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Organic farming promotes general disease suppression and modulates functional potential of rhizosphere microbiome in mustard

Priya Chaudhary · Annapurna Bhattacharjee · Y. S. Shivay · Martin Pabst · Shilpi Sharma

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Abstract

Purpose Organic farming practices enhance soil health by the addition of bio-amendments, which improve microbial diversity and abundance. Improved soil health, due to enhanced dynamic interactions between abiotic and biotic components of the environment, impedes the progression of diseases caused by soil-borne phytopathogens. The present study aimed to characterize the critical microbial and edaphic factors in correlation with phytopathogen

suppression in soil from mustard fields managed under different farming practices.

Methods and results Organic soil exhibited better suppression of phytopathogens, availability of macronutrients, and high biocontrol enzymatic activities than soil from conventionally managed field. In terms of maximal phytopathogen suppression, *Fusarium solani* was suppressed to 85% by fungal fraction of organic soil, whereas *F. fujikori* was suppressed to 77% by bacterial fraction of organic soil. However, available micronutrients were higher in conventionally managed soils. Positive correlations between enhanced biocontrol enzyme activities and organic farming practice were deciphered, highlighting improved disease suppressive potential of organic soil. Metagenomic sequencing of the rhizosphere soil from mustard plants grown using “*Jeevan Jyoti*” bio-amendment and conventional farming regimes revealed that microbial

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communities could play key roles in modulating general disease suppressiveness of soil. Functional annotation enabled the identification of dominant biological processes, impacting plant and soil health positively. Specifically, the open reading frames coding for bacterial proteins involved in transport and key cellular processes were enriched in datasets of organic farm soil.

Conclusion The evidences from this study delineate the correlation between microbial components present in rhizosphere soil and edaphic factors, in the context of general disease suppressiveness.

Keywords Biocontrol · Micronutrients · Phytopathogens · General disease suppression · Soil metagenomics

Introduction

Several environmental factors are responsible for governing plant and soil health. Abiotic and biotic stressors, coupled with excessive chemical use, often irreversibly jeopardize various agro-ecosystems, detrimentally affecting plant development and crop yield, besides compromising the soil health. There is an ardent need to advocate implementation of sustainable agricultural means to minimize adverse environmental effects worldwide. One such eco-friendly approach entails the promotion of organic farming regimes to facilitate the enhancement of soil and plant health by optimal usage of bio-amendments, which would eventually boost crop yield (Gamage et al. 2023; Jayaraman et al. 2021).

Soils from organic fields possess a disease-suppressive capacity to control the spread of various phytopathogens (Gómez Expósito et al. 2017). Soil disease suppression can be categorized into specific and general disease suppression; the latter leads to suppression of diseases against a wide range of phytopathogens. This disease-suppressive ability is a result of the activity of critical microbial agents, in soil and rhizospheres of plants (De Corato 2020; Schlatter et al. 2017). Numerous factors orchestrate the assembly and action of these antagonistic biocontrol agents in the disease-suppressive soil. This includes edaphic factors, agro-management practices, and crop type (Deltour et al. 2017; Palojarvi et al. 2020). Among the edaphic factors, soil nutrient status plays an

important role in governing competitive interactions in the rhizospheric microbial community, thereby influencing microbial diversity to confer the trait of general disease suppression in soil (Schlatter et al. 2017). Applying bio-amendments, under organic farming practice, has been beneficial for soil and plant health, and also exhibits the potential for inducing general disease suppression in soil (Al-Elwany et al. 2023; Deng et al. 2022).

Studies have established that organic farming practice positively impacts microbial diversity in soil and confers disease-suppressive traits to organic soils, improving plant health (Khatri et al. 2023a, b; Postma et al. 2008). However, limited studies have been carried out in the context of general disease suppressiveness traits of soil (Schlatter et al. 2017). So far, molecular markers and microbial members, conferring specific and general disease-suppressive trait in organic farm soils have been identified (Khatri and Sharma 2021; Khatri et al. 2024). To our knowledge, no study has been carried out to decipher how available nutrients and biocontrol enzymatic activities of rhizosphere soil under organic and conventional farming regimes, influence general disease suppressiveness in soil. Moreover, only a few recent reports have compared the functional potential of rhizospheric microbiomes from organically and conventionally managed farms (Raimi et al. 2023; Zhang et al. 2022a, b).

The current study hypothesized that organic farming practice influences the rhizospheric microbial communities and edaphic factors, which contribute to the development of general suppression against various phytopathogens. This study reports application of bio-amendment “*Jeevan Jyoti*” in organic farm, which may have a possible role in modulating the microbial dynamics and eventually disease-suppressive potential in soil. In totality, the present study was designed to decipher the role of soil nutrient status, biocontrol enzymatic activities, and key microbial members involved in suppression of a wide range of fungal and bacterial phytopathogens by analyzing the rhizospheric soil samples from mustard fields under organic and conventional management. To examine the functional potential of rhizosphere microbiomes under farming practices, and to further decipher the mechanisms involved in phytopathogen suppression, whole metagenome sequencing of soil samples was performed. This enabled the identification of major

microbial players and their functional potential to develop soil disease-suppressive traits.

Materials and methods

Field location and soil sampling

Soil was sampled from farmers' fields at Phaphund, Kanpur, Uttar Pradesh, India. The sampling site falls under the upper Indo-Gangetic plains with a sub-tropical climate (annual mean temperature min. 5.5 °C to max. 45 °C, and mean annual rainfall of 863 mm). The soil type was classified as alluvial, with alkaline pH. The mustard (T59 Varuna variety, Shriram Mustard Seeds) fields were managed under different farming practices, namely organic (coordinates: 26.586969, 79.467434), conventional (coordinates: 26.587043, 79.467845), and control (natural vegetation) soil (coordinates: 26.586609, 79.467362). Organic field management included the application of commercially available organic bio-amendment named *Jeevan Jyoti* (applied as a solution on field of ~0.5 acre, 35 ml per 15 l water) 15–25 days before and after sowing, and conventionally managed fields were amended with diammonium phosphate (DAP) (50 kg/ha) and urea (25 kg/ha). The bio-amendment *Jeevan Jyoti* was composed of cow urine, cow gallstones, jaggery cubes, and ayurvedic herbs like gokshura. Control soil was also sampled from area under natural vegetation. A randomized quadrat sampling experimental design was followed for sampling at each site. Rhizosphere soil was collected in five replicates using a hand auger from 0–30 cm depth from mustard cropping fields at harvest stage.

Before storage, visible roots and debris were manually removed from the soil samples. Soil samples were preserved at 4 °C and –80 °C. The remaining soil sample was air-dried in shade, followed by sieving, grinding, and storing at 4 °C for subsequent physicochemical analyses.

In vitro analysis of pathogen suppression potential of soil

Pathogen suppression efficacy of soil samples was assessed using in vitro dual culture assay against a range of phytopathogens as described previously (Khatri et al. 2023a, b). A set of soil-borne

phytopathogens with a wide range of hosts, were selected for the investigation. Phytopathogens, viz. *Fusarium udum* (ITCC No. 4968), *Fusarium fujikuroi* (ITCC10963.18), *Fusarium solani* (ITCC 6701), *Rhizoctonia solani* (MTCC No. 4633), *Fusarium oxysporum* (MTCC 4633), *Sclerotium rolfsii* (ITCC 6416), *Pythium aphanidermatum* (ITCC 9121), *Phytophthora* sp. (ITCC 7700), *Verticillium dahliae* (MTCC 2063), *Ralstonia solanacearum* (ITCC BI0001), and *Erwinia carotovora* (ITCC No. BL0001) were procured from Microbial Type Culture Collection and Gene Bank (MTCC), Chandigarh, India, and the Indian Type Culture Collection (ITCC), ICAR-Indian Agricultural Research Institute (IARI), New Delhi, India.

Ten grams of soil was added to 100 ml potato dextrose broth (HiMedia, India) containing combinations of different antibiotics (sulfadiazine 100 µg/ml, rifampicin 50 µg/ml, chloramphenicol 50 µg/ml, kanamycin 50 µg/ml, and streptomycin 50 µg/ml) to inhibit bacterial growth, as reported previously (Labiadh et al. 2021). To arrest the growth of varied members of the bacterial community a wide variety of antibiotics was used, thereby preferentially promoting the growth of fungal taxa present in soil. The fungal cultures were grown at 30 °C for five to seven days until the media became turbid or mycelium was visible in each culture. Subsequently, inhibition of the phytopathogens was assessed by the bacterial and fungal cultures, grown from soil suspensions of different treatments. In vitro dual culture assay for interaction between fungal/bacterial pathogen and fungal component was determined by spot inoculating an equal amount of pathogen and fungal suspension (~10⁶ spores/ml) on opposite ends (1.5 cm from the margin) of 90 mm petri plates after seven days of incubation. The plates were kept at 28 °C for 14–21 days or till complete growth was witnessed on the control plate for comparable results. Similarly, bacterial soil suspension was prepared by adding ten grams of soil in nutrient broth (HiMedia, India) containing antifungal compounds (50 µg/ml each of cycloheximide and fluconazole). The soil suspension was incubated at 30 °C for 48 h and spot inoculated on four ends of an equidistant quadrant position on plate. The fungal strain was spot inoculated at quadrant centre and the plates were incubated for 3–7 days at 30 °C. For inhibition of bacterial pathogen, the zone of inhibition was recorded.

The percentage inhibition of the fungal pathogen was calculated by measuring the radius of its growth in control (C) and other treatments (T) using the given formula (Rahman et al. 2009):

$$\% \text{Inhibition of pathogen} = (C - T) / C * 100$$

Physicochemical properties of soil

The physicochemical properties of soil, namely pH, electrical conductivity (EC), soil organic carbon (SOC), and availability of nutrients, nitrogen (N), phosphorus (P), potassium (K), sulphur (S), copper (Cu), iron (Fe), manganese (Mn), and zinc (Zn) levels were assessed. SOC was estimated using a previously described method (Walkley and Black 1934). Available P was extracted with 0.5 M NaHCO₃ solution (Olsen 1954), and available S was obtained using 0.01 M CaCl₂ solution (Chesnin and Yien 1951), respectively, and nutrient levels were recorded by spectrophotometric analysis. Available K levels in the soil were determined using a flame photometer after extracting with 1 M ammonium acetate. Available N levels in the soil were assessed based on alkaline permanganate method using Kjeldahl's apparatus (Subbiah and Asija 1956). Available micronutrients extracted by 0.005 M diethylenetriaminepentaacetic acid (DTPA)—0.01 M CaCl₂—0.1 M triethanolamine (TEA) solution, were quantified using flame atomic absorption spectroscopy (Lindsay and Norvell 1978). The pH and EC of soil samples were recorded using combined electrodes in a 1:2.5 ratio of soil:water.

Estimation of enzymatic activities and siderophore production in soil

The chitinase and cellulase activities in soil samples were quantified using the 3,5-dinitro salicylic acid (DNS) based colorimetric assay as reported earlier (Miller 1959; Rodriguez-Kabana et al. 1983), with few modifications. For enzymatic analysis, 0.5 g of soil was mixed with 0.2 ml of toluene for 10 min at room temperature. In the treated soil samples, 2 ml of substrates, viz. colloidal chitin (polymer of 2-(acetylamino)-2-deoxy-D-glucose) suspension [1.25% (w/v) of colloidal chitin in 0.1 ml of 100 mM potassium phosphate buffer (pH 6.0) and 1.0 mM calcium chloride], and carboxymethyl cellulose was

added to determine chitinase and cellulase activities, respectively. After 24 h of incubation at 28 °C, the suspensions were centrifuged at 10,000 rpm for 10 min to obtain clear supernatant. To 1 ml of clear supernatant, 1.5 ml of DNS reagent was added, and the suspension was kept for boiling in a water bath for 5 min. The reaction was stopped after addition of 2 ml of deionized water. Subsequently, the suspension was then subjected to spectrophotometry at 540 nm to determine the amount of N-acetyl-glucosamine and glucose released in 1 ml of the supernatant for chitinase and cellulase, respectively.

The soil protease activity was estimated using sodium casein as the substrate (Jesmin et al. 2022). The lipolytic activity in rhizosphere samples was assayed by titrimetric method using polysorbate 20 as substrate (Akhter et al. 2022; Sakai et al. 2002).

The level of siderophore production in soil was determined by inoculating (0.5 g) soil in a modified M9 minimal medium (without Fe) and incubating for 72 h at 28 °C. The culture was centrifuged at 10,000 rpm for 10 min to obtain clear supernatant. Universal chrome azurol-S (CAS) liquid assay was used to determine the siderophore levels in clear supernatant (Schwyn and Neilands 1987). The percent of siderophore units released was estimated (Chowdappa et al. 2020). Each reaction was performed with three replicates.

Isolation of rhizosphere soil DNA and whole metagenome sequencing

FastDNA™ SPIN Kit was used to isolate DNA from bulk soil, and soil samples from organic and conventional fields, as per the manufacturer's protocol (MP Biomedicals, USA). For each treatment, five replicates of soil samples were pooled to form composite sample, and 0.5 g of this was used for soil DNA isolation. The quantification and quality check for isolated DNA samples were performed using a NanoDrop™ 2000C spectrophotometer (Fischer, USA). The isolated soil DNA was kept at -20 °C till further analysis. Whole metagenome sequencing of soil DNA was performed using paired-end sequencing technology (2×150 bp) on the Illumina NOVASEQ6000 platform (Illumina, USA).

Initially, parameters like base quality score distribution, sequence quality score distribution, average base content per read, GC distribution in the reads from samples, PCR amplification issue,

overrepresented sequences and adapters, were checked from the sample fastq files. According to the quality control report, the fastq files were trimmed to retain high-quality sequences, whereas low-quality sequence reads were removed from the analysis. The trimming of adapters was done by the fastq-mcf tool (version- 1.04.803). The adapter trimmed reads were aligned to the human (hg19) genome to remove human contamination using BWA (0.7.12) and the reads were filtered for human DNA contamination. Further, de novo assembly was carried out using the pre-processed reads to obtain the scaffolds. For de novo metagenome assembly, the human unaligned reads, retrieved after human contamination removal step, were de novo assembled using Megahit (v. 1.2.9) (Li et al. 2015). The primarily assembled genome was used for ORF prediction and annotation using Prodigal (v. 2.6.3) (Hyatt et al. 2010). Taxonomic classification, preliminary functional annotation of predicted ORFs and identification of SEED pathway were performed using Megan 6 (Huson et al. 2007). The microbial abundance at the phylum, genus, and species level was recorded. The taxonomic quantification was carried out based on the fraction of reads assigned to individual taxa, and functional annotation was performed on the identified ORFs. Heatmaps were generated using Heatmapper software. The sequence data from the whole metagenome sequencing analysis was submitted to NCBI Sequence Read Archive (SRA) under BioProject ID PRJNA1105849. Functional annotation of predicted genes was performed by local installation of the eggNOG-mapper v. 2.1.12, using default parameters. Genes predicting relevant KOs, Prams, and CAZY annotations from the top 100 most frequent entries were normalized and visualized using Python and the seaborn cluster-map function.

Statistical analysis

To deduce the impact of specific farming practices on parameters of soil quality and suppression potential, one-way analysis of variance (ANOVA) was employed. Before one-way ANOVA, the data were examined for normal distribution using the Shapiro–Wilk test (Shapiro and Wilk 1965). The homogeneity of variance was assessed using Levene’s test. Means of treatments were separated using Tukey’s honestly significant post-hoc

analysis at $p < 0.05$. The data in tables and figures are represented as arithmetic means with standard error of the mean (SEM). Principal component analysis (PCA) was used to evaluate the multi-variable data. Factors with an eigenvalue greater than one were considered as per Kaiser’s criterion. The data was standardized before conducting PCA. Variables showing maximum variance in PCA were then subjected to two-tailed Pearson’s correlation. A two-tailed Pearson’s correlation test was employed to identify relationships between specific soil parameters and the percent inhibition potency of soils against different phytopathogens. A p -value ≤ 0.05 was considered significant. All the statistical analyses were carried out in Origin-Pro 2024 (Origin Lab Corporation, Northampton, MA, USA).

Results

In vitro dual culture assay for pathogen suppression

The pathogen suppression potential of culturable fungal and bacterial fractions of soil exhibited varying suppressive patterns. The soil managed organically showed enhanced pathogen suppression compared to conventional and control (natural vegetation) soils (Fig. 1).

To examine the bacterial fraction of the soil, seven of the shortlisted nine fungal phytopathogens showed significantly higher pathogen suppression in the soil from organic field than that from conventional field (Supplementary Table S1). *Fusarium oxysporum* ($61.79 \pm 2.52\%$, $p = 0.0231$), *F. solani* ($74.58 \pm 0.75\%$, $p = 0.0095$), *F. fujikuroi* ($77.54 \pm 0.41\%$, $p < 0.0001$), *Sclerotium rolfsii* ($56.66 \pm 1.66\%$, $p = 0.045$), *Pythium aphanidermatum* ($69.54 \pm 0.41\%$, $p = 0.0017$), *Phytophthora* sp. ($64.79 \pm 1.85\%$, $p = 0.0244$), and *Verticillium dahliae* ($67.7 \pm 2.75\%$, $p = 0.0182$) were highly suppressed in soil from organic fields. Similarly, fungal fraction from organically managed soil showed maximum suppression against the selected phytopathogens. The culturable fungal fraction of the community of organically managed soils showed maximum suppression compared to the same soil’s bacterial fraction. Organically managed soil showed significantly higher suppression of pathogens such as *Fusarium oxysporum* ($64 \pm 2.3\%$, $p = 0.0084$), *F. udum*

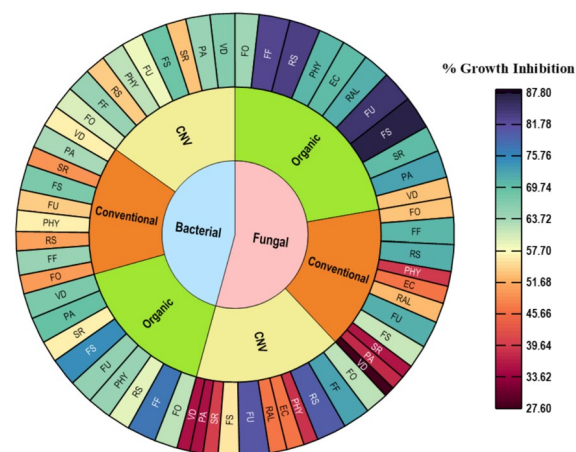


Fig. 1 Pathogen suppression potential of bacterial and fungal soil microbiome from mustard fields under organic, conventional, and control (natural vegetation) management. FO: *Fusarium oxysporum*, FU: *F. udum*, FF: *F. fujikuroi*, FS: *F. solani*, RS: *Rhizoctonia solani*, SR: *Sclerotium rolfsii*, PA: *Pythium aphanidermatum*, PHY: *Phytophthora* sp., VD: *Verticillium dahliae*, EC: *Erwinia carotovora*, RAL: *Ralstonia solanacearum*, CNV: Control (natural vegetation)

($85 \pm 2.54\%$, $p=0.0134$), *F. solani* ($82.66 \pm 1.45\%$, $p=0.0002$), *F. fujikuroi* ($87.77 \pm 2.42\%$, $p=0.0468$), *Rhizoctonia solani* ($83.33 \pm 0.96\%$, $p=0.0008$), *Sclerotium rolfsii* ($70 \pm 2.54\%$, $p=0.0005$), *Pythium aphanidermatum* ($72.55 \pm 2.95\%$, $p=0.0001$), *Phytophthora* sp. ($70.55 \pm 2.42\%$, $p<0.0001$), *Verticillium dahliae* ($53.33 \pm 0.96\%$, $p<0.0001$), *Erwinia carotovora* ($70 \pm 2.88\%$, $p=0.014$), and *Ralstonia solanacearum* ($71.73 \pm 2.04\%$, $p=0.0038$) than the conventionally managed soils.

Soil physicochemical properties under different farming types

Available macronutrient levels were significantly enhanced in organic farming as compared to conventional and control (natural vegetation) soils (Table 1). Sulphur (60.16 ± 1.92 mg/kg, $p=0.0031$), nitrogen (169.34 ± 6.27 kg/ha, $p<0.0001$), and phosphorus (20.1 ± 1.09 mg/kg, $p=0.0008$) were higher in the organic field compared to other farming practices. Contrary to this, available micronutrients were much higher in conventional and control (natural vegetation) soils than in organically managed soils. Besides

Table 1 Physicochemical and biocontrol parameters of rhizosphere soil under organic, conventional farming, and control (natural vegetation) soil in mustard field

Soil Properties	Parameters	Organic	Conventional	Control (Natural Vegetation)
Physicochemical	Available P (mg/kg)	20.1 ± 1.09^a	10.5 ± 0.86^b	13.6 ± 0.8^{ab}
	Available K (kg/ha)	450.24 ± 62.15^a	298.1 ± 27.5^{ab}	264.43 ± 18.97^b
	Available N (kg/ha)	169.34 ± 6.27^a	93.68 ± 1.98^c	108.71 ± 7.67^b
	Available S (mg/kg)	60.16 ± 1.92^a	50 ± 0.76^b	57.33 ± 0.72^a
	SOC (g/kg)	19.77 ± 0.98^a	12.27 ± 4.39^a	18.83 ± 0.75^a
	Available Cu (mg/kg)	0.38 ± 0.04^b	0.49 ± 0.04^b	0.79 ± 0.03^a
	Available Fe (mg/kg)	7.004 ± 1.05^b	11.44 ± 1.73^{ab}	13.97 ± 1.61^a
	Available Mn (mg/kg)	7.08 ± 1.04^b	11.46 ± 1.72^{ab}	15.42 ± 1.01^a
	Available Zn mg/kg)	0.11 ± 0.006^b	0.34 ± 0.02^a	0.29 ± 0.012^a
	Electrical Conductivity ($\mu\text{S}/\text{cm}$)	116.93 ± 0.75^b	104.76 ± 2.57^c	174.8 ± 1.25^a
	pH	6.46 ± 0.04^c	6.82 ± 0.09^b	7.44 ± 0.08^a
Biocontrol	Chitinase activity (IU/ml)	12.28 ± 0.23^a	10.71 ± 0.06^b	11.29 ± 0.54^{ab}
	Cellulase activity (IU/ml)	0.29 ± 0.017^a	0.09 ± 0.008^b	0.043 ± 0.002^c
	Lipase activity (μmol fatty acids/ml)	75.73 ± 0.88^a	58.06 ± 1.76^b	52.4 ± 0.57^c
	Protease activity (μmol tyrosine g^{-1} soil h^{-1})	0.75 ± 0.019^a	0.51 ± 0.02^b	0.49 ± 0.03^b
	Siderophore (% Units)	93.96 ± 1.31^a	92.03 ± 0.21^a	90.87 ± 1.48^a

Data are presented as mean \pm standard error. Mean values were compared among treatments using Tukey' -HSD following one-way ANOVA. Mean values with the same letter are not significantly different at $p \leq 0.05$. P: phosphorus; K: potassium; SOC: soil organic carbon; S: sulphur; N: nitrogen; Cu: copper; Mn: manganese; Zn: zinc; Fe: iron

nutrients, soil pH and EC were also measured to see the impact of these dynamic properties under different farming conditions on soil suppression and bio-control activities. Under organic farming, the soil was slightly more acidic (pH 6.4 ± 0.04) than in the conventional field (pH 6.8 ± 0.09) with a significant difference ($p=0.036$). The control (natural vegetation) soil showed an alkaline pH of 7.44 ± 0.08 . Soil EC was significantly lower in conventional ($104.76 \pm 2.57 \mu\text{S/cm}$) than in organically managed soil ($116.93 \pm 0.75 \mu\text{S/cm}$, $p=0.0057$).

PCA was performed to see the impact of soil physicochemical parameters on disease suppressiveness. The PCA extracted two components explaining 79.5% and 20.5% variance, respectively. The PC1 loadings exhibited a negative association between available micronutrients, soil pH, and EC (Fig. 2).

In PC2, loadings revealed a positive association among available Cu, Fe, Mn, pH, and EC, however, negative association among Zn levels and conventional farming practice was observed. Available micronutrients were closely related to soil pH and EC; and were influenced by conventional farming practices and control (natural vegetation) soils. The PC1 loadings were large and positive for pathogen suppression, which was positively influenced by the organic farming practice for the bacterial and fungal fractions of soil microbiome. Prominent positive associations were observed for biocontrol enzyme activities and organic farming practice, which indicated broad range of general disease-suppressive potential in organic soil. Loadings that showed maximum variance were then selected to find their relationship with soil suppressiveness and

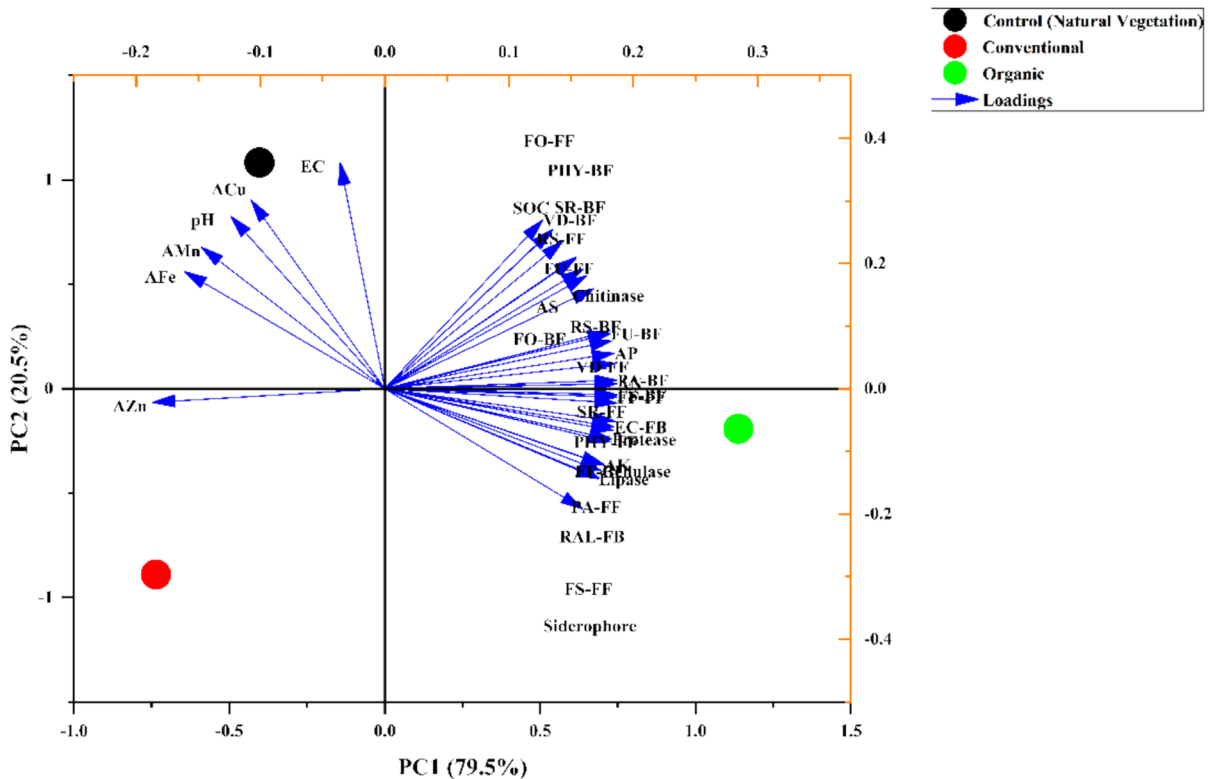


Fig. 2 Principal component analysis between physicochemical parameters and suppressiveness of soil from mustard fields under organic, conventional, and control (natural vegetation) practices. ACu: available copper, AMn available manganese, AZn: available zinc, AFe: available iron, FO: *F. oxysporum*, FU: *F. udum*, FF: *F. fujikuroi*, FS: *F. solani*, RS: *R. solani*, SR: *S. rolfsii*, PA: *Pythium aphanidermatum*, PHY: *Phytophthora*

sp., VD: *Verticillium dahliae*, EC: *Erwinia carotovora*, RAL: *Ralstonia solanacearum*. FF, FB, and BF are interactions studied in dual culture assay. FF: fungal soil suspension vs. fungal pathogen, FB: fungal soil suspension vs. bacterial pathogen, BF: bacterial soil suspension vs. fungal pathogen; CNV: control (natural vegetation)

biocontrol activity of soil. Pearson's correlation analysis exhibited a significant relationship between soil physicochemical properties and soil suppression potential (Fig. 3).

A positive correlation was found between SOC and *V. dahliae* ($r=0.99829$, $p=0.03$) suppression by the bacterial fraction. However, a negative correlation was observed in the context of available Zn and *Pythium aphanidermatum* ($r=-0.9997$, $p=0.014$) suppression by a bacterial fraction and *V. dahliae* ($r=-0.9986$, $p=0.032$) suppression by a fungal fraction. Similarly, disease suppression of a majority of the pathogens examined in the study was found to be affected by the availability of nutrients (Supplementary Table S2).

Biocontrol activity of soil

The biocontrol activity of soil was significantly greater in the organic field than in the conventional field (Table 1). Biocontrol enzymes like protease ($0.75 \pm 0.01 \mu\text{mol tyrosine g}^{-1} \text{ soil h}^{-1}$, $p=0.0017$), chitinase ($12.28 \pm 0.23 \text{ IU/ml}$, $p=0.04$), cellulase ($0.29 \pm 0.017 \text{ IU/ml}$, $p<0.0001$), and lipase ($75.73 \pm 0.88 \mu\text{mol fatty acids/ml}$, $p=0.0001$) had significantly greater activities in organic soils than in conventional soils. In the PCA analysis, the PC1, accounting for more than 75% variance, showed that the biocontrol activity was positively associated with pathogen suppression in organic farming practices (Fig. 2). Pearson's correlation determined that

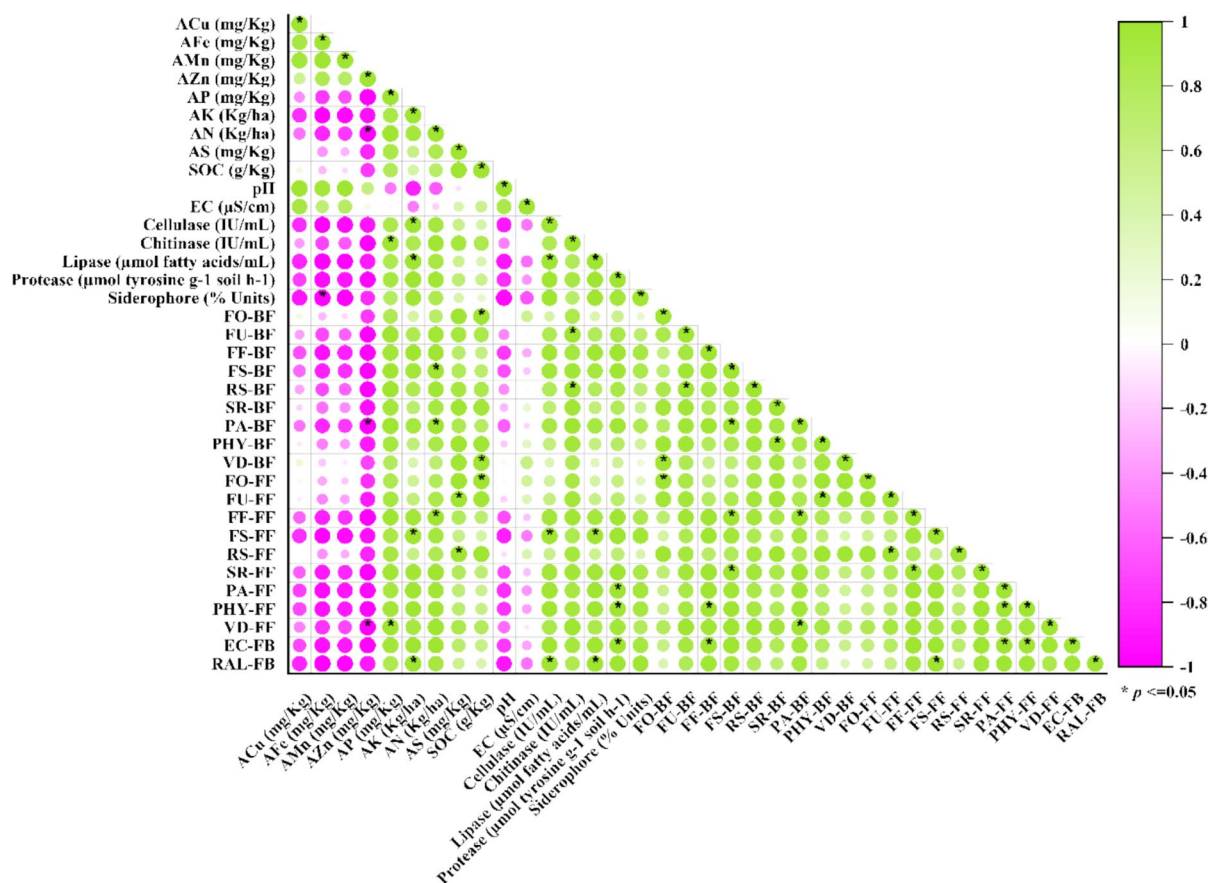


Fig. 3 Pearson Correlation analysis between physicochemical parameters and percent inhibition of pathogens by the soil from mustard fields. ACu: available copper, AMn available manganese, AZn: available zinc, AFc: available iron, FO: *F. oxysporum*, FU: *F. udum*, FF: *F. fujikuroi*, FS: *F. solani*, RS: *R. solani*, SR: *S. rolfisii*, PA: *Pythium aphanidermatum*, PHY: *Phytophthora* sp., VD: *Verticillium dahliae*, EC: *Erwinia carotovora*, RAL: *Ralstonia solanacearum*. FF, FB, and BF are interactions studied in dual culture assay. FF: fungal soil suspension vs. fungal pathogen, FB: fungal soil suspension vs. bacterial pathogen, BF: bacterial soil suspension vs. fungal pathogen

Phytophthora sp., VD: *Verticillium dahliae*, EC: *Erwinia carotovora*, RAL: *Ralstonia solanacearum*. FF, FB, and BF are interactions studied in dual culture assay. FF: fungal soil suspension vs. fungal pathogen, FB: fungal soil suspension vs. bacterial pathogen, BF: bacterial soil suspension vs. fungal pathogen

negative correlation was significant between available Fe and siderophore (% units) ($r = -0.9998$, $p = 0.01$). Cellulase and lipase activities were positively correlated with the available K in soils (Fig. 3). Protease activity was found to be significantly positive with suppression of *Pythium aphanidermatum* ($r = 0.9999$, $p = 0.008$), *Phytophthora* sp. ($r = 0.9992$, $p = 0.024$), and *Erwinia carotovora* ($r = 0.9985$, $p = 0.034$) by fungal fraction of soil.

Identification and comparison of bacterial taxa present in rhizospheric soil of mustard grown in organically and conventionally managed fields

The whole metagenome sequencing of rhizospheric soil from mustard plants grown in organically amended and conventional farms led to identifying different bacterial taxa that dominantly thrive in the plant's rhizosphere under specific farming practices.

A total of ~5–6 GB raw reads were generated per soil DNA sample from 3 input libraries for control (natural vegetation), conventional, and organic farm soil through whole metagenomic sequencing analysis. The data generated for control (natural vegetation), conventional, and organic soil samples was 15.24, 15.32, and 15.32 GB, respectively, and the percentage of GC content for control (natural vegetation), conventional, and organic datasets were 64.30, 65.03, and 65.35, respectively. Q30 was above 92%, and average GC% was around 60%. The contig length (bp) and N50 values for control (natural vegetation), conventional, and organic were 9097, 39,132, and 4724, and 657, 691, and 639, respectively. The total number of genes identified in control (natural vegetation), conventional, and organic soil datasets after ORF prediction were 118,104, 142,896, and 133,250, respectively. The Venn diagram depicts the distribution of taxonomies across all samples, revealing a high diversity (Supplementary Fig. S1). Particularly, the analysis led to identifying 10, 8, and 7 genera that were exclusively identified in the control (natural vegetation), conventional, and organic soil samples, respectively, whereas 35 genera were common to the three datasets (Supplementary Fig. S1). The common genera identified across all treatments likely represents the core microbiome of the mustard plant.

The ten dominant phyla among the identified phyla in all treatments were enlisted, and the stacked bar plot depicts the abundance of these dominant

bacterial phyla, in the mustard rhizosphere soil from organic and conventional farms, compared to control (natural vegetation) soil. *Actinobacteria* (49.3–74.5%), *Proteobacteria* (11.6–29.3%), *Chloroflexi* (3.3–9.2%), *Thaumarchaeota* (2.1–4.4%), and *Acidobacteria* (1.9–3.8%) were the most abundant phyla among all analyzed samples (Fig. 4A). In addition, *Planctomycetes* ranged from 0.7–1.2%. There was variability in the dominance of different bacterial taxa identified at the genus levels across the three treatments. At the genus level, unknown genus accounted for the maximum proportion of the total genera present (13.3–31.6%), followed by *Solirubrobacter* (3.7–9.8%), *Nocardioides* (9.3–23.5%), *Microvirga* (2.2–5.4%), and *Streptomyces* (2–13.8%), across control (natural vegetation), conventional, and organic soil datasets.

Interestingly, *Nocardioides* and *Microvirga* (2.2–5.4%) were more abundant under the organic farming regime (Fig. 4B). The relative abundance of *Bradyrhizobium* was comparable in the three treatments.

The abundance of bacterial taxa at the genus level across different treatments considered in the study has been represented as a heatmap (Fig. 5).

Besides the top ten genera identified in the three datasets (Fig. 4B), it was observed that the genera *Azospirillum*, *Nitrospira*, and *Mesorhizobium* were also relatively more abundant in the organic farms compared to the conventional farms and control (natural vegetation) soil. In contrast, genera *Anaeromyxobacter* and *Mycobacterium* were typically enriched in control (natural vegetation) soil, whereas *Kribbella* and *Streptomyces* were relatively more in conventional soil. Diversity analysis of the bacterial communities identified across all treatments was carried out, however, no significant difference was observed (Supplementary Table S3). Based on the Chao1 index, control (natural vegetation) soil (82) exhibited the lowest value, followed by organic (138) and conventional soil (138) datasets. The statistical analysis revealed that the Shannon and Simpson's indices did not differ significantly across the three datasets (Supplementary Table S3).

Functional annotation of the ORFs identified in the study indicated their roles in various biological processes. The pFAM terms corresponding to ABC_Trans, TcTC, and MarR, were typically higher in organic soil dataset, whereas BDP_transp_1,

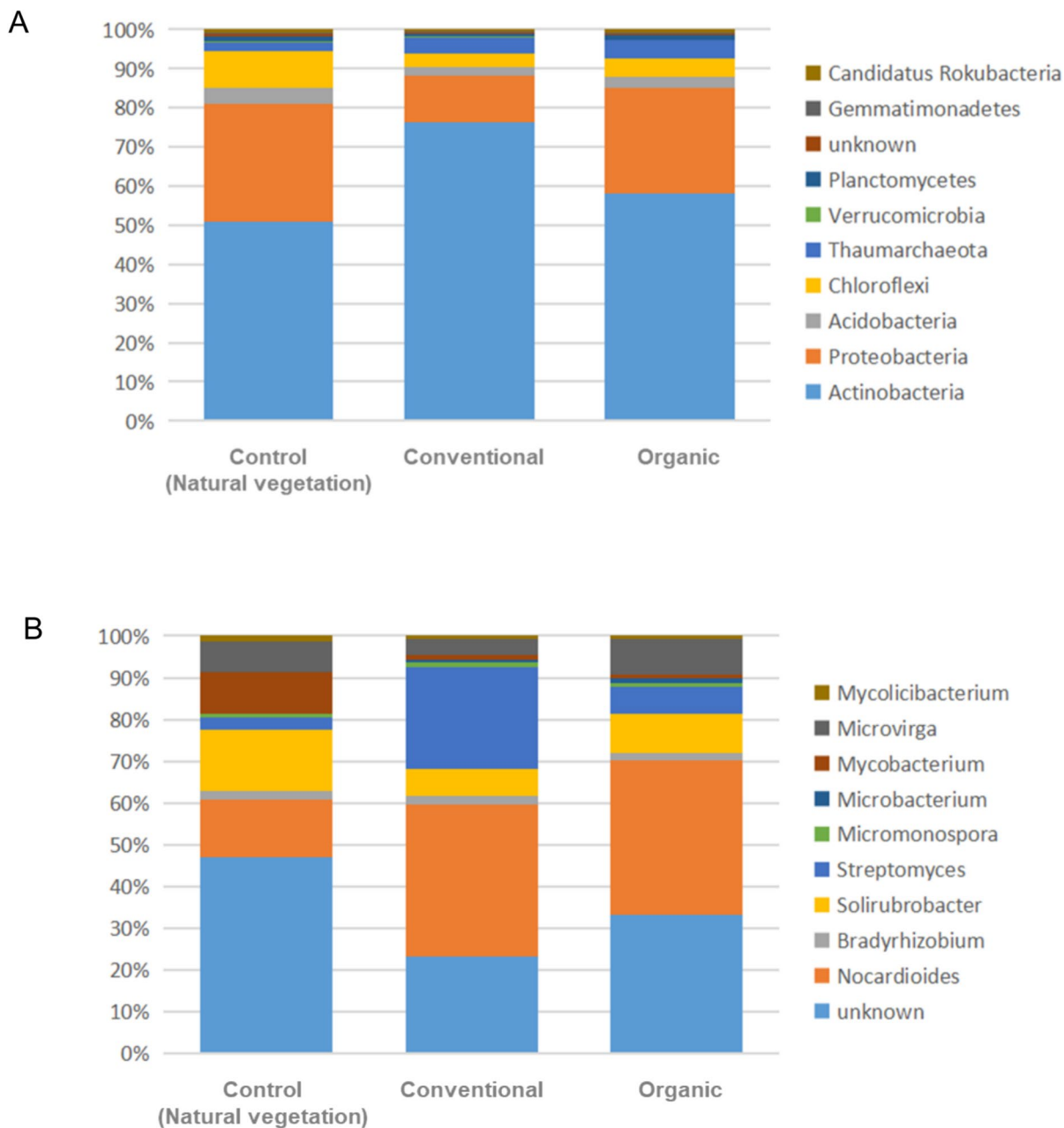


Fig. 4 Relative abundances (%) of different taxa at phyla (a), and genus (b) levels identified from soil of control (natural vegetation), organic and conventional rhizosphere from mustard field, Phaphund, depicted by stacked bar chart

HisKA, TetR_N, HTH28, and Acetyltransf_3 were specifically elevated in conventional soil dataset. The control (natural vegetation) soil detected a greater abundance of Response_reg, glyoxalase, HTH21, HTH29 and DUF4096 (Fig. 6A). The CAZy terms corresponding to GT85 and GH105

were specifically elevated in organic soil dataset, whereas GH99 and GT17 had enhanced abundance in conventional soil dataset (Fig. 6B). Similarly, several KO terms from KEGG database showed differential patterns across the three datasets (Supplementary Fig. S2). The above results indicate that ORFs

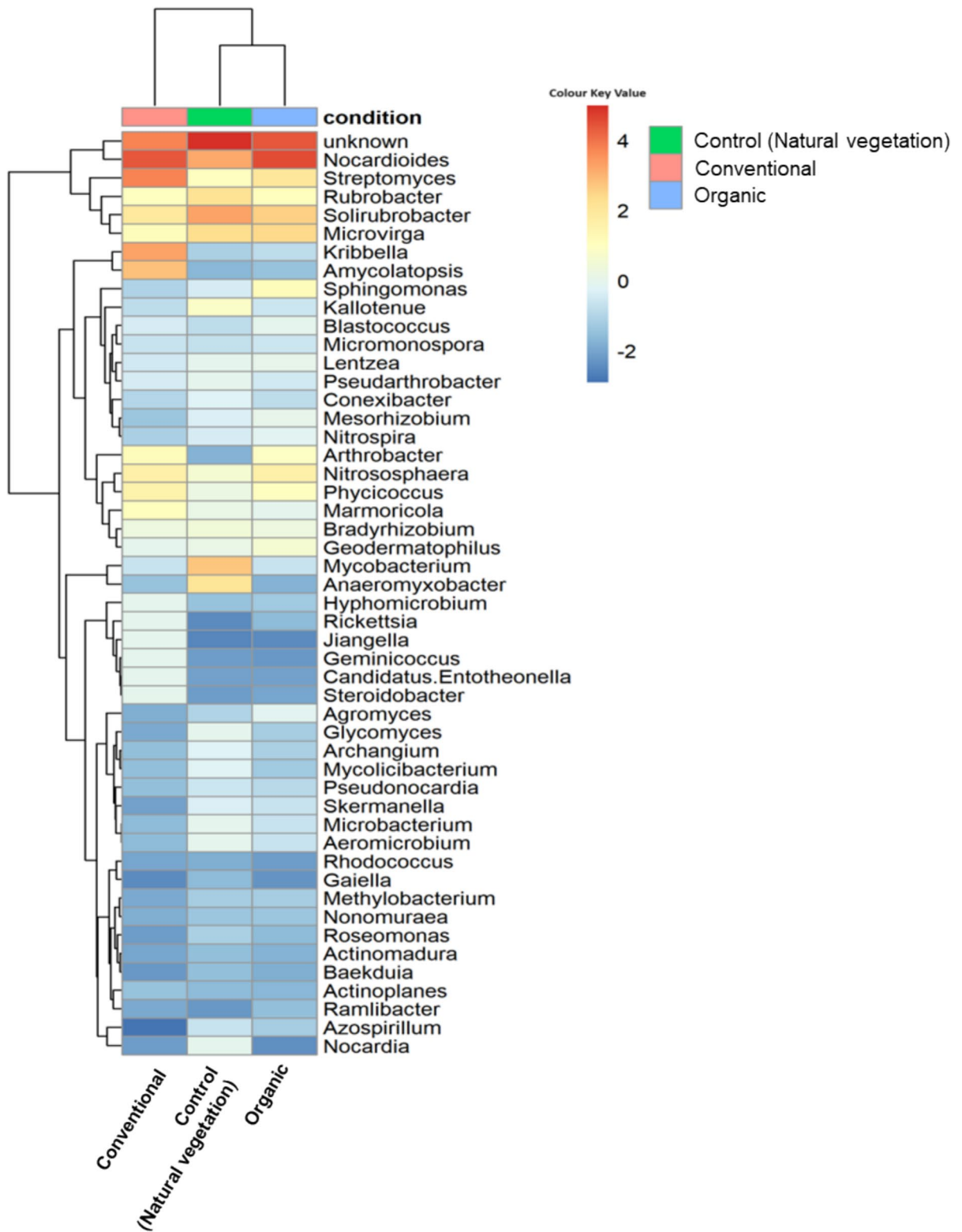


Fig. 5 Heatmap analysis depicting the relative abundance of taxa at the genus level identified from soil of control (natural vegetation), organic and conventional rhizosphere from mustard field, Phaphund

identified in these datasets were involved in crucial biological processes.

Discussion

Organically amended farms are known to increase microbial diversity, soil quality, and overall health,

whereas extensive use of chemical-based agricultural inputs leads to loss of microbial diversity and reduced nutrient availability (Gupta et al. 2022; Rani et al. 2023). The present study's data suggests that organic farming improved SOC and macronutrient availability, and also impacted enzymatic activities. The soils from organically managed systems showed enhanced immunity (i.e. suppressive ability) against

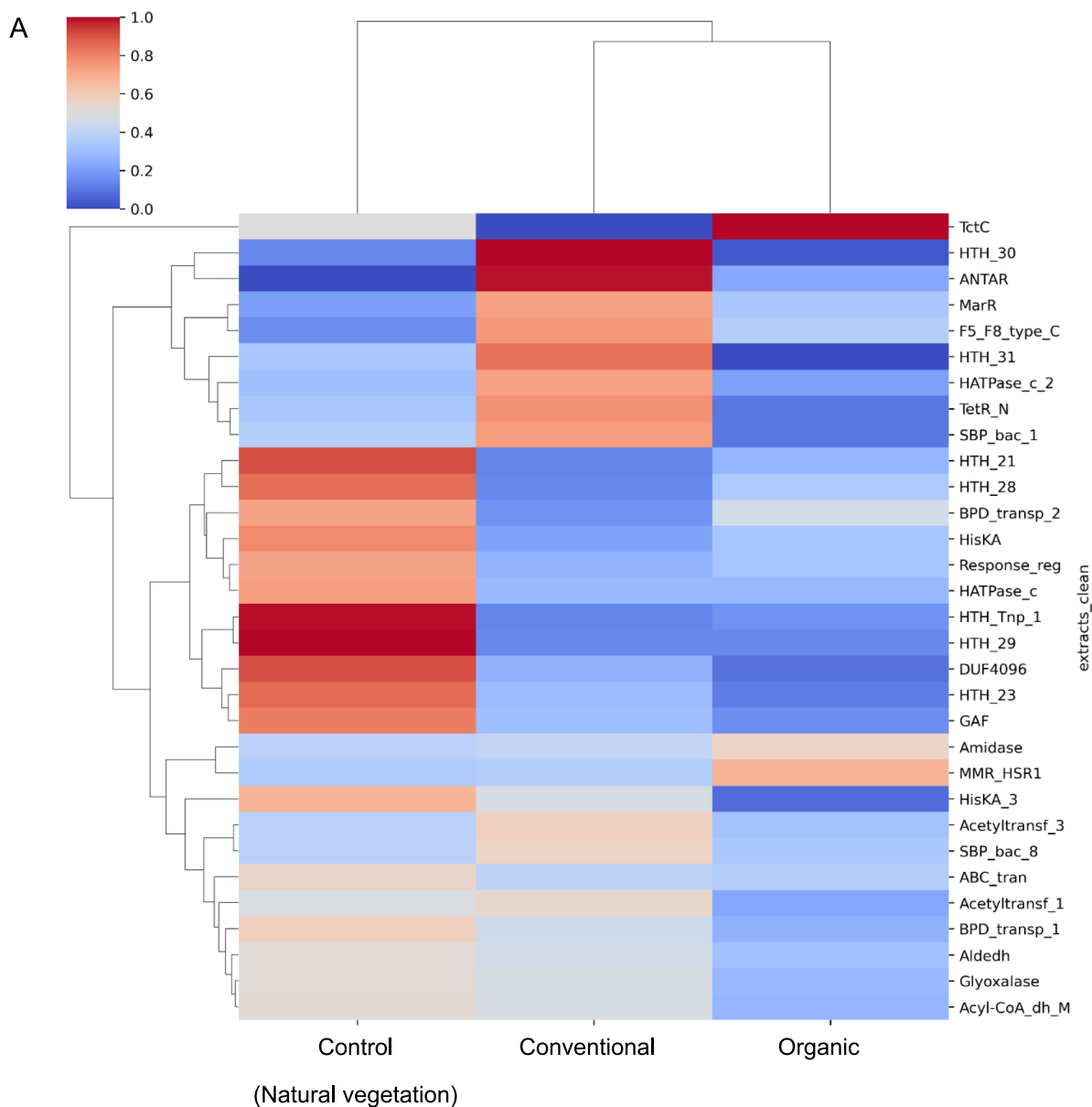


Fig. 6 Heatmap analysis depicting the distribution of pFAM terms (A) and CAZy terms (B) identified from soil of control (natural vegetation), organic and conventional rhizosphere from mustard field, Phaphund

B

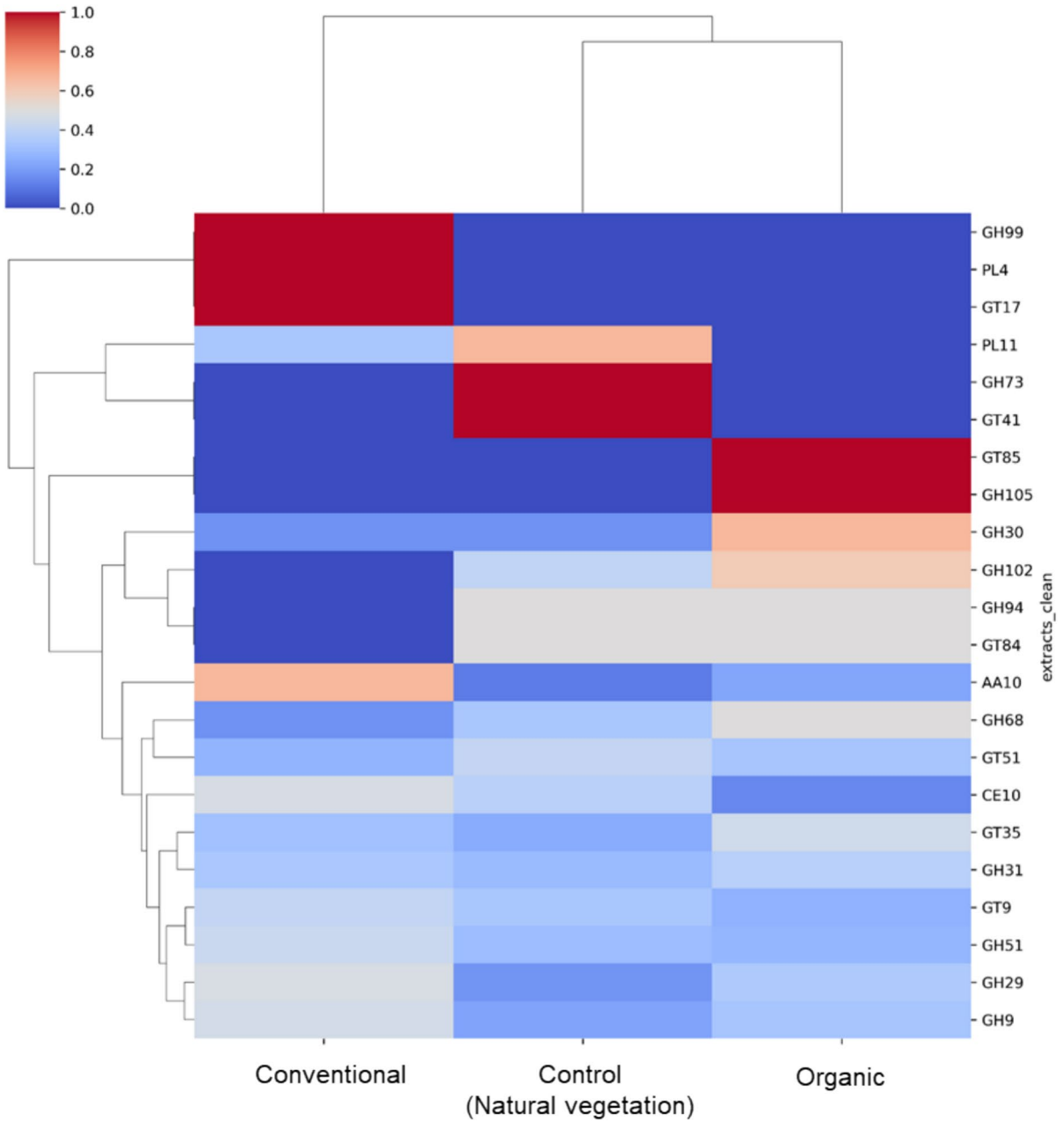


Fig. 6 (continued)

nine different fungal phytopathogens and two bacterial phytopathogens. The trend is similar to previously reported studies showing improved soil health

parameters and pathogen suppression potential of soils under organic farming systems (Deng et al. 2022; Khatri et al. 2023a, b).

Impact of farming practices on pathogen suppression

Soil-borne pathogens are major threats to agricultural production, leading to severe economic losses across the globe. Climate change further aggravates the issue due to its direct impact on soil health and the productivity of crops (Singh et al. 2023). Pathogen survival in soils depends on physicochemical parameters such as pH, EC, nutrient availability, etc. (Jayaraman et al. 2021). Our findings have shown that the pathogen suppression potential of bacterial and fungal fractions of soil was significantly greater in the organic fields than in the conventionally managed fields. Variable suppression was shown between fungal and bacterial fractions of soil. High microbial diversity, increased macronutrient availability, and high biocontrol enzymatic activities could be the plausible factors associated with high suppression against pathogens in organic farming (Jayaraman et al. 2021; Postma et al. 2008; Shu et al. 2022). Adding bio-amendments could be a reason for improved microbial diversity and SOC in organically managed fields (Deng et al. 2022; Shu et al. 2022). Organic farming contributes to restoring soil quality indices, resulting in enhanced soil functionality. To evaluate the individual impact of fungal and bacterial culturable fractions, a dual culture assay was performed, and a clear distinction between suppression effects was seen. This could be because of diverse microbes, which are functionally active under organic farming practices, specifically during pathogen attacks.

Impact of different farming practices on soil physicochemical parameters

Soil quality and health are impacted by different farming techniques and land use management. Various agricultural techniques impact the dynamic physicochemical attributes of soil and its microbial diversity (Rani et al. 2023). Compared with conventional farming methods, organic farming operations typically result in a significant increase in the availability of nutrients in the soil. When comparing organic soils to conventionally managed soils, high amounts of soil organic matter (SOM), total organic carbon (TOC), accessible P, N, and K, and a suitable pH have been recorded (Page et al. 2020). The availability of macronutrients, such as N, P, K,

and S, is vital for crop productivity, and hence, is an indicator of soil quality (Kumar et al. 2021). In the present study, available macronutrients N, P, K, and S were higher in organic than conventionally managed fields. Similar to our findings, many studies have reported enhanced nutrient availability under organic farms compared to conventional farms (Kaur et al. 2022; Xu et al. 2022). Soil pH influences the availability of both macro- and micronutrients. Organically managed soil with a mean pH of 6.4 had reduced availability of micronutrients Zn, Cu, Mn, and Fe, whereas conventional soil with a slightly acidic to neutral pH of 6.8 and control (natural vegetation) with an alkaline pH of 7.4 showed significantly higher availability of these micronutrients. The pH directly or indirectly impacts plant nutrient uptake due to the interaction with soil and plant root exudates (Barrow and Hartemink 2023). Most micronutrients are available at pH 5 to 7 except Fe, which is highly available below pH 5 (Thapa et al. 2021). However, the present study reports a higher availability of micronutrients ranging between 6.8 and 7.4. Plant mineral nutrients are key in defense against pathogens (Cabot et al. 2019; Tripathi et al. 2022). Several studies have reported the utilization of mineral nutrient amendments to improve the suppression of plant diseases (Dong et al. 2016; Li et al. 2012; Saikia et al. 2009). Similar to the present findings, where organic soils with pH 6.4 showed maximum suppression, enhanced suppression has been reported earlier in soil with pH 6 to 6.5 (Watanabe et al. 2011; Zhang et al. 2022a, b). In the future, correlation of edaphic factors, soil suppressiveness and microbiome function with plant performance and fitness can deepen our understanding of phytopathogen suppression trait prevalent in organic soil. However, in this study, plant parameters were not assessed as the objective was to compare the rhizosphere soil for its suppressive potential against a range of phytopathogens under different farming practices.

Studying EC levels may provide information about soil health and its potential to suppress disease since they can affect nutrient availability. Significantly higher soil EC was found in the organic fields than conventionally managed fields. Studies have reported an association of high EC levels with reduced pathogen growth (Garibaldi et al. 2012; Khalil 2011). Considering their significant roles in microbial diversity

and plant growth, available nutrients, EC, and soil pH may be significant indicators of the suppressive potential of the soil.

Biocontrol enzymatic activities of soil

Soil enzymatic activities are known to be modulated by the type of farming practice (Kaur et al. 2022; Wang et al. 2021). Soil enzymes mediate the mineralization of nutrients, their acquisition, and other biological activities, which may directly or indirectly impact the suppression (Mao and Jiang 2021; Zungu et al. 2022). The present study reported high enzymatic activities under organic management practices. It was also revealed that these activities were correlated with nutrient availability. A strong negative correlation existed between Fe availability and siderophore units released in soil under organic farming production (Fig. 3, Supplementary Table S2). Similarly, enhanced hydrolytic enzymes were found in organic soils. The same trend was observed in one of the reported studies, where organically managed soil showed increased cellulase activity compared to conventional soils (Sadeghi et al. 2017). Since iron chelation has a major role in determining how pathogens colonize different host plants, siderophore-mediated interaction by biocontrol agents may be essential for reducing phytopathogens (Gu et al. 2020). Siderophore producers are reported to be critical for disease suppression (Sheng et al. 2020; Srivastava et al. 2022). Since only a few studies have evaluated the role of biocontrol lytic enzymatic activities of soils against phytopathogens, under different farming practices, more studies need to be carried out in this context.

Identification and assessment of the functional potential of rhizosphere microbiome of mustard plant

The rhizosphere microbiome of mustard plays a key role in modulating its growth and development, because of the specific bacterial taxa associated with the plant (Liu et al. 2021). The present study conducted a whole metagenomic sequencing analysis of rhizosphere soil of mustard plants grown in conventional and organic farms, compared to bulk soil. The differences in the abundance of microbial taxa present in mustard plant rhizosphere soil were assessed at different levels in all the treatments. Although whole metagenomic sequencing should comprise other

microbial taxa like fungi, virus, protozoa, etc., the relative proportion of these was significantly lesser than the bacterial fraction. Hence, they were under-represented and were not detected in the analysis after the *de-novo* assembly of raw data. Such an observation could possibly be due to overrepresentation of bacteria in specific ecological niches like soil (Wang et al. 2024), albeit biases in DNA sequencing technology also cannot be ruled out.

It was found that *Actinobacteria* was the most abundant bacterial phylum detected across all samples analyzed. *Actinobacteria* can regulate plant growth, and they are known to positively impact plant and soil health (Boubekri et al. 2021; Boukhatem et al. 2022). Besides these, other dominant phyla identified in this study belonged to *Proteobacteria*, *Chloroflexi*, *Thaumarchaeota*, and *Acidobacteria*. Most of these bacterial phyla are involved in specific beneficial activities in soil, thereby affecting plant development (Nelkner et al. 2019; Zhang et al. 2022a, b). The phyla with lower relative abundance, like *Gemmatimonadetes* and *Cyanobacteria*, may also participate in complex rhizospheric interactions in the bacterial community.

There was a distinction between the prevalence of specific genera in the rhizospheric soil of mustard plants grown under organic farming and that under conventional farming practices. Specifically, *Nocardioideae*, and *Microvirga* were prevalent in organic farming practices. *Nocardioideae* can thrive under low nutrient conditions and exhibits plant growth promoting capabilities by P and K solubilization (Abdulla 2009; Ma et al. 2023). Additionally, the genus *Microvirga*, is reported to be an endosymbiont and promotes fixation of nitrogen and microbial interactions (Jimenez-Gomez et al. 2019; Msaddak et al. 2017). Further, the soil from conventional farming saw an enhanced abundance of *Kribbella* and *Streptomyces* in the mustard rhizosphere, as revealed in the present study. Although limited information is available for *Kribbella*, reports highlight the role of *Streptomyces* in pathogen biocontrol and plant growth promotion (Khan et al. 2023; Olanrewaju and Babalola 2019).

Functional annotation of the ORFs identified in the present study revealed key information about their involvement in governing mustard crops' developmental processes. ORFs encoding specific proteins are major drivers of primary and secondary active transport systems in bacteria. ATP-binding cassette (ABC) transporters govern the energy production

phenomena in microbial cellular processes and have recently been shown to regulate bacterial phytopathogenesis (Zeng and Charkowski 2021). Tripartite tricarboxylate transporter C (TcTC) belongs to the solute binding protein repertoire that binds to a single ligand type, tricarboxylates (Ortega et al. 2022). These protein moieties acting as transporters were detected in the dataset belonging to rhizospheric soil DNA sampled from organic fields of mustard. In contrast, the acetyltransferase (GNAT) domain and protein with histidine kinase domain encoding ORF were detected in rhizospheric soil DNA sampled from conventional fields of mustard. These acetyltransferases could determine antibiotic resistance in different bacterial species (Sanz-García et al. 2019), whereas histidine kinases are vital components of the signal transduction system in bacteria (Willett and Kirby 2012). Overall, functional analysis of the datasets in this study indicated that different farming practices can directly or indirectly impact the prevalence of specific bacterial regulators in the soil microenvironment, thereby also impacting plant health. Agro-management practices can influence the suppression potential of soil by shaping the microbial communities and changing the edaphic factors, steering the microbial structure towards a robust community, and deferring the propagation of plant disease-causing agents. Organic farming practices involve application of bio-amendments, which impact microbial diversity, leading to higher activity of biocontrol enzymes, and consequently accentuate phytopathogen suppression in organic soils.

Conclusion

To summarize, the present study deciphered the role of key microbial members and their biological activities in the rhizospheric soils in developing soil immunity (i.e. disease-suppressive potential) against various plant disease-causing pathogens. High biocontrol activities and available nutrients were significantly associated with organic farming practices. However, available micronutrients were found to be negatively associated with the suppression potential. Further, the metagenome sequencing revealed the specific members of the microbial community in the rhizospheric soil of mustard plants grown under organic and conventional farming regimes, and identified their roles

in the vital biological processes, possibly regulating plant and soil health. Optimizing the nutrient levels in soil could be useful in generating healthy soils. Understanding the role of particular biotic and abiotic factors could help in soil health management. To decipher the mechanisms behind enhanced general disease suppression in organic farms, extensive research is required to analyse both the abiotic and biotic components contributing to phytopathogen suppression. This will help elucidate how these factors interact to create a robust and resilient soil microenvironment that effectively mitigates plant diseases.

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Author contributions PC: Investigation, Methodology, Formal analysis Writing: Original draft; AB: Investigation, Methodology, Formal analysis Writing: Original draft; YSS: Investigation Writing: review; MP: Funding acquisition, Project administration, Formal analysis, Writing: review; SS: Conceptualisation, Experimental design, Funding acquisition, Project administration, Supervision, Writing: review.

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Data availability The sequence data from the whole metagenomic sequencing analysis was submitted at NCBI Sequence Read Archive (SRA) under BioProject ID PRJNA1105849.

Declarations

Competing interests The authors declare no conflict of interest.

References

- Abdulla H (2009) Bioweathering and biotransformation of granitic rock minerals by actinomycetes. *Microb Ecol* 58:753–761
- Akhter K, Karim I, Aziz B, Bibi A, Khan J, Akhtar T (2022) Optimization and characterization of alkaliphilic lipase from a novel *Bacillus cereus* NC7401 strain isolated from diesel fuel polluted soil. *PLoS One* 17:e0273368
- Al-Elwany OAAI, Mohamed AMHA, Abdelbaky AS et al (2023) Application of bio-organic amendments improves soil quality and yield of fennel (*Foeniculum vulgare* Mill.) plants in saline calcareous soil. *Sci Rep* 13:19876

- Barrow NJ, Hartemink AE (2023) The effects of pH on nutrient availability depend on both soils and plants. *Plant Soil* 487:21–37
- Boubekri K, Soumare A, Mardad I, Lyamlouli K, Hafidi M, Ouhdouch Y, Kouisni L (2021) The screening of potassium- and phosphate-solubilizing actinobacteria and the assessment of their ability to promote wheat growth parameters. *Microorganisms* 9:470
- Boukhatem ZF, Merabet C, Tsaki H (2022) Plant growth promoting actinobacteria, the most promising candidates as bioinoculants? *Front Agron* 4:849911
- Cabot C, Martos S, Llugany M, Gallego B, Tolrà R, Poschenrieder C (2019) A role for zinc in plant defense against pathogens and herbivores. *Front Plant Sci* 10
- Chesnin L, Yien CH (1951) Turbidimetric determination of available sulfates. *Soil Sci Soc Am J* 15(C):149–151
- Chowdappa S, Jagannath S, Konappa N, Udayashankar AC, Jogaiah S (2020) Detection and characterization of antibacterial siderophores secreted by endophytic fungi from *Cymbidium aloifolium*. *Biomolecules* 10:1412
- De Corato U (2020) Soil microbiota manipulation and its role in suppressing soil-borne plant pathogens in organic farming systems under the light of microbiome-assisted strategies. *Chem Biol Technol Agric* 7:17
- Deltour P, França SC, Liparini Pereira O, Cardoso I, De Neve S, Debode J, Höfte M (2017) Disease suppressiveness to *Fusarium* wilt of banana in an agroforestry system: influence of soil characteristics and plant community. *Agric Ecosyst Environ* 239:173–181
- Deng X, Zhang N, Li Y, Zhu C, Qu B, Liu H, Li R, Bai Y, Shen Q, Falcao Salles J (2022) Bio-organic soil amendment promotes the suppression of *Ralstonia solanacearum* by inducing changes in the functionality and composition of rhizosphere bacterial communities. *New Phytol* 235:1558–1574
- Dong X, Wang M, Ling N, Shen Q, Guo S (2016) Effects of iron and boron combinations on the suppression of *Fusarium* wilt in banana. *Sci Rep* 6:38944
- Gamage A, Gangahagedara R, Gamage J, Jayasinghe N, Kodikara N, Suraweera P, Merah O (2023) Role of organic farming for achieving sustainability in agriculture. *Farming System* 1(1):100005
- Garibaldi A, Gilardi G, Cogliati EE, Gullino ML (2012) Silicon and increased electrical conductivity reduce downy mildew of soilless grown lettuce. *Eur J Plant Pathol* 132:123–132
- Gómez Expósito R, de Bruijn I, Postma J, Raaijmakers JM (2017) Current insights into the role of rhizosphere bacteria in disease-suppressive soils. *Front Microbiol* 8:2529
- Gu S, Yang T, Shao Z, Wang T, Cao K, Jousset A, Friman V-P, Mallon C, Mei X, Wei Z, Xu Y, Shen Q, Pommier T (2020) Siderophore-mediated interactions determine the disease suppressiveness of microbial consortia. *mSystems* 5:e00811-19
- Gupta A, Singh UB, Sahu PK, Paul S, Kumar A, Malviya D, Singh S, Kuppasamy P, Singh P, Paul D, Rai JP, Singh HV, Manna MC, Crusberg TC, Kumar A, Saxena AK (2022) Linking soil microbial diversity to modern agriculture practices: a review. *Int J Environ Res Public Health*. <https://doi.org/10.3390/ijerph19053141>
- Huson DH, Auch AF, Qi J, Schuster SC (2007) Megan analysis of metagenomic data. *Genome Res* 17:377–386
- Hyatt D, Chen GL, LoCascio PF et al (2010) Prodigal: prokaryotic gene recognition and translation initiation site identification. *BMC Bioinformatics* 11:119
- Jayaraman S, Naorem AK, Lal R, Dalal RC, Sinha NK, Patra AK, Chaudhari SK (2021) Disease-suppressive soils—beyond food production: a critical review. *J Soil Sci Plant Nutr* 21:1437–1465
- Jesmin T, Margenot AJ, Mulvaney RL (2022) A comprehensive method for casein-based assay of soil protease activity. *Commun Soil Sci Plant Anal* 53:507–520
- Jimenez-Gomez A, Saati-Santamaria Z, Igual JM, Rivas R, Mateos PF, Garcia-Fraile P (2019) Genome insights into the novel species *Microvirga brassicacearum*, a rapeseed endophyte with biotechnological potential. *Microorganisms* 7:0
- Kaur M, Li J, Zhang P, Yang H, Wang L, Xu M (2022) Agricultural soil physico-chemical parameters and microbial abundance and diversity under long-run farming practices: a greenhouse study. *Front Ecol Evol*. <https://doi.org/10.3389/fevo.2022.1026771>
- Khalil S (2011) Influence of electrical conductivity on biological activity of *Pythium ultimum* and Binab T in a closed soilless system. *J Plant Dis Prot* 118:102–108
- Khan S, Srivastava S, Karnwal A, Malik T (2023) *Streptomyces* as a promising biological control agent for plant pathogens. *Front Microbiol* 14:1285543
- Khatri S, Bhattacharjee A, Shivay YS, Sharma S (2024) Transplantation of soil from organic field confers disease suppressive ability to conducive soil. *World J Microbiol Biotechnol* 40:112
- Khatri S, Dubey S, Shivay YS, Jelsbak L, Sharma S (2023a) Organic farming induces changes in bacterial community and disease suppressiveness against fungal phytopathogens. *Appl Soil Ecol* 181:104658
- Khatri S, Sharma S (2021) How does organic farming shape the soil- and plant-associated microbiota? *Symbiosis* 84:391–398
- Khatri S, Chaudhary P, Shivay YS, Sharma S (2023b) Role of fungi in imparting general disease suppressiveness in soil from organic field. *Microb Ecol* 86:2047–2059
- Kumar S, Kumar S, Mohapatra T (2021) Interaction between macro- and micro-nutrients in plants. *Front Plant Sci*. <https://doi.org/10.3389/fpls.2021.665583>
- Labiadh M, Dhaouadi S, Flahaut S, Kallel S (2021) Antimicrobial activity of *Bacillus subtilis* associated with *Dactylella gephyropaga* against *Arthrobotrys conoides* isolated from nematode infested citrus rhizosphere. *Biocontrol Sci Technol* 31(10):1052–1066
- Li D, Liu CM, Luo R, Sadakane K, Lam TW (2015) MEGAHIT: an ultra-fast single-node solution for large and complex metagenomics assembly via succinct de Bruijn graph. *Bioinformatics* 31:1674–1676
- Li Y, Yang Z, Bi Y, Zhang J, Wang D (2012) Antifungal effect of borates against *Fusarium sulphureum* on potato tubers and its possible mechanisms of action. *Postharvest Biol Technol* 74:55–61
- Lindsay WL, Norvell WA (1978) Development of a DTPA soil test for zinc, iron, manganese, and copper. *Soil Sci Soc Am J* 42:421–428
- Liu TC, Peng HM, Wollney S, Shen CH (2021) Rhizosphere microbiome regulates the growth of mustard under organic greenhouse cultivation. *Agriculture (Basel)* 11:987

- Ma Y, Wang J, Liu Y, Wang X, Zhang B, Zhang W, Cui X (2023) *Nocardioide*s: “specialists” for hard-to-degrade pollutants in the environment. *Molecules* 28:7433
- Mao T, Jiang X (2021) Changes in microbial community and enzyme activity in soil under continuous pepper cropping in response to *Trichoderma hamatum* MHT1134 application. *Sci Rep* 11:21585
- Miller GL (1959) Use of dinitrosalicylic acid reagent for determination of reducing sugar. *Anal Chem* 31:426–428
- Msaddak A, Rejili M, Durán D, Rey L, Imperial J, Palacios JM et al (2017) Members of *Microvirga* and *Bradyrhizobium* genera are native endosymbiotic bacteria nodulating *Lupinus luteus* in northern Tunisian soils. *FEMS Microbiol Ecol* 93:fix068
- Nelkner J, Henke C, Lin TW, Pätzold W, Hassa J, Jaenicke S, Grosch R, Pühler A, Sczyrba A, Schlüter A (2019) Effect of long-term farming practices on agricultural soil microbiome members represented by metagenomically assembled genomes (MAGs) and their predicted plant-beneficial genes. *Genes* 10:424
- Olanrewaju OS, Babalola OO (2019) *Streptomyces*: implications and interactions in plant growth promotion. *Appl Microbiol Biotechnol* 103:1179–1188
- Olsen SR (1954) Estimation of available phosphorus in soils by extraction with sodium bicarbonate (No. 939). US Department of Agriculture
- Ortega Á, Matilla MA, Krell T (2022) The repertoire of solute-binding proteins of model bacteria reveals large differences in number, type, and ligand range. *Microbiol Spectr* 10:e02054-22
- Page KL, Dang YP, Dalal RC (2020) The ability of conservation agriculture to conserve soil organic carbon and the subsequent impact on soil physical, chemical, and biological properties and yield. *Front Sustain Food Syst*. <https://doi.org/10.3389/fsufs.2020.00031>
- Palojärvi A, Kellock M, Parikka P, Jauhiainen L, Alakukku L (2020) Tillage system and crop sequence affect soil disease suppressiveness and carbon status in boreal climate. *Front Microbiol* 12:693341
- Postma J, Schilder MT, Bloem J, van Leeuwen WK (2008) Soil suppressiveness and functional diversity of the soil microflora in organic farming systems. *Soil Biol Biochem* 40:2394–2406
- Rahman MA, Begum MF, Alam MF (2009) Screening of *Trichoderma* isolates as a biological control agent against *Ceratocystis paradoxa* causing pineapple disease of sugarcane. *Mycobiology* 37:277–285
- Raimi AR, Ezeokoli OT, Adeleke RA (2023) Soil nutrient management influences diversity, community association, and functional structure of rhizosphere bacteriome under vegetable crop production. *Front Microbiol* 14:1229873
- Rani M, Kaushik P, Bhayana S, Kapoor S (2023) Impact of organic farming on soil health and nutritional quality of crops. *J Saudi Soc Agric Sci* 22:560–569
- Rodriguez-Kabana R, Godoy G, Morgan-Jones G, Shelby RA (1983) The determination of soil chitinase activity: conditions for assay and ecological studies. *Plant Soil* 75:95–106
- Sadeghi A, Koobaz P, Azimi H, Karimi E, Akbari AR (2017) Plant growth promotion and suppression of *Phytophthora drechsleri* damping-off in cucumber by cellulase-producing *Streptomyces*. *Biocontrol* 62:805–819
- Saikia R, Varghese SP, Singh BP, Arora DK (2009) Influence of mineral amendment on disease suppressive activity of *Pseudomonas fluorescens* to Fusarium wilt of chickpea. *Microbiol Res* 164:365–373
- Sakai Y, Hayatsu M, Hayano K (2002) Use of tween 20 as a substrate for assay of lipase activity in soils. *Soil Sci Plant Nutr* 48:729–734
- Sanz-García F, Anoz-Carbonell E, Pérez-Herrán E, Martín C, Lucía A, Rodrigues L et al (2019) Mycobacterial aminoglycoside acetyltransferases: a little of drug resistance, and a lot of other roles. *Front Microbiol* 10:46
- Schlatter D, Kinkel L, Thomashow L, Weller D, Paulitz T (2017) Disease-suppressive soils: new insights from the soil microbiome. *Phytopathology* 107:1284–1297
- Schwyn B, Neilands JB (1987) Universal chemical assay for the detection and determination of siderophores. *Anal Biochem* 160:47–56
- Shapiro SS, Wilk MB (1965) An analysis of variance test for normality (complete samples). *Biometrika* 52:591–611
- Sheng MM, Jia HK, Zhang GY, Zeng LN, Zhang TT, Long YH, Lan J, Hu ZQ, Zeng Z, Wang B, Liu HM (2020) Siderophore production by rhizosphere biological control bacteria *Brevibacillus brevis* GZDF3 of *Pinellia ternata* and its antifungal effects on *Candida albicans*. *J Microbiol Biotechnol* 30:689–699
- Shu X, He J, Zhou Z, Xia L, Hu Y, Zhang Y, Zhang Y, Luo Y, Chu H, Liu W, Yuan S, Gao X, Wang C (2022) Organic amendments enhance soil microbial diversity, microbial functionality and crop yields: a meta-analysis. *Sci Total Environ* 829:154627
- Singh BK, Delgado-Baquerizo M, Egidio E, Guirado E, Leach JE, Liu H, Trivedi P (2023) Climate change impacts on plant pathogens, food security, and paths forward. *Nat Rev Microbiol* 21:640–656
- Srivastava P, Sahgal M, Sharma K, Enshasy HAE, Gafur A, Alfarraj S, Ansari MJ, Sayyed RZ (2022) Optimization and identification of siderophores produced by *Pseudomonas monteilii* strain MN759447 and its antagonism toward fungi associated with mortality in *Dalbergia sissoo* plantation forests. *Front Plant Sci* 13:984522
- Subbiah BV, Asija GL (1956) A rapid procedure for the estimation of available nitrogen in soils. *Curr Sci* 25:259
- Thapa S, Bhandari A, Ghimire R, Xue Q, Kidwaro F, Ghatrhesamani S, Maharjan B, Goodwin M (2021) Managing micronutrients for improving soil fertility, health, and soybean yield. *Sustainability* 13:11766
- Tripathi R, Tewari R, Singh KP, Keswani C, Minkina T, Srivastava AK, De Corato U, Sansinenea E (2022) Plant mineral nutrition and disease resistance: a significant linkage for sustainable crop protection. *Front Plant Sci*. <https://doi.org/10.3389/fpls.2022.883970>
- Walkley A, Black IA (1934) An examination of the Degtjareff method for determining soil organic matter, and a proposed modification of the chromic acid titration method. *Soil Sci* 37:29
- Wang L, Kaur M, Zhang P, Li J, Xu M (2021) Effect of different agricultural farming practices on microbial biomass and enzyme activities of celery growing field soil. *Int J Environ Res Public Health* 18:12862

- Wang X, Chi Y, Song S (2024) Important soil microbiota's effects on plants and soils: a comprehensive 30-year systematic literature review. *Front Microbiol* 15:1347745
- Watanabe K, Matsui M, Honjo H, Becker JO, Fukui R (2011) Effects of soil pH on *rhizoctonia* damping-off of sugar beet and disease suppression induced by soil amendment with crop residues. *Plant Soil* 347:255–268
- Willett JW, Kirby JR (2012) Genetic and biochemical dissection of a HisKA domain identifies residues required exclusively for kinase and phosphatase activities. *PLoS Genet* 8:e1003084
- Xu C, Li Y, Hu X, Zang Q, Zhuang H, Huang L (2022) The influence of organic and conventional cultivation patterns on physicochemical property, enzyme activity, and microbial community characteristics of paddy soil. *Agriculture-Basel* 12(1):121
- Zeng Y, Charkowski AO (2021) The role of ATP-binding cassette transporters in bacterial phytopathogenesis. *Phytopathology* 111:600–610
- Zhang S, Liu X, Zhou L, Deng L, Zhao W, Liu Y, Ding W (2022a) Alleviating soil acidification could increase disease suppression of bacterial wilt by recruiting potentially beneficial rhizobacteria. *Microbiol Spectr* 10:e02333-21
- Zhang Z, Xiao YS, Zhan Y, Zhang Z, Liu Y, Wei Y, Li J (2022b) Tomato microbiome under long-term organic and conventional farming. *Imeta* 1:e48
- Zungu NS, Egbewale SO, Olaniran AO, Pérez-Fernández M, Magadlela A (2022) Soil nutrition, microbial composition and associated soil enzyme activities in KwaZulu-Natal grasslands and savannah ecosystems soils. *Appl Soil Ecol* 155:103663

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