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Organic matter content rather than farming practices modulates microbial activities in vineyard soils

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ABSTRACT

Soil functioning is a growing concern in intensively-managed agricultural landscapes such as vineyards. Mechanical disturbance of the soil and pesticide use have deleterious impact on microbial activity, which is a key parameter for organic matter decomposition and nutrient cycling. This study aims to assess the response of soil microbial activities under different farming systems (organic and conventional systems) and inter-rows management (grassy or tilled inter-rows). We selected 18 fields in the southwest of France, supporting tilled and grassy inter-rows (alternating treatment) - 9 fields were managed organically and 9 were managed conventionally. We assessed extracellular enzymatic activities relative to C, N, P acquisition and Microresp™, which allows to measure catabolic capacities of soil microbial communities. Our results showed that organic systems had a higher soil organic matter (SOM) content than conventional ones. At the inter-row scale, grassy inter-rows of organic vineyards differed from tilled inter-rows in catabolic capacities of microbial communities; with overall a higher complexity of C-substrates respired by microbial communities. Furthermore, N- and P-related enzymes were positively correlated to SOM and soil pH across sites and managements, suggesting that increasing SOM may positively impact nutrient recycling and notably NO_3^-. Altogether, our results pointed out the importance of soil organic matter content on soil microbial functioning in vineyards as well as the possible benefit of organic matter inputs on nutrient recycling and nitrogen directly available in the vineyard.

1. Introduction

Microorganisms play a central role in soil functioning, notably through their action on organic matter decomposition and nutrient cycling (Burns et al., 2013). The transition from traditional farming to intensive agriculture, coupled with the use of large amounts of pesticides, has led to a loss of soil organic carbon and microbial biomass (Okur et al., 2009). For instance, physical disturbance caused by tillage activities has been shown to reduce carbon microbial biomass by approximately 52 % (Cotton and Acosta-Martínez, 2018), but also enzyme activities (Zuber and Villamil, 2016) by approximately 87 % for β-glucosidase (Lagomarsino et al., 2011). There is an increasing number of studies addressing the influence of high-intensity management practices on the dynamics of soil organic matter (SOM) in vineyard soils (Abad et al., 2023; Syswerda et al., 2011). However, less is known about the potential positive effects of organic farming on soil microbial functioning and whether they have beneficial effects for vines through increasing nutrient availability in the soil.

The presence and the management of grass cover within vineyard rows and in inter-rows significantly influence SOM dynamics and microbial communities through various direct and indirect ways (Giffard et al., 2022). For instance, grass cover in vineyard inter-rows can enhance SOM accumulation through root turnover and organic matter deposition, contributing to an increase in soil carbon inputs (Garcia et al., 2018; Steenwerth and Belina, 2008). Moreover, root rhizodeposition can in turn stimulate soil microbial activity (Banerjee et al., 2019),

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notably by promoting the proliferation of beneficial soil microorganisms involved in nutrient cycling and disease suppression (Giffard et al., 2022). However, soil mechanical disturbance have detrimental effects on microbial activities reducing their biomass and activity (Belmonte et al., 2018). In addition, extensive management of vineyard supporting spontaneous vegetation and limiting soil tillage may promote competition for water and nutrients between spontaneous vegetation and vines which in turn may limit vine growth and yield (Novara et al., 2021). Such a trade-off between soil and crop functioning requires clear information about the consequences of within-field management on crop and soil functioning to develop management strategies optimizing soil functioning without compromising crop productivity.

The effect of grass cover in vineyards on microbial activities is highly context-dependent in relation with factors such as soil pH and the quantity of organic matter (Banerjee et al., 2019; Engell et al., 2022; Rousk et al., 2010). In situations where soil pH levels are relatively low, grass cover may facilitate nutrient availability, thereby promoting vine growth (Aciego Pietri and Brookes, 2009). Similarly, in environments where vineyard soils have low initial organic matter content, grass cover can significantly enhance SOM accumulation, fostering improved soil structure for microbial communities (Abad et al., 2021; Bommarco et al., 2013; Reilly et al., 2023). However, in soils with high SOM, we can expect that the presence of grass cover might exacerbate nutrient immobilization (Belmonte et al., 2018; Peregrina et al., 2012), but the consequences on microbial activity and organic matter dynamics are still relatively unknown. Therefore, considering the quantity of SOM and the pH level is crucial for understanding the variability in responses of grass cover on soil microbial functioning in vineyards, guiding tailored management practices to optimize both soil health and grapevine productivity.

In this study, our main objective was to assess the impact of management by comparing organic and conventional vineyards, and the effect of grass cover management on soil microbial activity (i.e., enzymes and catabolic capacities). We evaluated the context-dependency of these effects by using 18 sites across a wide range of soil types, which vary strongly in their SOM and pH values. We further compared tilled *vs* grassy inter-rows within each of the two types of management. First, we hypothesized that microbial activity should be higher in organically managed vineyards compared to conventionally managed vineyards due to a supposed more extensive management practices and reduced use of phytosanitary products (Hypothesis, H_1) (Engell et al., 2022; Sannino and Gianfreda, 2001). Second, we hypothesized that the effect of vineyard management should also depend on inter-row management, with greater microbial activity and functional abilities of microbial communities in grassy inter-rows compared to tilled inter-rows due to a lower soil disturbance coupled to higher C inputs with the presence of an herbaceous cover (Hypothesis, H_2) (Burns et al., 2013; Syswerda et al., 2011). Finally, we hypothesized that the effects of management would be stronger when soil C contents and pH are low, notably because increasing soil pH is known to increase enzymatic efficiency while increasing C inputs should stimulate microbial biomass and activity (Maxwell et al., 2020; Sinsabaugh et al., 2008) (Hypothesis, H_3). The main originality of our study lies in assessing the context-dependency of vineyard management across various soil types and environmental conditions, with the objective to assess if this may impact soil C:N stoichiometry and nitrogen that can then be available for plant growth and grape quality.

2. Material and methods

2.1. Study site and management characteristics

The study site was in Nouvelle-Aquitaine, in the southwest of France in the long-term living lab BACCHUS. This represents a 910 km^2 area in a vineyard-dominated landscape (Muneret et al., 2019; Ostandie et al., 2021). Nine pairs of vineyards close to each other in the landscape were selected and each pair was composed of one vineyard managed organically and the other conventionally (Supplementary material, Fig. S1). Each vineyard has an alternate row management with one row tilled out of two, the other one is covered by spontaneous vegetation mainly composed of ruderal and gramineous species (e.g: *Agrostis stolonifera*, *Cynodon dactylon*, *Potentilla reptans*, *Lolium* and *Trifolium* species). These vineyards presented a wide range of pH values (from 5.8 to 8.3) and diverse soil textures (Supplementary material, Table 1). The fields were in viticulture for a few decades to over 156 years. As they were in real production context, tillage was superficial in tilled inter-rows with an important variety of mechanical tools (< 10 cm). Most of the rows in conventional vineyards were both mechanically and chemically weeded whereas the use of herbicides was banned in organic vineyards.

2.2. Soil sampling

Vineyards were sampled during early spring 2022. Each inter-row was sampled at three points in the middle of the field in the 0–10 cm layer. These sampling points were distant from the edge by 15 m and each point was 10 m apart from the next and were mixed in order to obtain composite sample. Plant debris were removed from these composite samples. The composite samples were then sieved at 5 mm and sent to a laboratory for soil analyses (AUREA AgroSciences) to measure pH with glass electrode (NF ISO 10390) and organic matter content using sulphochromic oxidation of carbon followed by colorimetric dosage (NF ISO 14235) at the inter-row level (Supplementary material, Table S1). During the same period, we also collected and sieved soils for enzyme activities and MicroResp™ analyses. Composite samples for enzymatic activities were stored at −20°C, while composite samples for MicroResp™ were stored at ambient temperature.

We assessed available NO_3^- in soils through anion exchangeable (2 cm x 5 cm) membranes following Biofunctool methodology (Thoumazeau et al., 2019) based on Qian and Schoenau, (2002) and Saggar et al. (1990). Briefly, exchangeable membranes were charged with $NaHCO_3$ 0.5 M solution for at least 24 h and kept at 4 °C. Then, membranes were buried in vineyard soils the 1st or the 3rd of March, 2022 (3 replicates per inter-row per vineyard; points were located 15 m from the, with each point 10 m apart from the next, resulting in 108 membranes in total), and collected two weeks later and kept at 4 °C. The collected membranes were extracted with 35 mL of KCl 1 M solution to assess NO_3^- (mg/L) through Skalar San++®.

2.3. Enzymatic activities

To measure potential enzymatic activities, we selected 7 hydrolytic enzymes: Cellobiohydrolase (EC 3.2.1.91), α-Glucosidase (EC 3.2.1.20) and β-Glucosidase (EC 3.2.1.21), which degrade cellulose; xylosidase (EC 3.2.1.37), which breaks down hemicellulose; acid Phosphatase (EC 3.1.3.2), which hydrolyzes organic phosphate bounds; N-acetyl

Table 1
Effects of vineyard and inter-row managements (MNGT: 4 levels of management corresponding to organic and conventional crossed with tilled and grassy inter-rows plots) and of soil OM or pH on carbon (Cenz), nitrogen (Nenz), and phosphorus (Penz) enzymatic activities, C:N stoichiometry (CNenz) and NO_3^-. Results (F-values) of the models with management (MNGT) and OM are shown in the upper part and independent of the results of the models with management (MNGT) and pH indicated in the lower part of the table. Significant effects are shown in bold (***$P < 0.001$ and * $P < 0.05$).

Models	Variables	C_{enz}	N_{enz}	P_{enz}	CNenz	NO_3^-
MNGT + OM	OM	0.44	**56.69** ***	**19.96** ***	3.10	**14.40** ***
	MNGT	0.17	1.07	1.24	0.26	1.75
MNGT + pH	pH	1.62	**67.00** ***	**33.07** ***	**21.18** ***	**15.11** ***
	MNGT	0.25	1.80	0.73	0.01	**3.18** *

Glucosaminidase (EC 3.2.1.52) which breaks osidic bonds and Leucine aminopeptidase (EC 3.4.11.1) which breaks proteic bonds. Enzyme activities were assayed using fluorochromes 7-Amino-4-MethylCoumarine (7-AMC) for the Leucine aminopeptidase and the 4-MethylUmBelliferone (4-MUB) for the six other enzymes via a microplate reader (Synergy H1M Biotek®).

Firstly, the soil samples were thawed to 4°C. Then 2.750 g of each sub-sample (triplicate) was weighed and suspended by grinding with 91 mL of a 0.1 M Tris-HCl extraction buffer with a pH similar to the respective soil pH, then stirred. Secondly, 800 μL of each soil solution was added to the microplates containing 200 μL of each of the 7 substrates at 200 μM, which had previously been thawed in the dark to avoid instability due to light exposure (Bell et al., 2013). Substrates were given in excess in order to measure potential enzymatic activities (Nannipieri et al., 2012). We also prepared 2 microplates containing 800 μL of our soil solutions and 200 μL of 4-MUB for one microplate and 7-AMC for the second at 0, 2.5, 5, 10, 25, 50 and 100 μM. Another microplate was prepared with 800 μL of buffer solution and 200 μL of 4-MUB, and 800 μL of buffer solution and 200 μL of 7-AMC at the same molarity range. Microplates were then placed in incubation for 3 hours at 25°C, agitated every 30 min. After the incubation time, microplates were centrifuged at 3000 rpm for 3 minutes and 250 μL of supernatant of each deep well were transferred to a reading microplate for measurement by the microplate reader. For the calculation of enzymatic activities, soil moisture was taken into account. The excitation wavelength was set at 365 nm and re-emission wavelength at 450 nm for both fluorochromes.

To assess potential enzyme activities linked to C, N and P, we selected β-Glucosidase, Cellobiohydrolase, Xylosidase and α-Glucosidase for C potential enzyme activity. N-acetyl Glucosaminidase and Leucine amino-peptidase for N potential enzyme activity and the value of acid Phosphatase for P potential enzyme activity.

2.4. Respiration analyses

MicroResp™ was used to assess Community-Level physiological profiles (CLPP) of soil microorganisms. The procedure was similar to the one described by Campbell et al. (2003), with the exception of calcareous soils. Because $CaCO_3$ interferes with respiration, it was removed by adding 2 M HCl (instead of water) until boiling was complete, before adding substrate solutions. Different carbon sources were used, ranging from simple to complex, to assess the diversity of microbial communities. We used Carbohydrates: D-Glucose (CAS 50–99–7), D-Fructose (CAS 57–48–7), D-Arabinose (CAS 10323–20–3) and D-Xylose (CAS 58–86–6); Amino acids: N-Acetyl D-Glucosamine (CAS 7515–17–6), L-Lysine (CAS 56–87–1), L-Serine (CAS 56–45–1), γ-Amino Butyric acid (CAS 56–12–2) and L-Glutamine (CAS 56–85–9); Carboxylic acids: Malic acid (CAS 6915–15–7), Citric acid (CAS 77–92–9) and Oxalic acid (CAS 144–62–7); and phenolic acids: Gallic acid (CAS 149–91–7), Syringic acid (CAS 530–57–4) and Vanillic acid (CAS 121–34–6). Optical density at 570 nm was measured and converted into substrate-induced respiration (SIR) (μg $C\text{-}CO_2.g^{-1}.h^{-1}$). Afterwards, we added values of the 15 SIR_i to assess the total catabolic activity (SIRtot) and we calculated Shannon catabolic diversity index (H') for all soil samples and all these compounds (Bourget et al., 2023; Fromin et al., 2020). H' was calculated to assess the soil microbial functional diversity, through the following equation (Bourget et al., 2023):

$$H' = \sum_{i=1}^{15} SIRi\ ln(SIRi) \tag{1}$$

2.5. Statistical analyses

Firstly, we used linear models to compare if there was any difference in C, N, P potential enzyme activities, SIRtot and H' between organic and conventional vineyards, whatever the management of the inter-row (considered as replicates of measures). The second set of analyses was focused on the effect of inter-row management, with a comparison of C, N, and P potential enzyme activities, SIRtot and H' between grassy and tilled inter-rows, regardless of whether the management was organic or conventional.

Effects of management (organic vs conventional and grassy vs tilled inter-rows) on OM and pH were also assessed through linear models (without interactions). Prior to linear models, we checked for correlation using Pearson's correlation test. We found that OM and pH values were correlated ($r = 0{,}56$, $P = 3{,}4\ 10^{-4}$).

The quality of substrates respired between field managements in interaction with inter-row managements were analyzed through non-metric multidimensional scaling analysis (NMDS) (using metaMDS from *vegan* package v2.6–4) with Bray-Curtis distance matrix. PCA and ANOVAs were then computed to quantify effects of retained soil parameters (OM, pH) on microorganism total activities: SIRtot, H', enzymatic activities linked to carbon (C_{enz}), enzymatic activities linked to nitrogen (N_{enz}) and enzymatic activities linked to phosphorus (P_{enz}); and specific potential enzymatic activities (Cellobiohydrolase, α-Glucosidase, β-Glucosidase, Xylosidase, acid Phosphatase, N-acetyl Glucosaminidase and Leucine aminopeptidase).

Then, ANCOVAs were performed to assess the potential interactions between qualitative (management) and quantitative (OM, pH) retained parameters on C_{enz}, N_{enz} and P_{enz}. We chose to analyze the management factor as a 4-level factor: grassy and organic inter-rows, tilled and organic inter-rows, grassy and conventional inter-rows; and tilled and conventional inter-rows. pH and OM effects and their respective interactive effects with management were assessed in different models because they were correlated. The same procedure was repeated to assess differences between managements in the C_{enz}:N_{enz} stoichiometry and nitrogen availability by comparing C_{enz}:N_{enz} and NO_3^- between the four different managements. When the management effect was significant, a multiple comparison using Tukey HSD test was performed (using TukeyHSD from *stats* package v4.2.2). All statistical analyses were performed on R version 4.2.2 (2022–10–31-urct) (R Core Team, 2022).

3. Results

3.1. Management effects

3.1.1. Organic versus conventional

We did not find differences in pH between organic and conventional farming (mean ± sd: 7.03 ± 0.82 and 7.06 ± 0.90 for organically- and conventionally-managed vineyards respectively) (Table S2). However, we found that OM content was higher (t-value = 2,08; df = 34; $P = 4{,}5.10^{-2}$) in organic (mean of 2.77 ± 1.04 % across all sites) compared to conventional vineyards (2.16 ± 0.68 %) (Fig. 1). No significant differences were found between organic and conventional managements concerning potential enzymatic activities on carbon C_{enz} (0.20 ± 0.17 and 0.15 ± 0.16 $mmol.kg^{-1}$ for organic and conventional vineyards, respectively), nitrogen N_{enz} (0.52 ± 0.36 and 0.43 ± 0.26 $mmol.kg^{-1}$ respectively) and phosphorus P_{enz} (0.59 ± 0.35 and 0.62 ± 0.36 $mmol.kg^{-1}$ respectively) potential enzymatic activities (Supplementary material Fig. S2, S3 and S4, S7, S8 and S9). We also observed no significant difference in catabolic capacities between organic and conventional vineyards regarding SIRtot (30.6 ± 27.0 and 23.5 ± 16.1 $mmol.kg^{-1}$, respectively) and H' (2.41 ± 0.12 and 2.38 ± 0.12, respectively) (Supplementary material Fig. S5, S6 and S10). We also found no significant differences between organic and conventional vineyards in Cellobiohydrolase, α-Glucosidase, β-Glucosidase, Xylosidase, acid Phosphatase, N-acetyl Glucosaminidase and Leucine aminopeptidase potential enzymatic activities.

3.1.2. Inter-row management: grassy versus tilled inter-rows

We did not find significant differences in pH between grassy and tilled inter-rows (7.02 ± 0.84 and 7.08 ± 0.87 for grassy- and tilled-

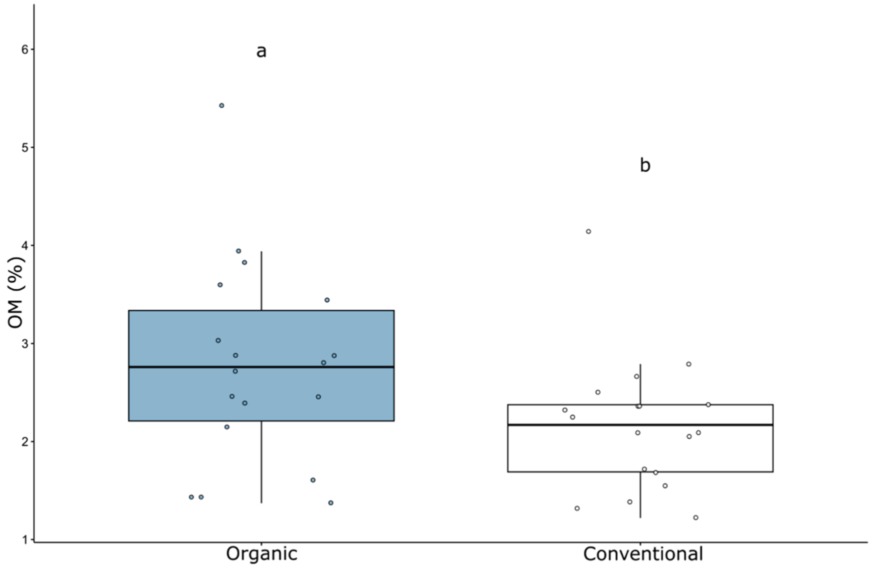

Fig. 1. Differences in organic matter (OM) content between organic and conventional vineyards. A significant difference was observed, with a higher OM content among organic (2.77 ± 1.04 %) fields compared to conventional ones (2.16 ± 0.68 %).

managed inter-rows respectively). The same observation was made for OM (mean 2.66 ± 1.09 % and 2.27 ± 0.69 % for grassy- and tilled inter-rows, respectively). No significant differences were found between grassy and tilled inter-rows concerning potential enzymatic activities for carbon C_{enz} (0.17 ± 0.19 and 0.17 ± 0.14 $mmol.kg^{-1}$ for grassy and tilled inter-rows, respectively), nitrogen N_{enz} (0.49 ± 0.36 and 0.45 ± 0.27 $mmol.kg^{-1}$, respectively) and phosphorus P_{enz} (0.65 ± 0.37 and 0.57 ± 0.34 $mmol.kg^{-1}$, respectively) potential enzymatic activities. We did not observe significant differences in catabolic capacities between grassy and tilled inter-rows regarding SIR_{tot} (22.48 ± 18.73 and 31.59 ± 24.92 $mmol.kg^{-1}$, respectively) and H' (2.36 ± 0.12 and 2.42 ± 0.12, respectively). Regarding specific potential enzymatic activities, we found no significant differences between grassy and tilled inter-rows on Cellobiohydrolase, α-Glucosidase, β-Glucosidase, Xylosidase, acid Phosphatase, N-acetyl Glucosaminidase and Leucine aminopeptidase.

3.2. *Substrate quality and diversity*

3.2.1. *Management organic vs conventional*

The grassy inter-rows in organic vineyards differed from those in conventional management by the quality of C-substrates respired, with higher levels of complex substrates such as vanillic and syringic acids (Fig. 2). NMDS showed that grassy inter-rows of organic vineyards respired higher complex C-substrates while grassy inter-rows in conventional vineyards showed communities more oriented towards simpler C-substrates. C_{enz} as well as a higher C_{enz}:N_{enz} ratio seemed to be favored by organic management while N_{enz} and NO_3^- were higher in conventional vineyards.

3.2.2. *Inter-row management*

To observe differences in C-substrate quality between inter-rows, we

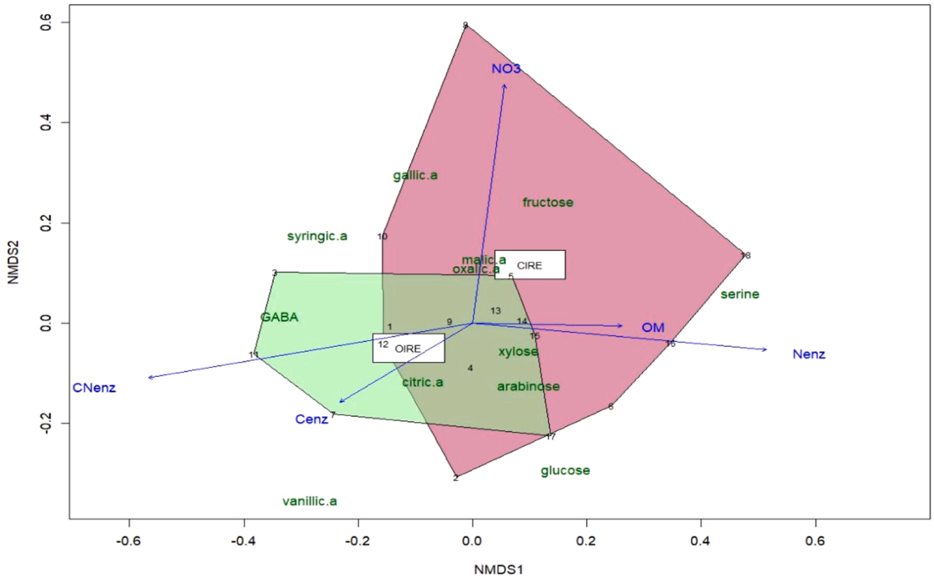

Fig. 2. Results of the NMDS on total and specific enzymatic catabolic activities regarding Carbon-substrates respired by microbial communities (Bray-Curtis distances) in grassy inter-rows of organic and conventional vineyards. Green polygon (OIRE) corresponds to grassy inter-rows of organic vineyards. Red polygon (CIRE) corresponds to grassy inter-rows of conventional vineyards (stress = 0.14). The different C-substrates were assessed from Microresp™. Blue axis correspond to organic matter content (OM), N enzymatic activity (Nenz), C enzymatic activity (Cenz), C:N stoichiometry (CNenz) and NO_3^- (NO_3).

separately analyzed the values obtained in organic and conventional vineyards. In organic vineyards, NMDS analysis showed that vanillic acid, syringic acid and GABA were more respired in grassy inter-rows, whereas malic acid was more respired in tilled inter-rows (Fig. 3). All C-substrates are respired in both inter-rows since H' did not significantly differ between grassy and tilled inter-rows. However, NMDS showed that there was a difference in the complexity of C-substrates preferentially respired by soils, with higher complexed C-substrates in grassy inter-rows. In conventional vineyards, no difference was observed in the quality of respired C-substrates between inter-rows managements.

3.3. *Effect of OM and pH on specific enzymatic activities*

We found that an increase in pH significantly decreased the activity of N-acetyl Glucosaminidase (t-value = −3,57; df = 34; $P = 1{,}1.10^{-3}$), but increased those of acid Phosphatase (t-value = 5,74; df = 34; $P = 1{,}9.10^{-6}$) and Leucine aminopeptidase (t-value = 8,55; df = 34; $P = 5{,}42.10^{-10}$). The regression analysis conducted with soil OM content revealed a significant positive increase in the activity of acid Phosphatase (t-value = 4,11; df = 34; $P = 2{,}38.10^{-4}$) and Leucine aminopeptidase (t-value = 6,98; df = 34; $P = 4{,}74.10^{-8}$) enzymatic activities with an increase of OM content.

3.4. *Effects of management in interaction with soil parameters*

We assessed for the relationships between organic matter content levels, pH and their respective interaction with management with 4 levels (organic + grassy inter-row; organic + tilled inter-row; conventional + grassy inter-row; conventional + tilled inter-row) on enzymatic activities (C, N, and P enzymatic activities) and specific enzymatic activities.

None of the interaction terms were significant regarding total and specific enzymatic activities and the interaction term was then removed from all models (all *P-values* > 0.05; Table 1). We found a significant and positive effect of OM content or of pH on N_{enz} and on P_{enz} (Table 1), whatever the field and inter-row managements (Fig. 4) while there was no significant effect observed on C_{enz}. There was no significant effect of management on total and specific enzymatic activities (Table 1).

3.5. *Implications on C_{enz}:N_{enz} and NO_3^-*

We observed no differences in C_{enz}:N_{enz} stoichiometry between vineyards with different managements (organic and conventional) neither between inter-row management (grassy and tilled). Linear models indicate no significant effect on SOM content on C_{enz}:N_{enz} while pH negatively impacted the C_{enz}:N_{enz} stoichiometry (t-value = 4,83; df = 34; $P = 2{,}89.10^{-5}$), favoring nitrogen enzymatic activities (Fig. 5). The following ANCOVAs revealed no interaction effects of pH or OM with management on C_{enz}:N_{enz} ratio. Organic vineyard management significantly increased NO_3^- compared to conventional management (t-value = 2,46; df = 34; $P = 1{,}92.10^{-2}$) (Fig. 6A) while inter-row management has no significant effect. Linear models indicate a positive effect of OM (t-value = 4,12; df = 34; $P = 2{,}27.10^{-4}$) and pH (t-value = 3.51; df = 34; $P = 1{,}29.10^{-3}$) on NO_3^- (Figs. 6B and 6C). The ANCOVAs analyses did not show a significant interactive effect of management and OM or pH, but we observed a significant simple effect of management on NO_3^- (Table 1). However, the multiple comparisons using Tukey HSD revealed one only marginally significant difference between the values of NO_3^- with a higher value in tilled inter-rows of organic vineyards compared to grassy inter-rows of conventional vineyards (Tukey adjusted t-value = 6.98 and $P = 0058$).

4. Discussion

Our study assessed the effect of soil management on soil microbial functioning at both vineyard and inter-row scales, and whether the effects of management depended on the level of soil organic matter and pH across 18 sites in Bordeaux vineyards. For this purpose, we measured C, N and P enzymatic activities and catabolic capacities of soil microbial communities in organic and conventional vineyards in interaction with alternating inter-row management. We found that enzymatic activities were not affected by vineyard management (i.e. organic or conventional) nor inter-row management (i.e. grassy or tilled) but rather by soil organic matter and pH. Our results contrast with previous studies, e.g. Peregrina et al. (2014), which observed a positive effect of cover crop on β-glucosidase activity. This opposite result could be attributed to methodological differences between studies (i.e., differences in the sampling depth). Positive effects of cover crop have been observed on top-soil layers (between 0 and 2.5 cm and 2.5 and 5 cm) but not deeper

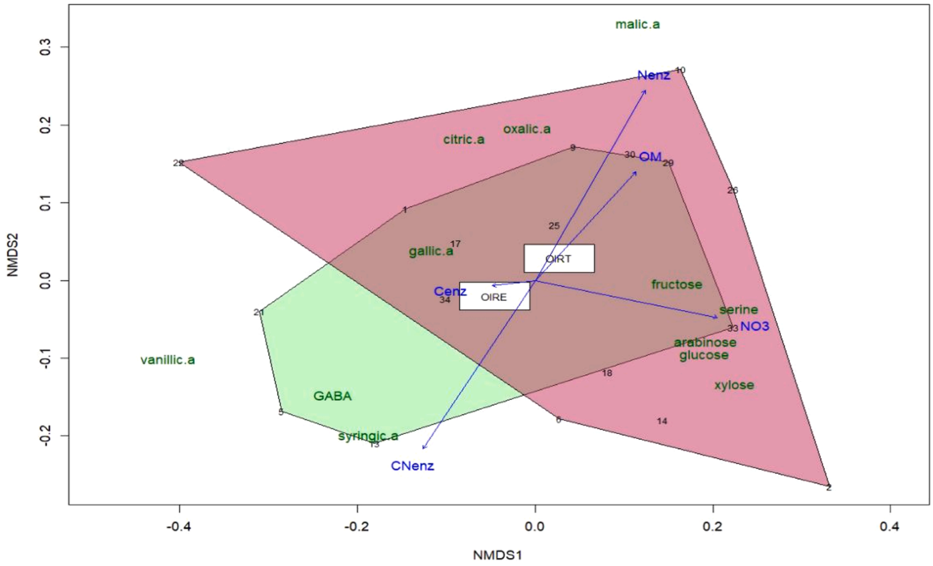

Fig. 3. Results of the NMDS on total and specific enzymatic catabolic activities regarding Carbon-substrates respired by microbial communities (Bray-Curtis distances) in tilled compared to grassy inter-rows of organic vineyards. Green polygon (OIRE) corresponds to grassy inter-rows. Red polygon (OIRT) corresponds to tilled inter-rows (stress = 0.13). The different C-substrates were assessed from Microresp™. Blue axis correspond to organic matter content (OM), N enzymatic activity (Nenz), C enzymatic activity (Cenz), C:N stoichiometry (CNenz) and NO_3^- (NO_3).

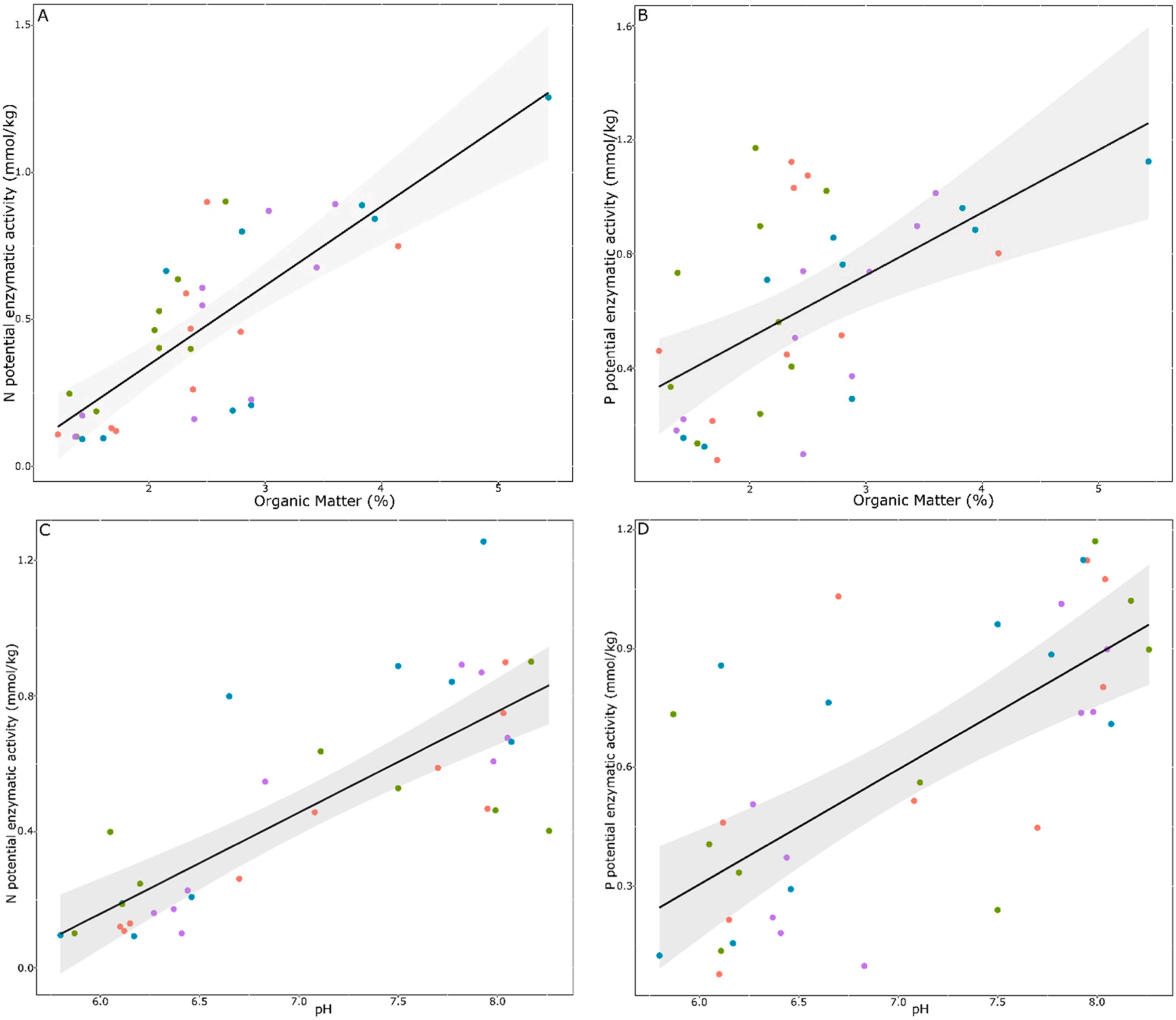

Fig. 4. Relationships between soil organic matter (%) and (A) nitrogen (N) potential enzymatic activities (mmol/kg) and (B) phosphorus (P) potential enzymatic activities (mmol/kg), and between pH and (C) nitrogen (N) potential enzymatic activities (mmol/kg) and (D) phosphorus (P) potential enzymatic activities (mmol/kg). Red dots represent grassy inter-rows of conventional vineyards. Green dots represent tilled inter-rows of conventional vineyards. Blue dots represent grassy inter-rows of organic vineyards and purple dots represent tilled inter-rows of organic vineyards.

while we sampled and analyzed the 0–10 cm depth. In contrast to our results on enzymatic activities, vineyard and inter-row managements influence catabolic capacities. The effect of vineyard system depended on soil organic matter (SOM) content and pH, suggesting that these parameters are predominant for enzymatic activities, nitrogen availability and soil functionality.

4.1. *Management effect on soil microbial activity*

Overall, we found that SOM content was significantly higher in organically managed vineyards than in conventional vineyards, probably because of application of organic amendments (Reilly et al., 2023) or increased tillage frequency in some conventional vineyards aimed at reducing weed competition (Giffard et al., 2022). Furthermore, we found slight differences (albeit marginally significant) in SOM content between organic grassy inter-rows compared to conventional tilled inter-rows. These observations are in accordance with results from other studies showing that tillage increased organic matter decomposition (Balesdent et al., 2000; De Santiago et al., 2008; Reilly et al., 2023; Tilman et al., 2002). Similarly, Reilly et al. (2023), found a significant difference between organic management and conventional management on SOM, which can be explained by tillage practices, notably because it affected soil organic carbon distribution along the soil profile. However, these two types of managements can also have indirect effects on soil structure and the quantity of soil aggregates (Balesdent et al., 2000) with further detrimental effects of tillage on fauna diversity (Ranjard and Richaume, 2001) and activity such as that of earthworms (Capowiez et al., 2009). Further studies should investigate the effect of tillage and of various tools (tillage depth and frequency) to better understand its impacts on soil communities and functioning.

Although we expected a positive effect of increasing SOM while reducing disturbance on soil microbial activity, we did not find that vineyard management (i.e., organic vs conventional) significantly affected enzymatic activities (C_{enz}, N_{enz} and P_{enz}), thus rejecting our first hypothesis. Contrary to our expectations, this suggests that vineyard and inter-row managements did not influence, alone, enzymatic activities.

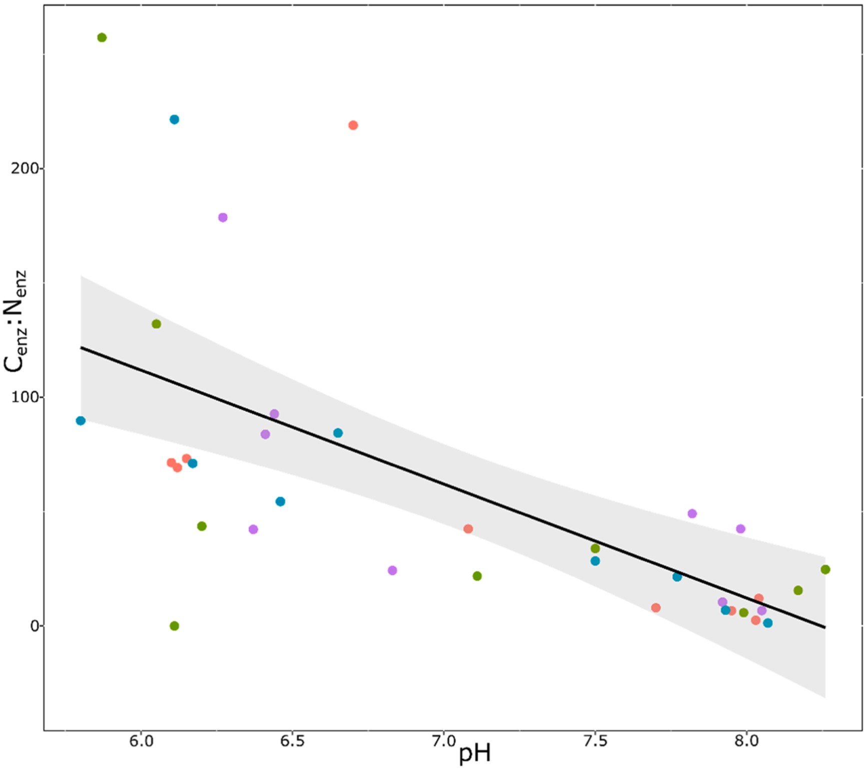

Fig. 5. Change in $C_{enz}:N_{enz}$ stoichiometry relative to soil pH. Red dots represent grassy inter-rows of conventional vineyards, green dots represent tilled inter-rows of conventional vineyards, blue dots represent grassy inter-rows of organic vineyards and purple dots represent tilled inter-rows of organic vineyards. pH significantly decreased $C_{enz}:N_{enz}$ stoichiometry while no interaction with any studied management method was observed ($y = 410.6 - 49.8x$; adjusted $R^2 = 0.39$; $P = 2.89.10^{-5}$; $n = 36$: 18 vineyards with 2 modalities/vineyard).

We observed the same result for total catabolic activities (SIR_{tot}), whatever the management considered. This absence of tillage effect on enzymatic activities (C_{enz}, N_{enz}, P_{enz}) and total catabolic activities (SIR_{tot}) could be attributed to relatively shallow tillage in our study case, instead of deeper tillage or intensive tillage that has been shown to decreased bulk density (Zehetner et al., 2015). The sampling depth used in our study may contribute to explain our result as changes in SOM content and enzymatic activities could be higher in top-soil layers (Peregrina et al., 2014) but slightly impacted at 10 cm depth (which correspond to our sampling protocol). Furthermore, in the present study we did not take into account the type of tool used for tillage, which can influence microbial community and enzymatic activities (Zuber and Villamil, 2016). For instance, Celik et al. (2011), observed significant differences in enzymatic activities between high-tilled intensity, reduced-tillage and no-tilled agricultural systems mainly because mycorrhizal spore number and soil respiration were negatively affected by high tillage intensity. This latter parameter also decreased fungal diversity and hyphal growing (Pingel et al., 2023).

4.2. Inter-rows effect

In partial agreement with our second hypothesis, we found a significant difference in the diversity of catabolic capacities (H'), with higher values in conventional tilled inter-rows compared to conventional grassy inter-rows. In particular, our NMDS revealed that microbial communities in grassy inter-rows were able to respire at higher rates using more complex C substrates as GABA, syringic and vanillic acids, which led to a higher specialization towards complex C-substrates for the grassy inter-row community. The observed difference between inter-rows may reflect variations in microbial activity driven by more diverse C inputs in grassy inter-rows (Celik et al., 2011; Pingel et al., 2023). Alternatively, this difference could be attributed to a shift in microbial community composition, particularly a reduction in fungal biomass due to the negative impact of tillage on hyphal growth. Based on these observations, we hypothesize that grassy inter-rows present microbial communities that are more specialized and potentially more efficient at degrading specific complex substrates (Orwin et al., 2006). These results could be also influenced by the cover and diversity of weed communities which is also known to strongly influence the quantity and the quality of substrates and exudates available for soil communities (Ingels et al., 2005; McDaniel et al., 2014).

4.3. The major role of organic matter and pH

In line with our third hypothesis, we found that OM and pH had a positive influence on nitrogen and phosphorus enzymatic activities across the 18 sites studied. These results suggest that organic matter and pH are primary drivers of enzymatic activities compared to soil management practices. In line with this idea, Creamer et al., 2016, found stronger effects of OM on enzymatic activities by comparing different land-use and suggested the positive impact of labile C on bacterial diversity. However, our results contrast to those of Lagomarsino et al. (2011), who found negative effect of tillage on α-glucosidase nor β-glucosidase. This difference can be due to the fact that they exported pruning residues in tilled management and left the residues in grassy cover, suggesting that beyond grass cover or tillage, other management methods such as residues management and the choice of cover crop (instead of spontaneous grass) must be taken into account. Nonetheless, it is important to mention that not all enzymatic activities did response the same way to OM and pH. Indeed, we observed a significant decrease in N-acetyl Glucosaminidase activity in vineyards with higher soil pH values (Creamer et al., 2016), probably because soil pH can shape community composition. For instance, it has been shown that *Bacteroidetes* are predominant at high pH in agricultural soils (Acosta-Martínez

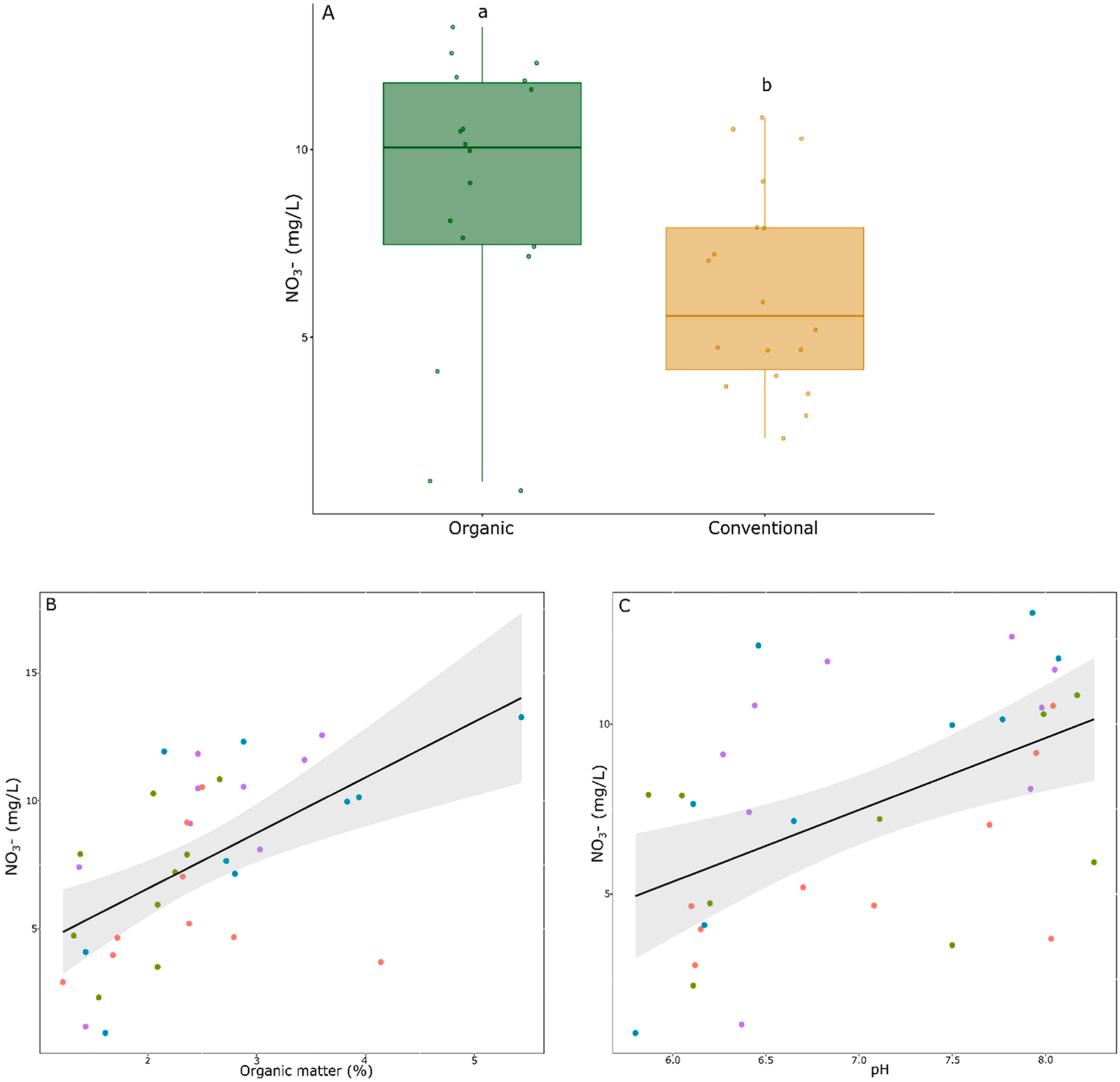

Fig. 6. Effect of organic (green) and conventional (brown) vineyard managements on soil NO_3^- (mg/L). NO_3^- reflects the availability of nitrogen in soils, which is enhanced by (A) organic management, (B) soil organic matter content (%) and (C) pH. In the Figs. B et C, red dots represent grassy inter-rows of conventional vineyards, green dots represent tilled inter-rows of conventional vineyards, blue dots represent grassy inter-rows of organic vineyards and purple dots represent tilled inter-rows of organic vineyards. NO_3^- values significantly increased in organic vineyards (A) and were enhanced with soil organic matter content (B: $y = 2.22 + 2.18x$; adjusted $R^2 = 0.31$; $P = 2.27.10^{-4}$; n = 36) and with soil pH (C: $y = -7.31 + 2.11x$; adjusted $R^2 = 0.24$; $P = 1.29.10^{-3}$; n = 36).

et al., 2008; Lauber et al., 2009), and take over *Acidobacteria* that are known to be more oligotrophic and contribute less to organic matter decomposition. Alternatively, the observed effects could result from the co-variation between organic and pH, although disentangling the effects between these two factors will require further investigations.

4.4. Consequences on nitrogen availability

The C_{enz}:N_{enz} stoichiometry did not differ between the different managements tested. Moreover, we did not observe significant interactive effect between management and OM or pH. This suggests that increasing OM would increase enzymatic activities overall, without specifically promoting N related enzymatic activities. Our results regarding pH followed a similar trend, with no effect of pH on C_{enz}:N_{enz} stoichiometry.

We observed significantly higher rates of NO_3^- in organic vineyards compared with conventional ones, which suggests that the management is important to increase N availability for plants. This result was unexpected, as mineral fertilization, which is not allowed from organic viticulture, would lead to a higher level of nitrogen availability in conventional vineyards (Peregrina et al., 2012). This can be due to the presence of higher SOM content and potential fresh organic matter inputs, which may contribute to a “priming effect” that enhances nitrogen availability in the studied organic vineyards (Kuzyakov et al., 2000).

However, at the site scale, there was no differences in NO_3^- between inter-row managements (grassy, tilled) while previous studies, generally reported lower rates of NO_3^- due to the competition for resources between cover crop and vines (Peregrina et al., 2012; Pérez-Álvarez et al., 2015, 2013). Such a difference can be due to the higher rates of SOM we observed in organic management, enhancing N availability, while we did not observe significant differences in SOM between inter-row managements. This result could be also due to the an increased water infiltration under cover crop, and of nitrogen mineralization (Celette et al., 2009), which can dampen the observed effects reported in the previous studies (Peregrina et al., 2012; Pérez-Álvarez et al., 2015, 2013). Thus, increasing soil organic matter enhances N and P potential enzymatic activities, highlighting the importance of maintaining high OM level in soils is essential to preserve microbial communities and their activity. This is possible and recommended by organic viticulture certification and by preserving grassy-inter-rows in vineyards, which efficiently respire more complex C-substrates. In this regard, further studies should focus on the effects of soil properties and agricultural practices on water infiltration between inter-rows, and on microbial activities at different samplings depths.

5. Conclusion

This study investigated the impacts of vineyard and inter-row managements as well as the effect of pH and OM on soil microorganism activities. We highlighted the benefits of organic management over conventional practices, as it is associated in our study sites with higher soil organic matter content. Organic matter is a major driver of enzymatic activities, particularly those related to N and P related enzymatic activities. pH was also an important parameter to control to ensure sufficient enzymatic activities. The presence of grassy inter-rows in vineyards contributed to enhanced soil functionality by promoting the respiration of complex C-substrates, in contrast to tilled inter-rows. Organic viticulture and grassy inter-rows appeared to not affect the C_{enz}:N_{enz} stoichiometry and enhanced nitrogen availability in vineyard soils. Further analyses such as phospholipid fatty acid (PLFA) could provide insight into whether community composition is impacted by soil management. Additional studies focusing on vineyards transitioning to organic management would also be valuable. Moreover, it would be beneficial to examine the resilience of microbial communities and activities after tillage operations, by analyzing microbial functions at different periods during the growing season.

CRediT authorship contribution statement

Benjamin Joubard: Writing – review & editing, Methodology, Investigation. **Sylvie Milin:** Methodology, Investigation. **Adrien Rusch:** Writing – review & editing, Project administration, Funding acquisition, Conceptualization. **Brice Giffard:** Writing – review & editing, Project administration, Funding acquisition, Conceptualization. **Pierre Blondel:** Writing – original draft, Methodology, Investigation, Formal analysis, Data curation. **Nicolas Fanin:** Writing – review & editing, Conceptualization.

Declaration of Competing Interest

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

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.pedobi.2024.151017.

Data Availability

Data will be made available on request.

References

Abad, F.J., Marín, D., Imbert, B., Virto, I., Garbisu, C., Santesteban, L.G., 2023. Under-vine cover crops: impact on physical and biological soil proprieties in an irrigated Mediterranean vineyard. Sci. Hortic. 311, 111797. https://doi.org/10.1016/j.scienta.2022.111797.

Abad, J., Hermoso De Mendoza, I., Marín, D., Orcaray, L., Santesteban, L.G., 2021. Cover crops in viticulture. A systematic review (1): implications on soil characteristics and biodiversity in vineyard. OENO One 55, 295–312. https://doi.org/10.20870/oeno-one.2021.55.1.3599.

Aciego Pietri, J.C., Brookes, P.C., 2009. Substrate inputs and pH as factors controlling microbial biomass, activity and community structure in an arable soil. Soil Biol. Biochem. 41, 1396–1405. https://doi.org/10.1016/j.soilbio.2009.03.017.

Acosta-Martínez, V., Dowd, S., Sun, Y., Allen, V., 2008. Tag-encoded pyrosequencing analysis of bacterial diversity in a single soil type as affected by management and land use. Soil Biol. Biochem. 40, 2762–2770. https://doi.org/10.1016/j.soilbio.2008.07.022.

Balesdent, J., Chenu, C., Balabane, M., 2000. Relationship of soil organic matter dynamics to physical protection and tillage. Soil Tillage Res 53, 215–230. https://doi.org/10.1016/S0167-1987(99)00107-5.

Banerjee, S., Walder, F., Büchi, L., Meyer, M., Held, A.Y., Gattinger, A., Keller, T., Charles, R., van der Heijden, M.G.A., 2019. Agricultural intensification reduces microbial network complexity and the abundance of keystone taxa in roots. ISME J. 13, 1722–1736. https://doi.org/10.1038/s41396-019-0383-2.

Bell, C.W., Fricks, B.E., Rocca, J.D., Steinweg, J.M., McMahon, S.K., Wallenstein, M.D., 2013. High-throughput fluorometric measurement of potential soil extracellular enzyme activities. J. Vis. Exp. 50961. https://doi.org/10.3791/50961.

Belmonte, S.A., Celi, L., Stahel, R.J., Bonifacio, E., Novello, V., Zanini, E., Steenwerth, K. L., 2018. Effect of long-term soil management on the mutual interaction among soil organic matter, microbial activity and aggregate stability in a vineyard. Pedosphere 28, 288–298. https://doi.org/10.1016/S1002-0160(18)60015-3.

Bommarco, R., Kleijn, D., Potts, S.G., 2013. Ecological intensification: harnessing ecosystem services for food security. Trends Ecol. Evol. 28, 230–238. https://doi.org/10.1016/j.tree.2012.10.012.

Bourget, M.Y., Fanin, N., Fromin, N., Hättenschwiler, S., Roumet, C., Shihan, A., Huys, R., Sauvadet, M., Freschet, G.T., 2023. Plant litter chemistry drives long-lasting changes in the catabolic capacities of soil microbial communities. Funct. Ecol. 37, 2014–2028. https://doi.org/10.1111/1365-2435.14379.

Burns, R.G., DeForest, J.L., Marxsen, J., Sinsabaugh, R.L., Stromberger, M.E., Wallenstein, M.D., Weintraub, M.N., Zoppini, A., 2013. Soil enzymes in a changing environment: current knowledge and future directions. Soil Biol. Biochem. 58, 216–234. https://doi.org/10.1016/j.soilbio.2012.11.009.

Campbell, C.D., Chapman, S.J., Cameron, C.M., Davidson, M.S., Potts, J.M., 2003. A rapid microtiter plate method to measure carbon dioxide evolved from carbon substrate amendments so as to determine the physiological profiles of soil microbial communities by using whole soil. Appl. Environ. Microbiol. 69, 3593–3599. https://doi.org/10.1128/AEM.69.6.3593-3599.2003.

Capowiez, Y., Cadoux, S., Bouchant, P., Ruy, S., Roger-Estrade, J., Richard, G., Boizard, H., 2009. The effect of tillage type and cropping system on earthworm communities, macroporosity and water infiltration. Soil Tillage Res 105, 209–216. https://doi.org/10.1016/j.still.2009.09.002.

Celette, F., Findeling, A., Gary, C., 2009. Competition for nitrogen in an unfertilized intercropping system: the case of an association of grapevine and grass cover in a Mediterranean climate. Eur. J. Agron. 30, 41–51. https://doi.org/10.1016/j.eja.2008.07.003.

Celik, I., Barut, Z.B., Ortas, I., Gok, M., Demirbas, A., Tulun, Y., Akpinar, C., 2011. Impacts of different tillage practices on some soil microbiological properties and crop yield under semi-arid Mediterranean conditions. Int. J. Plant Prod. https://doi.org/10.22069/IJPP.2012.736.

Cotton, J., Acosta-Martínez, V., 2018. Intensive tillage converting grassland to cropland immediately reduces soil microbial community size and organic carbon. Agric. Environ. Lett. 3, 180047. https://doi.org/10.2134/ael2018.09.0047.

Creamer, R.E., Stone, D., Berry, P., Kuiper, I., 2016. Measuring respiration profiles of soil microbial communities across Europe using MicroResp™ method. Appl. Soil Ecol. 97, 36–43. https://doi.org/10.1016/j.apsoil.2015.08.004.

De Santiago, A., Quintero, J.M., Delgado, A., 2008. Long-term effects of tillage on the availability of iron, copper, manganese, and zinc in a Spanish Vertisol. Soil Tillage Res 98, 200–207. https://doi.org/10.1016/j.still.2008.01.002.

Engell, I., Linsler, D., Sandor, M., Joergensen, R.G., Meinen, C., Potthoff, M., 2022. The effects of conservation tillage on chemical and microbial soil parameters at four sites across Europe. Plants 11, 1747. https://doi.org/10.3390/plants11131747.

Fromin, N., Shihan, A., Santonja, M., Baldy, V., Hättenschwiler, S., 2020. Soil microbial activity in a Mediterranean garrigue responds more to changing shrub community than to reduced rainfall. Plant Soil 449, 405–421. https://doi.org/10.1007/s11104-020-04501-8.

Garcia, L., Celette, F., Gary, C., Ripoche, A., Valdés-Gómez, H., Metay, A., 2018. Management of service crops for the provision of ecosystem services in vineyards: A review. Agric. Ecosyst. Environ. 251, 158–170. https://doi.org/10.1016/j.agee.2017.09.030.

Giffard, B., Winter, S., Guidoni, S., Nicolai, A., Castaldini, M., Cluzeau, D., Coll, P., Cortet, J., Le Cadre, E., d'Errico, G., Forneck, A., Gagnarli, E., Griesser, M., Guernion, M., Lagomarsino, A., Landi, S., Bissonnais, Y.L., Mania, E., Mocali, S., Preda, C., Priori, S., Reineke, A., Rusch, A., Schroers, H.-J., Simoni, S., Steiner, M., Temneanu, E., Bacher, S., Costantini, E.A.C., Zaller, J., Leyer, I., 2022. Vineyard management and its impacts on soil biodiversity, functions, and ecosystem services. Front. Ecol. Evol. 10, 850272. https://doi.org/10.3389/fevo.2022.850272.

Ingels, C.A., Scow, K.M., Whisson, D.A., Drenovsky, R.E., 2005. Effects of cover crops on grapevines, yield, juice composition, soil microbial ecology, and gopher activity. Am. J. Enol. Vitic. 56, 19–29. https://doi.org/10.5344/ajev.2005.56.1.19.

Kuzyakov, Y., Friedel, J.K., Stahr, K., 2000. Review of mechanisms and quantification of priming effects. Soil Biol.

Lagomarsino, A., Benedetti, A., Marinari, S., Pompili, L., Moscatelli, M.C., Roggero, P.P., Lai, R., Ledda, L., Grego, S., 2011. Soil organic C variability and microbial functions in a Mediterranean agro-forest ecosystem. Biol. Fertil. Soils 47, 283–291. https://doi.org/10.1007/s00374-010-0530-4.

Lauber, C.L., Hamady, M., Knight, R., Fierer, N., 2009. Pyrosequencing-based assessment of soil ph as a predictor of soil bacterial community structure at the continental scale. Appl. Environ. Microbiol. 75, 5111–5120. https://doi.org/10.1128/AEM.00335-09.

Maxwell, T.L., Augusto, L., Bon, L., Courbineau, A., Altinalmazis-Kondylis, A., Milin, S., Bakker, M.R., Jactel, H., Fanin, N., 2020. Effect of a tree mixture and water availability on soil nutrients and extracellular enzyme activities along the soil profile in an experimental forest. Soil Biol. Biochem. 148, 107864. https://doi.org/10.1016/j.soilbio.2020.107864.

McDaniel, M.D., Tiemann, L.K., Grandy, A.S., 2014. Does agricultural crop diversity enhance soil microbial biomass and organic matter dynamics? a meta-analysis. Ecol. Appl. 24, 560–570. https://doi.org/10.1890/13-0616.1.

Muneret, L., Auriol, A., Bonnard, O., Richart-Cervera, S., Thiéry, D., Rusch, A., 2019. Organic farming expansion drives natural enemy abundance but not diversity in vineyard-dominated landscapes. Ecol. Evol. 9, 13532–13542. https://doi.org/10.1002/ece3.5810.

Nannipieri, P., Giagnoni, L., Renella, G., Puglisi, E., Ceccanti, B., Masciandaro, G., Fornasier, F., Moscatelli, M.C., Marinari, S., 2012. Soil enzymology: classical and molecular approaches. Biol. Fertil. Soils 48, 743–762. https://doi.org/10.1007/s00374-012-0723-0.

Novara, A., Cerda, A., Barone, E., Gristina, L., 2021. Cover crop management and water conservation in vineyard and olive orchards. Soil Tillage Res 208, 104896. https://doi.org/10.1016/j.still.2020.104896.

Okur, N., AltindİŞlİ, A., Çengel, M., Göçmez, S., Kayikçioğlu, H.H., 2009. Microbial biomass and enzyme activity in vineyard soils under organic and conventional farming systems. Turk. J. Agric. For. https://doi.org/10.3906/tar-0806-23.

Orwin, K.H., Wardle, D.A., Greenfield, L.G., 2006. Ecological consequences of carbon substrate identity and diversity in a laboratory study. Ecology 87, 580–593. https://doi.org/10.1890/05-0383.

Ostandie, N., Giffard, B., Bonnard, O., Joubard, B., Richart-Cervera, S., Thiéry, D., Rusch, A., 2021. Multi-community effects of organic and conventional farming practices in vineyards. Sci. Rep. 11, 11979. https://doi.org/10.1038/s41598-021-91095-5.

Peregrina, F., Pérez-Álvarez, E.P., Colina, M., García-Escudero, E., 2012. Cover crops and tillage influence soil organic matter and nitrogen availability in a semi-arid vineyard. Arch. Agron. Soil Sci. 58, SS95–SS102. https://doi.org/10.1080/03650340.2011.648182.

Peregrina, F., Pilar Pérez-Álvarez, E., García-Escudero, E., 2014. Soil microbiological properties and its stratification ratios for soil quality assessment under different cover crop management systems in a semiarid vineyard. J. Plant Nutr. Soil Sci. 177, 548–559. https://doi.org/10.1002/jpln.201300371.

Pérez-Álvarez, E.P., Pérez-Sotés, J.L., García-Escudero, E., Peregrina, F., 2013. Cover Crop Short-Term Effects on Soil NO3 −-N availability, nitrogen nutritional status, yield, and must quality in a calcareous vineyard of the AOC Rioja, Spain. Commun. Soil Sci. Plant Anal. 44, 711–721. https://doi.org/10.1080/00103624.2013.748122.

Pérez-Álvarez, E.P., Garde-Cerdán, T., Santamaría, P., García-Escudero, E., Peregrina, F., 2015. Influence of two different cover crops on soil N availability, N nutritional status, and grape yeast-assimilable N (YAN) in a cv. Tempranillo vineyard. Plant Soil 390, 143–156. https://doi.org/10.1007/s11104-015-2387-7.

Pingel, M., Reineke, A., Leyer, I., 2023. Disentangling the mixed effects of soil management on microbial diversity and soil functions: a case study in vineyards. Sci. Rep. 13, 3568. https://doi.org/10.1038/s41598-023-30338-z.

Qian, P., Schoenau, J.J., 2002. Practical applications of ion exchange resins in agricultural and environmental soil research. Can. J. Soil Sci. 82, 9–21. https://doi.org/10.4141/S00-091.

R Core Team, 2022. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL ⟨https://www.R-project.org/⟩.

Ranjard, L., Richaume, A., 2001. Quantitative and qualitative microscale distribution of bacteria in soil. Res. Microbiol. 152, 707–716. https://doi.org/10.1016/S0923-2508(01)01251-7.

Reilly, K., Cavigelli, M., Szlavecz, K., 2023. Agricultural management practices impact soil properties more than soil microarthropods. Eur. J. Soil Biol. 117, 103516. https://doi.org/10.1016/j.ejsobi.2023.103516.

Rousk, J., Bååth, E., Brookes, P.C., Lauber, C.L., Lozupone, C., Caporaso, J.G., Knight, R., Fierer, N., 2010. Soil bacterial and fungal communities across a pH gradient in an arable soil. ISME J. 4, 1340–1351. https://doi.org/10.1038/ismej.2010.58.

Saggar, S., Hedley, M.J., White, R.E., 1990. A simplified resin membrane technique for extracting phosphorus from soils. Fertil. Res. 24, 173–180. https://doi.org/10.1007/BF01073586.

Sannino, F., Gianfreda, L., 2001. Pesticide influence on soil enzymatic activities. Chemosphere 417–425. https://doi.org/10.1016/S0045-6535(01)00045-5.

Sinsabaugh, R.L., Lauber, C.L., Weintraub, M.N., Ahmed, B., Allison, S.D., Crenshaw, C., Contosta, A.R., Cusack, D., Frey, S., Gallo, M.E., Gartner, T.B., Hobbie, S.E., Holland, K., Keeler, B.L., Powers, J.S., Stursova, M., Takacs-Vesbach, C., Waldrop, M.P., Wallenstein, M.D., Zak, D.R., Zeglin, L.H., 2008. Stoichiometry of soil enzyme activity at global scale. Ecol. Lett. 11, 1252–1264. https://doi.org/10.1111/j.1461-0248.2008.01245.x.

Steenwerth, K., Belina, K.M., 2008. Cover crops enhance soil organic matter, carbon dynamics and microbiological function in a vineyard agroecosystem. Appl. Soil Ecol. 40, 359–369. https://doi.org/10.1016/j.apsoil.2008.06.006.

Syswerda, S.P., Corbin, A.T., Mokma, D.L., Kravchenko, A.N., Robertson, G.P., 2011. Agricultural management and soil carbon storage in surface vs. Deep Layers. Soil Sci. Soc. Am. J. 75, 92–101. https://doi.org/10.2136/sssaj2009.0414.

Thoumazeau, A., Bessou, C., Renevier, M.-S., Trap, J., Marichal, R., Mareschal, L., Decaëns, T., Bottinelli, N., Jaillard, B., Chevallier, T., Suvannang, N., Sajjaphan, K., Thaler, P., Gay, F., Brauman, A., 2019. Biofunctool®: a new framework to assess the impact of land management on soil quality. Part A: concept and validation of the set of indicators. Ecol. Indic. 97, 100–110. https://doi.org/10.1016/j.ecolind.2018.09.023.

Tilman, D., Cassman, K.G., Matson, P.A., Naylor, R., Polasky, S., 2002. Agricultural sustainability and intensive production practices. Nature 418, 671–677. https://doi.org/10.1038/nature01014.

Zehetner, F., Djukic, I., Hofmann, R., Kühnen, L., Rampazzo-Todorovic, G., Gerzabek, M.H., Soja, G., 2015. Soil organic carbon and microbial communities respond to vineyard management. Soil Use Manag 31, 528–533. https://doi.org/10.1111/sum.12204.

Zuber, S.M., Villamil, M.B., 2016. Meta-analysis approach to assess effect of tillage on microbial biomass and enzyme activities. Soil Biol. Biochem. 97, 176–187. https://doi.org/10.1016/j.soilbio.2016.03.011.