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RESEARCH ARTICLE

Comparative analysis of rhizosphere bacterial communities in tomato (*Solanum lycopersicum* L.) through 16S rRNA amplicon-based taxonomic and functional profiling

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Abstract

Microorganisms in the soil play essential roles in the growth and development of plants. However, there is limited understanding of how the health status of plants influences the functions of these microorganisms. This study aims to analyze the composition of bacterial communities in the rhizosphere soil of tomato plants (*Solanum lycopersicum* L.) from the Beggli micro-watershed in Kolar, Karnataka using high throughput 16S rRNA amplicon sequencing. Four different rhizosphere soil samples of tomato were taken and subjected to microbial diversity analysis. Analysis of the soil showed differences in pH, Electrical conductivity (EC), percent organic carbon and macronutrients (N, P, K) that affected microbial composition. DNA sequencing, bioinformatic analysis and amplicon sequencing detected 350 amplicon sequence variants (ASVs) in all the rhizosphere soil samples. Among them, TSB2 showed the highest ASVs (210). Proteobacteria were the phylum with the highest abundance in all the samples, followed by *Firmicutes, Actinobacteria, Acidobacteriota* and *Chloroflexi*. Taxonomic analysis showed *Gammaproteobacteria, Alphaproteobacteria* and *Bacilli* to be the most dominant classes of bacteria while *Bacillus*, *Acinetobacter*, *Sphingomonas* and *Flavobacterium* were the most predominant genera. Alpha diversity indices showed remarkable diversity in microbial richness with the Shannon Index ranging from 8.25 to 9.11. Beta diversity analysis revealed a clear clustering of microbial communities based on soil characteristics. Functional annotation by Kyoto Encyclopedia of Genes and Genomes (KEGG) and Clusters of Orthologous Groups of Proteins (COG) analysis revealed genes involved in nutrient cycling, oxidative stress response and plant-microbe interactions. These findings enhance our understanding of tomato rhizosphere bacterial community structure and guide sustainable soil management practices.

Keywords: amplicon sequencing; bacterial diversity; functional annotations; micro-watershed; tomato

Introduction

A watershed is a natural hydrological unit where surface and subsurface water converge to a common outlet, such as a river, lake or ocean. It encompasses land, water bodies and biological constituents that together shape soil development, nutrient cycling and agricultural properties (1, 2). In general, these components of a watershed have a significant impact on cropping patterns by controlling soil moisture availability, nutrient parameters such as soil texture, organic matter level and microbial activity which directly affect plant growth and yield (3). In rainfed agriculture, cropping patterns are significantly influenced by watershed characteristics as they determine the retention and movement of water and nutrients in the soil profile (4, 5). Based on these considerations, watershed management is greatly needed. Therefore, the primary objective of effective watershed management is to preserve soil, plant and water resources, thereby enhancing agricultural practices and ecosystem health (5). To do so, the watershed was categorized into macro watershed (> 50000 ha), sub watershed (10000 to 50000 ha) and micro watershed (100 to 1000 ha) according to the area (6, 7). India possesses 321324 micro-watersheds, 49618 sub-watersheds and 3854 macro watersheds, as per the Micro-watershed Atlas of India, out of which 234 watersheds are mapped based upon the size, drainage, shape and land use pattern in Karnataka. Among these, Beggli is a micro-watershed covering 537 ha and is situated in the Kolar district. The area is characterized by low rainfall, erratic monsoons and soil degradation problems, hence contributing to increased nutrient loss and water deficit (8). Despite these factors, the major crops growing in this micro-watershed are tomato (S. *lycopersicum* L.), cabbage (*Brassica oleracea* var. *capitata*) and cauliflower

(*Brassica oleracea* var. *botrytis*). Among these, tomato is the most cultivated crop and variability in their yields may be due to poor water availability and spatial variation in soil properties (nutrient and biological properties). The roots of tomato (S. *lycopersicum* L.) plants have a significant connection to the microbiota present in the surrounding rhizosphere soil in natural environments (9, 10). This microbiota forms a unique bacterial community that plays a vital role in the growth and development of tomato plants, enhancing their overall health (11). Understanding the characteristics of this microbiota is essential for ensuring plant health and maintaining the effective functioning of the rhizosphere microbiome (12). Since, crop productivity is dependent on these properties, after exhaustive literature search, it is found that limited information reported on microbial community dynamics associated with tomato rhizosphere soils whereas few studies has been reported on available nutrients status (13, 14). However, this information alone is not enough for profitable crop production. The structure of the microbial community, especially the bacteria responsible for nitrogen, phosphorus and potassium (NPK) recycling, is closely associated with watershed characteristics and cropping patterns (15). Different bacterial populations such as nitrogen fixers, phosphate solubilizers and potassium mobilizers, interact to regulate nutrient availability. Their abundance and activity depend on soil physicochemical properties which help in the recommendation of fertilizers for crops and management of natural resources which ultimately improve crop productivity (16).

Therefore, understanding the variability of the microbial community in the Beggli micro-watershed using a 16S rRNA amplicon sequencing-based metagenomics approach, as it is a culture-independent approach, overcomes the limitations of traditional culture-dependent methods by allowing direct extraction and sequencing of total microbial DNA from environmental samples. This high-throughput sequencing technique offers a detailed profile of microbial diversity, functional genes and metabolic pathways enabling researchers to examine microbial communities in their natural state (17, 18). Tomato (*Solanum lycopersicum* L.) is a globally important crop whose productivity is strongly influenced by rhizosphere microbial interactions. Although the microbiome plays a vital role in nutrient cycling and plant growth, most tomato studies rely on culturable isolates or broad surveys, providing limited resolution. To address this gap, we applied high throughput 16S rRNA amplicon sequencing on four strategically selected rhizosphere soil samples from the Beggli micro-watershed, representing variations in plant vigor, soil texture and prior microbial data. This targeted design ensured high-resolution insights into taxonomic and functional shifts of bacterial communities, while balancing sequencing depth, cost and analytical complexity. Our study thus provides novel evidence on the links between rhizosphere bacterial diversity, soil properties and nutrient management strategies for sustainable tomato cultivation.

Materials and Methods

Overview of sample site and sample collection

The soil samples were collected from the Beggli micro-watershed (78.1320° E, 13.1350° N) which is located in Kolar district, Karnataka state, India. The annual temperature of this micro-watershed is between (18 °C-34 °C) and the rainfall pattern is low and irregular with an average rainfall of 650–750 mm annually. The red sandy loam soil type makes up the majority of the soil in this area with a low organic matter level and varying nutrient availability. Four tomato rhizosphere soil samples from different locations of Beggli were collected in the period of January 2024 and were coded as TSB (Tomato Soil Sample Beggli) (Supplementary Fig. 1). Samples were collected by uprooting tomato plants at a depth of 0-15 cm. The soil adhered to the root surface (50 g) was collected in a sterile plastic container and stored at -20 °C for further processing. Half of the collected samples (25 g) were used for metagenomic analysis and the other half was used to analyse soil physicochemical properties by following the standard protocol viz. pH, electrical conductivity (19), percent organic carbon (20), available nitrogen (21), available phosphorus (22) and total potassium (K) (23).

Metagenomic DNA extraction, qualitative and quantitative analysis

Metagenomic DNA was extracted from 0.5 g of soil samples using a commercially available nucleospin soil kit (which is designed for the isolation of total microbial DNA directly from soil, sediment, compost and other environmental samples rich in PCR inhibitors) following the manufacturer's instructions. The quality of the DNA was assessed with a Nanodrop, measuring the A260/280 ratio (24). Amplicon libraries were prepared using the Nextera XT Index Kit (Illumina Inc., USA) following the manufacturer's instructions. The libraries were quantified, normalized and pooled before sequencing. Paired-end sequencing (2 x 250 bp) was performed on the Illumina MiSeq platform, generating high-quality reads suitable for downstream taxonomic and functional profiling. Bacterial-specific primers were designed at Eurofins Genomic Lab and used to amplify the 16S region. 3 µL PCR products were resolved on a 1.2 % agarose gel at 120 V for approximately 60 min or till the samples reached ¾th of the gel and the primers targeting the V3-V4 region were 16S rRNA F GCCTACGGGNGGCWGCAG and 16S rRNA R ACTACHVGGGTATCTAATCC (25). QC-passed amplicons were amplified with i5 and i7 primers for multiplexing and purified with AMPureXP beads and then quantified using a Qubit Fluorometer. Libraries were analysed on 4200 Tape stations (Agilent Technologies) and loaded onto MiSeq for paired-end sequencing. The sequencing used kit reagents to bind samples to adapter oligos allowing selective cleavage of forward strands after reverse strand synthesis (25).

Bioinformatics analysis

Quantitative Insights into Microbial Ecology version 2 (QIIME2) is a microbiome analysis tool that converts sequence data into visualizations and statistical results suitable for publication (26). Clean reads were obtained using Trimmomatic v0.38 (27) to remove adapter sequences, ambiguous reads (more than 5 % unknown nucleotides) and low-quality sequences (over 10 % QV < 25 phred scores). Paired-end data were stitched into single-end reads using FLASH (v1.2.11) (28). The reads were then denoised and chimeric sequences filtered using DADA2 (29), while taxonomic classification was performed with the q2-feature classifier leveraging the SILVA database (30). Diversity metrics of within-sample (α-diversity; Shannon's Index) were calculated and between-sample diversity (β-diversity; Weighted and Unweighted UniFrac) was calculated.

Functional annotations

PICRUSt2 (Phylogenetic Investigation of Communities by Reconstruction of Unobserved States) software was used to functionally annotate the assigned ASVs by the SILVA database (31). By normalizing changes in gene copy number, the functional content of microbial communities can be predicted by comparing the sample's features to a reference with known or imputed gene content. To obtain relative KEGG and COG abundance information, the representative sequences were fed into PICRUSt2. The most prevalent COD and KEGG IDs were considered and examined (31).

Statistical analysis

The statistical analysis was performed using R software (version 4.1.3) to assess the diversity and composition of microbial communities from tomato rhizosphere and bulk soil samples. ANOVA, Kruskal–Wallis and t-tests were used to compare diversity across treatments. A heatmap with hierarchical clustering based on a Z-score transformation was generated to visualize the distribution patterns of dominant microbial taxa across treatments. Alpha diversity indices such as Shannon, Simpson and Chao1 were used to evaluate species richness and evenness while Pielou's index assessed species evenness. Beta diversity was assessed using weighted UniFrac and unweighted distance to evaluate phylogenetic similarities and differences among communities. Principal Coordinates Analysis (PCoA) based on UniFrac was employed to visualize microbial community separation across samples. All visualizations and statistical tests were carried out using relevant R packages including phyloseq, vegan, ggplot2 and DESeq2.

Results

Physicochemical properties of tomato rhizosphere soil samples

Analysis of soil chemical properties showed significant variations between the rhizosphere soils (TSB1, TSB2, TSB3 and TSB4) as shown in Table 1. Soil pH ranged from 5.94 to 7.22 with TSB2 being neutral and TSB4 acidic. TSB2 had the highest EC (0.52 dS/m), organic carbon (0.98 %) and macronutrients (nitrogen, phosphorus, potassium) while TSB4 showed the lowest values, indicating poor fertility. These variations impact microbial composition as soil pH and organic carbon are known to influence bacterial diversity (32, 33).

Quality check (QC) on agarose gel

The QC of tomato rhizosphere soil samples (TSB1, TSB2, TSB3 and TSB4) generated on a 1.2 % agarose gel showed a bright band at approximately 50 kb, indicating the high molecular weight DNA. No significant degradation or shearing was observed (Fig. 1). The concentrations of extracted metagenomic DNA from four tomato rhizosphere soil samples were measured as follows: 26.4 ng/µL for TSB1, 129.4 ng/µL for TSB2, 26.6 ng/µL for TSB3 and 48.1 ng/µL for TSB4. The A260/280 ratios indicated high-purity DNA with minimal protein contamination, measuring 1.86 for TSB1, 1.49 for TSB2, 1.57 for TSB3 and 1.77 for TSB4. All the four samples successfully passed the quality control assessment based on these Nanodrop readings. Following the Nanodrop qualification, a Tape Station analysis was conducted to assess the fragment size distribution, concentration, regional molarity and the proportion of total fragments within the desired range for the tomato rhizosphere soil DNA libraries (TSB1, TSB2, TSB3 and TSB4).

16S rRNA amplicon sequence and taxonomic analysis of bacterial community

The 16S rRNA gene sequencing of four tomato rhizosphere soil samples (TSB1, TSB2, TSB3 and TSB4) showed a diverse and

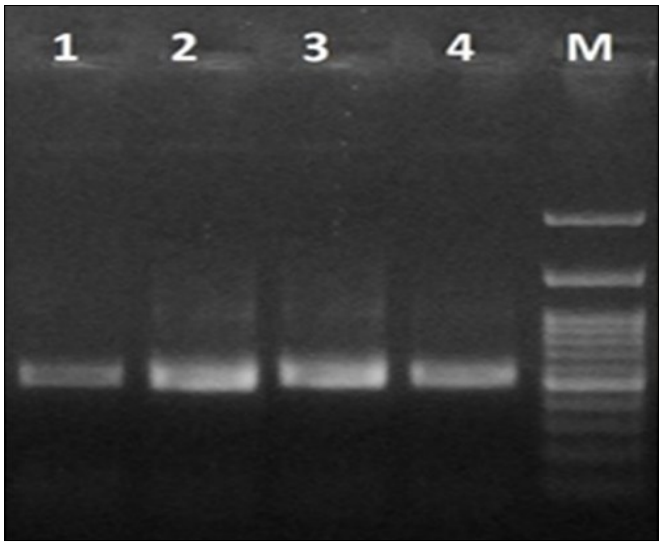

Fig. 1. DNA QC on agarose gel: 1, 2, 3, 4 represent the samples TSB1, TSB2, TSB3 and TSB4, respectively and M is the ladder.

complex bacterial community with differences in ASV richness and taxonomic structure. There are 350 ASVs detected in all the rhizosphere soil samples, of which TSB1 contains 120 ASVs, TSB2 contains the maximum number of 210 ASVs, TSB3 contains 75 ASVs and TSB4 contains 140 ASVs. The analysis, conducted via Illumina sequencing, demonstrated a progressive increase in unique taxonomic classifications from phylum to species level, indicating a hierarchical structure of microbial diversity. Specifically, the data exhibited a range of 30 to 44 distinct phyla, 78 to 112 classes, 190 to 273 orders, 278 to 416 families, 390 to 611 genera and 462 to 813 species across the four samples. As mentioned earlier, TSB2 displayed the highest ASV richness,

Table 1. Results of soil physicochemical properties of all four tomato rhizosphere soils of Beggli micro-watershed

S.NO	Physicochemical properties	TSB1	TSB2	TSB3	TSB4
1	pH	6.78 ± 0.02	7.22 ± 0.01	6.60 ± 0.08	5.94 ± 0.02
2	EC (dS/m)	0.45 ± 0.01	0.52 ± 0.00	0.48 ± 0.00	0.35 ± 0.02
3	OC (%)	0.78 ± 0.00	0.98 ± 0.02	0.85 ± 0.01	0.63 ± 0.00
4	N (kg/ha)	190.73 ± 0.64	211.00 ± 0.58	201.00 ± 0.58	170.52 ± 0.29
5	P (kg/ha)	32.00 ± 0.29	41.36 ± 0.32	35.39 ± 0.20	27.43 ± 0.23
6	K (kg/ha)	281.00 ± 3.79	310.38 ± 0.20	290.13 ± 0.07	261.67 ± 1.20

Note: All the values are mean ± standard error (n=3) at p ≤ 0.05. TSB (Tomato soil Beggli), electrical conductivity (EC), organic carbon (OC), available nitrogen (N), available phosphorus (P), available potassium (K).

suggesting a more complex and potentially functionally redundant microbial ecosystem compared to the other samples. In contrast, TSB4 demonstrated the lowest phylum-level diversity, indicating a potentially distinct ecological niche or environmental influence. The cumulative total of unique taxonomic classifications across all samples underscored the substantial microbial richness within the tomato rhizosphere soils, implying a potentially robust and functionally diverse ecosystem. These findings highlight the inherent variability in bacterial community structure across different tomato rhizosphere soil samples and provide a foundation for further investigations into the ecological roles of specific taxa.

Comparative t-analysis of bacterial community distribution in four tomato rhizosphere soil samples

The relative abundance of bacterial species showed considerable variations between the tomato rhizosphere soils as represented in the stacked bar plots (Fig. 2, Table 2). The 16S amplicon sequence revealed that Proteobacteria emerged as the dominant phylum across all four samples with TSB2 and TSB3 showing the highest relative abundance at 47.46 % and 51.40 % respectively. Firmicutes were particularly abundant in TSB1 (25.52 %) while TSB4 had a higher proportion of Acidobacteriota (1.46 %). Other commonly observed phyla included Chloroflexi, Planctomycetota and Gemmatimonadota though their relative abundances varied among the samples (Fig. 2A). At the class level, Gammaproteobacteria dominated TSB2 (26.90 %) and TSB3 (27.44 %) whereas TSB1 was primarily composed of Bacilli (24.83 %). TSB4, on the other hand, exhibited a higher abundance of Alphaproteobacteria (18.69 %). Other bacterial classes such as Bacteroidia, Vicinamibacteria, Actinobacteria and Acidimicrobia were present in varying proportions across all samples (Fig. 2B). The most prevalent bacterial order across the four samples was Bacillales (35.73 %) followed by Sphingomonadales (20.76 %), Vicinamibacterales (22.20 %), Rhizobiales (14.57 %) and Burkholderiales (15.75 %). However, variations were observed at the individual sample level: TSB1 and TSB4 were mainly dominated by Bacillales (18.54 % and 11.40 % respectively) whereas TSB2 had a higher proportion of Vicinamibacterales (5.13 %) and TSB3 was dominated by Burkholderiales (3.21 %) (Fig. 2C). At the family level, Bacillaceae was the most abundant in TSB1 and TSB4 (16.03 % and 10.59 % respectively) while Flavobacteriaceae was more prominent in TSB2 and TSB4 (4.46 % and 7.69 %). Other bacterial families commonly detected in all four samples included Sphingomonadaceae, SAR 11 clade, Rhodobacteraceae and Vicinamibacteraceae (Fig. 2D). The genus-level analysis showed that *Bacillus* was predominant in TSB1 (14.26 %) and TSB4 (9.55 %) while *Acinetobacter* was the dominant genus in TSB2 (3.91 %). Additionally, uncultured bacterial genera were prevalent in TSB4 (5.07 %). A significant proportion of bacterial genera remained unidentified in all four samples (Fig. 2E). At the species level, unidentified species from the genus *Bacillus* were dominant in TSB1 (13.05 %) and TSB4 (9.15 %). Similarly, unidentified species from the genus were observed in TSB2 (3.70 %) and TSB3 (5.03 %) (Fig. 2F).

Alpha diversity indices

Alpha diversity metrics provided insights into the richness and evenness of microbial communities within individual soils. The key indices analyzed in this study include the Shannon Index, Simpson Index, Observed Features, Goods Coverage, Simpson Reciprocal and Chao1 for all four tomato rhizosphere samples (TSB1, TSB2, TSB3 and TSB4) of the Beggli micro-watershed (Table 3). The analysis of microbial diversity across the samples revealed significant variations in several indices. The Shannon Index scores varied between 8.25 for TSB3 and 9.11 for TSB4, showing that TSB4 supported a heterogeneous microbial community while TSB3 indicated relatively low diversity. TSB1 and TSB2 showed comparable diversity with 8.79 and 9.10 for Shannon values respectively, representing an even distribution of microbial species. Species dominance, according to Simpson Index values, was nearly 1.00 in all samples, reflecting a mostly even microbial community. TSB3 was the only one that deviated slightly with a value of 0.99, reflecting slightly less evenness than the others. Observed species richness also differed with the highest number being 1370 for TSB4 and then 1295 for TSB2. TSB1 had 1100 species whereas TSB3 had the lowest richness at 625. It noted that its environment had a significantly less complex variety of microbes. All of the samples had a goods coverage value of 1.0, indicating that the sequencing efforts had captured the microbial diversity that was present to a reasonable extent with not too many undiscovered species. Moreover, Simpson Reciprocal Index values varied from 169.97 in TSB3 to 364.71 in TSB4, indicating that TSB4 contained a very even and stable microbial community as compared to TSB3 where some dominant species were more abundant. Finally, the Chao1 index showed the same trends in estimating species richness where TSB4 (1370) and TSB2 (1295) showed the greatest estimated richness while TSB1 had a mid-range number of 1100 and TSB3 the lowest at 625, again supporting the seen patterns in microbial diversity between the samples. Further, a refraction curve is used to justify the results between the samples obtained from alpha diversity (Fig. 3a). The rarefaction curves confirm that

Table 2. Most abundant taxonomy identified in the samples at different taxonomic levels

S. No.	TSB1 (%)	TSB2 (%)	TSB3 (%)	TSB4 (%)
Phylum	Proteobacteria (26.62)	Proteobacteria (47.46)	Proteobacteria (51.40)	Proteobacteria (27.46)
Class	Bacilli (24.83)	Gammaproteobacteria (26.90)	Gammaproteobacteria (27.44)	Alphaproteobacteria (18.69)
Order	Bacillales (18.54)	SAR11 clade (5.86)	SAR11 clade (9.73)	Bacillales (11.40)
Family	Bacillaceae (16.03)	Flavobacteriaceae (4.46)	Flavobacteriaceae (7.69)	Bacillaceae (10.59)
Genus	*Bacillus* (14.26)	*Acinetobacter* (3.91)	*Clade Ia* (5.07)	*Bacillus* (9.55)
Species	unidentified species from genus *Bacillus* (13.05)	unidentified species from genus *Clade Ia* (3.70)	unidentified species from genus *Clade Ia* (5.03)	unidentified species from genus *Bacillus* (9.15)

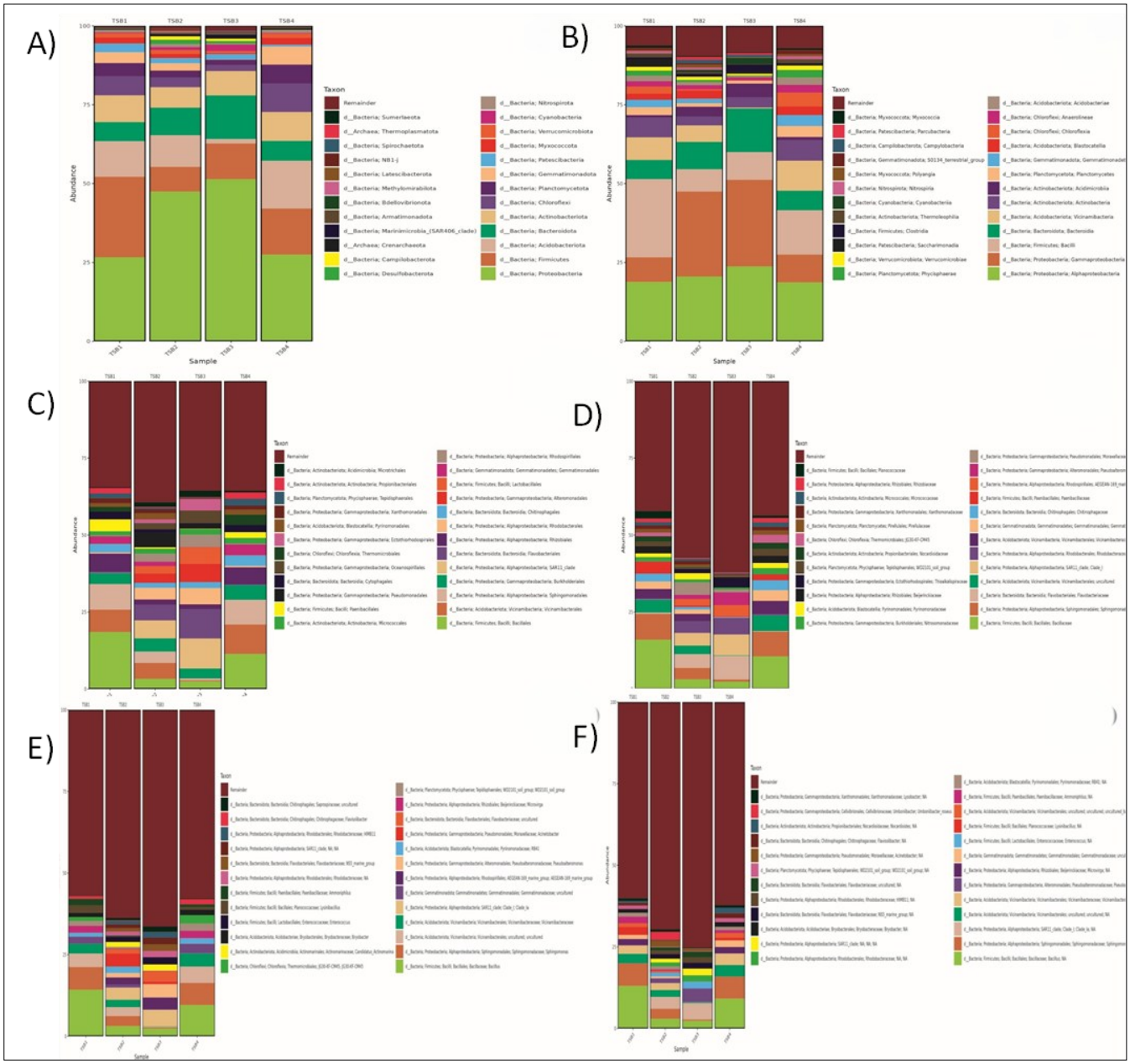

Fig. 2. The image presents stacked bar plots that illustrate the relative abundance of bacterial community composition across four tomato rhizosphere soil samples (TSB1, TSB2, TSB3 and TSB4). Each plot categorizes the bacterial community at various taxonomic levels including A) phylum, B) class, C) order, D) family, E) genus and F) species, showcasing the distribution and dominance of specific bacterial groups within each sample. The visual representation highlights the diversity and complexity of microbial communities present in the tomato rhizosphere.

Table 3. Species diversity was observed in all the tomato rhizosphere samples

Sample ID	Shannon index	Simpson index	Observed features	Goods coverage	Simpson reciprocal	Chao1
TSB1	8.79	1.00	1,100	1.0	274.23	1,100
TSB2	9.10	1.00	1295	1.0	308.85	1.100
TSB3	8.25	0.99	625	1.0	169.97	1,295
TSB4	9.11	1.00	1,370	1.0	364.71	625

sequencing depth was sufficient for most samples except for TSB3 which exhibits lower diversity. These findings align with alpha diversity indices, reinforcing differences in microbial richness across the samples. The abundance distribution of the dominant phylum in the four tomato rhizosphere soil samples is shown in the abundance heatmap (Fig. 3b). This study employed Krona to analyse the microbial community composition of tomato rhizosphere soil samples, allowing for a comprehensive examination of microbial taxa from domain to genus level. The resulting Krona charts effectively illustrate the relative abundance of these microbial taxa. (..\..\2) obj2_metagenomics\9_Krona_charts\index.html)

Beta diversity

A distance matrix was calculated to reflect the dissimilarity between samples to explore the beta diversity and assess the similarities or dissimilarities in microbial community composition across the four tomato rhizosphere soil samples. The data in this distance matrix can be visualized with the weighted and unweighted PCoA. The plot illustrates how these samples cluster together or separates from one another according to their similarities (Fig. 4).

KEGG functional annotation of tomato rhizosphere microbiome

To better understand the functional potential of the tomato

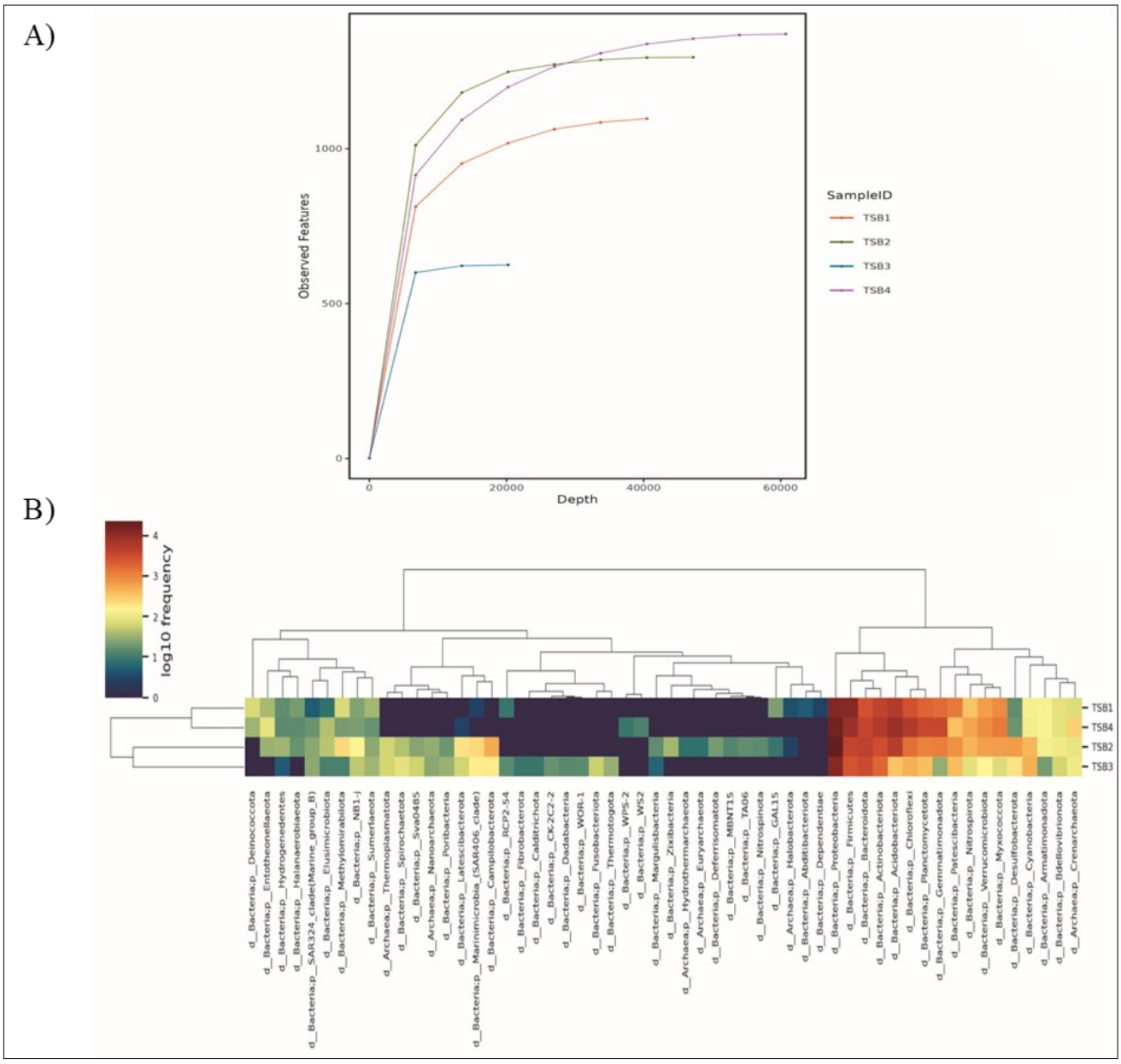

Fig. 3A. Rarefaction curves showing the observed bacterial features in four rhizosphere soil samples (TSB1-TSB4) as sequencing depth increases. TSB4 and TSB2 show the highest richness while TSB3 shows the lowest, indicating differences in microbial diversity across samples.
Fig. 3B. Heatmap with hierarchical clustering of log_{10}-transformed bacterial and archaeal taxa abundance across samples. Distinct clustering patterns highlight variations in microbial community structure with TSB2 and TSB4 showing similar profiles.

rhizosphere microbiome, KEGG pathway annotations were applied. A heatmap was generated to represent the abundance of the top 25 key functional genes across four samples (TSB1, TSB2, TSB3 and TSB4) along with KEGG IDs highlighting notable variations in metabolic activities and transport functions (Fig. 5A). A significant proportion of the identified genes were associated with ABC transporters including those related to the peptide/ Nickel Transport System (ABC.PE, ABC.PE.S, ABC.PE.P1) and the Iron Complex Transport System (ABC.FEV.P, TC.FEV.OM). The presence of these genes suggests that microbial strategies for iron acquisition are essential for effective plant-microbe interactions. Additionally, several genes responsible for regulating oxidative stress and redox reactions were identified. Thioredoxin Reductase (trxB, TRR) showed slight expression in TSB2 while Glutathione S-transferase (GST, gst) was detected in moderate abundance across all samples. Genes involved in fatty acid metabolism and energy production were also enriched, including Acetyl-CoA Acetyltransferase (atoB, EC:2.3.1.9) and Long-Chain Acyl-CoA Synthetase (fadD, ACSL, EC:6.2.1.3). These genes were present at varying levels indicating active processes of fatty acid degradation and synthesis. Dihydrolipoamide dehydrogenase (DLD, lpd, pdhD EC:1.8.1.4) and Aldehyde dehydrogenase (ALDH, EC:1.2.1.3) were abundant in all samples. Across all four samples, the cold shock protein gene (cspA) was also observed, suggesting mechanisms by which microbial communities adapt to environmental fluctuations. Furthermore, the ParA (soj) Chromosome Partitioning Protein was identified. Overall, KEGG pathway analyses provided valuable insights into the microbial community structure and functional potential of the tomato rhizosphere microbiome, highlighting its complex interactions and adaptive strategies in response to environmental changes.

Functional annotation predicted by COG analysis

The COG functional annotations were analysed for all four tomato rhizosphere soil samples. The relative abundance and the percentage of enriched annotations among the samples along with their COG gene IDs are represented through a heatmap (Fig. 5B). The most abundant key functional categories of COG

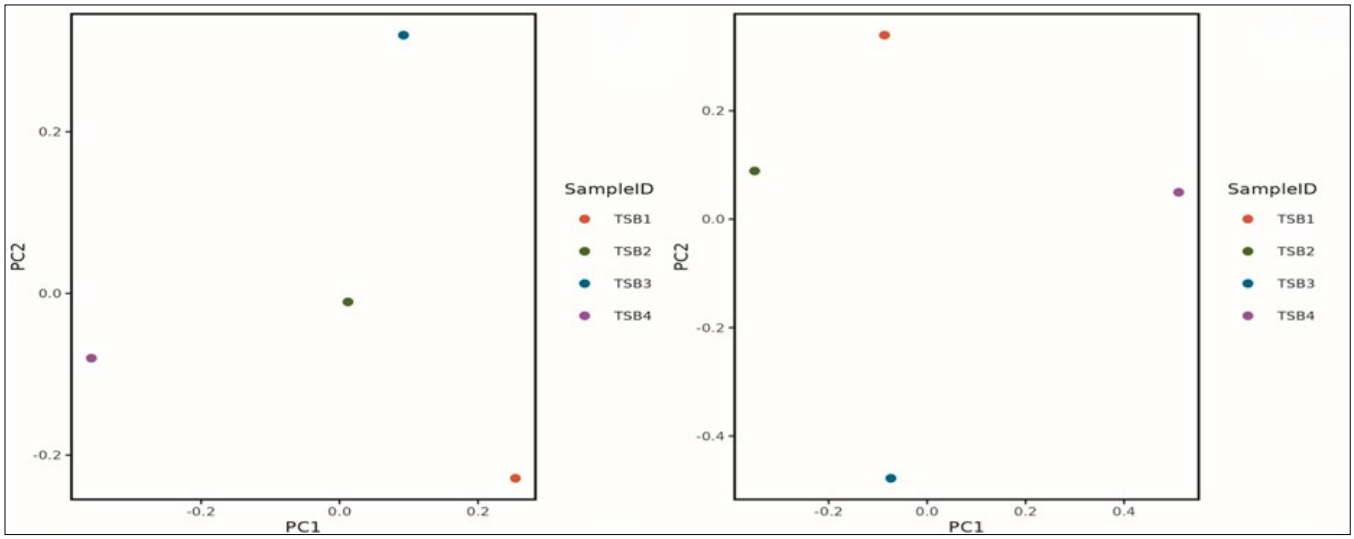

Fig. 4. PCA was employed to explore the variation in microbial functional profiles among the four tomato rhizosphere soil samples (TSB1-TSB4). The unweighted PCA (panel a, top) highlighted clear separation among samples with PC1 capturing the majority of variance due to differences in the core functional genes present in each community. In contrast, the weighted PCA (panel b, top) reveals stronger separation, especially of TSB3, suggesting distinct metabolic potential and community specialization. Together, PC1 and PC2 accounted for the major variation in community function.

annotations identified in all the samples are Transport and metabolism: ABC-type multidrug transport system (COG1131, COG1132); Acyl-CoA synthetase, dehydrogenase and reductase (COG0318, COG1960, COG1024, COG1012, COG0183) and Predicted arabinose efflux permease (COG2814). Transcription and Regulation: DNA-binding transcriptional regulators (COG1846, COG1309, COG0583, COG0745); DNA-directed RNA polymerase specialized sigma subunit (COG1595); Signal transduction histidine kinase (COG0642). Enzymatic activities: Catechol 2,3-dioxygenase (COG0346); Acetylornithine deacetylase (COG0624); Glycine/D-amino acid oxidase (COG0665); Predicted dehydrogenases (COG0673, COG1028); Cell wall biosynthesis: Glycosyltransferases (COG0438, COG0463); Nucleoside-diphosphate-sugar epimerase (COG0451); Recombination and repair: Site-specific recombinase XerD (COG4974). Other metabolic functions: Short-chain alcohol dehydrogenase (COG1028); Pimeloyl-ACP methyl ester carboxylesterase (COG0596) and Acetyl-CoA acetyltransferase (COG0183).

Discussion

The comprehensive 16S rRNA amplicon-based analysis of tomato rhizosphere soil samples from the Beggli micro-watershed, Kolar, Karnataka provides critical insights into the complex interplay

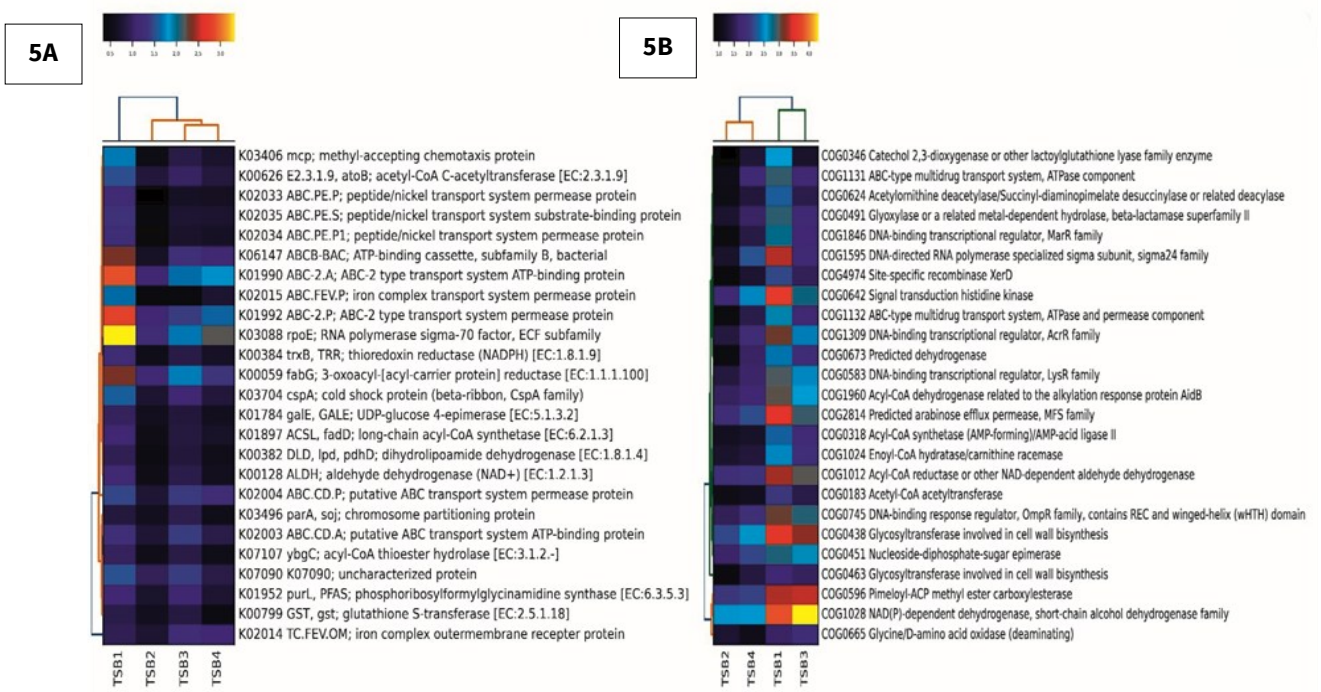

Fig. 5A. KEGG-based heatmap analysis (panel a, bottom) revealed functional divergence across samples, particularly in transport systems (ABC, iron complex), metabolic enzymes (*acetyl-CoA*, *NADH dehydrogenases*) and stress-related proteins. The hierarchical clustering grouped TSB2 and TSB4 closer indicating similar functional traits. On the other hand, **Fig. 5B**. COG-based heatmap (panel b, bottom) showed notable variation in genes related to transcription regulation, cell wall biosynthesis and degradation pathways. The distinct clustering patterns and expression intensities across both KEGG and COG datasets underscore the functional heterogeneity and potential microbial adaptation in different tomato rhizosphere environments.

between soil physicochemical properties and microbial community structure. Similar to previous studies, this research highlights how soil parameters drive microbial diversity, functional potential and ecological interactions within the rhizosphere environment (34). The assembly of core microbiota in crop plants is driven by biotic and abiotic factors including climate conditions, growth stage and different fertilization regimes (35, 36). According to findings from the current study, soil microbial diversity is greatly influenced by the chemical characteristics of the soil which are consistent with earlier research (34). Variations in the microbial diversity among the rhizosphere soils may be due to the variances we saw within the soil physicochemical properties (Fig. 6), particularly EC, organic carbon, nitrogen, phosphorus, potassium, zinc, boron and magnesium which exerted the greatest influence on microbial community structure in the tomato rhizosphere. While these nutrients showed strong positive associations at the class level, they exhibited consistent negative correlations from order to species levels indicating differential responses of microbial taxa to soil fertility gradients. In contrast, pH and calcium displayed only weak or variable correlations suggesting a relatively minor role in shaping microbial diversity. These findings highlight that nutrient availability and soil fertility parameters are the key drivers of microbial community shifts which in turn may affect nutrient cycling and plant growth in tomato rhizospheres (34, 37). The physicochemical characterization of all four tomato rhizosphere soil samples (TSB1, TSB2, TSB3 and TSB4) revealed significant variability in organic carbon, macronutrients (N, P, K). These variations have intense implications for microbial composition as studies have shown that soil pH and organic carbon significantly influence bacterial richness and functional diversity in the tomato rhizosphere (32, 33). The highest microbial abundance and diversity observed in TSB2 with its neutral pH (7.2) and high organic carbon (1.02 %) align with findings from previous metagenomic studies which indicate that neutral to slightly alkaline soils support greater microbial diversity and plant-beneficial interactions (38). By contrast, TSB4 with its acidic pH (5.9) and reduced organic matter content, had lower microbial diversity as expected by studies showing that acidic conditions tend to constrain microbial community complexity in the tomato rhizosphere (39). DNA extraction and quality checks ensured high-quality molecular weight DNA for sequencing. Maximum DNA content in TSB2 (129.4 ng/µL) indicates an enhanced microbial biomass while less DNA content in TSB3 (26.6 ng/µL) points towards compromised microbial load as was noticed earlier in other tomato rhizosphere experiments (40). These results support the hypothesis that availability of soil nutrient and organic carbon are major controllers of microbial community structure and biomass. The 16S rRNA gene sequencing disclosed a very diverse bacterial community among the four rhizosphere soil samples with a stepwise increase in taxonomic detail from phylum to species level. Proteobacteria became the predominant phylum in all samples followed by Firmicutes and Actinobacteria, a pattern supported by previous studies of tomato rhizosphere microbiomes indicating that by changing their cell membrane, employing alternative metabolic pathways and maintaining internal pH homeostasis, proteobacteria can adapt to alkaline conditions (41). Notably, TSB2 exhibited the highest ASV richness, suggesting a functionally redundant and resilient microbial ecosystem while TSB4 displayed the lowest phylum-level diversity, indicating a potential microbial niche specialization adapted to its acidic and nutrient-poor conditions. These findings align with research demonstrating that variations in soil nutrient status directly impact microbial community assembly and functional potential in tomato cropping systems (18, 42). Comparative taxonomic analysis across hierarchical levels showed that Gammaproteobacteria were highly abundant in TSB2 and TSB3, consistent with their known role in plant growth promotion and biocontrol activity within tomato rhizospheres (43). The genus *Bacillus* was dominant in TSB1 and TSB4 indicating the presence of spore-forming, stress-tolerant bacteria which have been widely reported in tomato rhizosphere metagenomics studies (44). Acinetobacter, a genus associated with organic matter degradation and biocontrol properties was particularly enriched in TSB2, further emphasizing the link between soil organic carbon and beneficial microbial colonization (45). The study found that conservation agriculture enhances bacterial community structure and diversity in rhizosphere soils compared to conventional practices, positively influencing soil health and

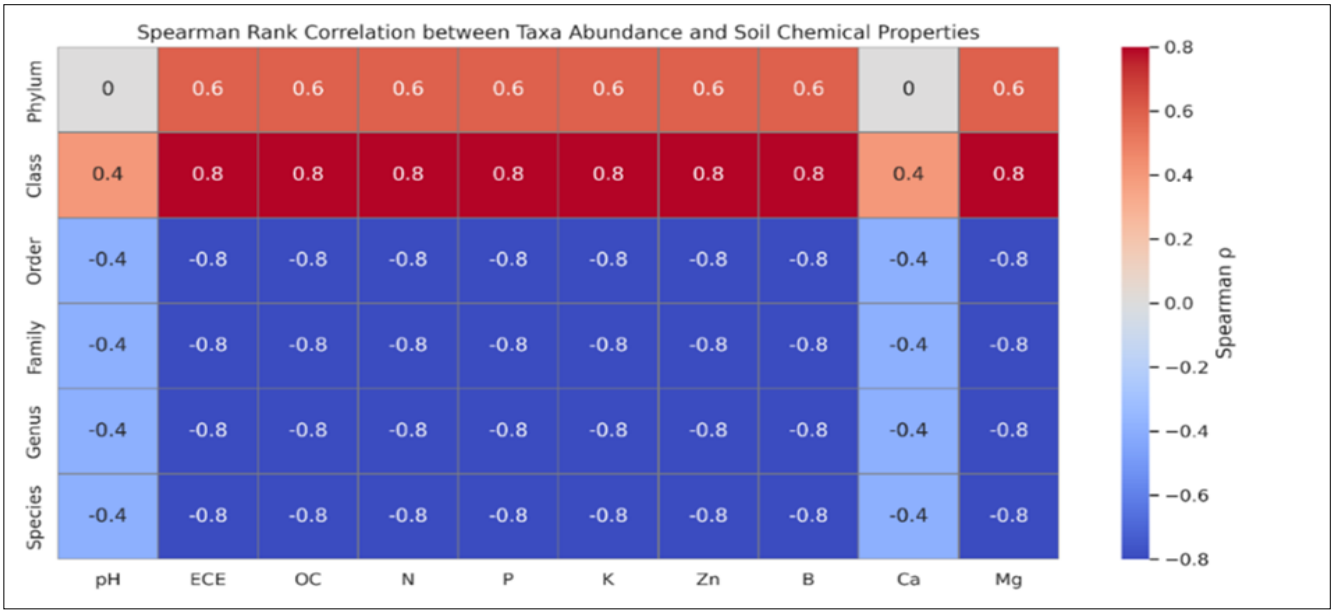

Fig. 6. Spearman rank correlation (ρ) between microbial taxa abundance (phylum to species) and soil chemical properties (pH, ECE, OC, N, P, K, Zn, B, Ca, Mg) in tomato rhizosphere soils. Positive correlations are indicated by red shades and negative correlations by blue shades. Strong positive correlations (ρ = + 0.8) were observed at the class level while consistent strong negative correlations (ρ = - 0.8) were seen at the order, family, genus and species levels.

potentially improving growth, particularly during the early growth stage (46). Alpha diversity indices provided further evidence of microbial richness and evenness across the four soil samples. The Shannon Index values ranged from 8.25 in TSB3 to 9.11 in TSB4, indicating significant differences in microbial diversity. The Simpson Index values remained close to 1.00, suggesting a relatively even microbial distribution, a trend commonly reported in tomato rhizosphere studies where bacterial communities exhibit balanced interactions due to root exudate-driven selection (17). Observed species richness was greatest in TSB4 (1370 species) supporting the idea that even with reduced pH and nutrient content, some bacterial groups are capable of flourishing in niches as earlier reported in acidic tomato rhizosphere soils (39). Beta diversity PCoA analysis showed that there were clear-cut clustering patterns of the samples and that TSB2 and TSB4 segregated into different clusters which points to significant variations in microbial makeup. These findings are consistent with previous research showing soil pH and organic carbon to be important drivers of microbial community grouping in tomato rhizospheres (18). Grouping of TSB1 and TSB3 implies common microbial properties, possibly prompted by comparable soil nutrient composition and root exudate chemistry. Functional annotation through the use of KEGG and COG analyses offered more informative insight into the metabolic capabilities of the tomato rhizosphere microbiome. Genes involved in ABC transporters, oxidative stress response, fatty acid metabolism and nutrient cycling were widespread across all samples, as would be expected from metagenomic findings that emphasize the functional significance of nutrient acquisition and stress tolerance processes in microbial communities associated with tomatoes (47). The enrichment of genes related to iron acquisition including iron complex transporters suggests that microbial iron metabolism plays a crucial role in plant-microbe interactions particularly in nutrient-limited soils (18). Additionally, the presence of oxidative stress mitigation genes such as Thioredoxin reductase (trxB) and Glutathione S-transferase (GST) supports the hypothesis that tomato rhizosphere microbes employ stress-response pathways to enhance survival under fluctuating environmental conditions (44). The identification of cold shock protein genes (cspA) highlights microbial adaptation mechanisms to temperature fluctuations while the presence of chromosome partitioning protein genes (ParA) underscores the role of genetic stability in sustaining rhizosphere microbial populations. These findings are consistent with studies demonstrating that tomato rhizosphere bacteria exhibit robust genetic mechanisms to cope with environmental stressors and maintain functional stability (17).

Conclusion

This study highlights the comparative taxonomic and functional composition of bacterial communities in the tomato rhizosphere within the Beggli micro-watershed using 16S rRNA amplicon sequencing. Observation revealed that the optimal conditions for a tomato crop to grow are well-drained loamy or sandy-loam soils rich in organic matter with an optimum pH of 6.0-7.0. Overall, a diverse community dominated by Proteobacteria, Firmicutes, Actinobacteria and Bacteroidetes is commonly associated with healthy tomato rhizospheres enhancing nutrient cycling, stress tolerance and disease resistance. Importantly, this study provides novel insights into the tomato rhizosphere within watershed-scale ecosystems, offering a scientific basis for location-specific biofertilizer recommendations. The direct application of these findings can support sustainable soil fertility management and enhance tomato productivity under diverse watershed conditions. The observed variations in microbial diversity and functional potential were closely linked to differences in soil physicochemical properties, emphasizing the role of the soil environment in shaping bacterial community structure. Future research should focus on experimental validation of predominant microbial functions, particularly through culture-based approaches, meta-transcriptomics or enzyme assays. Isolating and characterizing key culturable bacterial taxa may also help elucidate their specific roles in promoting plant growth and transforming soil nutrients. Such integrative approaches will enhance the functional understanding of rhizosphere microbial communities and contribute to the development of sustainable, microbe-driven soil management strategies in tomato-based agroecosystems.

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Authors' contributions

SB contributed to writing the original draft, methodology, data curation and conceptualization. UN contributed to conceptualization, supervision and data curation. AS contributed to visualization. BPS contributed to data curation and methodology. RTK contributed to methodology and conceptualization and LKN contributed to review and editing. All authors read and approved the final manuscript.

Compliance with ethical standards

Conflict of 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.

Ethical issues: None

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