a relative abundance higher than 0,01% were considered. To identify differentially abundant taxa in between extreme irrigation treatments, the Analysis of Compositions of Microbiomes with Bias Correction (ANCOM-BC) was applied within each year, between independent groups of soils subjected to no irrigation (NI) and full irrigation (FI); for a better resolution prokaryotic and fungal ASVs were collapsed at genus and species levels, respectively. Afterwards, a Multiple Linear Regression with Covariate Adjustment (MaAsLin2) was calculated comparing the irrigation strategies previously mentioned, using the sampling year as a covariate, and integrating with the ANCOM-BC data.

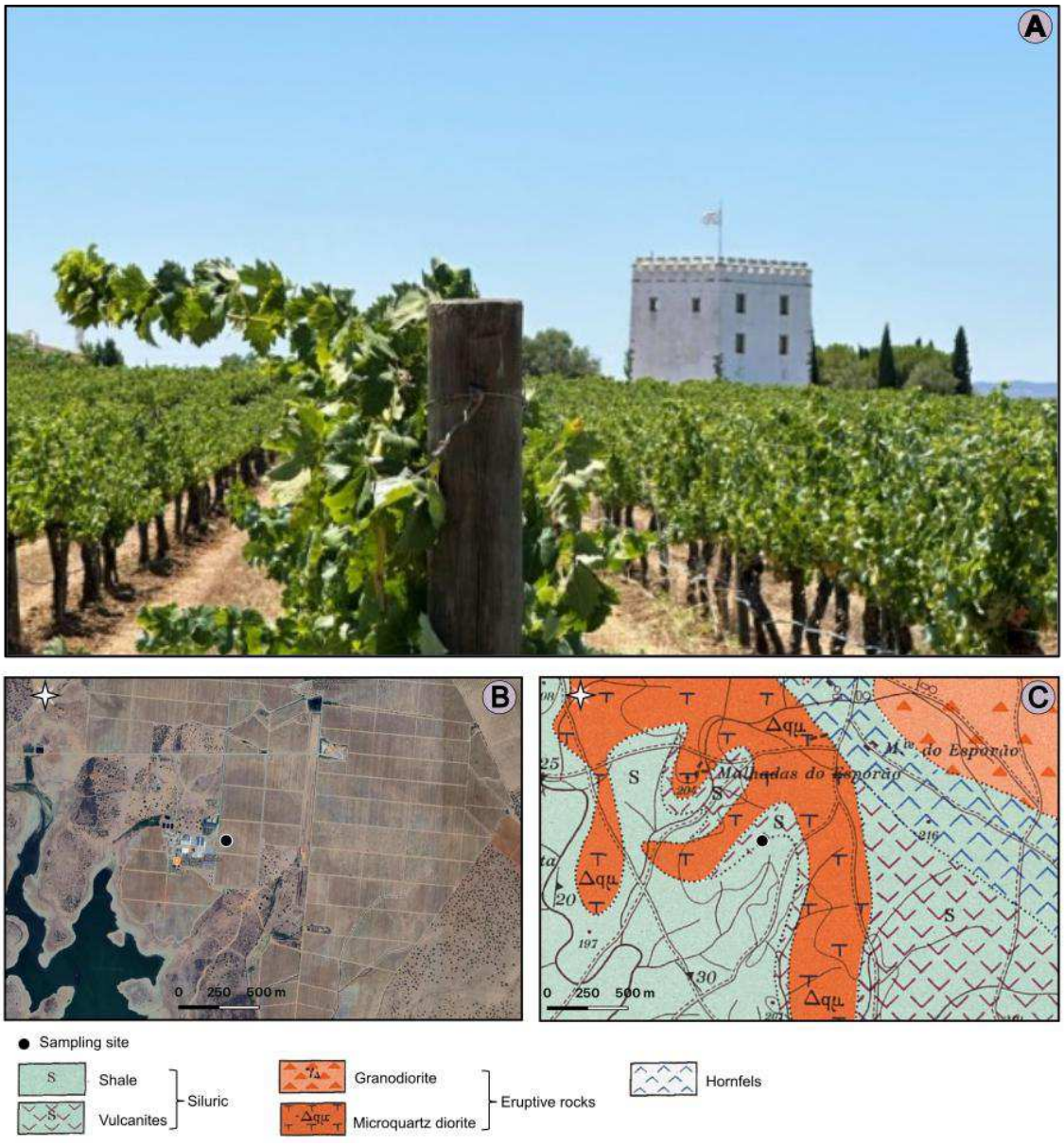
Results

Characterization of Vineyard's Soil and Climate

Climate conditions and irrigation regime are known to affect soil parameters. In this study, we conducted diverse analyses in two consecutive years in a vineyard located in a dryland in Southern Portugal (Figure 1A and 1B). The years 2022 and 2023 were distinct regarding the pattern of precipitation and temperature. While the first year of sampling was characterized by heavy precipitation events in March and April, 2023 was characterized by rain evenly distributed throughout the period of growth, and fruit ripening. In terms of temperature, 2022 was generally

hotter than 2023, except in the months during which heavy precipitation events occurred (Figure S I, Additional File 1). Moreover, 2022 experienced prolonged heatwaves throughout the growing season starting in May, as shown by IPMA data (IPMA, 2025)

The vineyard's soil is classified as a rhodic-luvisol, which formation is typical of weathered basic to intermediate parent material, such as the main rocks that outcrop the study area (vulcanites and microquartz diorite), as shown in Figure 1C. The soil exhibits granulometric characteristics typical of a sandy loam (Figure S II, Additional File 1), with about 50% of sand, proving excellent drainage, good aeration, and moderate water retention capacity, greater than that of sandy soils but lower than that of clay soils. The 2023 samples exhibit a slight increase in sand content compared to the 2022 samples, likely due to differing climatic conditions between those years.



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253 **Figure 1.** View of the vineyard under study in Alentejo (Southern Portugal) from A) the sampling site
254 and its respective B) satellite view and C) geologic context (Carvalhosa, 1967).

255 The assessment of edaphic parameters revealed that the irrigation regimes led to more pronounced
256 differences in terms of soil humidity and pH (Figure 2). These parameters show significant
257 differences among the irrigation strategies adopted in the soils in both years but are consistent
258 within the same strategy across the two years (i.e. 22SN vs 23SN). Dry Bulk Density did not reveal
259 significant differences between water treatments in both years. The differences that this parameter
260 returned were observed in the sampling year ($p < 0.01$, ANOVA), where 2022 showed a higher DBD
261 than 2023 (Figure S IIIA, Additional File 1). In terms of organic matter content, the soils of the first

sampling year showed significant differences among water treatments ($p < 0.01$, ANOVA), but the same did not occur in the next year ($p = 0.12$, ANOVA) (Figure S IIIB, Additional File 1). Finally, the relative soil particle contents as assessed with the grain size distribution showed no significant differences between the irrigation strategy or the sampling year.

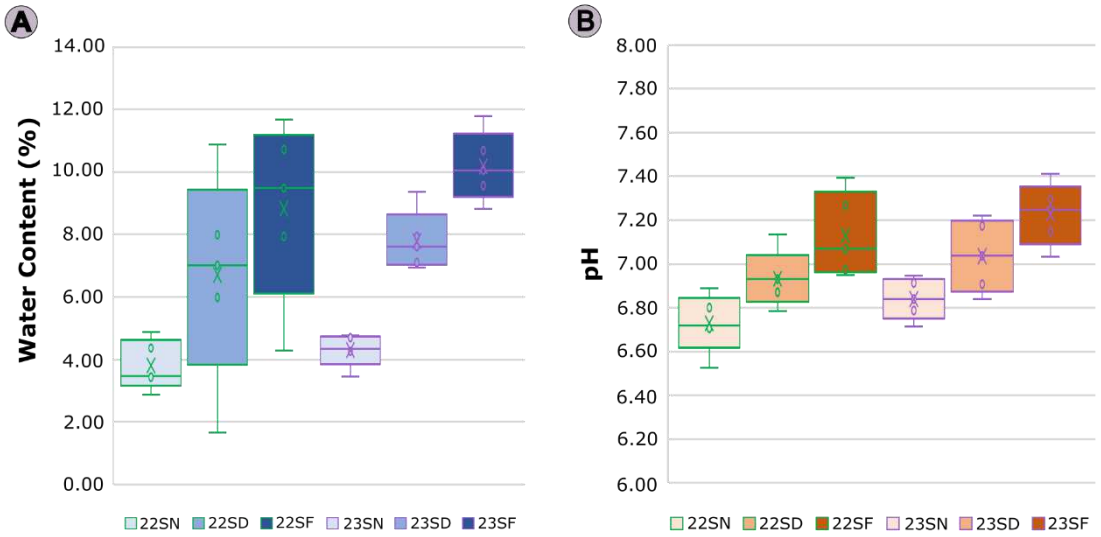

Figure 2. Water content (A) and pH (B) of soils sampled in 2022 and 2023, with lower dispersion of water content in 2023. ANOVA showed statistically significant differences in the soils in function of the irrigation strategy adopted both in terms of water content (2022: $p = 0.03$; 2023: $p < 0.01$) and pH (2022: $p < 0.01$; 2023: $p < 0.01$). 22SN: 2022 Syrah No irrigation (corresponding to Rainfed irrigation), 22SD: 2022 Syrah Deficit irrigation, 22SF: 2022 Syrah Full irrigation, 23SN: 2023 Syrah No irrigation (corresponding to Rainfed irrigation), 23SD: 2023 Syrah Deficit irrigation, 23SF: 2023 Syrah Full irrigation.

Geochemical analyses showed that most soil nutrients were significantly influenced by the irrigation strategy applied, with a more pronounced effect observed in 2022 (Table S I, Additional File 2). Among the metallic oxides that showed significant differences in both sampling years ($p < 0.05$), sodium oxide (Na_2O), potassium oxide (K_2O), and phosphorus pentoxide (P_2O_5) stood out. These oxides showed no significant difference between rainfed and deficit-irrigated soils, but their levels were markedly higher in soils under full irrigation. Their concentration in fully irrigated soils were nearly double those found in rainfed and deficit irrigation conditions (Figures S IVA, S IVB, and S IVC,

Additional File 1). An opposite trend was observed for magnesium oxide (MgO) and calcium oxide (CaO), with the highest concentrations found in rainfed soils and the lowest in fully irrigated soils (Figure S IVD, and S IVE, Additional File 1). However, these differences were only significant in 2022 ($p < 0.05$).

Assessment of Grapevine Water Status

Irrigation strategies affected grapevine physiological performance. Based on diverse physiological parameters, it can be assumed that harsher conditions were experienced in the 2022 season compared to 2023. As shown in Table 1, the most negative Ψ_{pd} value was registered in the non-irrigated grapevines in 2022, indicating the limited soil water availability. Irrigation improved the grapevine's water status in both years, in which Ψ_{pd} showed similar values for the plants under deficit- and full irrigation. This suggests that despite different stress conditions, irrigation in the vineyards alleviated the drought stress in a similar manner. Stomatal conductance (g_s) showed differences in accordance with irrigation treatments applied, particularly in 2023. As for evapotranspiration, the accumulated ETo was similar between years of sample collection, indicating that the total seasonal water need was the same; the key difference lies in the intensity of daily demand, which was higher in 2022, likely due to the high frequency of heatwave occurrences. Taking into account these three different physiological parameters, it appears that the vineyard in 2022 experienced a higher water stress pressure than in 2023.

Table 1. Physiological parameters measured from *V. vinifera* cv. Syrah on the day of soil sample collection at Herdade do Esporão. For the predawn water potential (Ψ_{pd}) and stomatal conductance (g_s), 5 plants from each irrigation strategy were randomly picked for these measurements. The reference evapotranspiration (ETo), both daily and accumulated, refers to the effect of

meteorological conditions on total crop water exportation. NI: No irrigation (corresponding to Rainfed irrigation), DI: Deficit irrigation, FI: Full irrigation.

	2022						2023					
	Ψ_{pd} (MPa)	St. Error	g_s (mol m^{-2} s^{-1})	St. Error	ETo (daily mm)	ETo (accumulated mm)	Ψ_{pd} (MPa)	St. Error	g_s (mol m^{-2} s^{-1})	St. Error	ETo (daily mm)	ETo (accumulated mm)
NI	-0.63	0.07	0.13	0.01			-0.56	0.01	0.05	0.01		
DI	-0.28	0.03	0.22	0.01	5.7	642.1	-0.27	0.02	0.16	0.01	3.9	647.1
FI	-0.08	0.01	0.28	0.01			-0.09	0.07	0.38	0.02		

Attributes of Sequencing Datasets

The total number of raw reads obtained for the 16S rRNA and ITS1 amplicons were 601 765 and 1 038 163, respectively. After quality and abundance filtering, removing unassigned sequences, and retaining only reads classified to prokaryotes and fungi, the number of sequences decreased to 553 401 for the 16S rRNA and 888 447 for the ITS1 datasets. In the prokaryotic set of sequences, a minimum of 13 703 and a maximum of 25 499 reads per sample were found, while the fungi sequences retrieved a minimum of 17 293 and a maximum of 46 007 per sample. The final number of ASVs retained for further analyses was 5164 for the prokaryotes and 1601 for the fungi.

Irrigation Drives Microbial Community and Structure

The prokaryotic and fungal portions of the microbiome showed statistically significant differences for the Shannon Index and Observed Richness when comparing the sampling year ($p < 0.05$, Kruskal-Wallis test – all groups). The same could be found for the type of samples, however, this was mostly due to the effect of the sampling year; in fact, only the mycobiome sampled in 2022 showed statically significant differences for the communities' richness in function of the irrigation strategy employed, highlighting the non-irrigated samples (Table S II, Additional File 2). A curious trend could be observed for both types of microbial communities in the first year of sampling, where the highest diversity was harbored in the non-irrigated soils, while the lowest was found in the fully irrigated soils (Figure 3). The same could not be said for the sampling in 2023, which, although it showed higher

diversity than the 2022 communities, the irrigation regime did not seem to show great differences for the α-diversity measurements assessed.

The distances between the communities calculated with the Bray-Curtis Dissimilarity Index of β-diversity and its corresponding ordination plot revealed the effect of the sampling year within the communities, although more pronounced in the prokaryotic part of the soil microbiome. Nevertheless, for both datasets – prokaryotes and fungi, it could be observed that the samples seemed to organize by the gradient of water supplied in the soils, the communities from non-irrigated and fully-irrigated soils being the most distant from each other, and the communities from deficit-irrigated soils being as an intermediary between them (Figure 4). Corroborating these observations, the results from PERMANOVA revealed a statistical significance ($p < 0.05$) that could be attributed to the sampling year, the type of samples, and the irrigation strategy for both types of communities and both years, with the exception of the prokaryotic community of 2023 that revealed a *p*-value higher than 0.05 (Table S III, Additional File 2).

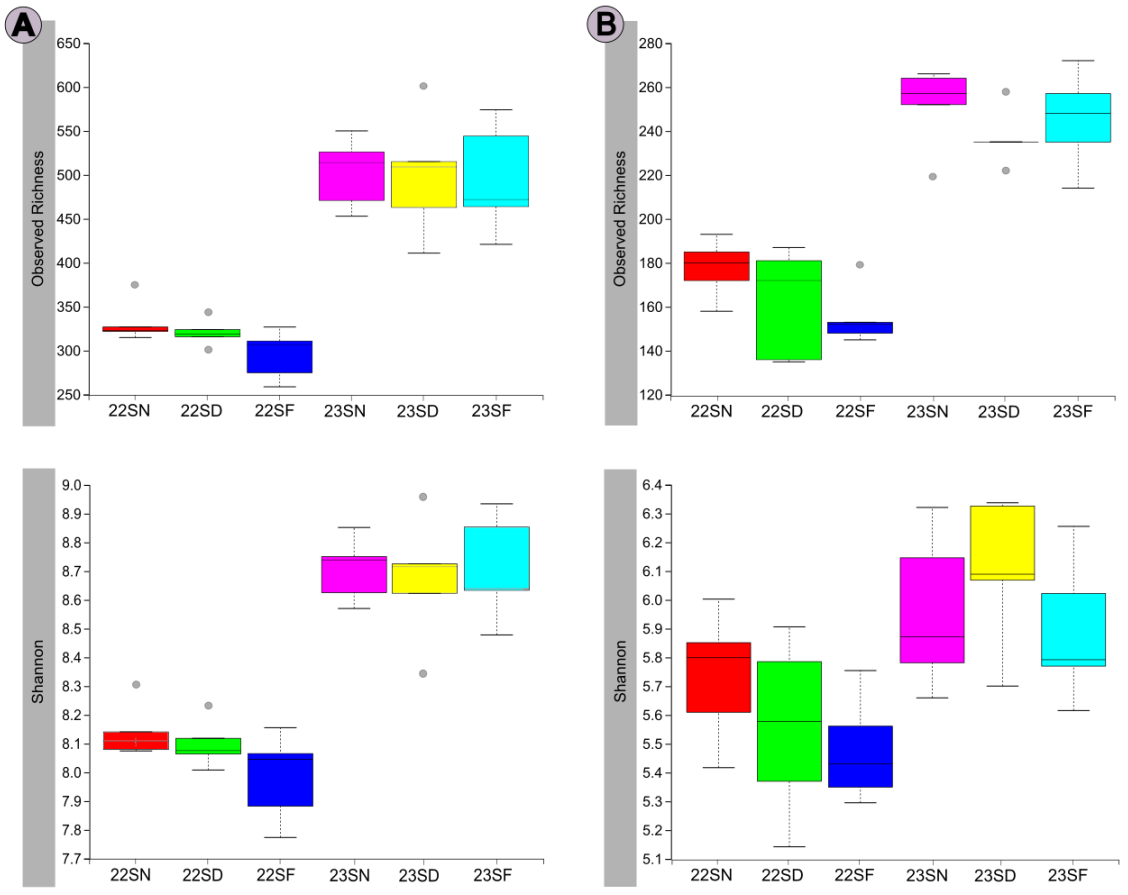

Figure 3. Prokaryotic (A) and fungal (B) α-diversity measurements of richness (top) and diversity (bottom) for the type of sample assessed. For all measurements, significance was found when comparing sampling year ($p < 0.05$). Irrigation strategy didn't show significantly different diversity, with the exception of fungal Observed Richness in 2022 ($p = 0.016$) 22SN: 2022 Syrah No irrigation (corresponding to Rainfed irrigation), 22SD: 2022 Syrah Deficit irrigation, 22SF: 2022 Syrah Full irrigation, 23SN: 2023 Syrah No irrigation (corresponding to Rainfed irrigation), 23SD: 2023 Syrah Deficit irrigation, 23SF: 2023 Syrah Full irrigation.

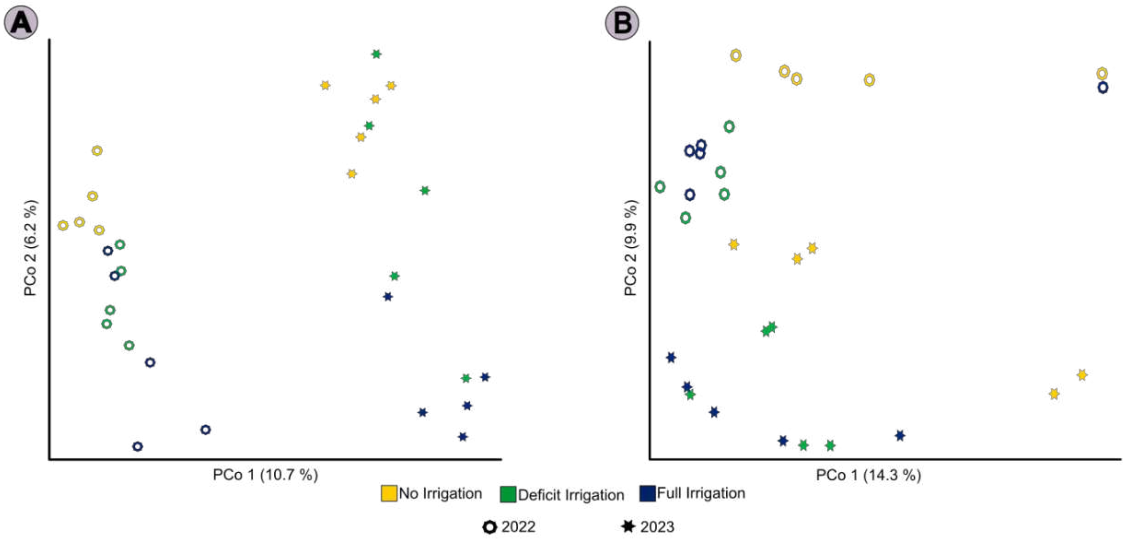

Figure 4. Principal coordinates analyses of the A) prokaryotic and B) fungal communities. Ordination plots were calculated using the Bray-Curtis Dissimilarity Index for each sample type. Beta diversity measurement revealed significant grouping both in terms of sampling year and irrigation strategy ($p < 0.01$), except for prokaryotic community of 2023 ($p = 0.08$).

Composition of Syrah's Soil Microbiome

The grapevines soil microbial communities were highly diverse with over 10 distinct phyla identified in both datasets. The prokaryotic communities were dominated by bacteria belonging to Pseudomonadota, followed by Actinobacteriota, and Acidobacteriota, accounting for around 60% of total sequences between the samples (Figure 5A). As for the top 3 most abundant fungal phyla,

these represented around 90% of the total communities, Basidiomycota being the phylum with highest abundance, Ascomycota and Mortierellomycota coming after (Figure 5B).

The most abundant prokaryotic species belonged to uncultured lineages of bacteria and archaea, and to mitigate these information gaps, it was chosen to analyze the prokaryotic microbiome to the family level. Although the abundance differences between the types of samples were very subtle, it could be seen that the samples collected in 2022 showed a higher relative abundance for the families with the highest number of sequences (Figure S VA, Additional File 1). These families were present among all samples, and, as expected, most of those were estimated to be part of the prokaryotic core microbiota (Figure 6). Between these 12 families, only one belonged to the domain of Archaea, this being *Nitrososphaeraceae*; the family with highest prevalence among samples was *Chitinophagaceae* (Bacteroidota), the following being *Gaiellaceae* (Actinobacteriota), and the third most prevalent being the metagenomically assembled genome UBA 2999, belonging to the order Vicinamibacterales (Acidobacteriota). Curiously, none of these three earlier mentioned bacteria belong to the most abundant prokaryotic phylum in our soil samples, Pseudomonadota. Additionally, a few other ASVs were classified to an uncultured lineage of bacteria presented as a core microbe, this being Env.OPS12 of the order Anaerolinales (Chloroflexota).

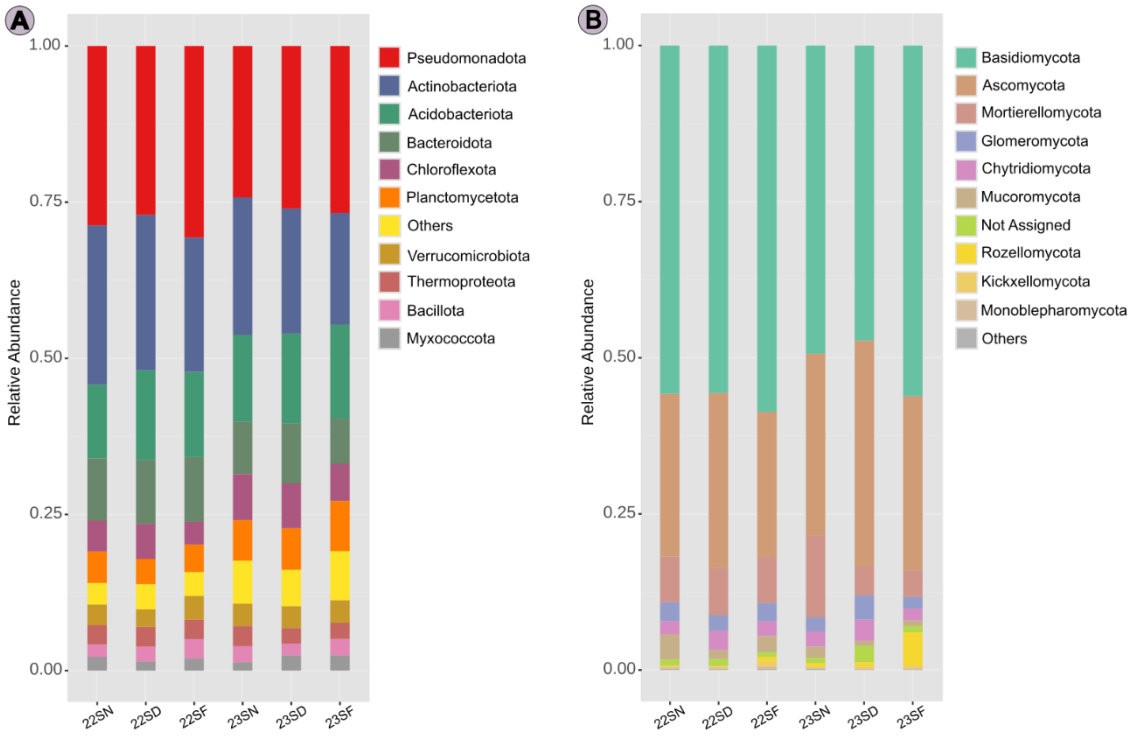

Figure 5. Taxonomic partition of A) prokaryotes and B) fungi found in the soils of the grapevine cv. Syrah put through three different water regimes for two seasons. Microbial composition is shown at phylum level and top 10 most abundant taxa are presented. 'Others' refers to more than one phylum in the datasets (total abundance was lower than the top 10 shown). 'Not Assigned' in the fungal dataset refers to sequences that could only be classified to the kingdom level (Fungi). 22SN: 2022 Syrah No irrigation (corresponding to Rainfed irrigation), 22SD: 2022 Syrah Deficit irrigation, 22SF: 2022 Syrah Full irrigation, 23SN: 2023 Syrah No irrigation (corresponding to Rainfed irrigation), 23SD: 2023 Syrah Deficit irrigation, 23SF: 2023 Syrah Full irrigation.

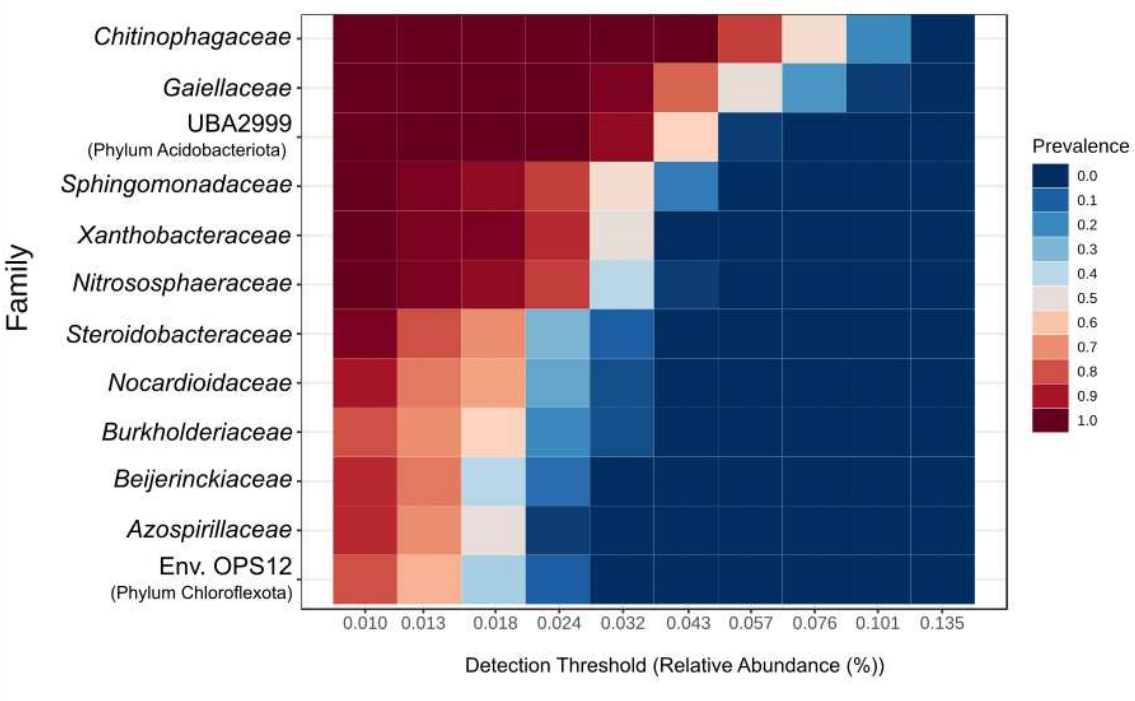

Figure 6.Hypothesized core prokaryotic families prevalent in at least 75% of samples and with relative abundance higher than 0.01% found in the soils of the grapevine cv. Syrah

Contrary to the prokaryotes, the majority of the most abundant fungal species could be classified to this level (Figure S VB, Additional File 1). The most abundant fungal species across all samples was *Solicoccozyma aeria*, where in both years it was observed a slightly higher relative abundance in soil samples that had been supplied water. Most of these fungi were evenly distributed throughtout the irrigation regimes employed in the soil, with a few exceptions; for instance, sequences belonging to *Coprinellus verrucispermus* were only found in soils sampled in 2023, and with a much higher

abundance among the non-irrigated soils. As for the core mycobiome, species from the three most abundant phyla were identified as members of the core, the basidiomycete *S. aeria* found with the highest prevalence, followed by the ascomycete *Hormonema viticola*, and the mortierellomycete *Mortierella alpina* (Figure 7).

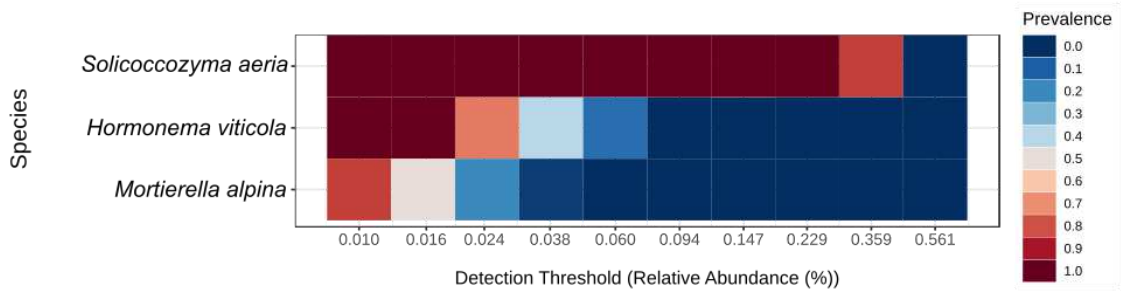

Figure 7. Hypothesized core fungal species prevalent in at least 75% of samples and with relative abundance higher than 0.01% found in the soils of the grapevine cv. Syrah.

Rare Taxa Found between Water Extremes

Diversity analysis revealed the communities from non- and fully irrigated soils to be the most distant from each other in both types of microorganisms, hence, only among these samples were rare taxa scanned for. Both prokaryotes and fungi had more differentially abundant taxa in 2022 than in 2023 as discovered by the ANCOM-BC analyses. These datasets showcased a similar pattern, where in 2022 there was a somewhat even partition of taxa enriched between the irrigation strategies tested. In 2023 the bacteria only seemed to be enriched in the fully irrigated soils, and the fungi mostly in the non-irrigated soils (Table S IV, Additional File 2).

In the first year of sampling, bacteria belonging to the genus *Actinoallomurus* showed the highest enrichment among soils under no irrigation (q = 1.16E-3), followed by the non-cultivated genus FEB-22 from the family *Xanthobacteraceae* (q = 1.06E-3), and *Rhizorhabdus* (q = 2.77E-3). Under full irrigation, the taxa enriched were mostly uncultivated genera, the most significant being SCUD01 from the family *Steroidobacteraceae* (q = 8.19E-205). Interestingly, this same taxon was also shown to be enriched in 2023 under soils put through full irrigation, although with a much higher false

discovery rate than in the previous year (q = 1.13E-3). The remaining enriched prokaryotic genera were also found only between fully irrigated soils.

Among the fungi differentially abundant in 2022, *Penicillium canescens* (q = 0), *Phialophora* sp. (q = 1.36E-12), and *Penicillago nodositata* (q = 7.84E-5), were the taxa with the highest enrichment between non-irrigated soils. In the soils with 100% ETc, the fungi enriched belonged to *Mortierella* sp. (q = 7.80E-67), followed by *Gongronella brasiliensis* (q = 2.49E-2), and an unclassified genus from the family *Herpotrichiellaceae* (q = 1.92E-30). In the next year of sampling, only one taxa was enriched among the fully irrigated soils, this being *Bovista plumbea* (q = 3.66E-102). The soils with no water supplied to them observed the enrichment of six taxa, *Vishniacozyma globispora* (q = 2.00E-4), *Ascotricha erinacea* (q = 2.15E-2), and *Filobasidium oeirense* (q = 2.32E-4), being the ones with the highest Log fold-change. Contrary to the prokaryotes, no fungal taxa were conserved between years with a statistical significance.

Most taxa discovered with MaAsLin2, could also be found in the ANCOM-BC results (Table S V, Additional File 2). In total, the prokaryotes observed eight enriched taxa in which only three did not require an adjustment for their significance, these being SCUD01, PALSA_1355, and *Noviherbaspirillum*. From the seven enriched fungal taxa, only two were not adjusted for their significance, these being *Mortierella* sp. and *P. canescens*.

Additionally, the correlation of the microbiota to the irrigation strategy was calculated with the Pearson distance for each year of sampling (Figure S VI, Additional File 1). However, only in 2022 was it found to be a significant correlation and only to prokaryotes, these being the metagenomically assembled genera SCUD01(q = 0.03), WYBL01(q = 0.03), and QUBU01(q = 0.03) to the fully irrigated soils, and *Noviherbaspirillum* (q = 0.05) to the samples that went through no irrigation.

Discussion

Climate and irrigation regime influence grapevine physiology and soil parameters

The summer of 2022 has been reported as one of the hottest and dryest seasons in Europe in a long time (Toreti et al., 2022) and for Portugal it was the third dryest summer since 1931, leading to great losses in agricultural production (Governo da República Portuguesa, 2022). This comes in line with the data obtained between January 1st and June 30th in 2022 and 2023 for the Reguengos de Monsaraz area (Figure S I, Additional File 1), where most of the rain observed in 2022 was attributed to an abnormal event between March and April. Extreme precipitation like this increases soil erosion, leading to reduced water infiltration, which may affect water availability (Eekhout et al., 2018). Additionally, the high frequency and prolonged heatwaves in 2022 may increase soil evaporation and plant transpiration contributing to exacerbated water deficit. As expected, these climate conditions were reflected in the physiological parameters. The leaf water potential at predawn being a reliable indicator of drought exposure and soil water potential (Da Sois et al., 2024), revealed the higher hydric pressure felt by the grapevines under non-irrigated conditions in 2022. It should be noted that the Syrah cultivar, generally classified as drought-sensitive, anisohydric cultivar (Hochberg et al., 2013; Schultz, 2003; Tramontini et al., 2014) has recently been shown to tightly regulate stomatal opening under water stress in the Alentejo region. This response is likely the result of plastic adaptation to local conditions, associated with a high [ABA]/[IAA] ratio under water deficit, which enhances hydraulic control and reduces water loss through transpiration (Damásio et al., 2025).

On the other hand, both leaf water potential and stomatal conductance align with the irrigation regime applied, confirming its impact on grapevine physiological responses. Interestingly, annual differences in g_s values were detected in NI and DI, with lower g_s in 2023 compared to 2022, while no year-to-year differences were found in water potential. This suggests a possible decoupling between stomatal aperture and plant water status, likely driven by the high sensitivity of stressed grapevines to elevated vapor pressure deficit during 2023. These findings corroborate previous reports indicating that grapevine stomata are relatively insensitive to vapor pressure deficit under well-watered conditions (Charrier et al., 2018; Dayer et al., 2020; Rogiers et al., 2012) but become highly responsive when subjected to water stress.

Regarding soil water content and pH, the season seemed to have a lesser profound effect than the irrigation strategy in these parameters. Nevertheless, the dry bulk density indicated that more

compact soils were sampled in 2022 (Figure S IIIA, Additional File 1); this parameter is directly linked to soil compaction and permeability, with an increase of this density, the soil water retention decreases (Indoria et al., 2020).

Microbial dynamics is altered more significantly by climate than by irrigation regime

Climate and irrigation strategy are known to impact ecotype-like microbial assemblies. Statistically significant differences were found between the communities α- (Table S II, Additional File 2) and β-diversity (Table S III, Additional File 2) regarding the year the soils were sampled. The same could not be found when comparing the α-diversity of the year specific irrigation strategy communities (except for the fungal microbiome sampled in 2022). Nevertheless, communities under the same irrigation strategy revealed significance when comparing its β-diversity, except for the prokaryotic communities sampled in 2023.

The extent of differences found in the microbial communities is dependent on the scale we are looking at. It is true that most prokaryotic and fungal microbiomes seemed to be highly conserved at higher levels of classification, not only between irrigation strategies adopted but also between years of sample collection (Figure 5). This may be due to the influence of the plant's genotype on the assemblage of the microbial communities (Marasco et al., 2018) but also due to the impact of recurrent long-term drought events. Ecological memory developed over six years of water stress could be attributed to these homogenizing assemblies (Canarini et al., 2021). Soil microbial communities seem to have a higher degree of homogenization under drought stress (Swift et al., 2024; Ullah et al., 2019).

The compositional differences in the microbiomes start becoming evident at lower levels of classification (Figure SIII, Additional File 1), in which rare and differentially abundant taxa create the distinction between the irrigation strategies. Despite the higher diversity found in the soils sampled in 2023 (Figure 3), it was in 2022 that the highest amount of differentially enriched taxa was found (Table S IV, Additional File 2). This microbiota may eventually make part of a functional microbiome that mitigates the effects of drought Besides this, rare taxa may help bridge the functional gaps found

494 in the core microbiome, even though this assembly is thought to be a highly host-specialized
495 selection of microbial life (Darriaut et al., 2022a; Kaminsky et al., 2021; Wang et al., 2023).

496

497 Prokaryotic microbiota exhibits resilience under water stress and putative growth promoting
498 properties

499 Soil-borne prokaryotes have been shown to display a high degree of resilience towards drought
500 stress in forest management, agricultural systems, and greenhouse experiments (Bastida et al.,
501 2017; Kost et al., 2024; Zhang et al., 2019). This goes in line with data obtained here for the
502 prokaryotic microbiome, where its intraspecific diversity did not change in function of the soil water
503 content (Table S II, Additional File 2). In terms of composition, the higher relative abundance of the
504 prokaryotic phyla Pseudomonadota, Actinobacteriota, and Acidobacteriota goes in agreement with
505 what was previously recorded from grapevine soil bacterial communities (Berlanas et al., 2019;
506 Marasco et al., 2018, 2022; Zarraonaindia et al., 2015).

507 Among the core prokaryotic families, the one with the highest prevalence, the Bacteroidota
508 *Chitinophagaceae*, has been shown to be part of the wood microbiome of healthy grapevines as
509 opposed to plants afflicted with esca disease (Bruez et al., 2020). In fact, not only most members of
510 this bacterial family present chitinolytic properties (Kämpfer, 2011), but also its capability of fungal
511 disease suppression at plant root-level has been highlighted (Carrión et al., 2019). Additionally, this
512 clade has been strongly linked to priming the rhizosphere (Cui et al., 2023), likely due to its high
513 organic matter degradation power, increasing soil mineralization, and in turn promoting plant-
514 growth (Jia et al., 2024). And although there have been many reports of the presence of this bacterial
515 family in agroecosystems, it is the first time that it is described at this high relative abundance to the
516 best of our knowledge.

517 The second most prevalent family was the actinobacteria *Gaiellaceae*. Although very little is known
518 about this taxon, its presence is often verified in viticultural soils across the globe (Gamalero et al.,
519 2020; Gupta et al., 2019; Novello et al., 2017), but also observed in enrichment in other plant-
520 associated soils (Bañeras et al., 2022; Reis et al., 2019). Bacteria from this family have also been

linked to the soil's available phosphorus content and phosphatase activity (W. Wang et al., 2022), as well as the ratio of soil C:N (Hermans et al., 2017). Even though poorly understood, the ubiquitous presence of this actinobacteria and its strong correlation to several soil nutrient mechanisms make it a good candidate for further exploration in relation to its plant-growth promoting properties.

Recently, a few prokaryotic families presented in our core were found in higher relative abundance in soils under drought than in control conditions, namely *Gaiellaceae*, *Steroidobacteraceae*, *Xanthobacteraceae*, *Beijerinckiaceae* and *Nitrosospheraceae* (Goemann et al., 2024). Interestingly, most of these have been linked to plant-growth promotion. For instance, the archaeal family *Nitrosospheraceae*, besides being constantly reported in vineyard soils (Gobbi et al., 2022), is a group of ammonia-oxidizing archaea that have been strongly correlated to agricultural practices (Naylor et al., 2023; Zhalnina et al., 2013), displaying its role in the soil's nitrogen cycling. *Beijerinckiaceae* and *Xanthobacteraceae* families are also frequently related to their ability to increase nitrogen availability in the soil (Bullergahn et al., 2024), this last one also being involved in other plant-growth promotion mechanisms like phosphate solubilization and auxin synthesis (Sánchez-Yañez, 2022). Metagenomically assembled genomes of *Steroidobacteraceae* seem to present all the genes encoding for the nitrogen cycle in its genome (Richy et al., 2024); on the other hand, there are only two validly published genera within this family, *Steroidobacter*, commonly isolated from rhizosphere soils (Huang et al., 2019; Huang et al., 2021) and first described by its steroid degradation properties (Fahrbach et al., 2008), and *Povalibacter*, a bacterium first isolated from grape berries (Nogi et al., 2014). Taking this into account, it is possible that this family may be involved not only in plant growth promotion, but also in biocontrol by steroid hydrolysis, such as ergosterol, the main steroid in fungal membranes (Rodrigues, 2018).

Regarding rare bacteria, *Actinoallomurus,* that was enriched in non-irrigated soils in 2022, has not only been seen to be enriched under drought conditions (Li et al., 2021), but also to be part of the core soil microbiome of drought-tolerant plant species (Legeay et al., 2024). Other bacteria enriched in these conditions, like *Noviherbaspirillum* and *Rhizorhabdus* have been isolated from agricultural soils (Francis et al., 2014; Ishii et al., 2017), this last one even showing biodegradation properties of soil contaminants (Aulestia et al., 2022; Yao et al., 2016). The remaining bacteria enriched under the

549 non-irrigated soils of 2022 were classified as FEB-22 from the family *Xanthobacteraceae*, and that
550 has only been identified once copulated to the anaerobic oxidation of methane (Cai et al., 2018), and
551 WS-7 belonging to the phylum *Candidatus* Eisenbacteriota, which have recently shown to possess
552 biosynthetic gene clusters encoding for compounds with antimicrobial activity that could be
553 compared to those of Actinobacteriota, known for their high biosynthetic capacity (Chen et al.,
554 2020). From the fully irrigated soils the abundance of SCUD001 in both years of sample collection is
555 highlighted. This uncultured genus is present in highly water saturated soil environments (Mosley et
556 al., 2022; Tian et al., 2020); it is also known that it belongs to the family *Steroidobacteraceae*, being
557 very likely that it performs similar activities as discussed previously. Additionally, another rare
558 bacterium found in fully irrigated soils (but only in 2022) was *Nitrospira*, known for its ability to
559 complete nitrification (Daims et al., 2015) and high sensitivity to drought conditions (Hafeez et al.,
560 2023; Séneca et al., 2020).

561 In conclusion, the soil prokaryotic microbiota harbored by the drought tolerant cultivar Syrah seem
562 to be highly static in terms of composition and may be already adapted to the *terroir* while eventually
563 providing aid to the host through biofertilization, biocontrol, among other processes.

564 Mycobiome seems to present lower ecological memory than prokaryotic microbiota

565 Contrary to the prokaryotic microbiota, the fungi seemed to present a more pronounced drought-
566 related effect as revealed by its community α- and β-diversity (Table S II and Table S III, Additional
567 File 2). In fact, this is not the first account of different irrigation regimes, water limitation, or drought
568 inducing a more noticeable response in fungi than in prokaryotes (Hopkins et al., 2018; Kost et al.,
569 2024; Lozano et al., 2021) And as for the prokaryotes, this effect had a higher impact in 2022.
570 However, this higher sensitivity should not be mistaken with higher susceptibility to drought, since
571 these organisms showcase a great plasticity to very diverse environmental conditions (Fierer, 2017).
572 Nonetheless, it has been shown previously that the combination of abiotic stressors, namely
573 drought and heat, had a stronger effect on the fungal community's diversity and structure than the
574 stressors alone (de Oliveira et al., 2020), which seems to be the case for the 2022 season.

Regarding community composition, our results come in a slight contradiction to what has been recorded before for the fungal soil microbiome harbored by the grapevine. As seen in Figure 5B, the most abundant fungal phyla in our soils were Basidiomycota, followed by Ascomycota and Mortierellomycota. However, in literature, ascomycetes tend to show a much higher abundance than basidiomycetes (Berlanas et al., 2019; Remenyik et al., 2024; Teixeira et al., 2024). This high abundance of Basidiomycota could be attributed to the high number of reads recovered from the soil yeast *Solicoccozyma aeria*, which showed to be the most abundant fungal species in both years of sampling and irrigation regimes (Figure S IIIB, Additional File 1), accounting for almost 50% of total relative abundance in soils that had been irrigated, and close to 40% in soils that had not. This fungus seems to have a global distribution in vineyard soils, generally being the dominant fungal genus when present (Gobbi et al., 2022). Still, not only was this trend not observed for other Portuguese *terroirs*, but the relative abundance for this basidiomycete seemed to be higher in the soils here analyzed than what was described by Gobbi and co-workers (2022). Recently it was shown that the inoculation of plants with *S. aeria* resulted in increased biomass and root lateralization, as well as the modulation of auxin ethylene phytohormonal metabolism (Carvajal et al., 2024). It was also shown that *Solicoccozyma* favors long-term monoculture soils (Wolińska et al., 2022) as in Herdade do Esporão.

The second most prevalent taxon in our fungal core was the ascomycete *Hormonema viticola*, which was the most abundant fungi present in plants affected with grapevine trunk disease (GTD) in Alentejo (Billar de Almeida et al., 2020). Nonetheless, the recent reclassification of this fungus into *Dothiora viticola* (Crous et al., 2022) raises questions about its role in association with its host. Most of the species from *Dothiora* are saprobes, found in decaying parts of woody host plants (Senwanna et al., 2024), and pathogenicity is only hypothesized on already stressed plant tissues (Crous & Groenewald, 2017). Although not present in the fungal core, there were other highly abundant fungal taxa (Figure S IIIB, Additional File 1) that have been reported to take part in the GTD-complex, like *Truncatella angustata* (Arzanlou et al., 2013).

At last, the remaining taxon in our core mycobiome was attributed to *Mortierella alpina*. This mortierellomycete has been traditionally used for the industrial production of arachidonic acid

(Chang et al., 2021); in turn, this lipid with high biotechnological interest has been shown to be an elicitor of plant defense response against phytopathogens (Dedyukhina et al., 2014). Additionally, *M. alpina* has been shown to be a great biocontrol agent, increasing plant biomass and mitigating the effects of phytopathogens (Nouri et al., 2024). Moreover, this *Mortierella* species has also been shown to be enriched in drought-tolerant wheat cultivars, not only contributing to the plant's drought resistance, but also enhancing stress response in drought-susceptible cultivars (Yue et al., 2024).

Between absent and complete irrigation, the soils sampled in 2022 observed a more even distribution of differentially abundant taxa than in 2023, which only observed the agaricomycete *Bovista plumbea* in fully irrigated soils (Table S IV, Additional File 2). The soils under full irrigation in 2022 observed the enrichment of six species, however only *Mortierella capitata* seems to display plant-growth promotion properties, increasing the diversity of the rhizosphere microbiota and leading to increased crop biomass (Li et al., 2020). The remaining taxa seem to be pathogenic (Bruez et al., 2016; Lombard et al., 2016; Meza et al., 2024). As for the rare taxa under no irrigation, more functionality could be attributed to them; for instance, many microbes that have shown biocontrol potential against grey mold and other phytopathogens were enriched under these conditions like *Penicillium canescens* (Pazooki et al., 2024) in 2022, and *Filobasidium oeirense* (Reyes-Bravo et al., 2022), *Vishniacozyma* (Lutz et al., 2013; Nian et al., 2023), and the well-known mycoparasite *Clonostachys rosea* (Funck Jensen et al., 2021) in 2023. In the first year of sampling, it was also observed the enrichment of *Penicillago nodositata*, a fungus that has been described as an enhancer of root nodulation, hence increased nutrient exchange, triggered by low nutrient conditions (Mohd-Radzman & Drapek, 2023). Some pathogens were also found differentially abundant under non-irrigated soils, namely *Phialophora* sp. (Ferreira et al., 1999; Meza et al., 2024) in 2022, and *Dactylonectria macrodidyma,* a causal agent of black foot disease in grapevines (Probst et al., 2019), in 2023.

In summary, fungal microbiota presented a higher sensitivity to environmental conditions than its prokaryotic counterparts but a wider array of putative functionalities were identified ranging from pathogenicity and biofertilization to biocontrol. Only in the mycobiome were identified

630 microorganisms with known biostimulant properties (since the biostimulant prokaryotes could only
631 be classified to the family level), namely *S. aeria*.

632

633 **Conclusions and Perspectives**

634 Soil characteristics, plant physiological parameters, and microbiome composition were affected to
635 some extent differentially by the climate/season and irrigation regimes. Interestingly, ecological
636 memory of prokaryotes seems to be higher than fungi under prolonged drought, but our mycobiome
637 revealed a composition that had never been reported before in other studies of grapevine associated
638 soil microbiome, with basidiomycetes showcasing higher relative abundance than ascomycetes.
639 This abundance could be attributed to the most present fungal taxa across all conditions,
640 *Solicoccozyma aeria*. As for the prokaryotes, the bacterial family *Chitinophagaceae* revealed
641 abundances that had not been described in other soil studies up to date. This highlights the
642 specificities of *terroir* associated microbiomes under drought stress where the plant genotype is
643 known to play a role. Syrah's microbiota showed not only high taxa redundancy, but also putative
644 growth promoting properties that may be directly linked to drought mitigation and increased
645 pathogen resilience. This may be involved in the higher plastic adaptation of Syrah in Alentejo. The
646 undergoing cultivation of this microbiota and the consequent application of these microorganisms
647 *in vivo* may provide further insights regarding the involvement of the microbiome in grapevine
648 plasticity under stress aiming at achieving more sustainable agricultural practices.

649

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Data availability

The datasets generated during the current study are available in the European Nucleotide Archive (ENA) repository, under the Project ID PRJEB90149 (https://www.ebi.ac.uk/ena/browser/view/PRJEB90149).

References

Abarenkov, K., Zirk, A., Piirmann, T., Pöhönen, R., Ivanov, F., Nilsson, R. H., & Kõljalg, U. (2022). *UNITE QIIME release for eukaryotes*. UNITE Community. https://doi.org/https://dx.doi.org/10.15156/BIO/1264819

Arzanlou, M., Narmani, A., Moshari, S., Khodaei, S., & Babai-Ahari, A. (2013). *Truncatella angustata* associated with grapevine trunk disease in northern Iran. *Archives Of Phytopathology And Plant Protection*, **46**(10), 1168–1181. https://doi.org/10.1080/03235408.2012.761417

Aulestia, M., Flores, A., Acosta-Jurado, S., Santero, E., & Camacho, E. M. (2022). Genetic Characterization of the Ibuprofen-Degradative Pathway of *Rhizorhabdus wittichii* MPO218. *Applied and Environmental Microbiology*, **88**(11). https://doi.org/10.1128/aem.00388-22

Azorín, P. R., & García, J. G. (2020). The productive, economic, and social efficiency of vineyards using combined drought-tolerant rootstocks and efficient lowwater volume deficit irrigation techniques under mediterranean semiarid conditions. *Sustainability (Switzerland)*, **12**(5). https://doi.org/10.3390/su12051930

Bañeras, L., Llorens, L., Díaz-Guerra, L., Gispert, M., Hernández-del Amo, E., Massart, S., & Verdaguer, D. (2022). Resilience of microbial communities in Mediterranean soil after induced drought and

manipulated *UV* radiation. *European Journal of Soil Science*, **73**(1). https://doi.org/10.1111/ejss.13218

Bastida, F., Torres, I. F., Andrés-Abellán, M., Baldrian, P., López-Mondéjar, R., Větrovský, T., Richnow, H. H., Starke, R., Ondoño, S., García, C., López-Serrano, F. R., & Jehmlich, N. (2017). Differential sensitivity of total and active soil microbial communities to drought and forest management. *Global Change Biology*, **23**(10), 4185–4203. https://doi.org/10.1111/gcb.13790

Berlanas, C., Berbegal, M., Elena, G., Laidani, M., Cibriain, J. F., Sagües, A., & Gramaje, D. (2019). The Fungal and Bacterial Rhizosphere Microbiome Associated With Grapevine Rootstock Genotypes in Mature and Young Vineyards. *Frontiers in Microbiology*, **10**. https://doi.org/10.3389/fmicb.2019.01142

Bettenfeld, P., Cadena i Canals, J., Jacquens, L., Fernandez, O., Fontaine, F., van Schaik, E., Courty, P. E., & Trouvelot, S. (2022). The microbiota of the grapevine holobiont: A key component of plant health. *Journal of Advanced Research*, **40**,1–15. https://doi.org/10.1016/j.jare.2021.12.008

Bollar de Almeida, A., Concas, J., Campos, M. D., Materatski, P., Varanda, C., Patanita, M., Murolo, S., Romanazzi, G., & Félix, M. do R. (2020). Endophytic Fungi as Potential Biological Control Agents against Grapevine Trunk Diseases in Alentejo Region. *Biology*, **9**(12), 420. https://doi.org/10.3390/biology9120420

Bokulich, N. A., Subramanian, S., Faith, J. J., Gevers, D., Gordon, J. I., Knight, R., Mills, D. A., & Caporaso, J. G. (2013). Quality-filtering vastly improves diversity estimates from Illumina amplicon sequencing. *Nature Methods*, **10**(1), 57–59. https://doi.org/10.1038/nmeth.2276

Bolyen, E., Rideout, J. R., Dillon, M. R., Bokulich, N. A., Abnet, C. C., Al-Ghalith, G. A., Alexander, H., Alm, E. J., Arumugam, M., Asnicar, F., Bai, Y., Bisanz, J. E., Bittinger, K., Brejnrod, A., Brislawn, C. J., Brown, C. T., Callahan, B. J., Caraballo-Rodríguez, A. M., Chase, J., … Caporaso, J. G. (2019). Reproducible, interactive, scalable and extensible microbiome data science using QIIME 2. *Nature Biotechnology*, **37**(8), 852–857. https://doi.org/10.1038/s41587-019-0209-9

Bruez, E., Baumgartner, K., Bastien, S., Travadon, R., Guérin-Dubrana, L., & Rey, P. (2016). Various fungal communities colonise the functional wood tissues of old grapevines externally free from grapevine trunk disease symptoms. *Australian Journal of Grape and Wine Research*, **22**(2), 288–295. https://doi.org/10.1111/ajgw.12209

Bruez, E., Vallance, J., Gautier, A., Laval, V., Compant, S., Maurer, W., Sessitsch, A., Lebrun, M., & Rey, P. (2020). Major changes in grapevine wood microbiota are associated with the onset of esca, a devastating trunk disease. *Environmental Microbiology*, **22**(12), 5189–5206. https://doi.org/10.1111/1462-2920.15180

Bullergahn, V. B., Menezes, K. M. S., Veloso, T. G. R., da Luz, J. M. R., Castanheira, L. F., Pereira, L. L., & da Silva, M. de C. S. (2024). Diversity of potential nitrogen-fixing bacteria from rhizosphere of the *Coffea arabica* L. and *Coffea canephora* L. *3 Biotech*, **14**(1), 27. https://doi.org/10.1007/s13205-023-03875-7

Cai, C., Leu, A. O., Xie, G.-J., Guo, J., Feng, Y., Zhao, J.-X., Tyson, G. W., Yuan, Z., & Hu, S. (2018). A methanotrophic archaeon couples anaerobic oxidation of methane to Fe(III) reduction. *The ISME Journal*, **12**(8), 1929–1939. https://doi.org/10.1038/s41396-018-0109-x

Canarini, A., Schmidt, H., Fuchslueger, L., Martin, V., Herbold, C. W., Zezula, D., Gündler, P., Hasibeder, R., Jecmenica, M., Bahn, M., & Richter, A. (2021). Ecological memory of recurrent drought modifies soil processes via changes in soil microbial community. *Nature Communications*, **12**(1), 5308. https://doi.org/10.1038/s41467-021-25675-4

Carrión, V. J., Perez-Jaramillo, J., Cordovez, V., Tracanna, V., de Hollander, M., Ruiz-Buck, D., Mendes, L. W., van Ijcken, W. F. J., Gomez-Exposito, R., Elsayed, S. S., Mohanraju, P., Arifah, A., van der Oost, J., Paulson, J. N., Mendes, R., van Wezel, G. P., Medema, M. H., & Raaijmakers, J. M. (2019). Pathogen-induced activation of disease-suppressive functions in the endophytic root microbiome. *Science*, **366**(6465), 606–612. https://doi.org/10.1126/science.aaw9285

Carvajal, M., Godoy, L., Gebauer, M., Catrileo, D., & Albornoz, F. (2024). Screening for indole-3-acetic acid synthesis and 1-aminocyclopropane-carboxylate deaminase activity in soil yeasts from Chile

733 uncovers *Solicoccozyma aeria* as an effective plant growth promoter. *Plant and Soil*, **496**(1–2), 83–
734 93. https://doi.org/10.1007/s11104-023-05906-x

735 Carvalhosa, A.B. (1967). Carta Geológica de Portugal, à escala 1:50 000, Folha 40D Portel. Serviços
736 Geológicos de Portugal. Direção Geral de Minas e Serviços Geológicos, Lisboa.
737 https://geoportal.lneg.pt/download/maps/50k/news/40-D.pdf

738 Chang, L., Chen, H., Tang, X., Zhao, J., Zhang, H., Chen, Y. Q., & Chen, W. (2021). Advances in improving
739 the biotechnological application of oleaginous fungus *Mortierella alpina*. *Applied Microbiology and*
740 *Biotechnology*, **105**(16–17), 6275–6289. https://doi.org/10.1007/s00253-021-11480-y

741 Charrier, G., Delzon, S., Domec, J. C., Zhang, L., Delmas, C. E. L., Merlin, I., Corso, D., Barrios-Masias, F.
742 H., Ojeda, H., Ollat, N., & Gambetta, G. A. (2018). Drought will not leave your glass empty: low risk
743 of hydraulic failure revealed by long-term drought observations in world's top wine regions. *Science*
744 *Advances*, **4**(1). https://doi.org/10.1126/sciadv.aao6969

745 Chen, R., Wong, H. L., Kindler, G. S., MacLeod, F. I., Benaud, N., Ferrari, B. C., & Burns, B. P. (2020).
746 Discovery of an Abundance of Biosynthetic Gene Clusters in Shark Bay Microbial Mats. *Frontiers in*
747 *Microbiology*, **11**. https://doi.org/10.3389/fmicb.2020.01950

748 Cherni, M., Ferjani, R., Mapelli, F., Boudabous, A., Borin, S., & Ouzari, H.-I. (2019). Soil parameters drive
749 the diversity of *Citrus sinensis* rhizosphere microbiota which exhibits a potential in plant drought
750 stress alleviation. *Applied Soil Ecology*, **135**, 182–193. https://doi.org/10.1016/j.apsoil.2018.12.006

751 Costa, J. M., Vaz, M., Escalona, J., Egipto, R., Lopes, C., Medrano, H., & Chaves, M. M. (2016). Modern
752 viticulture in southern Europe: Vulnerabilities and strategies for adaptation to water scarcity.
753 *Agricultural Water Management*, **164**(1), 5–18. https://doi.org/10.1016/j.agwat.2015.08.021

754 Crous, P. W., Begoude, B. A. D., Boers, J., Braun, U., Declercq, B., Dijksterhuis, J., Elliott, T. F., Garay-
755 Rodriguez, G. A., Jurjević, Ž., Kruse, J., Linde, C. C., Loyd, A., Mound, L., Osieck, E. R., Rivera-Vargas,
756 L. I., Quimbita, A. M., Rodas, C. A., Roux, J., Schumacher, R. K., … Groenewald, J. Z. (2022). New and
757 Interesting Fungi. *Fungal Systematics and Evolution*, **10**(1), 19–90.
758 https://doi.org/10.3114/fuse.2022.10.02

759 59 Crous, P. W., & Groenewald, J. Z. (2017). The Genera of Fungi — G 4: *Camarosporium* and *Dothiora*. *IMA*
760 *Fungus*, **8**(1), 131–152. https://doi.org/10.5598/imafungus.2017.08.01.10

761 61 Cui, H., Chen, P., He, C., Jiang, Z., Lan, R., & Yang, J. (2023). Soil microbial community structure dynamics
762 shape the rhizosphere priming effect patterns in the paddy soil. *Science of The Total Environment*,
763 **857**, 159459. https://doi.org/10.1016/j.scitotenv.2022.159459

764 64 de la Sois, L., Mencuccini, M., Castells, E., Sanchez-Martinez, P., & Martínez-Vilalta, J. (2024). How are
765 physiological responses to drought modulated by water relations and leaf economics' traits in
766 woody plants? *Agricultural Water Management*, **291**, 108613.
767 https://doi.org/10.1016/j.agwat.2023.108613

768 68 Daims, H., Lebedeva, E. V., Pjevac, P., Han, P., Herbold, C., Albertsen, M., Jehmlich, N., Palatinszky, M.,
769 Vierheilig, J., Bulaev, A., Kirkegaard, R. H., von Bergen, M., Rattei, T., Bendinger, B., Nielsen, P. H., &
770 Wagner, M. (2015). Complete nitrification by *Nitrospira* bacteria. *Nature*, **528**(7583), 504–509.
771 https://doi.org/10.1038/nature16461

772 72 Damásio, M., Pinto, C., Salguero, J., Alarcon, M.V., de Deus, J., Soares-David, T., Silvestre, J., Carvalho,
773 L.C., & Zarrouk, O. (2025). Molecular and hydraulic responses of grapevine to water status and
774 phenology under long-term differential irrigation treatments. *Agricultural Water Management*
775 **318**(109708). https://doi.org/10.1016/j.agwat.2025.109708

776 76 Garriaut, R., Antonielli, L., Martins, G., Ballestra, P., Vivin, P., Marguerit, E., Mitter, B., Masneuf-Pomarède,
777 I., Compant, S., Ollat, N., & Lauvergeat, V. (2022a). Soil composition and rootstock genotype drive
778 the root associated microbial communities in young grapevines. *Frontiers in Microbiology*, **13**.
779 https://doi.org/10.3389/fmicb.2022.1031064

780 80 Garriaut, R., Lailheugue, V., Masneuf-Pomarède, I., Marguerit, E., Martins, G., Compant, S., Ballestra, P.,
781 Upton, S., Ollat, N., & Lauvergeat, V. (2022b). Grapevine rootstock and soil microbiome interactions:
782 Keys for a resilient viticulture. *Horticulture Research*, **9**. https://doi.org/10.1093/hr/uhac019

783 83 Gayer, S., Scharwies, J. D., Ramesh, S. A., Sullivan, W., Doerflinger, F. C., Pagay, V., & Tyerman, S. D.
784 (2020). Comparing hydraulics between two grapevine cultivars reveals differences in stomatal

785 regulation under water stress and exogenous ABA applications. *Frontiers in Plant Science*, **11**.
786 https://doi.org/10.3389/fpls.2020.00705

787 de Oliveira, T. B., de Lucas, R. C., Scarcella, A. S. de A., Contato, A. G., Pasin, T. M., Martinez, C. A., &
788 Polizeli, M. de L. T. de M. (2020). Fungal communities differentially respond to warming and drought
789 in tropical grassland soil. *Molecular Ecology*, **29**(8), 1550–1559. https://doi.org/10.1111/mec.15423

790 Dedyukhina, E. G., Kamzolova, S. V, & Vainshtein, M. B. (2014). Arachidonic acid as an elicitor of the plant
791 defense response to phytopathogens. *Chemical and Biological Technologies in Agriculture*, **1**(1), 18.
792 https://doi.org/10.1186/s40538-014-0018-9

793 Eekhout, J. P. C., Hunink, J. E., Terink, W., & de Vente, J. (2018). Why increased extreme precipitation under
794 climate change negatively affects water security. *Hydrology and Earth System Sciences*, **22**(11),
795 5935–5946. https://doi.org/10.5194/hess-22-5935-2018

796 Fahrbach, M., Kuever, J., Remesch, M., Huber, B. E., Kampfer, P., Dott, W., & Hollender, J. (2008).
797 *Steroidobacter denitrificans* gen. nov., sp. nov., a steroidal hormone-degrading
798 gammaproteobacterium. *International Journal of Systematic and Evolutionary Microbiology*, **58**(9),
799 2215–2223. https://doi.org/10.1099/ijs.0.65342-0

800 Ferreira, J. H. S., van Wyk, P. S., & Calitz, F. J. (1999). Slow Dieback of Grapevine in South Africa: Stress-
801 Related Predisposition of Young Vines for Infection by *Phaeoacremonium chlamydosporum*. *South*
802 *African Journal of Enology & Viticulture*, **20**(2). https://doi.org/10.21548/20-2-2228

803 Fierer, N. (2017). Embracing the unknown: Disentangling the complexities of the soil microbiome. *Nature*
804 *Reviews Microbiology*, **15**(10), 579–590. https://doi.org/10.1038/nrmicro.2017.87

805 Francis, I. M., Jochimsen, K. N., De Vos, P., & van Bruggen, A. H. C. (2014). Reclassification of rhizosphere
806 bacteria including strains causing corky root of lettuce and proposal of *Rhizorhapis suberifaciens*
807 gen. nov., comb. nov., *Sphingobium mellinum* sp. nov., *Sphingobium xanthum* sp. nov. and
808 *Rhizorhabdus argentea* gen. nov., sp. nov. *International Journal of Systematic and Evolutionary*
809 *Microbiology*, **64**(4), 1340–1350. https://doi.org/10.1099/ijs.0.058909-0

Funck Jensen, D., Dubey, M., Jensen, B., & Karlsson, M. (2021). *Clonostachys rosea* to control plant diseases. In J. Köhl & W. J. Ravensberg (Eds.), *Microbial bioprotectants for plant disease management* (pp. 429–472). Burleigh Dodds Science Publishing. https://doi.org/10.19103/AS.2021.0093.14

Gamalero, E., Bona, E., Novello, G., Boatti, L., Mignone, F., Massa, N., Cesaro, P., Berta, G., & Lingua, G. (2020). Discovering the bacteriome of *Vitis vinifera* cv. Pinot Noir in a conventionally managed vineyard. *Scientific Reports*, **10**(1), 6453. https://doi.org/10.1038/s41598-020-63154-w

Gobbi, A., Acedo, A., Imam, N., Santini, R. G., Ortiz-Álvarez, R., Ellegaard-Jensen, L., Belda, I., & Hansen, L. H. (2022). A global microbiome survey of vineyard soils highlights the microbial dimension of viticultural terroirs. *Communications Biology*, **5**(1). https://doi.org/10.1038/s42003-022-03202-5

Goemann, H. M., Ulrich, D. E. M., Peyton, B. M., Gallegos-Graves, L. V., & Mueller, R. C. (2024). Severe and mild drought cause distinct phylogenetically linked shifts in the blue grama (*Bouteloua gracilis*) rhizobiome. *Frontiers in Microbiomes*, **2**. https://doi.org/10.3389/frmbi.2023.1310790

Governo da República Portuguesa. (2022, October 14). Seca hidrológica mais grave do século devido à conjugação de temperaturas altas e fraca precipitação. *Comissão Permanente de Prevenção, Monitorização e Acompanhamento Dos Efeitos Da Seca*.

Greer, D. H., & Weston, C. (2010). Heat stress affects flowering, berry growth, sugar accumulation and photosynthesis of *Vitis vinifera* cv. Semillon grapevines grown in a controlled environment. *Functional Plant Biology*, **37**(3), 206–214. https://doi.org/10.1071/FP09209

Gupta, V. V. S. R., Bramley, R. G. V., Greenfield, P., Yu, J., & Herderich, M. J. (2019). Vineyard Soil Microbiome Composition Related to Rotundone Concentration in Australian Cool Climate ‘Peppery’ Shiraz Grapes. *Frontiers in Microbiology*, **10**. https://doi.org/10.3389/fmicb.2019.01607

Hafeez, F., Clément, J., Bernard, L., Poly, F., & Pommier, T. (2023). Early spring snowmelt and summer droughts strongly impair the resilience of bacterial community and N cycling functions in a subalpine grassland ecosystem. *Oikos*, **2023**(7). https://doi.org/10.1111/oik.09836

[35] Heiri, O., Lotter, A.F. & Lemcke, G. (2001). Loss on ignition as a method for estimating organic and carbonate content in sediments: reproducibility and comparability of results. *Journal of Paleolimnology* **25**, 101–110. https://doi.org/10.1023/A:1008119611481

[36] Hermans, S. M., Buckley, H. L., Case, B. S., Curran-Cournane, F., Taylor, M., & Lear, G. (2017). Bacteria as Emerging Indicators of Soil Condition. *Applied and Environmental Microbiology*, **83**(1). https://doi.org/10.1128/AEM.02826-16

[41] Hochberg, U., Degu, A., Fait, A., & Rachmilevitch, S. (2013). Near isohydric grapevine cultivar displays higher photosynthetic efficiency and photorespiration rates under drought stress as compared with near anisohydric grapevine cultivar. *Physiologia Plantarum*, **147**(4). https://doi.org/10.1111/j.1399-3054.2012.01671.x

[45] Hopkins, A. J. M., Ruthrof, K. X., Fontaine, J. B., Matusick, G., Dundas, S. J., & Hardy, G. Es. (2018). Forest die-off following global-change-type drought alters rhizosphere fungal communities. *Environmental Research Letters*, **13**(9), 095006. https://doi.org/10.1088/1748-9326/aadc19

[48] Huang, J.-W., Hu, S.-L., Cheng, X.-K., Chen, D., Kong, X.-K., & Jiang, J.-D. (2019). *Steroidobacter soli* sp. nov., isolated from farmland soil. *International Journal of Systematic and Evolutionary Microbiology*, **69**(11), 3443–3447. https://doi.org/10.1099/ijsem.0.003639

[51] Huang, R.-R., Ge, X.-F., Chen, X.-K., Yang, S.-R., Zhen, C., Wen, Z.-Q., Li, Y.-N., & Liu, W.-Z. (2021). *Steroidobacter gossypii* sp. nov., isolated from cotton field soil. *International Journal of Systematic and Evolutionary Microbiology*, **71**(8). https://doi.org/10.1099/ijsem.0.004935

[54] Kadoria, A. K., Sharma, K. L., & Reddy, K. S. (2020). Hydraulic properties of soil under warming climate. In M. N. Prasad & M. Pietrykowski (Eds.), *Climate Change and Soil Interactions* (pp. 473–508). Elsevier. https://doi.org/10.1016/B978-0-12-818032-7.00018-7

[57] IPMA – Instituto Português do Mar e da Atmosfera. (2025). *Ondas de Calor,* IPMA https://www.ipma.pt/pt/oclima/ondascalor (visited at 20th March 2025).

[59] Ishii, S., Ashida, N., Ohno, H., Segawa, T., Yabe, S., Otsuka, S., Yokota, A., & Senoo, K. (2017). *Noviherbaspirillum denitrificans* sp. nov., a denitrifying bacterium isolated from rice paddy soil and

Noviherbaspirillum autotrophicum sp. nov., a denitrifying, facultatively autotrophic bacterium isolated from rice paddy soil and proposal to reclassify *Herbaspirillum massiliense* as *Noviherbaspirillum massiliense* comb. nov. *International Journal of Systematic and Evolutionary Microbiology*, **67**(6), 1841–1848. https://doi.org/10.1099/ijsem.0.001875

Ma, X., Shang, H., Chen, Y., Lin, M., Wei, Y., Li, Y., Li, R., Dong, P., Chen, Y., Zhang, Y., & Wang, Q. (2024). Improved bacterial composition and co-occurrence patterns of rhizosphere increased nutrient uptake and grain yield through cultivars mixtures in maize. *Science of The Total Environment*, **926**, 172102. https://doi.org/10.1016/j.scitotenv.2024.172102

Maminsky, L. M., Esker, P. D., & Bell, T. H. (2021). Abiotic conditions outweigh microbial origin during bacterial assembly in soils. *Environmental Microbiology*, **23**(1), 358–371. https://doi.org/10.1111/1462-2920.15322

Kämpfer, P. (2011). Family II. *Chitinophagaceae* fam. nov. Kämpfer, Lodders and Falsen. In A. Parte, N. R. Krieg, W. Ludwig, W. B. Whitman, B. P. Hedlund, B. J. Paster, J. T. Staley, N. Ward, & D. Brown (Eds.), *Bergey's Manual of Systematic Bacteriology: Volume 4: The Bacteroidetes, Spirochaetes, Tenericutes (Mollicutes), Acidobacteria, Fibrobacteres, Fusobacteria, Dictyooglomi, Gemmatimonadetes, Lentisphaerae, Verrucomicrobia, Chlamydiae, and Planctomycetes* (Vol. 4, pp. 351–357). Springer Science & Business Media.

Rost, E., Kundel, D., Conz, R. F., Mäder, P., Krause, H.-M., Six, J., Mayer, J., & Hartmann, M. (2024). Microbial resistance and resilience to drought under organic and conventional farming. *bioRxiv*. https://doi.org/10.1101/2024.04.17.589021

Laboratório Nacional de Engenharia Civil. (1967). E 203 – Solos: Determinação da do pH. Lisboa, Portugal: LNEC

Lambers, H., & Barrow, N. J. (2021). The pervasive use of P2O5, K2O, CaO, MgO and other molecules that do not exist in soil or fertiliser bags. *New Phytologist*, **232**(5), 1901–1903. https://doi.org/10.1111/nph.17715

Ibegeay, J., Errafii, K., Ziami, A., & Hijri, M. (2024). The rhizosphere of a drought-tolerant plant species in Morocco: A refuge of high microbial diversity with no taxon preference. *Environmental Microbiology Reports*, **16**(3). https://doi.org/10.1111/1758-2229.13254

Li, F., Zhang, S., Wang, Y., Li, Y., Li, P., Chen, L., Jie, X., Hu, D., Feng, B., Yue, K., & Han, Y. (2020). Rare fungus, *Mortierella capitata*, promotes crop growth by stimulating primary metabolisms related genes and reshaping rhizosphere bacterial community. *Soil Biology and Biochemistry*, **151**, 108017. https://doi.org/10.1016/j.soilbio.2020.108017

Li, L., Preece, C., Lin, Q., Bréchet, L. M., Stahl, C., Courtois, E. A., & Verbruggen, E. (2021). Resistance and resilience of soil prokaryotic communities in response to prolonged drought in a tropical forest. *FEMS Microbiology Ecology*, **97**(9). https://doi.org/10.1093/femsec/fiab116

Liang, Y., Xiao, X., E. Nuccio, E., Yuan, M., Zhang, N., Xue, K., M. Cohan, F., Zhou, J., & Sun, B. (2020). Differentiation strategies of soil rare and abundant microbial taxa in response to changing climatic regimes. *Environmental Microbiology*, **22**(4), 1327–1340. https://doi.org/10.1111/1462-2920.14945

Liu, T., Ye, N., Wang, X., Das, D., Tan, Y., You, X., Long, M., Hu, T., Dai, L., Zhang, J., & Chen, M. (2021). Drought stress and plant ecotype drive microbiome recruitment in switchgrass rhizosheath. *Journal of Integrative Plant Biology*, **63**(10), 1753–1774. https://doi.org/10.1111/jipb.13154

Lombard, L., Houbraken, J., Decock, C., Samson, R. A., Meijer, M., Réblová, M., Groenewald, J. Z., & Crous, P. W. (2016). Generic hyper-diversity in *Stachybotriaceae*. *Persoonia - Molecular Phylogeny and Evolution of Fungi*, **36**(1), 156–246. https://doi.org/10.3767/003158516X691582

Lozano, Y. M., Aguilar-Trigueros, C. A., Roy, J., & Rillig, M. C. (2021). Drought induces shifts in soil fungal communities that can be linked to root traits across 24 plant species. *New Phytologist*, **232**(5), 1917–1929. https://doi.org/10.1111/nph.17707

Lu, Y., Zhou, G., Ewald, J., Pang, Z., Shiri, T., & Xia, J. (2023). MicrobiomeAnalyst 2.0: comprehensive statistical, functional and integrative analysis of microbiome data. *Nucleic Acids Research*, **51**(W1), W310–W318. https://doi.org/10.1093/nar/gkad407

911 Lutz, M. C., Lopes, C. A., Rodriguez, M. E., Sosa, M. C., & Sangorrín, M. P. (2013). Efficacy and putative
912 mode of action of native and commercial antagonistic yeasts against postharvest pathogens of pear.
913 *International Journal of Food Microbiology*, **164**(2–3), 166–172.
914 https://doi.org/10.1016/j.ijfoodmicro.2013.04.005

915 Marasco, R., Alturkey, H., Fusi, M., Brandi, M., Ghiglieno, I., Valenti, L., & Daffonchio, D. (2022). Rootstock–
916 scion combination contributes to shape diversity and composition of microbial communities
917 associated with grapevine root system. *Environmental Microbiology*, **24**(8), 3791-3808.
918 https://doi.org/10.1111/1462-2920.16042

919 Marasco, R., Rolli, E., Ettoumi, B., Vigani, G., Mapelli, F., Borin, S., Abou-Hadid, A. F., El-Behairy, U. A.,
920 Sorlini, C., Cherif, A., Zocchi, G., & Daffonchio, D. (2012). A Drought Resistance-Promoting
921 Microbiome Is Selected by Root System under Desert Farming. *PLoS ONE*, **7**(10), e48479.
922 https://doi.org/10.1371/journal.pone.0048479

923 Marasco, R., Rolli, E., Fusi, M., Michoud, G., & Daffonchio, D. (2018). Grapevine rootstocks shape
924 underground bacterial microbiome and networking but not potential functionality. *Microbiome*, **6**(1).
925 https://doi.org/10.1186/s40168-017-0391-2

926 Marín, D., Armengol, J., Carbonell-Bejerano, P., Escalona, J. M., Gramaje, D., Hernández-Montes, E.,
927 Intrigliolo, D. S., Martínez-Zapater, J. M., Medrano, H., Mirás-Avalos, J. M., Palomares-Rius, J. E.,
928 Romero-Azorín, P., Savé, R., Santesteban, L. G., & de Herralde, F. (2021). Challenges of viticulture
929 adaptation to global change: tackling the issue from the roots. *Australian Journal of Grape and Wine*
930 *Research*, **27**(1), 8–25. https://doi.org/10.1111/ajgw.12463

931 McDonald, D., Jiang, Y., Balaban, M., Cantrell, K., Zhu, Q., Gonzalez, A., Morton, J. T., Nicolaou, G., Parks,
932 D. H., Karst, S. M., Albertsen, M., Hugenholtz, P., DeSantis, T., Song, S. J., Bartko, A., Havulinna, A.
933 S., Jousilahti, P., Cheng, S., Inouye, M., … Knight, R. (2023). Greengenes2 unifies microbial data in a
934 single reference tree. *Nature Biotechnology*, **42**, 715-718. https://doi.org/10.1038/s41587-023-
935 01845-1

Meisner, A., Jacquiod, S., Snoek, B. L., ten Hooven, F. C., & van der Putten, W. H. (2018). Drought Legacy Effects on the Composition of Soil Fungal and Prokaryote Communities. *Frontiers in Microbiology*, **9**. https://doi.org/10.3389/fmicb.2018.00294

Mezza, L., Deyett, E., Vallance, J., Gendre, L., Garcia, J. F., Cantu, D., Rey, P., Lecomte, P., & Rolshausen, P. E. (2024). Grapevine pruning strategy affects trunk disease symptoms, wood pathobiome and mycobiome. *Phytopathologia Mediterranea*, **63**(1), 91–102. https://doi.org/10.36253/phyto-14778

Mohd-Radzman, N. A., & Drapek, C. (2023). Compartmentalisation: A strategy for optimising symbiosis and tradeoff management. *Plant, Cell & Environment*, **46**(10), 2998–3011. https://doi.org/10.1111/pce.14553

Mosley, O. E., Gios, E., Weaver, L., Close, M., Daughney, C., van der Raaij, R., Martindale, H., & Handley, K. M. (2022). Metabolic Diversity and Aero-Tolerance in Anammox Bacteria from Geochemically Distinct Aquifers. *mSystems*, **7**(1). https://doi.org/10.1128/msystems.01255-21

Naylor, D., Naasko, K., Smith, M., Couvillion, S., Nicora, C., Trejo, J., Fransen, S., Danczak, R., McClure, R., Hofmockel, K. S., & Jansson, J. K. (2023). Interactive effects of depth and differential irrigation on soil microbiome composition and functioning. *Frontiers in Microbiomes*, **2**. https://doi.org/10.3389/frmbi.2023.1078024

Nerva, L., Sandrini, M., Moffa, L., Velasco, R., Balestrini, R., & Chitarra, W. (2022). Breeding toward improved ecological plant–microbiome interactions. *Trends in Plant Science*, **27**(11), 1134–1143. https://doi.org/10.1016/j.tplants.2022.06.004

Nian, L., Xie, Y., Zhang, H., Wang, M., Yuan, B., Cheng, S., & Cao, C. (2023). *Vishniacozyma victoriae*: An endophytic antagonist yeast of kiwifruit with biocontrol effect to *Botrytis cinerea*. *Food Chemistry*, **411**, 135442. https://doi.org/10.1016/j.foodchem.2023.135442

Nogi, Y., Yoshizumi, M., Hamana, K., Miyazaki, M., & Horikoshi, K. (2014). *Povalibacter uvarum* gen. nov., sp. nov., a polyvinyl-alcohol-degrading bacterium isolated from grapes. *International Journal of Systematic and Evolutionary Microbiology*, **64**(8), 2712–2717. https://doi.org/10.1099/ijs.0.062620-0

962 Abouri, C., Saadaoui, M., Morlevat, T., Esserti, S., Faize, L., Rifai, A., Tayeb, K., Smaili, A., Faize, M., &
963 Venisse, J.-S. (2024). Seed treatment with *Mortierella alpina* M01 promotes tomato growth and
964 mitigates verticillium wilt and bacterial speck disease infections by potentiating plant antioxidant
965 responses. *Journal of Plant Pathology*. https://doi.org/10.1007/s42161-024-01669-1

966 Bovello, G., Gamalero, E., Bona, E., Boatti, L., Mignone, F., Massa, N., Cesaro, P., Lingua, G., & Berta, G.
967 (2017). The Rhizosphere Bacterial Microbiota of *Vitis vinifera* cv. Pinot Noir in an Integrated Pest
968 Management Vineyard. *Frontiers in Microbiology*, **8**. https://doi.org/10.3389/fmicb.2017.01528

969 Fazooki, S., Shekariesfahlan, A., Maleki, M., & Naeimi, S. (2024). Isolation and identification of endophytic
970 and grapevine trunk diseases associated fungi with antagonistic potential against *Cytospora*
971 *chrysosperma*. *Journal of Plant Pathology*. https://doi.org/10.1007/s42161-024-01731-y

972 Pereira, S. C., Carvalho, D., & Rocha, A. (2021). Temperature and precipitation extremes over the iberian
973 peninsula under climate change scenarios: A review. *Climate*, **9**(9).
974 https://doi.org/10.3390/cli9090139

975 Soudel, M., Mendes, R., Costa, L. A. S., Bueno, C. G., Meng, Y., Folimonova, S. Y., Garrett, K. A., & Martins,
976 S. J. (2021). The Role of Plant-Associated Bacteria, Fungi, and Viruses in Drought Stress Mitigation.
977 *Frontiers in Microbiology*, **12**. https://doi.org/10.3389/fmicb.2021.743512

978 Probst, C. M., Ridgway, H. J., Jaspers, M. V., & Eirian Jones, E. (2019). Pathogenicity of *Ilyonectria*
979 *liriodendri* and *Dactylonectria macrodidyma* propagules in grapevines. *European Journal of Plant*
980 *Pathology*, **154**(2), 405–421. https://doi.org/10.1007/s10658-018-01664-0

981 Reis, F., Soares-Castro, P., Costa, D., Tavares, R. M., Baptista, P., Santos, P. M., & Lino-Neto, T. (2019).
982 Climatic impacts on the bacterial community profiles of cork oak soils. *Applied Soil Ecology*, **143**,
983 89–97. https://doi.org/10.1016/j.apsoil.2019.05.031

984 Semenyik, J., Csige, L., Dávid, P., Fauszt, P., Szilágyi-Rácz, A. A., Szőllősi, E., Bacsó, Z. R., Szepsy Jnr, I.,
985 Molnár, K., Rácz, C., Fidler, G., Kállai, Z., Stündl, L., Dobos, A. C., & Paholcsek, M. (2024). Exploring
986 the interplay between the core microbiota, physicochemical factors, agrobiochemical cycles in the

soil of the historic tokaj mád wine region. *PLOS ONE*, **19**(4), e0300563. https://doi.org/10.1371/journal.pone.0300563

Reyes-Bravo, P., Acuña-Fontecilla, A., Rosales, I. M., & Godoy, L. (2022). Non-conventional yeasts as biocontrol agents against fungal pathogens related to postharvest diseases. *Sydowia*, **74**, 71–78. https://doi.org/10.12905/0380.sydowia74-2021-0071

Richy, E., Dobbler, P. T., Tláskal, V., López-Mondéjar, R., Baldrian, P., & Kyselková, M. (2024). Pacbio HiFi sequencing sheds light on key bacteria contributing to deadwood decomposition processes. *Research Square*. https://doi.org/10.21203/rs.3.rs-4181686/v1

Rodrigues, M. L. (2018). The Multifunctional Fungal Ergosterol. *mBio*, **9**(5). https://doi.org/10.1128/mBio.01755-18

Rogiers, S. Y., Greer, D. H., Hatfield, J. M., Hutton, R. J., Clarke, S. J., Hutchinson, P. A., & Sommers, A. (2012). Stomatal response of an anisohydric grapevine cultivar to evaporative demand, available soil moisture and abscisic acid. *Tree Physiology*, **32**(2), 249-261. https://doi.org/10.1093/treephys/tpr131

Rolli, E., Marasco, R., Vigani, G., Ettoumi, B., Mapelli, F., Deangelis, M. L., Gandolfi, C., Casati, E., Previtali, F., Gerbino, R., Pierotti Cei, F., Borin, S., Sorlini, C., Zocchi, G., & Daffonchio, D. (2015). Improved plant resistance to drought is promoted by the root-associated microbiome as a water stress-dependent trait. *Environmental Microbiology*, **17**(2), 316–331. https://doi.org/10.1111/1462-2920.12439

Sánchez-Yañez, J. M. (2022). Xanthobacter autotrophicus an Endophytic Beneficial Bacterium for Wheat and Other Plants: A Short Review. In M.-R. Ansari (Ed.), *Current Trends in Wheat Research* (1st ed., pp. 73–102). IntechOpen. https://doi.org/http://dx.doi.org/10.5772/intechopen.102066

Schleypen, J. R., Mistry, M. N., Saeed, F., & Dasgupta, S. (2022). Sharing the burden: quantifying climate change spillovers in the European Union under the Paris Agreement. *Spatial Economic Analysis*, **17**(1), 67–82. https://doi.org/10.1080/17421772.2021.1904150

1012 Schultz, H. R. (2003). Differences in hydraulic architecture account for near-isohydric and anisohydric
1013 behaviour of two field-grown *Vitis vinifera* L. cultivars during drought. *Plant, Cell & Environment*,
1014 **26**(8), 1393-1405. https://doi.org/10.1046/j.1365-3040.2003.01064.x

1015 Séneca, J., Pjevac, P., Canarini, A., Herbold, C. W., Zioutis, C., Dietrich, M., Simon, E., Prommer, J., Bahn,
1016 M., Pötsch, E. M., Wagner, M., Wanek, W., & Richter, A. (2020). Composition and activity of nitrifier
1017 communities in soil are unresponsive to elevated temperature and CO2, but strongly affected by
1018 drought. *The ISME Journal*, **14**(12), 3038–3053. https://doi.org/10.1038/s41396-020-00735-7

1019 Senwanna, C., Hongsanan, S., Khuna, S., Kumla, J., Yarasheva, M., Gafforov, Y., Abdurazakov, A., &
1020 Suwannarach, N. (2024). Insights into the molecular phylogeny and morphology of three novel
1021 *Dothiora* species, along with a worldwide checklist of *Dothiora*. *Frontiers in Cellular and Infection*
1022 *Microbiology*, **14**. https://doi.org/10.3389/fcimb.2024.1367673

1023 Swift, J. F., Kolp, M. R., Carmichael, A., Ford, N. E., Hansen, P. M., Sikes, B. A., Kleiner, M., & Wagner, M.
1024 R. (2024). Drought stress homogenizes maize growth responses to diverse natural soil microbiomes.
1025 *Plant and Soil*. https://doi.org/10.1007/s11104-024-06853-x

1026 Teixeira, A., Martins, V., & Gerós, H. (2024). From the vineyard soil to the grape berry surface: Unravelling
1027 the dynamics of the microbial terroir. *Agriculture, Ecosystems & Environment*, **374**, 109145.
1028 https://doi.org/10.1016/j.agee.2024.109145

1029 Tian, R., Ning, D., He, Z., Zhang, P., Spencer, S. J., Gao, S., Shi, W., Wu, L., Zhang, Y., Yang, Y., Adams, B.
1030 G., Rocha, A. M., Detienne, B. L., Lowe, K. A., Joyner, D. C., Klingeman, D. M., Arkin, A. P., Fields, M.
1031 W., Hazen, T. C., … Zhou, J. (2020). Small and mighty: adaptation of superphylum Patescibacteria to
1032 groundwater environment drives their genome simplicity. *Microbiome*, **8**(1), 51.
1033 https://doi.org/10.1186/s40168-020-00825-w

1034 Toreti, A., Masante, D., Acosta Navarro, J., Bavera, D., Cammalleri, C., De Jager, A., Di Ciollo, C., Hrast
1035 Essenfelder, A., Maetens, W., Magni, D., Mazzeschi, M., Spinoni, J., & De Felice, M. (2022). Drought
1036 in Europe July 2022. *July 2022: GDO Analytical Report*. https://doi.org/10.2760/014884

Tramontini, S., Döring, J., Vitali, M., Ferrandino, A., Stoll, M., & Lovisolo, C. (2014). Soil water-holding capacity mediates hydraulic and hormonal signals of near-isohydric and near-anisohydric *Vitis* cultivars in potted grapevines. *Functional Plant Biology*, **41**(11), 1119-1128. https://doi.org/10.1071/FP13263

Ullah, A., Akbar, A., Luo, Q., Khan, A. H., Manghwar, H., Shaban, M., & Yang, X. (2019). Microbiome Diversity in Cotton Rhizosphere Under Normal and Drought Conditions. *Microbial Ecology*, **77**(2), 429–439. https://doi.org/10.1007/s00248-018-1260-7

Van Leeuwen, C., & Darriet, P. (2016). The Impact of Climate Change on Viticulture and Wine Quality. *Journal of Wine Economics*, **11**(1), 150–167. https://doi.org/10.1017/jwe.2015.21

Vaz, M., Coelho, R., Rato, A., Samara-Lima, R., Silva, L. L., Campostrini, E., & Mota, J. B. (2016). Adaptive strategies of two Mediterranean grapevines varieties (Aragonez syn. Tempranillo and Trincadeira) face drought: physiological and structural responses. *Theoretical and Experimental Plant Physiology*, **28**(2), 205–220. https://doi.org/10.1007/s40626-016-0074-6

Venios, X., Korkas, E., Nisiotou, A., & Banilas, G. (2020). Grapevine responses to heat stress and global warming. *Plants*, **9**(12), 1–15. https://doi.org/10.3390/plants9121754

Vink, S. N., Chrysargyris, A., Tzortzakis, N., & Salles, J. F. (2021). Bacterial community dynamics varies with soil management and irrigation practices in grapevines (*Vitis vinifera* L.). *Applied Soil Ecology*, **158**. https://doi.org/10.1016/j.apsoil.2020.103807

Wang, B., Wang, X., Wang, Z., Zhu, K., & Wu, W. (2023). Comparative metagenomic analysis reveals rhizosphere microbial community composition and functions help protect grapevines against salt stress. *Frontiers in Microbiology*, **14**. https://doi.org/10.3389/fmicb.2023.1102547

Wang, W., Wang, J., Wang, Q., Bermudez, R. S., Yu, S., Bu, P., Wang, Z., Chen, D., & Feng, J. (2022). Effects of Plantation Type and Soil Depth on Microbial Community Structure and Nutrient Cycling Function. *Frontiers in Microbiology*, **13**. https://doi.org/10.3389/fmicb.2022.846468

Wolińska, A., Podlewski, J., Słomczewski, A., Grządziel, J., Gałązka, A., & Kuźniar, A. (2022). Fungal Indicators of Sensitivity and Resistance to Long-Term Maize Monoculture: A Culture-Independent Approach. *Frontiers in Microbiology*, **12**. https://doi.org/10.3389/fmicb.2021.799378

Xiao, L., Zhang, J.-J., Yu, L.-L., Chen, Q., Zhu, J.-C., He, J., & Ding, D.-R. (2016). *Rhizorhabdus dicambivorans* sp. nov., a dicamba-degrading bacterium isolated from compost. *International Journal of Systematic and Evolutionary Microbiology*, **66**(9), 3317–3323. https://doi.org/10.1099/ijsem.0.001194

Xue, H., Sun, X., Wang, T., Zhang, A., Han, D., Wei, G., Song, W., & Shu, D. (2024). Host genotype-specific rhizosphere fungus enhances drought resistance in wheat. *Microbiome*, **12**(1), 44. https://doi.org/10.1186/s40168-024-01770-8

Zarraonaindia, I., Owens, S. M., Weisenhorn, P., West, K., Hampton-Marcell, J., Lax, S., Bokulich, N. A., Mills, D. A., Martin, G., Taghavi, S., van der Lelie, D., & Gilbert, J. A. (2015). The soil microbiome influences grapevine-associated microbiota. *mBio*, **6**(2). https://doi.org/10.1128/mBio.02527-14

Zarrouk, O., Costa, J. M., Francisco, R., Lopes, C., & Chaves, M. M. (2016). Drought and water management in Mediterranean vineyards. In H. Gerós, M. M. Chaves, H. M. Gil, & S. Delrot (Eds.), *Grapevine in a Changing Environment: A Molecular and Ecophysiological Perspective* (1st ed.). John Wiley & Sons. https://doi.org/https://doi.org/10.1002/9781118735985.ch3

Zhalnina, K., de Quadros, P. D., Gano, K. A., Davis-Richardson, A., Fagen, J. R., Brown, C. T., Giongo, A., Drew, J. C., Sayavedra-Soto, L. A., Arp, D. J., Camargo, F. A. O., Daroub, S. H., Clark, I. M., McGrath, S. P., Hirsch, P. R., & Triplett, E. W. (2013). *Ca.* Nitrososphaera and *Bradyrhizobium* are inversely correlated and related to agricultural practices in long-term field experiments. *Frontiers in Microbiology*, **4.** https://doi.org/10.3389/fmicb.2013.00104

Zhang, R., Chen, L., Niu, Z., Song, S., & Zhao, Y. (2019). Water stress affects the frequency of Firmicutes, Clostridiales and *Lysobacter* in rhizosphere soils of greenhouse grape. *Agricultural Water Management*, **226**, 105776. https://doi.org/10.1016/j.agwat.2019.105776

1085 Liao, G., Li, S., Zhou, W., He, L., Zou, R., Yu, J., Chen, Z., Bai, X., Zhang, J., & Sun, X. (2024). Comparative
1086 Analysis of Soil Organic Carbon and Soil Oxide Minerals across Different Climates and Forest Types
1087 [JD]. *Centralblatt Für Das Gesamte Forstwesen*, **2024**(1), 53–78. https://doi.org/10.53203/fs.2401.3

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