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VITICULTURE ORIGINAL RESEARCH ARTICLES

Pedological origin and edaphic factors drive biota in vineyard soils of Northeast Italy

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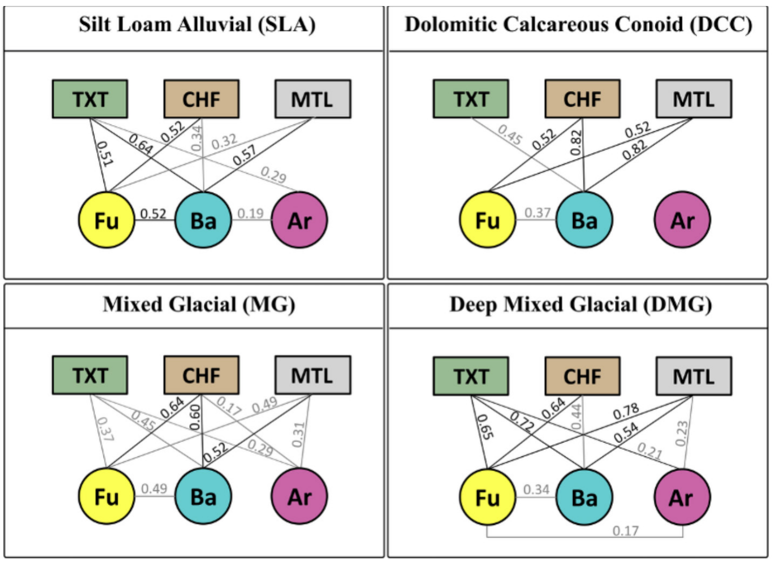
ABSTRACT

Soil biota is responsible for essential biological processes occurring in the soil. Biota composition, biodiversity and activity can be affected by soil properties, biogeography and human activities. This study, conducted in vineyards of Northeast Italy, aimed to understand the combined effect of edaphic and agronomic factors on the composition and biodiversity of soil biota in four soil types characterised by different pedological origin. The soil biota was studied by simultaneously investigating the composition and the biodiversity of fungal, bacterial and microarthropod communities and their interactions with abiotic factors. The results show that the impact of natural soil characteristics and viticulture activity on biota depends on soil type. Some fungal, bacterial and microarthropod community groups were characteristic only of certain soil types. Geographical position and edaphic factors mainly affected the composition of microbial communities, while microarthropods seemed to respond less to these variables. Depending on the origin of the soil, the biodiversity of the biota responded differently to viticulture practices. The study shows that understanding how natural and agronomic factors drive soil biota makes it possible to predict the effect of natural or artificial changes on soil biological processes.

KEYWORDS: bedrock material, biodiversity, soil biota, soil properties, viticulture



GRAPHICAL ABSTRACT. Spearman rank correlations between edaphic factors and soil biota ($p \leq 0.05$) in four vineyard soil types. The numbers represent the ρS value. **TXT** (texture): sand, silt and clay. **CHF** (chemical factors): pH, soil organic matter, total N, total cabonates and C/N. **MTL** (metals): available Cu, Zn, Pb and Cd. **Fu**: fungal community. **Ba**: bacterial community. **Ar**: microarthropod community.

INTRODUCTION

Biota represents one of the most significant components of soil. It includes a huge diversity of organisms such as plants, soil fauna and microorganisms (Fortuna, 2012). The microorganisms include bacteria, fungi, archaea and algae. Soil fauna is grouped according to size class: microfauna, 20-200 µm (mainly protozoa and nematodes), mesofauna, 0.2-2 mm (including microarthropods) and macrofauna, > 2 mm (including earthworms and macroarthropods) (Menta, 2012). Microorganisms provide a large number of functions: they are responsible for the nutrient cycle, are involved in the decomposition of organic matter and in C sequestration, contribute to the growth and nutrition of plants, limit parasite expansion (Schlatter *et al.*, 2017), reduce the toxicity of pollutants and improve chemical and physical soil properties (Gupta *et al.*, 1998). Mesofauna has a key role in decomposition processes, shredding dead organic matter, preparing the substrate for microbial attack and transporting nutrients through the soil (Fortuna, 2012); for this reason, interest in soil biota and its distribution in the environment has increased rapidly in recent decades. Several studies have investigated the ecosystem services and functions supplied by the soil community and the impact of natural and anthropic stresses on biotic activities (Coller *et al.*, 2019; Guerra *et al.*, 2022). Soil properties, habitat, biogeography and land use guide the composition and biodiversity of microbiota (Xue *et al.*, 2018; Zheng *et al.*, 2019) and soil fauna (Keith *et al.*, 2006; Minor & Cianciolo, 2007). A study by Nielsen *et al.* (2010) showed that the composition of soil communities is strongly influenced by soil properties. The differentiated responses of distinct groups (mites, fungi, bacteria and archaea) highlight their potential usefulness as bio-indicators of soil degradation. The influence of individual soil characteristics on biota composition and biodiversity has been well demonstrated (Rousk *et al.*, 2010; Brockett *et al.*, 2012), but the scientific literature lacks studies that consider edaphic properties and soil origin as a matrix and that investigates their combined effect on the soil community. Zheng *et al.* (2019) demonstrated for the first time that, compared to individual variables, a combination of soil factors increased the influence of the soil environment on bacterial and fungal community composition and diversity. Moreover, several studies have proved that anthropic activities affect soil biodiversity, compromising ecosystem functioning and reducing its ability to respond and adapt to stresses (Wertz *et al.*, 2007; Gardi *et al.*, 2013). An example is the use of copper as a fungicide in viticulture, which reduces the abundance and biodiversity of the soil bacterial community (Li *et al.*, 2015). de Boer *et al.* (2012) found the structure of a microbial community to exhibit the historical impact of Cu contamination, and the analysis of Collembola *Folsomia candida* gene expression showed it was related to the level of bioavailable Cu. Numerous studies have reported a decrease in the abundance of some Collembola species and an increase in the abundance of species tolerant to metal pollution (Filser *et al.*, 2000; Fiera, 2009). Therefore, soil biodiversity and community structure can be excellent indicators of soil quality and good predictors of environmental changes (Arias *et al.*, 2005).

The novelty of this study is that it aimed to understand the combined effect of pedological and edaphic factors and agronomic practices on the composition and biodiversity of soil biota in the vineyard. For this reason, we investigated fungal, bacterial and microarthropod communities simultaneously, and we set out to identify the dominant natural and viticultural factors driving the biota of different pedological sites in order to predict the effect of natural or artificial changes on biological processes. For this purpose, we investigated soil properties (texture, total carbonates, soil organic matter, total nitrogen and pH) and available concentrations of four metals (Cu, Zn, Pb and Cd), which are the main metals involved in plant protection and fertilisation (Mantovi *et al.*, 2003). We hypothesised that pedological origin, soil characteristics and agricultural practices affect the three components of the soil communities, which were studied in different ways, and that their response to viticultural impacts depends on their adaptability to natural soil properties.

MATERIALS AND METHODS

1. Site description and soil collection

Twelve sites (vineyards) located in a valley in Trentino (Northeast Italy) were investigated. The area covers 230 km^2 in a N-S direction and is crossed by the Adige River. The south-western part of the area is characterised by the presence of several lakes. According to the *Köppen-Geiger* climate classification, the entire area is classified as being warm-temperate (*Cfb*). The sites differ in their associated bedrock material and the soils are classified as four types:

- silt loam alluvial (SLA) - soils widespread in the valley floor and developed on fine, calcareous, deep and hydromorphic alluvial deposits
- dolomitic calcareous conoid (DCC) - soils originating from dejection cones at the base of the slopes; superficial to shallow, extremely calcareous and very skeletal
- mixed glacial (MG) - soils on moderately deep glacial materials with mixed lithology, dominant in hilly, calcareous and moderately skeletal areas
- deep mixed glacial (DMG) - soils on deep glacial materials with mixed lithology, present in hilly sub-flat areas, very deep and slightly calcareous.

The soil types were also characterised according to their elevation, available water capacity (AWC) and soil texture (Figure S1). For each soil type, three previously uninvestigated sites were identified in different geographic positions (Figure S2, Table S1). Six replicates per site were chose at the centre of the inter-rows. A random sampling design was used and the edges of the vineyard were omitted from the sampling. The Figure S3 shows the sampling design. Sampling was conducted in spring 2017. Table S1 shows some details that help contextualise the sites: municipality, site elevation, soil texture class and AWC (data collected from Trentino Soil

Map - http://meteogis.fmach.it/cartaSuoli/indexnew.php), vineyard planting year, agronomic management, soil history (data collected from the registers of agronomic practices supplied by farmers) and the average of meteorological parameters over the previous ten years (data collected from the network of meteorological stations of Trentino - https://meteo.fmach.it/meteo/index.php). In all the vineyards, the ground was covered with permanent grass.

For microarthropod analysis, soil cubes of (10 × 10 × 10) cm^3 were sampled between the rows. For the chemical and metataxonomic analyses, the soil was collected from the 0-20 cm layer after removal of the first few millimetres of the surface organic layer. Each sample (replicate per site) consisted of four cores sampled from around the sampled cube for microarthropod analysis and homogenised to obtain a representative sample. For each analysis type, 72 samples were assessed.

2. Soil properties

Chemical and texture analyses were carried out on the air-dried fine soil fraction (< 2 mm). Soil texture was determined as percentage of sand (2 mm - 50 µm), silt (50 µm - 2 µm) and clay (< 2 µm) by wet sieving and hydrometric assay of soil dispersant solution (sodium hexametaphosphate). The pH was measured using a pH meter on the soil-water suspension (*w/v* 1:2.5). Total carbonates were determined from powdered samples by volumetric method, measuring evolved CO_2 after the addition of HCl. Organic carbon content was obtained by calculating the difference between total carbon - measured by Dumas combustion of powdered soil and thermal conductivity detection using a CN analyser - and total carbonates. Soil organic matter (SOM) content was calculated using the determined organic carbon content (conversion factor 1.724). Total nitrogen (N) was measured simultaneously with total carbon. The available fraction of Cu, Zn, Pb and Cd were extracted in a DTPA solution and their concentrations were detected by ICP-OES.

3. Microbial community

For the soil microbial community analysis, total DNA was extracted from 0.25 g of fresh fine earth fraction (< 2 mm) that had been frozen at -80 °C immediately after sampling. To this end, a Power Soil DNA isolation kit (MO BIO Laboratories Inc., CA, USA) was used. Soil DNA amplification was performed using primers 515F (50-GTGYCAGCMGCCGCGGTAA-30) and 806R (50-GGACTACNVGGGTWTCTAAT-30) specific to the bacterial and archaeal 16S rRNA gene (Caporaso *et al.*, 2011), and ITS1F (50-CTTGGTCATTTAGAGGAAGTAA-30) (Gardes *et al.*, 1993; Berruti *et al.*, 2017) and ITS2 (50-GCTGCGTTCTTCATCGATGC-30) (White *et al.*, 1990) specific to the fungal ITS1 region. DNA purification, indexing, quantification, preparation of libraries for Illumina MiSeq (PE300) sequencing, data pre-processing and subsequent taxonomic classifications of operational taxonomic units (OTUs) were performed as previously described by Coller *et al.* (2019). The *de novo* greedy algorithm (MICCA) with 97 % identity was used to cluster the filtered sequences into OTUs. Subsequently, the Ribosomal Database Project (RDP) Classifier v2.11 was applied for taxonomic classification (Wang *et al.*, 2007) as described by Coller *et al.* (2019). Finally, a total of 3,551,358 amplicon sequences of the V4 region of the 16S rRNA gene and 4,585,869 sequences of the ITS region were acquired from 72 soil samples. The 16S and ITS sequences were clustered into 24,355 and 7,856 OTUs (97 % identity), respectively. The 16S and ITS sequences were rarefied evenly at 16,000 and 22,000 reads per sample, respectively. After rarefaction, the dataset consisted of 21,840 prokaryotic OTUs (henceforth referred to as "bacterial") and 6,929 fungal OTUs. The OTUs identified 409 bacterial and 314 fungal genera.

4. Microarthropods

The microarthropod community was assessed by taxa composition, abundance (number of individuals per m^2) and QBS-ar quality index. The latter is based on a direct correlation between soil quality and the number of microarthropods well-adapted to the soil habitat. QBS-ar divides the organisms into morphological classes according to their capacity to adapt to the environment and each "biological form" receives an ecomorphological score (EMI) within a range of 1 to 20, commensurate with its adaptation level (Menta *et al.*, 2008). The microarthropods were extracted from the soil samples using a Berlese-Tullgren funnel (Wallwork, 1970). The extracted individuals were observed using a stereomicroscope and assigned to the suitable biological form. The QBS-ar score represented the total of the highest EMI values of each taxon (Parisi *et al.*, 2005).

5. Statistical analysis

R software version 4.2.1 was used for the statistical analysis. The Wilcoxon non-parametric statistical test - with FDR correction following the Benjamini-Yekutieli procedure - was run to identify which parameters differed significantly under different conditions ($p \leq 0.05$). The same italic letters indicate non-significant differences. The richness and diversity indices (number of taxa - S, Chao1 index, Shannon index - *H'* and Pielou index - *J*) were calculated by the functions of the vegan R package. Site characteristics (elevation, available water capacity- (AWC) and texture) were determined using factor analysis for mixed data (FAMD) (FactoMineR package). The variance in microbial (bacterial and fungal OTUs) and microarthropod (taxa) composition was analysed by non-metric multidimensional scaling (NMDS) based on Bray-Curtis dissimilarity and 999 permutations (vegan R package). The significance of the differences between the communities of various soil types was tested using analysis of similarity (ANOSIM) (vegan R package). Non-parametric correlation test (Spearman correlation) was used to estimate the relationships between edaphic parameters and the biota. We considered correlations with $p \leq 0.05$ and $\rho S \geq |0.5|$ to be significant. The Mantel test was performed to evaluate Spearman rank correlations between single factors. Functional prediction of bacteria and fungi was calculated using Faprotax v1.2.10 (Louca *et al.*, 2016) based on 16S and ITS data, respectively (microeco R package).

RESULTS

1. Chemical and physical characteristics of soil types

The texture of the four soil types in the twelve sites varied from loam to silt loam to sandy loam. In detail, SLA was characterised by a higher silt level than the others, DCC and DMG soils had a higher clay content, while MG soils showed a lower silt and a higher sand content than the other soil types (Table 1). All soil types were subalkaline. DCC and MG soils had the highest levels of carbonates and organic matter, while DMG soils showed the lowest total carbonate values and C/N ratio, and organic matter and total N that were half of DCC soils (Table 1). The available Cu concentration in the four soil types was on average in the range of 76-136 mg kg^{-1} d.w., and MG soils had the highest mean value of all soils. DCC and MG soils contained the highest available fraction of Zn. The available Pb concentration was higher in the two glacial soils (MG and DMG) than in SLA and DCC soils. In all sites, the available fraction of Cd was less than 0.21 mg kg^{-1} d.w. (Table 1).

2. Fungal community

Overall, 314 genera of fungi were detected (191 in SLA, 210 in DCC, 200 in MG and 238 in DMG). Nine genera of fungi represented 70 % of the total frequency of genera in all soil types: *Mortierella* (29.2 %), *Cryptococcus* (8.0 %), *Alternaria* (7.12 %), *Mycoarthris* (6.2 %), *Tetracladium* (5.9 %), *Davidiella* (4.8 %), *Ilyonectria* (3.9 %), *Exophiala* (2.9 %) and *Clonostachys* (2.5 %). Considering the genera with a frequency greater than 1.0 %, *Mortierella*, *Tetracladium*, *Alternaria*, *Ilyonectria* and *Davidiella* were the predominant fungal genera in each soil type. *Minimedusa* was more abundant in DCC and *Cylindrocarpon* was more abundant in SLA than in the other soils (Figure 1a). *Cryptococcus* and *Mycoarthris* were mainly found in DCC and glacial soils, *Clonostachys* and *Exophiala* in glacial soils (MG and DMG) and SLA and *Botrytis*, *Nectria* and *Metarhizium* in SLA and DCC (Figure 1a). The biodiversity indices S, Chao1 and J were found to be statistically different between the various soil types. In particular, S and Chao1 indices were higher in DMG and DCC soils than in the others (Table 2). The NMDS and ANOSIM analyses showed that the composition of the fungal community of SLA soils differed from the other soil types (Figure 2a, Table S2) and available Cd, total carbonates, pH, total N, SOM and Zn were the chemical variables that contributed the most to separate groups (Table S3). Several correlations were found between the fungal community and the chemical parameters Table S5) and also among the different fungal genera. *Mortierella* in glacial soils (MG and DMG) showed negative correlations with metals (Cu, Zn and Cd), total N, SOM and clay. Additionally, *Mortierella* in glacial and DCC soils was found to be negatively correlated with some phytopathogenic genera (*Davidiella* in MG – ρ_S: -0.74, DMG – ρ_S: -0.68 and DCC – ρ_S: -0.72; *Fusarium* in MG – ρ_S: -0.62, DMG – ρ_S: -0.83; *Alternaria* in MG – ρ_S: -0.88). *Tetracladium* was found to be negatively correlated with the available fraction of Cu, Zn and Cd in all soil types, except

TABLE 1. Chemical and physical variables of four soil types (mean ± standard error). Different letters in brackets indicate significant differences between soil types (Wilcoxon test with BY correction, $p \leq 0.05$).

	SLA	DCC	MG	DMG
Sand (g kg^{-1} d.w.)	329 ± 40 (b)	404 ± 11 (b)	476 ± 18 (a)	410 ± 30 (ab)
Silt (g kg^{-1} d.w.)	577 ± 33 (a)	466 ± 7 (b)	419 ± 17 (c)	429 ± 19 (b)
Clay (g kg^{-1} d.w.)	95 ± 8 (b)	131 ± 12 (a)	105 ± 7 (b)	162 ± 14 (a)
pH	7.7 ± 0.0	7.8 ± 0.1	7.7 ± 0.0	7.4 ± 0.2
Total carbonates (g $CaCO_3$ kg^{-1} d.w.)	206 ± 26 (b)	405 ± 27 (a)	449 ± 23 (a)	73 ± 18 (c)
Total N (g kg^{-1} d.w.)	2.1 ± 0.1 (a)	3.1 ± 0.3 (a)	2.5 ± 0.4 (ab)	1.6 ± 0.1 (b)
SOM (g kg^{-1} d.w.)	39.7 ± 1.6 (b)	59.1 ± 5.6 (a)	49.6 ± 6.6 (ab)	28.1 ± 1.9 (c)
C/N	11.0 ± 0.2 (a)	11.2 ± 0.2 (a)	11.9 ± 0.3 (a)	10.4 ± 0.1 (b)
Cu (mg kg^{-1} d.w.)	75.9 ± 9.0 (b)	89.2 ± 10.2 (b)	136.1 ± 12.2 (a)	86.1 ± 17.2 (b)
Zn (mg kg^{-1} d.w.)	6.9 ± 0.7 (b)	15.5 ± 2.0 (a)	16.4 ± 2.6 (a)	6.9 ± 1.5 (b)
Pb (mg kg^{-1} d.w.)	6.4 ± 1.1 (b)	4.5 ± 0.5 (b)	9.2 ± 1.9 (ab)	10.1 ± 1.0 (a)
Cd (mg kg^{-1} d.w.)	0.17 ± 0.02 (ab)	0.21 ± 0.02 (a)	0.12 ± 0.01 (c)	0.14 ± 0.01 (b)

for Cu in DCC. A negative correlation was also found with Pb in DMG. In DCC and DMG soils, *Ilyonectria* showed a significant positive correlation with Cu and negative Spearman coefficients for SOM, total N and Cd in DCC only; meanwhile, *Davidiella* displayed positive correlations with $CaCO_3$, SOM, total N and Pb in both the soil types and opposite correlations with Cu between the two soil types. *Cylindrocarpon*, despite only characterising SLA soils, showed an opposite correlation with SOM and total N between SLA and DCC and a negative correlation with Pb in both the latter soil types. *Botrytis*, which characterised the DCC soils, displayed negative correlations with Cu concentrations and with the genus *Minimedusa* (ρ_S: -0.58) in this soil type. In all soil types, endophytic fungi were more frequent than epiphytic ones (Table S4b). The most frequent functional classes of the fungal community were, in order of abundance, saprotrophs/decomposers, pathogens/parasites and mycorrhizae (Table S4b). The arbuscular mycorrhizae were less frequent in DCC and MG.

3. Bacterial community

A total of 409 genera of bacteria were retrieved (335, 357, 336 and 351 in SLA, DCC, MG and DMG soils, respectively) and five genera (*Gp6*, *Nitrososphaera*, *Gp4*, *Gp16* and *Gp17*) represented 40 % of the total frequency of genera in all soil types. Regarding the genera with a frequency greater than 1.0 % in each soil type (Figure 1b), these five genera characterised all soil types, whereas *Gaiella* characterised only SLA, DCC and DMG soils, *Gp7* SLA and DMG soils and *Pirellula* DCC soils. The analysis of the biodiversity indices (Table 2) showed that those of S, Chao1 and J were higher in DCC than in the other soil types. No significant differences were found between SLA and glacial soils (MG and DMG). The bacterial community composition of the SLA soils, similarly to the fungal community, differed from the other soil types (Figure 2b, Table S2). The chemical parameters that contributed the most to differentiating the groups were available Cd, total carbonates, available Zn, total N and SOM (Table S3). Statistical correlations were found between some bacterial genera and the chemical parameters (Table S5). Negative and positive correlations were observed between the genera belonging to the phylum *Acidobacteria* (*Gp16*, *Gp17*, *Gp4*, *Gp7* and *Gp6*) and SOM, total N and pH, in DCC and DMG soils, respectively. Furthermore, several positive correlations were observed between *Acidobacteria* and metals in all soil types. Available Cu positively affected the genus *Gp4* in all soil types, *Gp7* in SLA and DCC, *Gp6* and *Gp17* in DCC and *Gp16* in DMG soils. Available Zn correlated positively with the genus *Gp4* in SLA and the glacial soils (MG and DMG), and with *Gp16* in SLA and DMG and *Gp7* in SLA. Moreover, *Gp7* showed a negative correlation with available Zn in MG. In DCC and MG soils, *Nitrososphaera* showed positive correlations with SOM, total N and available Cd, a negative correlation with the C/N ratio and an opposite correlation with available Cu and $CaCO_3$. Moreover, this genus correlated positively with available Zn and negatively with available Pb in MG soils. The genus *Gaiella* was found to be strongly related to edaphic parameters, particularly in DCC and DMG soils, and it exhibited negative correlations with metals, especially in DMG soils. A negative correlation between available Cu and *Gaiella* was also found in SLA and DCC soils. In the latter soils, Pb correlated positively with *Gaiella*. The genus *Pirellula* genus was positively related to SOM and total N in DCC and MG soils. The functional analysis (Table S4a) showed that the most represented bacterial functional groups in all soil types were those involved in C degradation and the N cycle. C degradation groups (cellulolysis, chitinolysis, hydrocarbon degradation and xilanolysis processes) were more frequent in CCD. Other C cycle-related functional groups (methanogenesis and utilisation of low molecular weight hydrocarbons) and denitrifiers were also among the highest in DCC.

4. Microarthropod community

A total of 42,412 specimens belonging to sixteen taxa were collected in all investigated soils (SLA: 8,732 individuals and 15 taxa, DCC: 8,458 individuals and 16 taxa, MG: 15,056 individuals and 15 taxa, DMG: 10,167 individuals and 13 taxa). The sixteen taxa found were *Acari*, *Araneidi*, *Chilopoda*, *Coleoptera* (adults and larvae), *Collembola*, *Diplopoda*, *Diplura*, *Diptera* (larvae), *Hemiptera*, *Hymenoptera*, *Isopoda*, *Lepidoptera*, *Pauropoda*, *Protura*, *Symphyla* and *Thysanoptera*. *Acari* (56.6 % ± 5.8 %), *Collembola* (31.5 % ± 6.0 %) and *Hymenoptera* (6.5 % ± 1.2 %), which were the most abundant groups in each soil type. *Diplopoda* were found in SLA and DCC soils only, *Diplura* in DCC and MG soils and *Isopoda* in all soil types except for DMG (Figure 1c). The composition of microarthropod communities showed no differences among the soil types (Figure 2c, Table S2). All biological indices of microarthropods (abundance, *S*, Chao1, *H′*, *J* and QBS-ar) showed the lowest values in DCC compared to the other soil types. The J and H′ indices were higher in SLA than in the other soil types, abundance and QBS-ar were higher in MG (Table 2). DCC soils were found to contain the microarthropod community (comprising *Isopoda*, *Diplura*, *Pauropoda*, *Symphyla*, *Hemiptera*, *Coleoptera* and *Hymenoptera*) that had the most negative correlations with available Cu (Table S5). *Hemiptera* and *Coleoptera* in SLA and *Hemiptera* and the larvae of *Lepidoptera* in MG soils also correlated negatively with this metal. By contrast, a positive correlation was found between *Pauropoda*, *Coleoptera* and *Hymenoptera* and available Cu in DMG soils. *Hymenoptera*, *Diplura*, the larvae of *Diptera* and *Isopoda* in DCC soils showed a higher number of correlations with other chemical parameters than the other soil types (Table S5).

5. Viticulture practices and soil biodiversity

The Spearman correlation analysis highlighted the effects of Cu and Zn on soil biodiversity in the four soil types (Table 3). The biodiversity indices for SLA and MG soils displayed fewer significant correlations than for the other soil types. In DCC, available Cu concentrations showed a negative impact on microarthropod, bacterial and fungal biological indices. In DMG, negative correlations were found between the available fractions of Cu and Zn and fungal and bacterial indices, whereas positive correlations were observed between these metals and the microarthropod indices. In MG, available Zn concentrations showed negative correlations with the number of microarthropod taxa (S index).

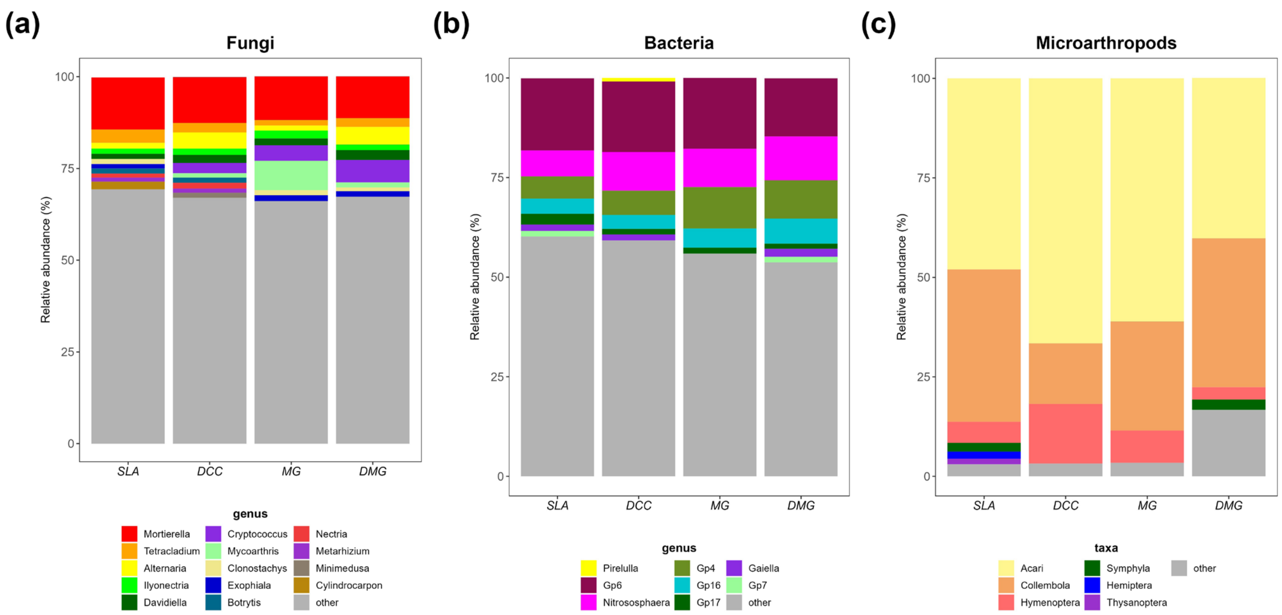


FIGURE 1. Relative abundance of (a) fungal, (b) bacterial and microarthropod communities at genus level for the first two and class/order level for the third, based on Illumina sequencing of the four soil types. "Other" includes taxa with average relative abundance < 1 %.

TABLE 2. Fungal, bacterial and microarthropod biodiversity indices (mean ± standard error) in four soil types. Different letters indicate significant differences between soil types (Wilcoxon test with BY correction, $p \leq 0.05$).

INDEX	SLA	DCC	MG	DMG
		Fungi		
S	69 ± 2 (b)	75 ± 4 (ab)	73 ± 1 (b)	83 ± 3 (a)
Chao1	73 ± 2 (b)	85 ± 4 (a)	79 ± 2 (b)	89 ± 3 (a)
H'	2.59 ± 0.05	2.49 ± 0.06	2.51 ± 0.08	2.59 ± 0.05
J	0.61 ± 0.01 (a)	0.58 ± 0.01 (b)	0.59 ± 0.02 (ab)	0.59 ± 0.01 (ab)
		Bacteria		
S	175 ± 4 (b)	197 ± 5 (a)	184 ± 2 (ab)	180 ± 3 (b)
Chao1	218 ± 5 (b)	240 ± 6 (a)	218 ± 3 (b)	218 ± 5 (b)
H'	2.67 ± 0.03	2.84 ± 0.06	2.66 ± 0.03	2.72 ± 0.05
J	0.52 ± 0.00 (b)	0.54 ± 0.01 (a)	0.51 ± 0.01 (b)	0.52 ± 0.01 (ab)
		Microarthropods		
S	9.2 ± 0.7 (a)	6.7 ± 0.9 (b)	8.8 ± 0.8 (ab)	8.3 ± 0.5 (a)
Chao1	11 ± 1	8 ± 1	11 ± 1	10 ± 1
H'	1.2 ± 0.05 (a)	0.68 ± 0.09 (c)	0.87 ± 0.07 (bc)	0.98 ± 0.04 (b)
J	0.57 ± 0.03 (a)	0.38 ± 0.04 (b)	0.42 ± 0.03 (b)	0.47 ± 0.02 (b)
Abundance (No m^{-2})	30893 ± 6792 (ab)	29927 ± 6268 (b)	53273 ± 9714 (a)	35974 ± 8453 (ab)
QBS-ar	104 ± 6 (ab)	77 ± 12 (c)	107 ± 7 (a)	90 ± 6 (b)

DISCUSSION

1. Chemical and physical characteristics of soil types

The available fraction of Cd in all soil types exhibited low concentrations, showing the natural origin of this metal (Kabata-Pendias & Pendias, 2010). Available Pb concentrations were similar to those found in non-acidic Italian agricultural soils (Barbafieri *et al.*, 1996) (range 0.5-5.0 mg kg^{-1}), indicating that they could have both natural and anthropic origins. In the twelve sites investigated, the available Zn concentrations were found to be within the range reported for non-acidic Italian wine-growing soils (2-30 mg kg^{-1}; Barbafieri *et al.*, 1996). The presence of the Zn in the present study may derive from either natural sources or the application of chemical products. Furthermore, the highest values of available Zn were found in DCC and MG soils, where carbonates had the highest levels, confirming that Zn in soil is strongly associated with the carbonate matrix (Lestan *et al.*, 2003). On average, available Cu in all soil types

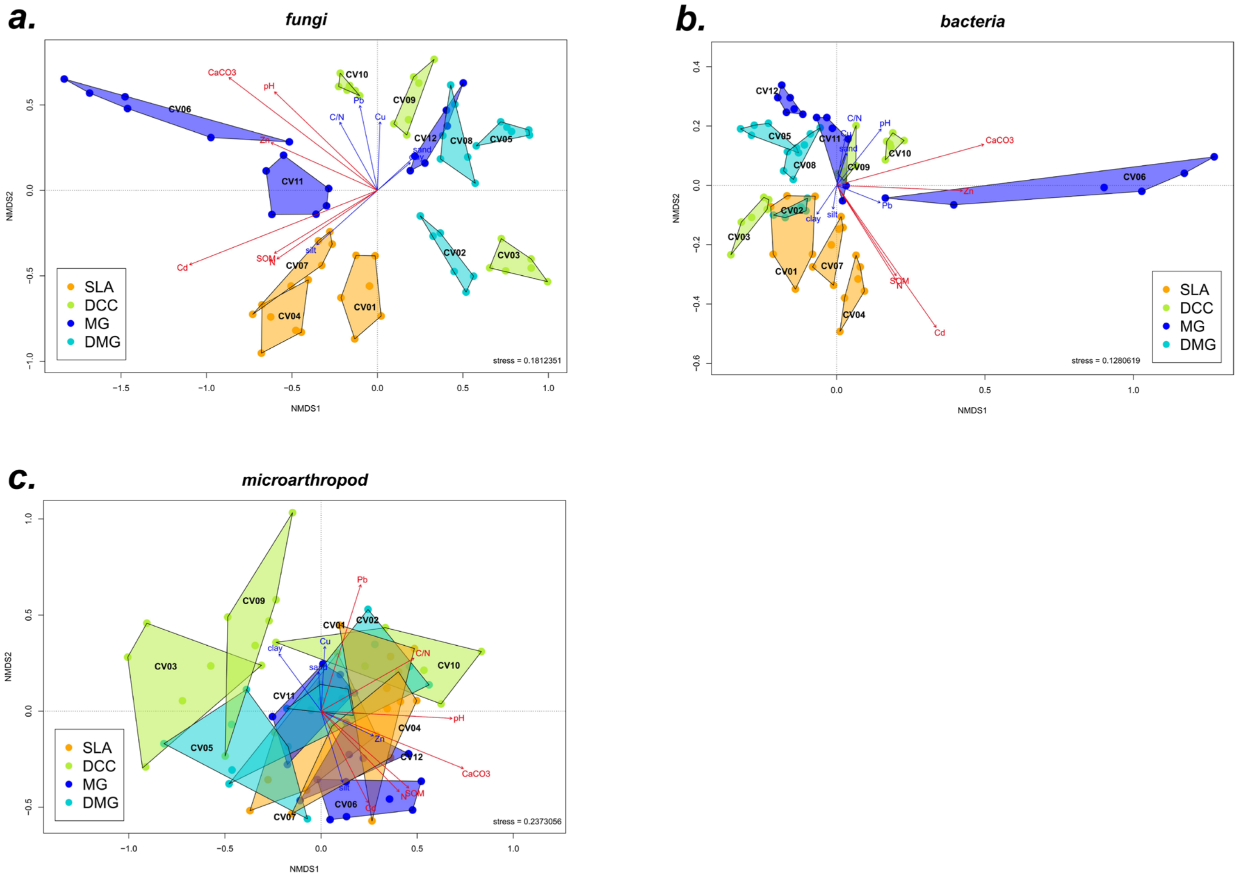


FIGURE 2. Ordination plot generated by nonmetric multidimensional scaling (NMDS) based on Bray-Curtis dissimilarity, displaying the soil biota composition of the sites investigated, (a) Fungi, (b) Bacteria, and (c) Microarthropods and the contribution of the edaphic variables. Red vectors contributed significantly ($p \leq 0.05$) to the separation of soil types, blue vectors did not contribute significantly. *p* is based on random data permutations.

had concentrations above the mean value for Italian vineyards (30 mg kg^{-1}; Barbafieri *et al.*, 1996). These levels of copper may result from anthropogenic activity due to the application of this metal as a fungicide in viticulture. It is important to emphasise that levels of available Cu above 100 mg kg^{-1} can influence the soil biota (Keiblinger *et al.*, 2018), and the European Union has thus restricted the application of plant protection products containing copper compounds to a maximum of 28 kg ha^{-1} of copper over a 7-year period (Regulation EU 1981/2018); this aims to minimise potential accumulation in the soil and reduce exposure to non-target organisms. Research also showed the possibility of reducing the amount of copper used for vine protection and developing innovative formulations (Cabús *et al.*, 2017; Battiston *et al.*, 2019).

2. Fungal community

The NMDS and ANOSIM analyses showed that the fungal communities of the twelve sites studied were affected by pedological origin. Moreover, the dissimilarity observed between fungal communities of different soil types highlighted how edaphic factors are essential in the selection of community structure (Zheng *et al.*, 2019). Among the most representative fungal genera of all four soil types were *Mortierella*, *Tetracladium*, *Alternaria*, *Ilyonectria* and *Davidiella*. The high frequency of *Mortierella* confirmed that it is one of the most abundant genera of fungi in agricultural and forest soils at all latitudes (Simon *et al.*, 2017; Ozimek & Hanaka, 2021). *Mortierella*, having shown negative relationships with several phytopathogenic genera in this study, could have an aptitude for suppressing fungal plant diseases. Several studies have demonstrated that it is a PGPF (plant growth-promoting fungi) and is able to improve the bioavailability of certain elements, especially P (Tamayo-Velez & Osorio, 2017) and Fe (Ozimek & Hanaka, 2021), as well as plant growth, stress tolerance (Yu *et al.*, 2016; Ozimek & Hanaka, 2021) and the protection of crops from pathogens (Jaroszuk-Scisel *et al.*, 2011). *Mortierella*, like other genera belonging to the phylum *Zygomycota*, plays a key role in the decomposition of plant material (Alexopoulos *et al.*, 1996) and the accumulation of organic carbon in the soil (Zhu *et al.*, 2022). In glacial soils, *Mortierella* has been found to have a negative correlation with SOM and N. In particular, MG soils were characterised as having a high SOM content (5 %) and a high C/N ratio (> 11), suggesting that they undergo slow mineralisation, contain stabilised carbon and have low nitrogen availability. The positive correlation with C/N suggests the involvement of *Mortierella* in the decomposition of organic matter more susceptible to mineralisation and a potential reduction in its ability to humify SOM due to low mineral nitrogen availability. Despite being a fungal genus mainly observed in aquatic environments, *Tetracladium* has also been found in agricultural soils, where it is involved in the degradation of plant debris (Klaubauf *et al.*, 2010) and is a typical root fungus capable of enhancing plant growth and nutrient uptake (Wang *et al.*, 2018). Cu and Zn appeared to adversely affect *Tetracladium*, although in aquatic habitats some species have shown wide variability in their susceptibility to metal pollution (Miersch *et al.*, 2005). The main species of *Ilyonectria* in soils are associated with root rot disease in numerous woody and herbaceous plants (Liao *et al.*, 2019; Sánchez *et al.*, 2019). In this study, this fungal genus characterised all soil types but appeared to be influenced only by the chemical characteristics of DCC and DMG soils, which had a similar texture but differed in other edaphic variables. In both soil types, *Ilyonectria* showed a positive relationship with Cu, demonstrating the ability of this fungus to tolerate metals (Torres-Cruza *et al.*, 2018). *Ilyonectria* species are ubiquitous soilborne fungi, associated with the "black foot disease" of grapevine (Petit, 2017; Viret & Gindro, 2025). They can persist in a latent state, infecting young vines under unfavourable soil and climatic conditions (*e.g.*, compacted or poorly drained soils; Petit, 2017; Viret & Gindro, 2025). With these characteristics, the widespread presence of this fungus in vineyards could be mainly due to the repeated cultivation of grapevine for long periods, rather than to the copper content. The genus *Davidiella*, whose members are mainly phytopathogens, characterised all the soil types, but showed a different response to edaphic characteristics depending on soil type. The abundance of arbuscular mycorrhizae appears to reflect the soil organic matter (SOM) content, which was higher in DCC and MG soils. However, in these soils, this functional group was less abundant compared to other soil types. A high SOM content likely indicates

TABLE 3. Spearman correlations between fungal, bacterial and microarthropod biodiversity indices and the available fraction of Cu and Zn (metals linked to the viticultural activity) in soil samples. Only correlations found to be significant with at least one of the two metals ($p \leq 0.05$) and with a $\rho_S \geq |0.5|$ are reported. The values in columns represents ρ_S and non-significant correlations are indicated with "n.s.".

Soil type	Kingdom	Biodiversity index	Cu	Zn
DCC	Bacteria	*H'*	–0.74	*n.s.*
		S	–0.75	*n.s.*
		J	–0.72	*n.s.*
		Chao1	–0.65	*n.s.*
	Fungi	*S*	–0.86	*n.s.*
		Chao1	–0.77	*n.s.*
	Microarthropods	*H'*	–0.75	–0.54
		S	–0.84	*n.s.*
		Chao1	–0.84	*n.s.*
		QBS-ar	–0.63	*n.s.*
DMG	Bacteria	*H'*	–0.75	–0.74
		J	–0.77	–0.77
	Fungi	*H'*	–0.78	–0.71
		S	–0.67	–0.61
		J	–0.77	–0.68
		Chao1	–0.71	–0.65
	Microarthropods	*H'*	0.5	*n.s.*
		S	*n.s.*	0.52
		Chao1	0.5	0.54
		QBS-ar	0.58	0.6
		No m^{-2}	*n.s.*	0.51
MG	Microarthropods	*S*	*n.s.*	–0.56
SLA	Microarthropods	*S*	–0.52	*n.s.*
		Chao1	–0.62	*n.s.*

higher concentrations of nutrients, including available phosphorus (P). In soils rich in available P, the growth of arbuscular mycorrhizae may be reduced, as the host plant is not metabolically advantaged enough to establish symbiosis with the endophyte (Nouri *et al.,* 2015).

3. Bacterial community

The pedological origin of the investigated sites also affected the bacterial community composition, in agreement with the NMDS and ANOSIM analyses, and Bray-Curtis analysis showed how soil parameters drive the bacterial community structure (Zheng *et al.*, 2019). Five of the most frequent genera in the four soil types (*Gp4*, *Gp6*, *Gp7*, *Gp16* and *Gp17*), with a total average frequency of over 32 %, belong to the phylum *Acidobacteria*. This bacterial group is one of the most common in soils (Dunbar *et al.*, 2002), and its abundance and diversity are driven by environmental factors, such as pH and nutrients (Kielak *et al.*, 2016). In this study, positive correlations between *Acidobacteria* and the available fraction of metals, particularly Cu and Zn, highlighted that the use of Cu in viticulture may have affected the soil bacterial community and confirmed the ability of this phylum to tolerate pollutants (Kielak *et al.*, 2016). *Nitrososphaera* was a dominant group in all soil types and showed positive correlations with total N in DCC and MG soils. It has been shown that this genus is closely related to organic and mineral forms of N (Zhalnina *et al.*, 2013), and in agricultural soils it is among the main contributors to the oxidation of ammonium to nitrite (Xia *et al.*, 2011), the first step in the nitrification process. This evidence is confirmed by functional analyses, showing that aerobic ammonia-oxidising bacteria were among the most abundant groups in all soil types and their frequency reflected the trend in total N in the diverse soil types. In this study, *Nitrososphaera* displayed both negative and positive relationships with metals. Several studies have demonstrated the tolerance of this genus of Archaea to high Cu concentrations, having been found in extreme environments such as mining sites with high metal concentrations (Maezato & Blum, 2012). *Pirellula* characterised the DCC soils, where SOM and total N exhibited the highest values compared to other soil types and were positively correlated with this genus. These results are consistent with those of Buckley *et al.* (2006), who found an over-representation of *Pirellula* in soils amended with organic fertilisers, in which an increase in SOM was noted. Moreover, the chitinolysis process was more pronounced in DCC soils than in others, and Rabus *et al.* (2002) found that *Pirellula* can grow with the chitin monomer N-acetylglucosamine as the sole source of C and N under aerobic conditions. Methanogens, methanotrophs and denitrifiers were found mainly in DCC soils, where clay, SOM and total N were higher than in the other soil types. This may indicate that temporary anaerobic conditions occur in DCC soils due to water saturation or oxygen consumption from SOM decomposition, inducing anaerobic processes such as methanogenesis and denitrification (Seo *et al.*, 2014).

4. Microarthropod community

This study confirms that *Acari*, *Collembola* and *Hymenoptera* are the predominant groups in vineyard soils (Gagnarli *et al.*, 2015). Diplopoda were predominant in SLA and DCC soils, where total N and C/N ratio were higher than in the other soil types. This is in line with the relationship between *Diplopoda*, N availability and C/N ratio found by Aerts *et al.* (2012), who observed that N content influences the decomposition rate of leaf litter, the main nutritional source for *Diplopoda*. *Diplura* were affected by high metal concentrations in DCC and MG soils, as also reported by Sendra *et al.* (2021). The lower amount of SOM and total carbonates in DMG soils could have limited the development of *Isopoda* in this soil type, as also shown by Hadjicharalampous *et al.* (2002). Conversely, DMG soils were hospitable for *Diptera* adults, which were absent in the other soil types. Moreover, a higher clay level and a greater number of fungal genera found in DMG soils are consistent with the positive relationship with the presence of *Diptera* (Garrido-Jurado *et al.*, 2011).

5. Viticulture practices and soil biodiversity

The concentrations of available Zn and Cu are thought to be linked to viticultural practices. The highest values of these elements were found in soils where vines were also the previous crop. These two elements are, in fact, active components of pesticides or fertilisers, which are widely used in viticulture, and it is highly likely this is where they originate from, given the concentrations found in the soils of the investigated vineyards. Cu and Zn are essential micronutrients for all plants and animals, although they become toxic at concentrations above certain values (Jaishankar *et al.*, 2014). The relationships between these metals and biodiversity indices are determined by soil types (Table 3), emphasising that tolerance of microorganisms to pollutants may depend on other soil characteristics, which could reduce their mobility and interaction with organisms or increase the adaptability and the liveability of the microbial community (Keiblinger *et al.*, 2018). In this study, Cu content showed a negative impact on bacterial and fungal biodiversity indices in DCC and DMG soils, as also demonstrated by Wang *et al.* (2018). Berg *et al.* (2012) also found that long-term Cu exposure causes changes in soil bacterial community composition. Zn concentrations in DMG soils negatively affected fungal richness and indices of bacterial biodiversity. Several studies have shown a reduction in OTU microbial diversity in soils with high Zn concentrations (Golebiewski *et al.,* 2014; Hur *et al.,* 2011). The biological indices of microarthropods were negatively affected by Cu in DCC and in SLA soils. Similar results were found by Pedersen *et al.* (1999) in a study conducted in Denmark on long-term Cu-contaminated agricultural soils: overall, DCC soils were the worst at promoting microarthropod biodiversity, showing the lowest values of the biological indices, despite the high level of some chemical quality indicators (SOM, total N and C/N ratio). The factors behind the limitation in arthropod biodiversity are probably related to the physical structure of DCC soils, which are characterised by a high skeleton content, thus reducing arthropod mobility (Duyar, 2018).

CONCLUSIONS

This study identified the dominant natural and viticulture factors driving the biota of different soil types characterised by different pedological origins in vineyards of Trentino (Northeast Italy). The combined effect of pedological factors and agronomic practices contributed to affecting the composition and biodiversity of the soil biota. Although some groups of fungal, bacterial and microarthropod communities were predominant in all the analysed soil types, some taxa were characteristic of only certain soil types. Edaphic factors determined the selection of community structure. Viticulturally related factors, such as the presence of Cu and Zn, influenced the biodiversity of the biota depending on the soil type, whose chemical and physical characteristics may have reduced metal mobility and interaction with organisms. Fungal and bacterial communities were affected by geographical position, whereas microarthropods seemed to respond less to pedological origin and geographical position. Understanding how natural and agronomic factors drive soil biota makes it possible to predict the effect of natural or artificial changes on soil biological processes.

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