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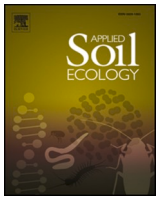

Enhancing vineyard soil mycorrhizal properties and grape and wine phenolic profiles through microbial inoculation and interrow green cover

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ABSTRACT

Grapevine cultivation has to face major challenges for maintaining its long-term resilience, in which soil health is a key factor. Sustainable management options, like service crops and beneficial microbial inocula, have been proposed for preserving soil health and biodiversity in vineyards.

Here, commercial and locally sourced arbuscular mycorrhiza-based inocula were applied in combination with a green cover mix in two organic Mediterranean vineyards with different intensity of soil disturbance. Chemical soil properties, mycorrhizal inoculum potential, arbuscular mycorrhizal fungal (AMF) ecology (using high-throughput DNA metabarcoding), and grape and wine physico-chemical characteristics were investigated in the short-term.

The local inoculum enhanced soil mycorrhizal activity by 179% in the more intensely cultivated vineyard. The sustainable management treatments increased AMF biodiversity by up to 42% in terms of richness, and induced significant shifts in the community composition at both sites. Nevertheless, the introduced AMF did not outcompete native communities. Grape and wine secondary metabolite profiles showed an enrichment of phenolic compounds by up to 35% – in particular that of anthocyanins, flavan-3-ols, hydroxycinnamic acids and phenolic alcohols – in plots treated with interrow green cover and microbial inocula. Additionally, grape anthocyanin and wine anthocyanin, flavonol and phenolic alcohol contents exhibited strong, and mostly positive correlations with soil AMF diversity. Our data highlighted the modulating effect of vineyard *terroir* on both mycorrhizal ecology and grape / wine quality responses to the applied treatments.

Therefore, service crops and mycorrhiza-based inocula may be feasible tools for improving soil health, microbial biodiversity and agro-ecosystem sustainability in viticulture. This work provides a novel insight into vineyard AMF ecology and the impact of sustainable agricultural practices on grape and wine characteristics in field conditions.

1. Introduction

Viticulture and winemaking are practices that have evolved alongside with human civilization (McGovern et al., 1996), nowadays representing an important share of global agricultural production and trade (FAOSTAT, 2024). Nevertheless, vineyards are prone to soil health and fertility decline caused by erosion, compaction, reduced soil water retention, loss of soil organic matter (SOM), loss of biodiversity, and imbalance in mineral nutrient budgets (Cataldo et al., 2021; Cerdan et al., 2010; Costantini et al., 2018; Lal, 2015). According to previous studies, these global patterns have even accelerated, supposedly, as a consequence of unsustainable agronomic practices and current climatic changes (Borrelli et al., 2017; Wiesmeier et al., 2016), posing significant challenges to the long-term resistance and resilience of Mediterranean grapevine cultivation (Valenzuela-Aragon et al., 2025).

Intensive, conventional agricultural management has long been

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recognized to take a toll on soil and plant-associated microbial communities (Banerjee et al., 2019; Idbella and Bonanomi, 2023; Matson et al., 1997; Zhang et al., 2024). The diversity, composition and functionality of such microbiota are of great importance, as they take part in soil nutrient cycling, they influence soil structure, and – given their extensive metabolic capabilities – they provide key auxiliary functions to plants, forming a flexible holobiont supporting plant growth, nutrition and health (Bettenfeld et al., 2022; Vandenkoornhuyse et al., 2015). Furthermore, in the context of viti- and viniculture, the environmental microbiome dwelling in the surroundings of grapevines constitutes the microbial *terroir*, an important source of distinctive wine characteristics (Griggs et al., 2021; Liu et al., 2019; Visconti et al., 2024).

Among plant-associated beneficial soil microorganisms, arbuscular mycorrhizal fungi (AMF) represent a pivotal taxonomic group (phylum *Glomeromycota*), establishing mutualistic symbioses with ca. 72% of vascular plants, including important food and industrial crops (Brundrett and Tedersoo, 2018; Smith and Read, 2008). Arbuscular mycorrhizal interactions primarily concern the exchange of photosynthetically produced phytometabolites for mineral nutrients and water scavenged by the extensive extraradical mycelium of the fungal partner, as they are capable of efficiently absorbing and transporting mineral nutrients from soil compartments otherwise less accessible to plant roots. In addition, AMF colonization shapes plant secondary metabolism, modulates phytohormonal balance and volatile organic compound (VOC) production, and induces systemic resistance, significantly contributing to their host's defense against biotic and abiotic stressors (Avio et al., 2018; Bitterlich et al., 2018; Smith and Read, 2008). Moreover, the growth, exudation and decay of glomeromycotan mycelia improve soil structure and aggregate stability, prevent soil erosion, supply a noteworthy amount of labile SOM, and regulate the microbial ecology of the mycorrhizosphere, overall providing complex agro-ecosystem services (Gianinazzi et al., 2010; Jansa et al., 2020; Kakouridis et al., 2024; Ujvári et al., 2021; Zhang et al., 2024). Therefore, AMF are considered as microbial indicators of soil health and quality (Schloter et al., 2018).

Previous findings have proven that AMF are crucial contributors to grapevine performance, associated with higher yields, improved resistance to severe drought and pests and increased production of VOCs, flavonols, anthocyanins and other phenolic compounds (Cardinale et al., 2022; Ganugi et al., 2023; Karoglan et al., 2021; Torres et al., 2018b; Velásquez et al., 2020) that could translate into enhanced wine quality traits (Gabriele et al., 2016). The compatible fungal partners get selected from the pool of resident AMF communities to colonize the grapevine root system (Lailheugue et al., 2024; Trouvelot et al., 2015), and the identity of available mycorrhizal partners may have differential effects on the vine nutrition due to their inherent metabolic traits, as demonstrated by Moukarzel et al. (2023). Consequently, higher AMF diversity in the surrounding soil may help to balance mycorrhizal trade-offs and may offer enhanced flexibility for the adaptation of grapevine to different environmental conditions. However, conventionally managed vineyards often harbor limited AMF diversity, mainly represented by members of the *Glomeraceae*, *Diversisporaceae* and *Entrophosporaceae* (previously known as *Claroideoglomeraceae*, and recently re-classified by Błaszkowski et al., 2022) families, resistant to soil perturbations (Berruti et al., 2017a; Lailheugue et al., 2024; Moukarzel et al., 2024; Nogales et al., 2021; Oehl and Koch, 2018; Van Geel et al., 2017). Indeed, frequent soil tillage, unbalanced fertilization and the lack of interrow vegetation were shown to affect AMF communities and general soil health negatively in vineyards (Aguilar-Paredes et al., 2024; Karimi et al., 2020; Vukicevich et al., 2016), leaving ample space for the improvement of sustainable agronomic practices in viticultural settings.

As such, service crops and plant-associated beneficial microorganisms (including AMF) have been proposed as powerful allies in combating soil degradation and achieving sustainability goals in vineyards and similar perennial agro-ecosystems (Berg et al., 2017; Cataldo et al., 2021; Darriaut et al., 2022; Novara et al., 2021; Rillig et al., 2019), although their extensive impacts have not been entirely uncovered in real-life scenarios. While several reports are available on the beneficial effects of interrow vegetation covers – e.g. facilitated SOM accumulation, erosion prevention, enhanced nutrient dynamics, increased soil microbial biomass (Abad et al., 2021; García-Díaz et al., 2018; Lazcano et al., 2020), capability to shape the soil microbiota and to regulate potential pests and pathogens (Bellabarba et al., 2025; Garcia et al., 2018; Pingel et al., 2019) – there is little knowledge on their ability of preserving mycorrhizal communities in viticultural settings (Trouvelot et al., 2015). Similarly, despite AMF-based inocula are often proposed as biofertilizers and biostimulants in various agro-ecosystems (Berruti et al., 2016; Jindo et al., 2022; Rouphael et al., 2015), with a potential to improve depleted vineyard soils and to help grapevines cope with the challenges of climate change (Holland et al., 2018; Nogales et al., 2021; Valenzuela-Aragon et al., 2025), key field trials are still very scarce. Current paradigms of microbial inoculation techniques are shifting towards a more holistic approach, exploiting diverse arrays of beneficial microorganisms in pre-established consortia rather than using single-strain inocula (Ray et al., 2020; Thirkell et al., 2017).

So far, only few studies investigated the native mycorrhizal communities and their potential manipulation in vineyards, especially by taking advantage of ad hoc meta-barcoding approaches (Battie-Laclau et al., 2025; Moukarzel et al., 2024; Nogales et al., 2021). There is also a severe lack of data on the field efficiency of commercially available AMF bioinocula in viticultural settings (Holland et al., 2018), however, some contrasting reports have drawn attention to this matter previously (Cardinale et al., 2022; Thomsen et al., 2021). Therefore, our objective was to elucidate the impact of sustainable agricultural practices aiming to promote soil health, such as interrow cover cropping and beneficial soil microbiome inoculation, on chemical soil properties, and on the colonizing activity and phylogenetic diversity of resident soil AMF communities (based on mycorrhizal inoculum potential measurements and 18S rRNA gene meta-barcoding, respectively) in two organic Mediterranean vineyards. Additionally, the physico-chemical characteristics of grapes and fermented wines were assessed via spectrophotometry and HPLC-DAD. We hypothesized that the interrow plant cover would boost innate soil mycorrhizal activity, causing moderate shifts in the community structure, while the combined soil inoculation treatments would re-shape and enrich AMF communities in intensely cultivated vineyard soils, ultimately affecting fruit and wine quality traits through the extensive plant-microbe interactions.

2. Materials and methods

2.1. Experimental sites

For the scope of this study, two commercial vineyards were selected in the Chianti region (Italy), both in the municipality of Greve in Chianti: Antico Borgo di Sugame (Sugame [S]; 43°35′40″N, 11°21′39″E; 475 m a.s.l.) and Palagio di Panzano (Panzano [P]; 43°32′50″N, 11°17′58″E; 450 m a.s.l.) (Table 1). The area is characterized by a mild Mediterranean climate. The vineyard in Sugame faced southwest and was characterized

Table 1
Summary of the sample groups, vineyard locations and interrow treatments.

Sample group	n[a]	Location	Treatment
SNN	6	Sugame (S)	No green cover, no inoculum (NN)
SGN	6	(43°35′46″N)	Green cover, no inoculum (GN)
SGC	6	(11°21′36″E)	Green cover, commercial inoculum (GC)
SGL	6	475 m a.s.l.	Green cover, local inoculum (GL)
PNN	3	Panzano (P)	No green cover, no inoculum (NN)
PGN	6	(43°32′50″N)	Green cover, no inoculum (GN)
PGC	6	(11°17′58″E)	Green cover, commercial inoculum (GC)
PGL	6	450 m a.s.l.	Green cover, local inoculum (GL)

[a] n: number of treated interrows.

by a sandy clay loam soil. The Panzano property had a similar southwest orientation, but a more clay-rich, calcareous loam soil. Both properties cultivated *Vitis vinifera* L. cv. Sangiovese vines trained with the Guyot method. The scions were grafted on either 1103 Paulsen (Sugame) or 420A (Panzano) rootstocks. Both producers adhered to organic viticultural standards (Regulation EU 2018/848); however, in Sugame, the interrows were tilled only once a year, favoring the incorporation of naturally occurring vegetation as green manure; while in Panzano, tillage was repeated as required as part of a more intense mechanical weed management, resulting in elevated soil disturbance and decreased interrow vegetation continuity.

2.2. Treatments and experimental design

Three experimental treatments aiming at improving soil health were introduced in both vineyards: interrow green cover (GN), interrow green cover with a commercial microbial inoculum (GC) and interrow green cover with a local microbiome inoculum (GL) (Table 1). Control parcels (NN) were maintained according to the long-term agronomic practices of the vinegrowers.

The interrow green cover treatment without microbial inoculum (GN) was established by sowing a mix of seeds of *Trifolium alexandrinum* L., *Trifolium incarnatum* L., *Vicia sativa* L., *Avena sativa* L., *Hordeum vulgare* L., *Phacelia tanacetifolia* Benth., *Sinapis alba* L. and *Raphanus sativus* L. (Locci Agricoltura, Castelfiorentino, Italy). The AMF-based field inoculum treatments (GC, GL) were introduced together with the same mix of seeds at the time of sowing. A commercial inoculum – Rizotech Plus (MS Biotech, Rome, Italy) containing 10% *Glomus* spp., 1×10^8 colony forming unit (CFU)/g rhizosphere bacteria and 1×10^6 CFU/g *Trichoderma* spp. – was utilized for the GC treatment. The local microbiome inoculum was sourced from experimental fields previously characterized as AMF biodiversity hot spots (Njeru et al., 2015) located in the "Selve Costiere di Toscana" UNESCO Man and Biosphere Reserve (Pisa, Italy) and maintained by the Interdepartmental Centre of Agro-Environmental Research 'Enrico Avanzi' (CIRAA), University of Pisa. Native AMF populations residing in the collected field soil were maintained in pot cultures using *Medicago sativa* L. as host plant. After several reproduction cycles, the pot substrate containing colonized roots and AMF propagules was applied as crude inoculum for the GL treatment. The taxonomic composition of the AMF community dwelling in the high-diversity GL inoculum was assessed in triplicate (Fig. S1) according to the molecular methods of Koskey et al. (2023) and the bioinformatic pipeline of the present study.

The experiment was conducted in two randomized blocks in each vineyard, where each treatment occupied 3 adjacent interrows per block. Unfortunately, the variability of soil conditions did not permit the establishment of the NN treatment within the second block in Panzano, therefore, the PNN samples for the mycorrhizal inoculum potential (MIP) and grape and wine quality measurements were collected in duplicates within the same parcel (Table 1).

Seeds for the GN, GC and GL interrow vegetation treatments were sown in May 2023, according to the manufacturer's instructions. At the same time, GC parcels received the commercial inoculum at a rate of 10 Kg/ha, while the GL interrows were treated with the local microbiome inoculum at a rate of 18 Kg/ha. Soil and mature grape samples were collected at the time of harvest in September 2023.

2.3. Soil sampling

For each replicate parcel, soil samples were taken in the middle, along the longitudinal transect of the central interrows. In each central interrow, 3 samples were collected at the distances of 5 m, 10 m and 15 m from the beginning of the grapevine row. For sampling 5–20 cm below the soil surface, a steel Edelman auger (d = 4 cm) (Eijkelkamp, Giesbeek, The Netherlands) was used. The individual samples were homogenized on site. Soil aliquots were separated for DNA extraction and transported to the laboratory on ice. The remaining soil was pooled for each sampled interrow, creating the reserve for soil chemical analysis and the substrate for MIP measurements.

2.4. Soil chemical analysis

Soil properties were determined by ISVEA (Eurofins, Poggibonsi, Italy), in accordance with standard procedures. Soil pH was measured in water (ISO 10390). Total and active $CaCO_3$ contents were analyzed according to the ISO 10693 and NF X31-106 procedures, respectively. Total nitrogen (N) content was determined with the modified Kjeldahl method (ISO 11261). Cation exchange capacity (CEC), SOM ratio and Olsen P content were tested according to internal standards (MT-CED, MT-COR and MT-OLS, respectively). Exchangeable K^+, Mg^{2+}, Ca^{2+} and Na^+ were quantified following the NF X31-108 manual. Cu, Zn and Mn were measured as required by the NF X31-120 procedure, while B was extracted in boiling water, and determined with internal methods (MT-BOR).

2.5. Mycorrhizal inoculum potential (MIP)

The infectivity of the experimental field soil was quantified by mycorrhizal inoculum potential (MIP) test. Briefly, *Cichorium intybus* L. "Zuccherina di Trieste" seeds were sown in 50 mL sterile Falcon tubes filled with 40 mL of homogenized and air-dried soil substrate. Five replicate tubes were prepared for each sampled interrow. After emergence, *C. intybus* plantlets were thinned to 3 plants per tube. The tubes were closed in transparent Sun bags (Sigma-Aldrich, St. Louis, MO, USA) and maintained in a growth chamber with 24/21 °C day/night temperatures and 16/8 h light/dark cycles. The plants were watered as needed, and they were provided with 2 mL of sterile modified Hoagland's solution (Hoagland and Arnon, 1938) containing ½ strength of the standard KH_2PO_4 concentration once a week. After 4 weeks of growth, the plants were extracted from the tubes, and their root systems were stained with 0.05% Trypan blue solution (Turrini et al., 2017). MIP was calculated as the proportion of colonized root length within the sample, determined by the grid-line intersect method (Giovannetti and Mosse, 1980).

2.6. Soil DNA extraction and the assessment of AMF diversity

Genomic DNA was extracted from 500 mg of soil samples using the FastDNA Spin Kit for Soil (MP Biomedicals, Solon, OH, USA), following the manufacturer's instructions. The concentration and the purity of the DNA extracts was confirmed by measurements on a Nanodrop ND-1000 device (Thermo Fisher Scientific, Wilmington, NC, USA) and by electrophoresis in 1% agarose gel stained with Midori Green Advance (Nippon Genetics, Tokyo, Japan).

For the in-depth assessment of the resident AMF community based on partial 18S rDNA sequences, an approach similar to that of Koskey et al. (2023) was implemented. Briefly, 1:10 diluted DNA samples were amplified by polymerase chain reaction (PCR) in a T100 thermocycler (Bio-Rad Laboratories, Hercules, CA, USA) using the *Glomeromycota*-specific AML1 / AML2 primer pair (Lee et al., 2008). The reaction mixture contained 1× Platinum™ Taq buffer, 2 mM $MgSO_4$, 0.2 mM dNTPs, 0.2 mM of each primer, 1 U of Platinum™ Taq (Invitrogen, Waltham, MA, USA) and 5 µL of template in a final volume of 25 µL. The thermal cycle consisted of 1′ of initial denaturation at 94 °C, 20 cycles of 30″ of denaturation at 94 °C, 40″ of annealing at 59 °C and 1′ of elongation at 68 °C, concluded by 7′ of final elongation at 68 °C. The PCR products were purified with the QIAquick PCR Purification Kit (Qiagen, Hilden, Germany), following the manufacturer's instructions, except the DNA was eluted in 50 µL of UltraPure H_2O (Merck, Darmstadt, Germany). Subsequently, 1:2 diluted purified DNA samples were subjected to a second, nested PCR step utilizing the nu-SSU-0450-5′ / nu-SSU-0899-3′ primer pair completed with heterogeneity spacers and Illumina

adapters, according to Stefani et al. (2020). The reaction mixture was similar to that of the first PCR, but a concentration of 0.4 mM for each primer set, 0.5 U of Platinum™ Taq and 2.5 μL of template was used in a final volume of 12.5 μL. The thermal cycle consisted of the same initial and final steps, while 25 cycles of 30″ of denaturation at 94 °C, 30″ of annealing at 59 °C and 45″ of elongation at 68 °C were executed in between. The success of the amplification procedure was confirmed by 1% gel electrophoresis.

Nested PCR products were treated with Thermolabile Exonuclease I (New England Biolabs, Ipswich, MA, USA), indexed using the Nextera XT DNA Library Preparation Kit (Illumina, San Diego, CA, USA), and normalized with the SequalPrep™ Normalization Plate (Thermo Fisher Scientific). Libraries were sequenced following the paired-end 300 bp protocol on an Illumina MiSeq device in the facility of BMR Genomics (Padua, Italy).

Raw sequence libraries were demultiplexed, and processed in the USEARCH v11 pipeline (Edgar, 2010). The primers were removed with Cutadapt v3.5 (Martin, 2011). Paired-end reads were merged and filtered for a maximum expected error threshold of 1.0. The assembled reads were dereplicated, and error-correction was performed using the UNOISE2 algorithm (Edgar, 2016a) with default parameters to generate the zero-radius operational taxonomic units (zOTUs). Chimeras were removed with the UCHIME2 tool (Edgar, 2016b). Subsequently, the reads were mapped against the zOTUs with default parameters. Taxonomic assignment for each zOTU was performed in R v4.2.1 (R Core Team, 2024) using the *assignTaxonomy* function of *dada2* v1.24.0 package (Callahan et al., 2016) with 70% confidence against a custom database (Online Resource 1), which was adapted from the Maarj*AM* SSU reference database v2021 containing virtual taxon (VTX) type sequences (Öpik et al., 2010) truncated at the binding site of the reverse primer (ca. 310 bp) and updated according to the current *Glomeromycota* taxonomy of GlobalAMFungi v1.0 (Větrovský et al., 2023), amended with the changes proposed by Kaonongbua et al. (2010) and Błaszkowski et al. (2022) regarding the genera *Kuklospora* and *Claroideoglomus*, as implemented by www.amf-phylogeny.com v04.2024. All zOTUs unclassified at the level of genus were searched by BLAST in the NCBI GenBank (www.ncbi.nlm.nih.gov/genbank), GlobalAMFungi and Maarj*AM* databases, considering the closest hits with 100% of query cover and at least 98% of identity. The sequences were deposited at the NCBI BioProject archive (https://www.ncbi.nlm.nih.gov/bioproject/) under the accession number PRJNA1298164 (SAMN50255625 - SAMN50255669).

2.7. Harvest and wine fermentation

Mature Sangiovese grapes from the two vineyards were handpicked at harvest in September 2023. Bunches were collected by selecting them along the entire length of the central row of each replicate treatment, mounting to a total of ca. 15 Kg of grapes per parcel. The samples were transferred to the laboratory for grape analysis and fermentation trials.

For the assessment of grape and wine quality, bunches were destemmed manually, and the berries were mixed well in a plastic bag creating a homogeneous lot for each sampled plot. Aliquots of 500–600 g of grapes were obtained for grape analysis. Berries destined for wine making were crushed and poured into steel tanks (10 L each). The musts were inoculated with 2×10^6 CFU/mL of *Saccharomyces cerevisiae* Lalvin ICV Opale 2.0 (Lallemand, Montreal, Canada) and supplied with 30 mg/L of SO_2. The tanks were maintained at 24 °C, and the depletion of sugars was monitored until the completion of the fermentation process. Afterwards, fermented musts were transferred into new tanks for cold stabilization at 4 °C for 40 days, and then the finished wines were bottled.

2.8. Grape and wine chemical analysis

Glucose and fructose concentrations were quantified using high performance liquid chromatography (HPLC) according to the method reported by Guerrini et al. (2018), utilizing a Rezex ROA-Organic Acid H+ (8%) column (8 μm particle size, 300 × 7.8 mm) (Phenomenex, Torrance, CA, USA), a ProStar 210 chromatograph equipped with a diode array detector (DAD) at 210 nm, and a refractive index detector in series (Varian Inc., Palo Alto, CA, USA). Tartaric acid, malic acid, ammoniacal N, free amino N, K^+ and Ca^{2+} concentrations were determined enzymatically through an automatic multi-parametric Hyperlab Plus analyzer (Steroglass, San Martino in Campo, Italy).

For determining the concentrations of anthocyanins, hydroxybenzoic acids, hydroxycinnamic acids, flavonols and flavan-3-ols in grapes, 40 berries were randomly selected respecting the relative proportion of each berry dimension in the aliquot. The berries were extracted in 150 mL of solvent (methanol: water: formic acid [500:485:15]) according to Rodríguez Montealegre et al. (2006) and macerated overnight at 20 °C. Wines were analyzed after filtration through a 0.45-μm regenerated cellulose membrane syringe filter (Phenomenex, Torrance, CA, USA).

The individual anthocyanins were separated and identified by HPLC as previously described by Mangani et al. (2011). Anthocyanins were quantified at 520 nm, using malvidin-3-*O*-glucoside as the standard. For the determination of flavonols and flavan-3-ol monomers, the analytical conditions were identical to those reported by Guerrini et al. (2023).

Total phenolic index was measured as absorbance at 280 nm, color intensity was calculated as the sum of absorbance at 420, 520 and 620 nm, whereas tonality as the ratio of absorbance at 420 nm and 520 nm using a V-730 spectrophotometer (Jasco International, Tokyo, Japan) according to Mangani et al. (2020). Total SO_2 was determined using a Flash automatic titrator (Steroglass). All chemical assessments were performed in duplicates.

2.9. Statistical analysis

Soil properties were confronted within and between vineyard locations using the Kruskal-Wallis test in R v4.4.1 (R Core Team, 2024).

The statistical significance of the differences in MIP among treatments was calculated using one-way analysis of variance (ANOVA) and Tukey's HSD post-hoc test in PAST v4.13 (Hammer et al., 2001).

AMF metabarcoding results were elaborated in R, mainly relying on the *vegan* v2.6–8 (Oksanen et al., 2001) and *phyloseq* v1.48.0 (McMurdie and Holmes, 2013) packages. Alpha diversity indices (Chao1, richness [*S*], Shannon-Wiener diversity [*H*], inverse Simpson diversity [inv*D*] and Pielou's evenness [*J*]) were calculated at the zOTU level based on sequence pools rarefied to 19,785 sequences per sample (Fig. S2). The alpha diversity data was tested for its normal distribution with the Shapiro-Wilk test ($p < 0.05$), and for its homogeneity of variances between groups with Levene's test ($p < 0.05$). Statistically significant differences were investigated with one-way ANOVA or Kruskal-Wallis tests, according to the suitability of the data. Differential abundances at the genus level were evaluated by Kruskal-Wallis and post-hoc Dunn tests, while at the zOTU level, similarity percentage (SIMPER) tests within and between locations were carried out. The identity and classification of significant zOTUs were confirmed by BLAST as above. Beta diversity was assessed at the zOTU level, relying on unrarefied abundance data standardized with the Hellinger transformation. Non-metric multidimensional scaling (NMDS), permutational multivariate ANOVA (PERMANOVA, $N = 9999$) and the homogeneity of multivariate dispersions (permutest.betadisper, $N = 9999$) (Anderson, 2006) were computed based on unweighted and weighted UniFrac distances. The maximum likelihood tree was constructed with the *phangorn* v2.12.1 tool (Schliep, 2011) according to sequence alignments provided by *DECIPHER* v3.0.0 (Wright, 2016), assigning the root to the longest terminal branch. PERMANOVA tests were executed with the *MiscMetabar* v0.12.1 (Taudière, 2024) package. The ordination plots were visualized in OriginPro v2023b (OriginLab Corp., Northampton, MA, USA).

The impact of soil properties on the AMF community structure was examined with distance-based redundancy analysis (db-RDA) as

implemented in the *vegan* package, considering standard scaled explanatory variables, relative abundance data on the zOTU level and distances calculated with the unweighted UniFrac formula. Explanatory variables were fitted onto the ordination plot using the "envfit" function ($N = 9999$), which projects vectors by maximizing their correlation with the ordination axes. Only significant variables were retained. For the scope of this analysis, triplicate metabarcoding samples were pooled to match the respective soil chemical data.

Grape and wine chemical determinations were elaborated with one-way ANOVA and post-hoc Tukey's HSD tests within vineyard locations in Statistica v7.0 (StatSoft GmbH, Hamburg, Germany).

Spearman correlations between chemical and mycorrhizal soil health indicators and grape and wine characteristics were computed using the *Hmisc* v5.2–2 (Harrell, 2025) and *corrplot* v0.95 (Wei and Simko, 2024) packages. The assessed grape and wine features were limited to those displaying significant alterations according to interrow treatments.

3. Results

3.1. Chemical soil properties

Soil chemical analyses did not reveal any significant differences between treatments in either of the vineyards (Table S1, S2). On the other hand, most assessed soil attributes displayed considerable differences among the two locations. Sugame soils were characterized by higher SOM, total N, K^+ and Mg^{2+} contents, while Panzano was distinguished by its elevated soil pH and CEC, moreover, by higher $CaCO_3$, P, Ca^{2+} and Na^+ contents.

3.2. Vineyard soil mycorrhizal inoculum potential (MIP)

Results of the MIP analysis in *C. intybus* revealed 23.7–30.8% of colonization potential in Sugame, and 17.5–48.8% of colonization potential in Panzano (Table 2). One-way ANOVA indicated no significant differences among treatments in Sugame, but evidenced notable improvements with all sustainable agricultural measures in Panzano. In particular, the treatment applying the local microbiome inoculum accompanied by the green cover mix (PGL) was consistently associated with a 179% higher MIP with respect to the control (PNN).

3.3. The diversity and composition of resident AMF communities

According to the rarefaction curves, the Illumina MiSeq runs recovered 19,785–100,243 high quality reads corresponding to a total of 1324 zOTUs in the vineyard soil samples, allowing a highly detailed analysis of AMF biodiversity and community composition (Fig. S2).

At the level of zOTUs, Sugame had a core community of 653 zOTUs (83.2% of the sequence reads), while 189 unique zOTUs (represented by 2.2% of the dataset) were found exclusively in one of the interrow treatments (Fig. S3a). Likewise, in Panzano, the core community was composed of 358 zOTUs (corresponding to 92.6% of the reads), and 154 unique zOTUs were observed (occupying less than 1% of the total number of sequences) (Fig. S3b). Overall, a higher number of zOTUs were found in Sugame (1294 zOTUs) than in Panzano (797 zOTUs) (Fig. S3c).

In Sugame, all alpha diversity indices differed among the treatment groups, showcasing the lowest AMF diversity in SNN (Chao1, *S*), SNN and SGL (*H*, inv*D*) or SGL (*J*) samples, while all index values were significantly boosted by the green cover treatment without any microbial inocula (SGN), presenting an increment of 41.8%, 12.2% and 81.1% in zOTU richness, *H* and inv*D*, respectively, compared with SNN. Similarly, in Panzano, PNN and PGL samples showed the lowest richness (Chao1, *S*), however, such differences were not statistically significant (Table 3). Only the *H* and *J* indices showed significant variations according to the interrow treatments, highlighting reduced biodiversity in the PGN samples, and improvements of *H* and *J* with the application of the commercial inoculum (PGC) and the locally produced inoculum (PGL), respectively. Additionally, Sugame soils showcased consistently higher Chao1, *S* and *H* indices when compared with Panzano soils (Table S3).

Further differences in the community composition were revealed by the beta diversity analysis at the zOTU level, considering unweighted and weighted UniFrac metrics (Fig. 1). In both vineyards, the applied treatments caused significant shifts (PERMANOVA $p < 0.05$) in the mycorrhizal community structure according to unweighted distances (Fig. 1a, c), while the weighted metrics indicated no considerable dissimilarities (PERMANOVA $p > 0.05$) between groups (Fig. 1b, d). According to unweighted UniFrac, SNN and SGN samples that had not received external microbial inocula clustered together on the NMDS biplot, while SGC and SGL mycorrhizal communities showed more divergence (Fig. 1a). On the other hand, PGN and PGC samples demonstrated higher similarities to one another, whereas PNN and PGL treatments grouped separately (Fig. 1c). Remarkably, in Panzano, the local microbial inoculum (PGL) induced the largest alterations in the community structure with respect to the control (PNN) (Fig. 1c). Regarding the between-site differences, the beta diversity assessment revealed highly dissimilar resident AMF communities in the two vineyards (Fig. S4).

Based on db-RDA, soil properties had a limited contribution to the compositional differences among AMF communities under different treatments (Fig. S5a, b). In particular, in Sugame, while the two main axes captured 60% of the variance, none of the examined chemical variables explained the distribution of samples. In Panzano, the two main axes covered 56% of the variance, and pH, active $CaCO_3$ and Mg^{2+} contents appeared to be potential drivers of beta diversity. Conversely, between-site dissimilarities aligned well with the differences in soil chemical attributes (Fig. S5c). The first main axis (CAP1) represented 36% of the total variance, and separated the samples according to vineyard location. Soil pH, CEC, $CaCO_3$ content along with P, Ca^{2+}, Mg^{2+}, Na^+, Mn and B concentrations acted as potential chemical determinants of the multivariate distribution of mycorrhizal communities.

The compositional assessment of AMF communities indicated the prevalence of the orders *Glomerales* (66.8%), *Entrophosporales* (25.1%) and *Paraglomerales* (6.0%) and their type families in all vineyard soils. Eight identified genera (*Archaeospora*, *Diversispora*, *Entrophospora*, *Funneliformis*, *Glomus* sensu lato, *Paraglomus*, *Rhizophagus* and *Septoglomus*) and unknown *Glomeraceae* occurred with at least 1% of relative abundance, occupying 98.8–99.7% of the recovered sequences in both vineyard settings (Fig. 2), while other genera such as *Acaulospora*, *Ambispora*, *Pacispora*, *Racocetra* e *Scutellospora* were less represented (data not shown). The most abundant genera were *Glomus* sensu lato

Table 2
Statistical analysis (one-way ANOVA) of the mycorrhizal inoculum potential (MIP) within locations. For significant differences ($p < 0.05$), post-hoc Tukey's HSD test was applied ($p < 0.05$), and the results were reported as lower-case letters.

Location	Treatment	MIP (%)	
		Mean	SD
Sugame	SNN[a]	25.8	5.9
	SGN	30.8	5.9
	SGC	23.7	1.8
	SGL	27.3	5.6
	p-value	0.610	
Panzano	PNN	17.5 **c**	1.2
	PGN	26.2 **b**	1.8
	PGC	25.8 **b**	1.2
	PGL	48.8 **a**	1.8
	p-value	**< 0.001**	

[a] NN: no green cover, no inoculum; GN: green cover, no inoculum; GC: green cover, commercial inoculum; GL: green cover, local inoculum.

Table 3
Statistical analysis (one-way ANOVA or Kruskal-Wallis test) of the biodiversity indices of AMF communities within locations. For significant differences ($p < 0.05$), post-hoc Tukey's HSD test (ANOVA) or Dunn test (Kruskal-Wallis) was applied ($p < 0.05$), respectively, and the results were reported as lower-case letters.

Location	Treatment	Chao1		S[a]		H		inv$D$		J	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Sugame	SNN[b]	400.40 **b**	85.12	351.17 **b**	71.73	4.316 **b**	0.324	29.862 **b**	13.400	0.738 **ab**	0.037
	SGN	564.56 **a**	72.38	498.00 **a**	68.87	4.844 **a**	0.225	54.072 **a**	14.204	0.781 **a**	0.021
	SGC	520.13 **ab**	91.99	457.67 **ab**	80.71	4.737 **ab**	0.226	45.751 **ab**	13.375	0.775 **ab**	0.018
	SGL	457.31 **ab**	70.69	403.50 **ab**	59.54	4.382 **b**	0.274	29.863 **b**	14.139	0.731 **b**	0.033
	p-value	**0.011**		**0.010**		**0.005**		**0.013**		**0.039**	
Panzano	PNN	277.73	12.57	258.00	11.53	4.244 **ab**	0.194	32.301	6.946	0.764 **ab**	0.035
	PGN	356.33	53.37	306.67	45.83	4.095 **b**	0.115	24.996	5.099	0.717 **b**	0.024
	PGC	349.89	38.94	315.17	30.33	4.384 **a**	0.203	35.905	13.098	0.763 **ab**	0.032
	PGL	315.39	36.95	285.00	34.77	4.345 **ab**	0.147	35.932	10.175	0.770 **a**	0.024
	p-value	0.053		0.138		**0.032**		0.207		**0.017**	

[a] S: richness; H: Shannon-Wiener diversity; inv$D$: inverse Simpson diversity, J: Pielou's evenness.
[b] NN: no green cover, no inoculum; GN: green cover, no inoculum; GC: green cover, commercial inoculum; GL: green cover, local inoculum.

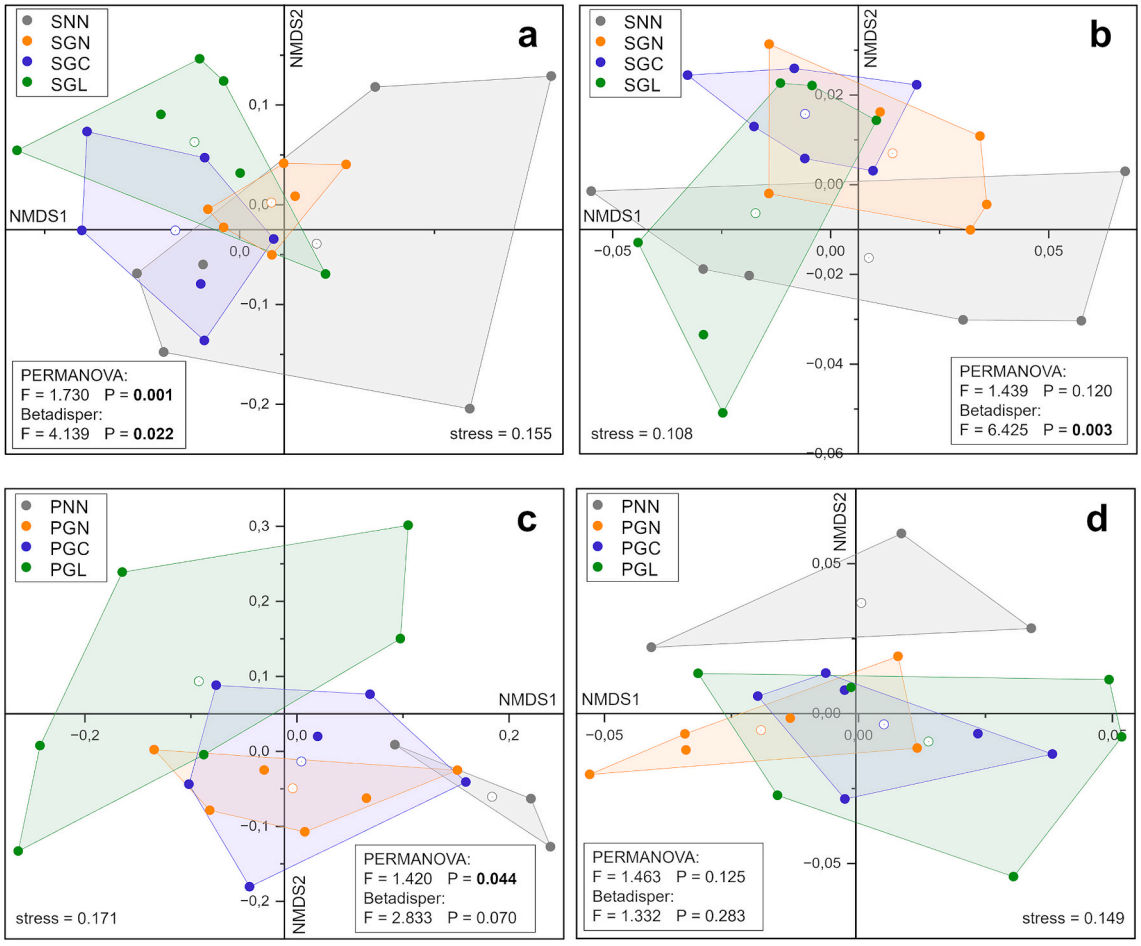

Fig. 1. NMDS and one-way PERMANOVA (factor: treatment) at the zOTU level, based on unweighted (**a**, **c**) or weighted (**b**, **d**) UniFrac distances in Sugame (**a**, **b**) and Panzano (**c**, **d**). Centroids were filled with white. Labels as in Table 1.

(42.9–60.0%), *Entrophospora* (17.2–29.3%) and *Septoglomus* (12.9–18.8%) in Sugame, and *Glomus* sensu lato (51.7–60.4%), *Entrophospora* (23.0–37.1%) and *Paraglomus* (5.1–10.9%) in Panzano. In Sugame, the genus *Archaeospora* and unknown *Glomeraceae* were more represented in the GN and GC treatments (Fig. S6). Moreover, five of the dominant AMF genera showed differential abundance among the two vineyard locations; namely, *Diversispora*, *Septoglomus* and unknown *Glomeraceae* favored Sugame, while larger populations of *Paraglomus* and *Rhizophagus* were dwelling in Panzano (Fig. 2).

According to the similarity percentage (SIMPER) assessment, in Sugame, interrow treatments were discriminated by 9 *Glomeromycota* zOTUs corresponding to *Septoglomus viscosum*, *Glomus* sensu lato spp. and *Entrophospora* sp. that were differentially abundant ($p < 0.05$), and contributed at least with 1% to the pairwise between-group divergences (Fig. 3a). In particular, zOTU_515 (*Glomus* sensu lato sp. VTX00064) was indicative of the SGC treatment. In Panzano, 14 differentially abundant mycorrhizal zOTUs were revealed, classified as *Glomus* sensu lato spp., *Paraglomus* sp. and *Entrophospora* sp. (Fig. 3b). The elevated abundance

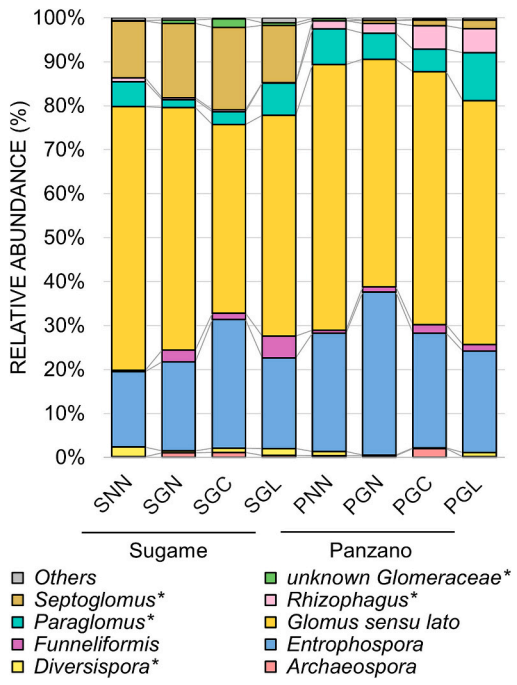

Fig. 2. The relative abundance of the dominant AMF genera (> 1%) in Sugame and Panzano. Asterisks mark differentially abundant (Kruskal-Wallis test, $p < 0.05$) taxa among vineyard locations. Labels as in Table 1.

of zOTU_793 (*Paraglomus* sp. VTX00001), zOTU_1214 and zOTU_180 (*Glomus* sensu lato sp. VTX00214) distinguished PNN samples, while PGL soils were characterized by zOTU_526 (*Glomus* sensu lato sp. VTX00069), zOTU_224 and zOTU_537 (*Glomus* sensu lato sp.) when compared with PGC and PGN treatments. Interestingly, *Glomus* sensu lato sp. VTX00342, and especially zOTU_437 appeared to be associated with GN samples in both vineyards. Between-site variations were mostly related to *Entrophospora* spp., *Glomus* sensu lato spp., *Paraglomus laccatum* and *Septoglomus viscosum* (Fig. S7). While zOTUs of *Septoglomus viscosum* VTX00063, *Paraglomus laccatum* VTX00281 and an unidentified *Entrophospora* sp. were linked to Sugame, other zOTUs belonging to *Entrophospora* sp. VTX00056, *Paraglomus laccatum* VTX00281 and several *Glomus* sensu lato sp. virtual taxa were found characteristic for Panzano soils.

3.4. *Sangiovese grape chemical attributes*

Grapes harvested from separate treatments showed different chemical profiles (Table S4). In Sugame, potassium (K^+) concentration was suppressed by the SGN and SGC treatments, while ammoniacal N content was elevated by SGN and diminished by SGL. Although the overall alterations were significant also for tartaric acid and free amino N contents, none of the treatment groups displayed substantial differences compared to SNN. On the contrary, the tartaric acid concentration varied significantly in Panzano grapes, reaching its highest and lowest values in PGC and PNN, respectively. In Sugame, the amount of anthocyanin-3-*O*-glucosides (cyanidin-3-*O*-glucoside and peonidin-3-*O*-glucoside in particular) was strongly influenced by the interrow

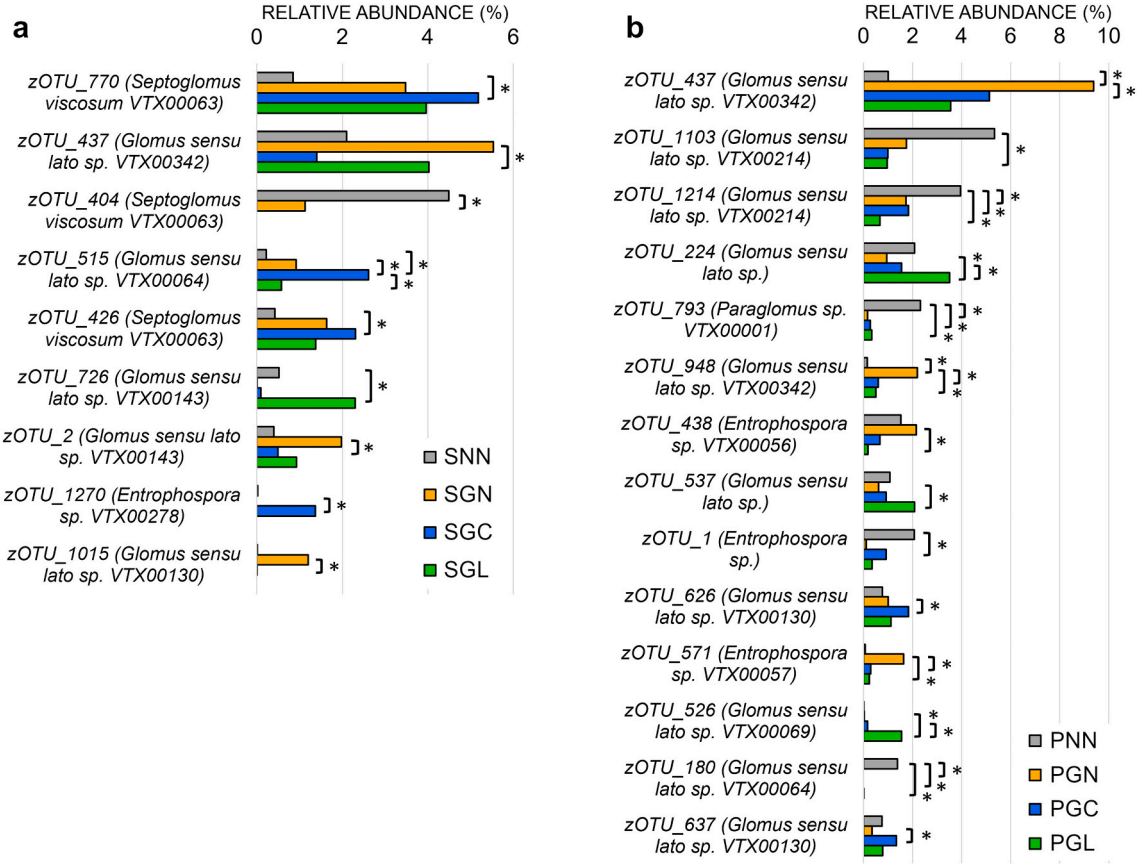

Fig. 3. SIMPER analysis of the AMF zOTUs differentially abundant among treatments in Sugame (**a**) and Panzano (**b**). Asterisks mark significant differences ($p < 0.05$). Only zOTUs with a contribution of ≥ 1% to the pairwise dissimilarities were considered. Labels as in Table 1.

treatments, showing a consequent accumulation in the SGN samples; furthermore, flavan-3-ol and catechin concentrations responded positively to any treatment involving the application of the green cover (SGN, SGC, SGL). Grape methylgallate content followed different tendencies, depleting completely in the SGN treatment. In Panzano, similar changes could be detected only for the cyanidin-3-*O*-glucoside.

Interestingly, soil AMF biodiversity strongly and positively correlated with grape anthocyanin-3-*O*-glucoside concentrations, but displayed a negative association with grape K^+ content in Sugame (Fig. S8). In Panzano, mycorrhizal richness (*S*) was positively correlated with grape tartaric acid content.

3.5. Sangiovese wine chemical analysis

Following the fermentation and cold stabilization of grape musts, wine physical characteristics and chemical profiles showed divergence according to the interrow treatments; however, most of these effects remained dependent on the vineyard location (Table S5).

In Sugame, wine color intensity has been enhanced in the SGN samples, while in Panzano, tonality was reduced in both microbial inoculation treatments (PGC, PGL). K^+ content was suppressed only in wines originating from the PGC parcels (Table S5).

The experimental interrow treatments strongly influenced the total amount and the profile of anthocyanins in the produced wines in Sugame, while no similar impact was observed in Panzano. In particular, almost all measured anthocyanin-3-*O*-glucosides reached significantly higher concentrations in the SGN and SGC plots, whereas vitisin A and B were depleted in the SGC wines. On the other hand, in Panzano, only the amount of malvidin-3-*O*-glucoside was affected, reaching higher concentrations in wines originating from plots treated with microbial inocula (PGC, PGL) (Table S5).

Among hydroxybenzoic acids, syringic acid was less concentrated in the SGC treatment compared with the control samples (SNN), while in Panzano wines, syringic and gallic acids have been augmented by the PGN treatment compared to the control (PNN) samples. In Sugame, interrow management had a significant influence on the total amount and on the profile of hydroxycinnamic acids as well. Notably, SGC parcels reached the highest concentrations for most, while such differences were less pronounced in Panzano. In the case of flavan-3-ols, wines from Panzano expressed a stronger response to the treatments, especially to that of the green cover mix (PGN), while in Sugame, only the catechin concentration was increased by the SGC commercial microbial inoculation. The interrow treatments had less impact on flavonol contents; however, SGN and SGC augmented the concentration of myricetin-3-glucoside, while SGN and PGN reduced the concentrations of quercetin-3-galactoside and myricetin, respectively. Moreover, tryptophol content was increased 1.6-fold by SGC and 1.7-fold by PGL compared with their respective within-location controls (SNN, PNN), and the amount of total phenolic alcohols followed the same trends in Sugame. Additionally, in Sugame, SGC wine samples showed a significant 1.4-fold increase in their contents of polymeric phenolic compounds compared to SNN (Table S5).

Remarkably, mycorrhizal biodiversity indices showed strong correlations with multiple wine chemical properties (Fig. S9). In Sugame, soil AMF diversity was positively associated with wine color intensity and anthocyanin-3-*O*-glucoside concentrations along with myricetin-3-glucoside, tryptophol and total phenolic alcohol concentration, while it had an opposite relationship with quercetin-3-galactoside. In Panzano, similar correlations were limited: only MIP and mycorrhizal richness (*S*) showed negative associations with cis-p-coumaric acid content and wine tonality, respectively. Nonetheless, soil CEC displayed correlations with catechin and myricetin-glycoside concentrations.

4. Discussion

Our work investigated the impact of an interrow green cover combined with either commercial or local microbial inocula on soil properties, on the resident AMF communities, as well as on grape and derived wine quality in two Mediterranean vineyards. To our knowledge, this is one of the first studies providing an insight into the ecology of vineyard AMF symbionts by high-throughput sequencing following manipulation by sustainable agricultural measures, and one of the few works assessing the effect of AMF inoculation on grape and wine physico-chemical attributes in field conditions.

4.1. Vineyard interrow sustainable management practices did not modify soil properties in the short term

Soil chemical variables, including main soil health indicators, remained unchanged for the duration of this study. This could be explained by the short timespan of the experiment; for example, in another case, two-year vineyard cover cropping treatments resulted in negligible alterations of the chemical soil properties (Fernando et al., 2024). According to Picone et al. (2025), sustainable viticultural management practices often needed decade-long continuous application for producing consistent and meaningful physico-chemical soil health improvements, however, biological responses are generally expected to be more rapid (Cusset et al., 2024; Semenov et al., 2025).

4.2. The interrow green cover practice combined with a local microbiome inoculum improved the vineyard soil mycorrhizal inoculum potential (MIP)

In Panzano, we found that the parcels treated with the local microbiome inoculum in combination with a vegetation cover possessed a significantly higher soil MIP compared with the control. Such differences were more moderate in other treatments and completely absent in Sugame. As suggested by the data recovered from control plots, AMF symbiotic networks may have been slightly impaired in Panzano soils due to a more intense interrow management, therefore becoming more responsive to the complex microbial inoculum that was providing a set of potential partners well adapted to local climatic and edaphic conditions. Mycorrhizal inoculation can be an effective tool for promoting soil health and productivity in agricultural contexts, despite previously published reports showing contrasting results (Berruti et al., 2016, 2017b; Pellegrino et al., 2011, 2012), supporting our variable results on AMF activity. In line with our findings in Panzano, recent studies suggested that soil environments with impoverished mycorrhizal communities (as showcased by our analysis of AMF diversity) may be suitable targets for AMF inoculation treatments (Bender et al., 2019; Holland et al., 2018). On the other hand, in Sugame, field AMF carrying capacities may have been already met by the native community (Verbruggen et al., 2013). Nevertheless, the commercial inoculum failed to improve MIP with respect to the sole green cover treatment at both locations. Indeed, concerns have emerged regarding the wide applicability and the production standards of commercial AMF-based inocula (Berruti et al., 2016; Salomon et al., 2022a, 2022b), while locally replicated microbial consortia may provide an alternative way for restoring and preserving soil health.

4.3. AMF biodiversity and community composition was significantly influenced by interrow green cover and mycorrhiza-based inoculum treatments

Our assessment of AMF community ecology revealed that sustainable interrow treatments enhanced mycorrhizal biodiversity in vineyard soils. In particular, the green cover alone was effective to increase mycorrhizal alpha diversity in Sugame, presumably by supporting the native AMF communities that were already characterized by a noteworthy biodiversity, as shown in the control parcels. On the other hand, in Panzano, the green cover alone was insufficient for significantly improving the biodiversity of arbuscular mycorrhizal symbionts.

However, inoculation treatments were able to raise the Shannon-Wiener diversity (*H*) and Pielou's evenness (*J*) indices, suggesting that Panzano – due to the more intensive management – has been deficient in naturally occurring mycorrhizal partners, and the external inocula aided soil health by enriching and equilibrating resident AMF communities.

Preserving mycorrhizal diversity has been suggested as a tool for promoting the long-term resilience of agro-ecosystems (Gianinazzi et al., 2010; Verbruggen and Kiers, 2010; Weber et al., 2025). Service crops, polycultures and even herbaceous weeds have been noted for their ability to boost AMF biodiversity in agricultural soils by improving the spatio-temporal consistency and biodiversity of available plant hosts (Guzman et al., 2021; Pellegrino et al., 2020; Radić et al., 2012; Shrestha et al., 2025; Verbruggen and Kiers, 2010), while conventional tillage was found to cause a 40% drop in mycorrhizal diversity metrics compared with no-till treatments (Brito et al., 2012). Indeed, similar to our results, organic management types involving green covers were shown to support a higher diversity of sporulating and root-colonizing AMF in Chilean (Aguilar-Paredes et al., 2024) and French (Battie-Laclau et al., 2025) vineyards.

Furthermore, our analysis of beta diversity indicated that the treatments had a significant influence on the structure of vineyard AMF communities. However, this effect may have mostly concerned the rare taxa, as such differences were evident only when considering unweighted distance metrics – an observation underpinned by the Venn diagrams as well. In particular, the treatment with local microbiota induced pronounced shifts at both locations, but most notably in Panzano, where native AMF may have been previously suppressed, as discussed above. Distance-based RDA revealed that within-site differences between AMF communities were barely aligned with chemical soil properties.

It is well established that agricultural management plays a key role in shaping soil microbiomes (Chou et al., 2018; Pingel et al., 2019; Schmidt et al., 2019; Velaz et al., 2025). Previously, mycorrhizal field inocula, herbaceous vegetation and organic practices were found to alter the composition of resident AMF communities in vineyards and other agro-ecosystems, although site- and genotype-specific interactions often occurred (Battie-Laclau et al., 2025; Islam et al., 2021; Moukarzel et al., 2024; Radić et al., 2012; Van Geel et al., 2017). On the other hand, mycorrhizal communities were shown to construct phylogenetic clusters on small spatial scales, regardless of soil chemical gradients (Horn et al., 2014), supporting the low explanatory power of chemical soil properties in our within-site comparisons. Interestingly, consistent with our results, other studies reported that mycorrhizal field inoculation did not lead to a widespread replacement of native taxa, while still exerting its beneficial effect on soil health (Arcidiacono et al., 2025; Berruti et al., 2017b; Nogales et al., 2021; Renaut et al., 2020).

Here, we recorded the dominance of the genera *Archaeospora*, *Diversispora*, *Entrophospora*, *Funneliformis*, *Glomus* sensu lato, *Paraglomus*, *Rhizophagus*, *Septoglomus* and unknown *Glomeraceae* in Chianti vineyard soils. Based on available data, the overall domination of *Glomeraceae* was expected, as many of its members can successfully proliferate in disturbed soils (Chagnon et al., 2013; Oehl et al., 2010; Torres et al., 2018a). Recently, sets of prevalent AMF taxa very similar to ours were described from vineyard soils and grapevine roots in New Zealand (Moukarzel et al., 2024), Spain (López-García et al., 2020) and France (Battie-Laclau et al., 2025). Conversely, utilizing a different sequencing workflow, both the works of Massa et al. (2020) and Cesaro et al. (2021) reported the absence of *Entrophosporaceae*, *Acaulosporaceae* and *Diversisporaceae* in grapevine rhizospheres from Piedmont (Italy), while our molecular approach was able to recover sequences affiliated with these families. Some of these discrepancies may be attributed to the peculiarities of glomeromycotan genetics, to the unresolved phylogeny of certain taxa, and to the lack of standard primer sets, sequencing strategies and optimized reference databases.

At the genus level, we observed a positive response of *Archaeospora* to all interrow green cover treatments in Sugame, similar to the abundance increases detected under oat-pea intercropping with respect to oat or pea monocropping (Lee et al., 2023), suggesting that elevated plant diversity may stimulate *Archaeospora* populations dwelling in agricultural soils. Moreover, we identified several zOTUs affiliated with *Septoglomus viscosum*, *Glomus* sensu lato spp., *Paraglomus* sp. and *Entrophospora* sp. that were stimulated or suppressed by the vineyard treatments, demonstrating the importance of intra-species diversity in AMF adaptation.

4.4. Between-site differences shaped the vineyard mycorrhizal communities

Confronting the data obtained from the two Chianti vineyards, we found that Sugame soils, that were subjected to relatively low-intensity cultivation over an extended period of time, had higher mycorrhizal activity in control conditions, and harbored richer AMF communities in general. Indeed, many conventional agronomic practices proved to be harmful to resident AMF, such as frequent tillage, the periodic lack of vegetation, reduced host plant diversity, excess inorganic fertilization and the dispersal of generic pesticides that may disrupt native mycorrhizal networks (Bowles et al., 2017; Trouvelot et al., 2015; Van Geel et al., 2017; Zaller et al., 2018).

Interestingly, the two vineyards were characterized by distinct AMF communities that conserved their structure even following the uniform interrow treatments. In this comparison, multiple soil chemical attributes emerged as potential drivers of sample distribution. The genera *Septoglomus*, *Diversispora*, *Paraglomus* and *Rhizophagus*, and several zOTUs affiliated with *Entrophospora* spp., *Glomus* sensu lato spp., *Paraglomus laccatum* and *Septoglomus viscosum* proved to be differentially abundant between sites. In fact, geographic location – and consequently, edaphic, climatic and other site-specific differences encompassed by the concept of *terroir* – was described as the main driver of AMF community assembly in vineyards so far (Battie-Laclau et al., 2025; Bouffaud et al., 2016), coincident with other observations regarding the broader grapevine-associated microbiota constructing the microbial *terroir* (Bokulich et al., 2014; Gobbi et al., 2022; Liu et al., 2019). Moreover, soil pH together with Mn and Zn contents were previously identified as important drivers of grassland mycorrhizal communities (Alguacil et al., 2016), while pH and soil type were found to determine the landscape-scale distribution of AMF across various habitats and land use types (Hazard et al., 2013).

4.5. The interrow green cover and the microbial inocula impacted grape and wine quality traits

Grapevines produce a wide variety of bioactive primary and secondary metabolites that are present in their berries and fermented juices (Ali et al., 2010). So far, there are plenty of reports on the impact of vineyard management practices on grape and wine quality (e.g. Cataldo et al., 2020a; Colì et al., 2024; Steiner et al., 2021), in which the grapevine-associated microbiota may play an important mediating role (Belda et al., 2017; Liu et al., 2019; Perpetuini et al., 2022).

In our assessment, grape and wine physico-chemical attributes were influenced by the use of interrow green cover and microbial inocula, however, such effects often appeared to be site-specific. Although cation contents and primary grape and wine metabolites were less affected by the treatments, the secondary metabolite profiles, associated with important organoleptic features and health-promoting potentials (El Rayess et al., 2024; Mitrović et al., 2024), differed greatly among interrow management practices. Interestingly, the concentrations of some of these phenolic compounds displayed significant (and mostly positive) correlations with soil AMF biodiversity.

Concordant with our data, vineyard cover cropping has been demonstrated to improve the quality of grapes, and consequently that of derived products, however, results may vary with cover crop and grapevine features, and with seasonal and regional differences (Abad

et al., 2021; Cataldo et al., 2020; Pérez-Álvarez et al., 2013; Tomaz et al., 2021). In line with our findings in cv. Sangiovese, interrow barley covers were found to decrease tonality, and to increase color intensity, polyphenol and anthocyanin contents in cv. Tempranillo grapes and wines from the first year of their introduction to the vineyard, while the concentrations of primary metabolites remained mostly unaffected (Pérez-Álvarez et al., 2013, 2015). Many of these changes may be ascribed to the competition between grapevines and service crops for available water and nutrient resources, resulting in a reduction of grapevine vigor (Cataldo et al., 2020; Nogales et al., 2021; Novara et al., 2021; Pérez-Álvarez et al., 2015).

Soil fungal communities – shaped by environmental and agronomic management factors – exert a multifaceted influence on the distinctive characteristics of regional wines (Belda et al., 2017; Cruz-Silva et al., 2023; Liu et al., 2020). The fundamental contributions of AMF to plant nutrition and health may translate into enhanced fruit quality traits, especially regarding the amounts of bioactive secondary metabolites, as it was observed in a variety of other crops (Avio et al., 2018). Indeed, when grapevines were grown in controlled conditions, mycorrhizal inoculation often stimulated the accumulation of sugars and phenolic compounds (Antolín et al., 2020; Torres et al., 2016, 2019), and systemic changes were detectable in the gene expression patterns as well (Velásquez et al., 2025). Remarkably, vineyard inoculations with mycorrhiza-based biostimulants delivered matching results in real-life conditions (Gabriele et al., 2016; Ganugi et al., 2023; Karoglan et al., 2021), confirming the data we obtained. In particular, Ganugi et al. (2023) documented an extensive reprogramming of grapevine primary and secondary metabolism following diverse mycorrhizal inoculation treatments, leading to the enrichment of phenolic acids, stilbenes and sugars in the produced berries. Similarly, Karoglan et al. (2021) registered higher concentrations of flavonols, flavan-3-ols, anthocyanins and total polyphenols in berry skins originating from plots that have been treated with a commercial mycorrhizal product. Furthermore, Gabriele et al. (2016) observed an increase of flavonol, flavonoid and total polyphenol contents in cv. Sangiovese wines produced in parcels receiving a mycorrhizal consortium inoculum. However, to our knowledge, there are no previous reports on positive correlations between soil AMF biodiversity and the enrichment of grape and wine phenolic profiles, nor on the negative association between soil mycorrhizal diversity and berry K^+ accumulation – another possible regulatory interaction that could hold technological potential (Mpelasoka et al., 2003).

Some of the aforementioned works described notably divergent responses in different grapevine varieties (Antolín et al., 2020), or to different mycorrhiza-based inocula (Ganugi et al., 2023), while our present paper showed contrasting effects according to vineyard location as well, underlining the relevance of viticultural context in mycorrhizal treatments. Indeed, some larger scale studies raised awareness of the context dependency of soil microbial research (Degrune et al., 2019; Steiner et al., 2023), while reports on the ecological impact of AMF field inocula are still very scarce, leaving ample space for future research (Hart et al., 2018; Rodriguez and Sanders, 2015; Valenzuela-Aragon et al., 2025). It is also important to note that higher AMF activity or diversity in the soil does not necessarily imply higher grapevine root colonization or better overall plant performance (Moukarzel et al., 2023; Nogales et al., 2021; Velaz et al., 2025). However, previous evidence showed that caring for soil health and maintaining an ample pool of potential microbial symbiotic partners can contribute to viticultural resilience (Moukarzel et al., 2024; Nogales et al., 2021; Rillig et al., 2019). Additionally, AMF in particular have been proposed as valuable assets in maintaining the quality of grape berries under climate change scenarios (Goicoechea et al., 2023; Torres et al., 2018a), rendering the related forthcoming research even more compelling and relevant.

5. Conclusions

In conclusion, our study showed that the high diversity local microbial inoculum combined with the interrow green cover boosted soil AMF activity in the more intensely managed vineyard. The sustainable agricultural treatments increased soil mycorrhizal biodiversity, and induced moderate, but significant shifts in the community structure. Nevertheless, the introduced AMF were not detrimental to the native communities. Furthermore, the applied treatments enriched grape and wine bioactive secondary metabolite profiles associated with organoleptic properties and health-promoting potentials. Remarkably, such improvements displayed positive correlations with soil AMF biodiversity. Nevertheless, the vineyard *terroir* appeared as an important modulating factor of outcomes.

As demonstrated here, service crops and mycorrhizal inoculation may be feasible options for improving soil health, microbial biodiversity and agro-ecosystem sustainability in viticulture, although further field studies would be necessary to elucidate long-term effects and interactions with the *terroir*.

CRediT authorship contribution statement

Gergely Ujvári: Writing – original draft, Methodology, Investigation, Formal analysis. **Agnese Bellabarba:** Writing – review & editing, Formal analysis. **Silvia Mangani:** Writing – review & editing, Methodology, Investigation, Formal analysis. **Matteo Daghio:** Writing – review & editing, Supervision, Methodology, Formal analysis. **Viola Galli:** Writing – review & editing, Formal analysis. **Lisa Granchi:** Writing – review & editing, Supervision, Funding acquisition. **Monica Agnolucci:** Writing – review & editing, Methodology, Funding acquisition, Formal analysis. **Alessandra Turrini:** Writing – review & editing, Methodology, Funding acquisition, Formal analysis. **Luciano Avio:** Writing – review & editing, Methodology, Funding acquisition, Formal analysis. **Giacomo Buscioni:** Writing – review & editing, Formal analysis. **Manuela Giovannetti:** Writing – review & editing, Supervision. **Simona Guerrini:** Writing – review & editing, Project administration, Funding acquisition, Conceptualization. **Carlo Viti:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization.

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Declaration of competing interest

The authors have no interests to declare.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.apsoil.2026.107129.

Data availability statement

The raw sequences obtained from the targeted Illumina MiSeq 18S rRNA gene sequencing were deposited at the NCBI BioProject archive (https://www.ncbi.nlm.nih.gov/bioproject/) under the accession

number PRJNA1298164 (SAMN50255625 - SAMN50255669).

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