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Different soil salinity imparts clear alteration in rhizospheric bacterial community dynamics in rice and peanut

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Abstract
The rhizospheric microbiome is capable of changing the physio-chemical properties of its own micro-environment and found to be indispensable in the overall health of the host plant. The interplay between the rhizospheric environment and the microbiota residing therein tune the physiology of the associated plant. In this study, we have determined how the soil properties and the host–plant remains as an important parameter for microbial community dynamics in the rhizosphere of rice and peanut. In addition to check the physio-chemical parameters of the rhizospheric soil, we have also prepared the metagenomic DNA from each rhizospheric soil followed by high-throughput sequencing and sequence analysis to predict the OTUs that represents the community structure. The alpha-diversity of the bacterial community in the RRN sample was highest, while the lowest was in PRS sample. Actinobacteria is the most predominant phylum in PRN, PRS and RRN, whereas Acidobacteria in RRS. We found a clear shift in bacterial community over the rice and peanut rhizosphere and also over these host–rhizospheres from normal and high saline region. The rhizospheric bacterial community composition found to be affected by the close-by environmental factors. Thus, the rhizospheric bacterial community structure is related to both the adjoining soil characters and the type of the hosts.

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Introduction

The root-adjoining soil where the plant has much higher influence through secretion of their different root exudates, mucilage, and sloughed cells is the rhizospheric region. The phytochemicals secreted in the rhizosphere are important for the establishment of the microbial community around it (Mendes et al. 2013). The rhizospheric region of the plant is a complicated and heterogeneous environment that dictates the type of allowed microbes therein. Molecular studies particularly metagenomics suggest that the soil is the habitat of the highest biodiversity which is approximated as 1000 Gbp of microbial genome sequence in each gram of soil (Vogel et al. 2009). The advantageous role of these rhizospheric microbes can be demonstrated through their direct role in plant-growth promotion, plant protection from phytopathogen and stress management of the plants (Penrose and Glick 2003). By virtue of having various microbes, the rhizosphere remains as the chemical factory, where complex physical, chemical and biochemical interactions are operating which in turn influence the nutrient cycling, nitrogen fixation, phosphate mobilization and solubilization, nutrient uptake, water uptake, production of plant growth regulators, seed germination and early plant growth promotion, development in soil structure and competing with plant pathogens (Sahu and Brahmaprakash 2016). Thus, the diversity of microorganisms plays a fundamental role in the maintenance of soil fertility and nutrient cycling. Mostly such rhizospheric microbiome is having a beneficial effect on the plants; however, in few cases, the rhizospheric community might have representatives which are either neutral or detrimental for the host plant.

The plant root exudates choose the type of microbes it will attract or repel from the rhizospheric region, but this is not the only parameter. The physicochemical composition of the soil remains another important criterion for building the rhizospheric community. Thus, it is, in general, the reciprocal action of the plant root and the soil which establishes a particular type of microbiota. The physiochemical characteristics of the soil are ever-changing mostly by various physical, chemical and biological means. The soil microbial community is influenced by crop rotation, use of fertilizers and tillage which in turn change the soil physiochemical parameters (Hinsinger et al. 2005). The compounds present in root exudates influence the rhizospheric microbial community structure and are different at each developmental stage (Chaparro et al. 2014). The microbial community-assisted nitrogen, phosphorous and other nutrients cycle are more rapid and dynamic in rhizospheric soil compared to the bulk soil (Sahu and Brahmaprakash 2016). Agricultural
management builds up soil physicochemical properties which control microbial community composition and nutrient cycling. Furthermore, the microbial diversity and heterogeneity in bulk soil are increased by organic fertilizer (Lupatini et al. 2017). Bacterial community compositions are different in the organically managed agricultural systems than the conventional system (Wang et al. 2016). Simultaneous analysis showed that the ecological interaction regulates structure, function and potential resilience of soil microbial communities (Berry and Widder 2014; Coyte et al. 2015). Plant root systems are the strong operators of microbial community congregation that build rhizosphere communities and are taxonomically and functionally different from bulk soil microbial communities (Turner et al. 2013; Zhang et al. 2018). The rhizosphere effect and plant selection are evident in the observation of microbiomes across different field environment (Hamonts et al. 2018). Agricultural management and plant relation with microbial community structure establish taxonomy to network structure. Rhizosphere network is often smaller, less densely connected and less complex than bulk soil microbial community (Sahu and Brahmaprakash 2016).

The abundance, diversity and composition of bacteria in the rice rhizosphere have been widely investigated. Bacterial population in the rice rhizosphere were double to those of bulk soil (Hamonts et al. 2018; Hussain et al. 2011). The structures of bacterial communities in the rice rhizosphere are diverse and dynamic which are related to soil type, geographical location and rice genotype (Santos-Medellín et al. 2017). Metagenomic studies have indicated that the bacterial communities in rice rhizosphere are broadly inhabited by Proteobacteria, mainly Alpha-, Beta- and Delta-proteobacteria classes, Acidobacteria, Actinobacteria and Chloroflexi phyla (Ding et al. 2019). Alpha-, Beta-proteobacteria classes are abundant in the rice rhizosphere and essential for ecosystem functioning (Handelsman 2004).

In this study, we have chosen the rhizospheric sample of peanut (dicotyledon) and rice (monocotyledon) from different geographical locations (Fig. 1) to analyze the microbiota, present therein. Here we have undertaken the characterization of rhizospheric soil of rice and peanut, grown in different salinity conditions, using targeted 16S rRNA genes through a metagenomic approach. We further analyzed the sequence of 16S rRNA variable region and highlighted the following prediction: the microbial community is notably different in rice rhizosphere grown in normal soil (RRN) than that of the saline soil growing rice (RRS) and rhizosphere of peanut grown in normal soil (PRN) over that of saline soil (PRS), and also from monocotyledons to dicotyledon grown in normal and saline soil.

**Materials and methods**

**Site description**

The study was performed with samples of the rhizospheric region associated with peanut and rice plants grown in normal and high saline soil conditions collected from places of West Bengal, India (Fig. 1). The geographical location of the sample collection sites is Galsi (23°19′48.00″N, 87°42′00.00″E) for rice rhizospheric soil with low salinity area (RRN). This is central plain areas of the district Burdwan of West Bengal, which sometimes encounter heavy floods during rainy seasons. The next sample collection site is Egra (21°53′58.09″N, 87°32′16.58″E) for the peanut rhizospheric soil with low salinity area (RRS). This is one of the main deltaic islands in the Sundarban region.
Sampling

Four samples of the peanut and rice rhizosphere having different soil salinity were collected in May 2017. The owner of all four sampling sites granted all necessary permits to access. On spot, surface soils around the plants were cleared of debris and unwanted pebbles and the soil sample were collected to an 8–10 cm depth from the surface on soil using an auger with 10 cm diameter around the roots. Roots are gently shaken to remove the non-rhizospheric soil. The rhizospheric soil samples were collected using brush. Each of the soil samples that is free of debris is kept in a labeled zipper storage bag in a cool place for further analysis. Samples were collected from three spots for each of the four cropland sites. These three replicates were mixed as one sample and further characterization has been done.

Analysis of the physio-chemical parameters of the sample

Soil samples were air-dried and ground. Soil pH and electrical conductivity were measured with Thermo Fisher Scientific Orion STAR A329 multi-parameter, following Sparks et al., (1996). Organic carbon and organic matter of the soil samples were estimated by the rapid titrimetric method (Walkley and Black 1934). The salinity of the soil samples was measured by Mohr’s method, often called the argentometric method (Eaton et al. 1995). Soil texture analysis was measured following ASTM standard method. The air-dried soil samples were ground finely with an agate mortar and pestle. The ground soil sample was digested with the help of the di-acid digestion process. 400 mg of soil samples were digested with 8 ml of 1:1 HNO₃: HCl (EMSURE grade) in a Teflon vessel for 1 h (modified USEPA 3051) at 200 °C. After cooling, the soil samples were diluted to 100 ml in a cleaned volumetric (modified USEPA 3051) at 200 °C. After cooling, the soil samples was measured by Mohr’s method, often called the argentometric method (Eaton et al. 1995). Soil texture analysis was measured following ASTM standard method. The air-dried soil samples were ground finely with an agate mortar and pestle. The ground soil sample was digested with the help of the di-acid digestion process. 400 mg of soil samples were digested with 8 ml of 1:1 HNO₃: HCl (EMSURE grade) in a Teflon vessel for 1 h (modified USEPA 3051) at 200 °C. After cooling, the soil samples were diluted to 100 ml in a cleaned volumetric flask using ultrapure water (18.2 ms cm⁻¹) and the solutes were filtered through Axiva 0.2 µ PTFE filter paper and stored at 4°C in 50 ml polypropylene tubes. Then samples were analyzed for metal using an inductive-coupled plasma optical emission spectrometer (ICP-OES) (Thermo Fisher Scientific, Model iCAP 7000 Series). The plastic and glassware used during the experiment were washed thoroughly with 10% v/v HNO₃ acid solution. Thereafter a series of washing was done using Milli-Q water and finally, it was air-dried. Merck standard solution IV and IX was used during the analysis. The coefficient of correlation for the calibrated curve was observed to be between 0.9990 and 0.9996. The quality of the data generated in ICP-OES was assessed using standard reference material (Estuarine Sediment-SRM 1646a) purchased from NIST (National Institute of Standard and Technology). Accuracy of the analysis in the form of percentage recovery ranging between 96.12 and 104.59% was observed for all the metals, the precision of <5% relative standard deviation was also obtained for all the metals. Concentration of metals was expressed in the form of mg/kg.

Estimation of culture dependent bacteria from the soil samples

To find the approximate number of culturable bacteria present in the soil sample, 1 g of each of the PRN, PRS, RRN and RRS samples were homogenized in 10 ml of 0.9% NaCl solution. Two types of agar media, Luria agar or LA (Tryptone, 10 gm/litre; yeast extract, 5 g/l; NaCl, 10 g/l; and agar, 15 g/l in 1000 ml of MilliQ-grade water) and International Streptomyces Project-2 or ISP-2 (malt extract, 10 g/l; yeast extract, 4 g/l; dextrose, 4 g/l; and agar, 20 g/l in 1000 ml of MilliQ-grade water) were used to get the total bacterial cfu/ml (colony forming unit/microliter) soil sample. The media pH was maintained between 7 and 8. Cycloheximide (50 µg/ml) was added to the media used as the anti-fungal agent to avoid the undesired growth of the fungi. These soil suspensions were then serially diluted and 100 µl from different selected dilutions from each sample were then used as inoculum and spread onto LA and ISP-2 agar plates. LA plates were used for estimating the cfu of all general types of bacteria, while the ISP-2 media were used for the estimation of cfu of actinobacteria. The LA and ISP-2 agar plates were then incubated at 37 °C and 30 °C for 2 and 5 days, respectively. Colonies were then counted to determine the cfu/ml from each sample.

Metagenomic DNA extraction, 16SrDNA amplicon library generation and sequencing

Metagenomic DNA preparation, 16SrDNA library generation and Illumina MiSeq sequencing were done by AgriGenome Labs, India. Total genomic DNA of four different rhizospheric soil was prepared separately using the DNeasy Power Soil Kit (Qiagen, USA) following the manufacturer’s protocol. The concentration and purity of DNA were determined by Nanodrop 2000c spectrophotometer and 1% agarose gel electrophoresis. After DNA extraction, the total DNA of the rhizospheric samples was used as the template and the bacterial V3 region-specific primers (V3 Forward primer CCTACGGGNGBCASCAG and V3 Reverse primer GACTACNVGGGTATCTAATCC). 5 ng of amplified product was used for library preparation using NEBNext Ultra DNA library preparation kit. The library quantification and quality estimation were done in Agilent 2200 TapeStation. The prepared library was sequenced in Illumina MiSeq 2500 with 2*150 cycles chemistry.
Sequence analysis

Paired-end FASTA sequences of four soil samples were analyzed using the standalone installation of QIIME 1.9.1 (Caporaso et al. 2010) and USEARCH (v.11.0) on Linux platform (Ubuntu 20.04) (Edgar 2010). USEARCH is the most followed software to analyze our sequence data for community studies. Initially, the raw sequences (in fastq format) were visualized using FastQC version 0.11.9 (Andrews 2010). PCR primer sequences, of V3 region of the respective samples were removed from the sequencing data using cutadapt (v.1.8.3) (Edgar 2013). Sequence data in FastQ format was quality trimmed using sickle (v.1.33) in paired-end mode with default settings (Joshi et al. 2011). Forward and reverse read were merged into a single amplicon read using fastq-join allowing fragments with a length of 200–250 bp for V3 (Lozupone and Knight 2005). A minimum Phred score of 38 was used for downstream analysis. The entire cleaned sequence data was concatenated into a single file. Minimum of 2 nucleotides similarity parameter was set up for OTU selection. Duplicated and chimeric sequences were checked by USEARCH (v.11.0) (Edgar 2010). Processed sequences were used for OTU picking with USEARCH using 97% sequence similarity against the silvagold database using the UCLUST algorithm (v.1.2.21) following most previous studies with a Phred score as 38 (Edgar 2010). However, analysis with Phred score of 40 produce exactly similar data with that of the Phred score set as 38. The OTUs were taxonomically annotated using the RDP classifier using RDP database (v 11.5) (Cole et al. 2014). Taxon-by-sample abundance tables were created for all taxonomic levels from phylum to genus, as well as for OTUs. QIIME was used to determine the alpha diversity and rarefaction curve that, respectively, represents community diversity (Inverse Simpson and Shannon) and species richness (observed OTUs and Chao1). Beta diversity was calculated by weighted UniFrac distance matrix (Lozupone and Knight 2005) and was visualized using the Principal Coordinate Analysis (PCoA) plot. To assess the stability of the PCoA plot was performed on the OTU table. Based on the relative abundance of genera from each sample Venny 2.1 software was used to construct the Venn diagram (Oliveros 2007), whereas the Circos-0.67–7 software has been used to construct the Circos diagram (Krzywinski et al. 2009). Associations among relative abundances of phylum in each sample and measured environmental factors (pH, EC, Salinity, Coarse Sand, Al, Cd, Cr, Fe, Ni, Pb and K) were determined using canonical correspondence analysis (CCA) (Ter Braak and Verdonschot 1995).

Statistical analysis

Statistical analyses were performed using the Paleontological Statistics package version 3.01 (PAST software1). All the data were subjected to one-way ANOVA analysis followed by Tukey’s post-hoc test. Differences were considered significant if \( p \leq 0.05 \) with multiple comparisons using 999 permutations.

Data deposition

Raw reads of four samples were deposited in fastq format to the National Center for Biotechnology Information. Sequences were deposited under Bioproject PRJNA660114. The accession number of PRN, PRS, RRS, RRN were SAMN15920910, SAMN15920911, SAMN15920912 and SAMN15920913, respectively (Following links https://www.ncbi.nlm.nih.gov/biosample/15920910).

Results

Physical and chemical characteristics of the rhizospheric soil

The physical and chemical characteristics of all the rhizospheric soil were analyzed to correlate with the rhizospheric microbiota (Table 1). pH analysis of the soil collected from the PRS and RRS showed 7.91 ± 0.01 and 7.84 ± 0.02, respectively, whereas soil samples from PRN and RRN showed 6.48 ± 0.04 and 6.75 ± 0.03. Thus, the PRS and RRS soil sample has been found to be slightly alkaline but near neutral in case of PRN and RRN. PRS and RRS showed significantly higher electrical conductivity (EC) than RRN and PRN. The organic carbon and organic matter present in these rhizospheric soils were found to be in a range between 0.64 and 2.79%. The salinity of PRS and RRS ranged between 1.5 and 1.9 mg/L and was found to be higher than PRN and RRN which were 0.2–0.3 mg/L. The rhizospheric soil samples showed higher silt and clay texture (34.19–38.25%) compared to the fine and coarse sand (5.83–15.84%). The metal analyses of the soil samples indicated the prevalence of Fe and Al. The prevalence Cd in these samples was found to be the least. All the soil samples have shown presence of micro and macronutrient (Cd, Co, Cr, Cu, Ni, Pb and Zn) which in general facilitated the growth of the microorganism.

Estimation of culturable bacteria present in rhizospheric soils

The 0.1 g suspension of RRN was plated on LA and ISP-2 media which upon estimation turned out to be \( 6 \times 10^6 \) and \( 1.8 \times 10^4 \) bacteria, respectively. Likewise, the RRS, PRN and PRS showed \( 4.8 \times 10^6 \) and \( 2.7 \times 10^4 \), \( 2.6 \times 10^6 \) and \( 1.5 \times 10^5 \), \( 3.5 \times 10^6 \) and \( 2.1 \times 10^4 \) cells, respectively (Table S1). The number of bacteria appeared higher on LA than on ISP-2.
as ISP-2 is generally supposed to be specific for isolation of actinobacteria.

**General characteristics of the amplicons and sequencing data**

Four amplicon samples from Illumina Miseq sequencing analysis of four different salinity regions were successfully sequenced (Table 2). The V3 region of PRN, PRS, RRN and RRS samples produced 1934241, 677182, 1840904 and 671840 pair-end sequences, respectively. After quality filtering of these sequences, the obtained reads of PRN, PRS, RRN and RRS were 1891967, 668518, 1805567 and 653697, respectively, with an average length range of 250 to 300 bp. Sequences were clustered into rarefaction curves of operational taxonomic units (OTUs) of four different samples of PRN, PRS, RRN and RRS with 7353, 7172, 9038 and 6391, respectively, based on ≥ 97% similarity. The Shannon index of PRN, PRS, RRN and RRS were 8.05, 7.86, 9.23 and 7.88, respectively. The Shannon index was higher in rhizospheric soil of both monocot and dicot growing in normal saline soil with a high diversity. Simpson index also indicates the

### Table 1 Characteristics of different rhizosphere soils and its elemental composition

| Soil characteristic | RRN          | RRS          | PRN          | PRS          |
|---------------------|--------------|--------------|--------------|--------------|
| pH                  | 6.75 ± 0.03  | 7.84 ± 0.02  | 6.48 ± 0.04  | 7.91 ± 0.01  |
| EC (µS/cm)          | 118.2 ± 9.39 | 311 ± 10.21  | 163.5 ± 2.26 | 315 ± 11.56  |
| Organic C (%)       | 1.62 ± 0.12  | 1.04 ± 0.21  | 0.64 ± 0.23  | 1.15 ± 0.39  |
| Organic matter (%)  | 2.79 ± 0.19  | 1.79 ± 0.11  | 1.1 ± 0.08   | 1.65 ± 0.16  |
| Salinity (mg/L)     | 0.3 ± 0.02   | 1.5 ± 0.27   | 0.2 ± 0.09   | 1.9 ± 0.14   |
| Soil texture        |              |              |              |              |
| Coarse Sand (%)     | 5.83 ± 0.03  | 10.84 ± 0.01 | 8.69 ± 0.02  | 11.35 ± 0.01 |
| Fine Sand (%)       | 12.25 ± 0.05 | 15.25 ± 0.02 | 15.84 ± 0.06 | 15.32 ± 0.07 |
| Silt (%)            | 38.25 ± 0.01 | 35.63 ± 0.03 | 34.19 ± 0.02 | 34.5 ± 0.01  |
| Clay (%)            | 43.67 ± 0.26 | 38.28 ± 0.12 | 41.28 ± 0.59 | 38.83 ± 0.42 |
| Soil profile        | silt clay loam| clay loam    | clay loam    | clay loam    |
| Metal concentrations (mg/kg) | | | | |
| Al      | 23,241.66 ± 1259.23 | 47,520.12 ± 2156.12 | 12,146.21 ± 1429.12 | 59,235.39 ± 1782.50 |
| Cd      | 0.12 ± 0.02 | 0.094 ± 0.02 | 0.19 ± 0.03 | 0.089 ± 0.01 |
| Co      | 10.16 ± 0.65 | 13.22 ± 0.87 | 11.56 ± 0.94 | 17.67 ± 0.45 |
| Cr      | 1.23 ± 0.03 | 64.25 ± 3.39 | 2.39 ± 0.02 | 72.26 ± 4.20 |
| Cu      | 83.18 ± 0.85 | 78.52 ± 4.22 | 91.23 ± 0.45 | 70.98 ± 5.12 |
| Fe      | 4201.55 ± 1654.24 | 55,012.87 ± 1278.24 | 10,231 ± 985.76 | 40,029.46 ± 3254.95 |
| Mn      | 332.23 ± 20.25 | 590.24 ± 39.56 | 410.23 ± 12.22 | 502.45 ± 56.23 |
| Ni      | 17.16 ± 5.75 | 54.22 ± 2.21 | 10.32 ± 1.97 | 69.67 ± 4.23 |
| Pb      | 7.13 ± 2.93 | 15.67 ± 4.19 | 2.25 ± 1.89 | 13.23 ± 2.11 |
| Zn      | 82 ± 3.87 | 70.13 ± 4.26 | 75.29 ± 5.76 | 59.53 ± 3.26 |
| Ca      | 3.23 ± 2.31 | 1.62 ± 0.32 | 5.22 ± 1.56 | 2.12 ± 1.33 |
| Na      | 7.79 ± 2.89 | 4.23 ± 1.12 | 9.13 ± 1.45 | 2.21 ± 1.45 |
| Mg      | 12.43 ± 5.67 | 3.02 ± 0.25 | 18.27 ± 2.58 | 10.12 ± 1.29 |
| K       | 2.56 ± 1.95 | 0.152 ± 0.03 | 3.25 ± 1.56 | 0.75 ± 0.06 |

### Table 2 Raw data summary of the Illumina Miseq sequences of the V3 region of 16S DNA of microbial communities in different hosts in different seasons

| Samples | 16SrDNA amplicon reads | No. of OTU | Chou1 index | Shannon (H) index | Simpson (D) index |
|---------|-------------------------|------------|-------------|-------------------|-------------------|
|         | Total                   | Filtered   | Total       | Percentage (%)    |                   |
| PRN     | 1934241                 | 1,891,967  | 7353        | 97.8              | 7995.66           |
|         |                         |            | 9038        | 98.0              | 9246.82           |
| RRN     | 1840904                 | 1,805,567  | 6391        | 97.29             | 7174.52           |
| RRS     | 671840                  | 668,518    | 7172        | 98.72             | 7646.33           |
| PRS     | 677182                  | 668,518    | 7172        | 98.72             | 7646.33           |

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alpha-diversity and its increase is directly proportional to the magnitude of the Simpson indices. Simpson index of PRN, PRS, RRN and RRS was 0.984, 0.974, 0.993 and 0.983, respectively. Chou1 indices, which indicates species richness, are low in the samples with higher salinity. Chou1 of PRN, PRS, RRN and RRS were 7995.66, 7646.33, 9246.82 and 7174.52, respectively (Table 2). Beta-diversity indices show random distribution of bacterial population in these rhizospheres.

**Microbial taxonomic analysis at the phylum and class level**

Classification of the high-quality sequences also demonstrated differences in the bacterial communities among the different samples at the phylum, class, family and genus level (Fig. 2). A total of 29 phyla were identified in all samples out of which 7 phyla showed dominance in their relative abundance (> 1% of relative abundance in at least one sample) ($p$ value < 0.05) (Fig. 2a). Actinobacteria was the most dominant phylum (> 20% relative abundance) across all samples, accounting for 20.4–59.23%. Acidobacteria, Chloroflexi, Cyanobacteria, Fermicutes, Gemmatimonadetes and Proteobacteria were the subdominant phyla with > 1% relative abundance in at least one sample (Table S2). The other 22 phyla had much lower abundances (less than 1% relative abundance in all samples).

A total of 85 bacterial classes were identified across all samples. There were twelve classes with a relative abundance of higher than 1% in at least one sample ($p$ value < 0.05) (Fig. 2b). Among these twelve classes, the significantly dominant class (> 20% relative abundance) was Actinobacteria with 20.31–59.01% of the total high-quality sequences. The class of Acidobacteria was also dominant in RRS sample with 35.99% relative abundance. The subdominant classes were Thermoleophilia, Anaerolineae, Chloroflexi, Bacilli, Clostridia, Gemmatimonadetes, Alpha-proteobacteria, Beta-proteobacteria, Delta-proteobacteria, Gamma-proteobacteria with the relative abundance of greater than 1% in at least one sample (Table S3). In the sample of PRN, Alpha-proteobacteria, Bacilli, Clostridia, Gemmatimonadetes, Beta-proteobacteria, Delta-proteobacteria, Gamma-proteobacteria, Acidobacteria were dominant with the relative abundance ranging from 1 to 16%. The class Proteobacteria was co-dominantly inhabited with Actinobacteria in the sample of PRN with 16.26% relative abundance. In the sample of PRS Acidobacteria, Anaerolineae, Clostridia, Alpha-proteobacteria were codominant with relative abundance of greater than 1%. Actinobacteria was also dominant in PRS sample such as PRN with 48.64% relative abundance. Next to Actinobacteria, Anaerolineae
was dominant in the sample of PRS with 19.96% relative abundance. Relative abundance of Alpha-proteobacteria was drastically reduced from 16 to 4% in PRS sample than the PRN. In the sample of RRN Alpha-proteobacteria was also codominant with 8.54% relative abundance next to Actinobacteria. Only class Gemmatimonadetes was lesser than 1% relative abundance (0.06%) in RRN. In RRS, the relative abundance of Acidobacteria was dominant over other classes with 35.99% relative abundance. RRS was the only sample, where Actinobacteria (20.31%) was not a dominant taxon. Class Anerolineae and Alpha-proteobacteria were co-dominantly present in RRS with the relative abundance of 6.27 and 8.04%, respectively. Comparative relative abundance among four samples was also represented by heatmap analysis (p value < 0.05) (Fig. 3). Phylum Acidobacteria was dominated in sample RRS. Actinobacteria was dominated in the low salt rhizospheric region of samples in both PRN and RRN. Phylum Chloroflexi was dominated in PRS (Fig. 3a). Relative abundance of rhizospheric bacteria at the class level also reflected the same abundance, such as phylum. The class Acidobacteria was also dominant in RRS. The class actinobacteria were also showed the dominant relative abundance in both PRN and RRN. Alpha-proteobacteria, Beta-proteobacteria, Delta-proteobacteria and Gamma-proteobacteria were also dominant in normal salt soil of both PRN and RRN (Fig. 3b). This dynamic behavior of bacteria, at phylum and class level in rhizospheric soils of monocot/ dicot growing in different saline soil, was very important to maintain the plant growth promotion.

Microbial taxonomic analysis at the family and genus level

The top 20 classified families with greater than 1% relative abundance at least in one sample, were represented in a bar diagram (Fig. 2c; Table S4). The distributions of the families differed greatly across the samples (p value < 0.05). Actinomycetales, Pseudonocardiaceae and Sphingomonadaceae were the dominant families in PRN among which Pseudonocardiaceae was the most dominant family (17.511% relative abundance). In the sample PRS, Anaerolineaeae and Nocardiodiaceae were the dominant families with 19.97 and 33.99% relative abundance, respectively. Actinomycetales and Acidobacteria were the most dominant families in the RRN and RRS, respectively. At the family level bacterial dynamic community structures were significant. Total 35 genera were selected by the greater than 1% relative abundance in atleast one sample, for comparative abundance studies (Fig. 2d; Table S5). Actinopolysporaceae, Bacteroidetes, Hydrogenedens, Nitriliruptor, Pseudonocardiaceae, Sphingopyxis were dominant in PRN. Whereas in the sample PRS Actinopolysporaceae, Bacteroidetes, Bellilinea, Longilinea, Nocardiodioides were the enriched genera. Actinopolysporaceae group of genera was the most dominant bacteria in the sample PRN. Nocardiodioides was the enriched bacteria in the sample PRS. Actinocorallia, Actinomycetales, Actinopolysporaceae, Bacteroidetes, Hydrogenedens, Nitriliruptor, Nocardiodioides, Streptomycetaceae were the most dominant genus present in the sample of RRN. Actinopolysporaceae, Koribacter and Telmatobacter were the most dominant in RRS sample. Telmatobacter was the most dominant genus with 25.285% relative abundance in the RRS. Comparative relative abundance of family and genus level was also represented by heatmap (p value < 0.05) (Fig. 3c, d). The family Acidobacteria was dominant in the rice rhizosphere growing in saline soil. Actinomycetales was also dominant in PRN, RRN than the high-salt growing rice peanut rhizosphere PRS and RRS.

Comparative fold-shift of families and genera between low and high-salt rhizosphere

We have tried to highlight the dominance of different bacterial groups present in the rhizosphere of both the host growing in normal and saline soil between samples in phylum, class, family and genus level (Figs. 4, 5, S1, S2). We have also compared the relative abundance of bacterial families in the peanut and rice rhizosphere. It is striking to note that there are many taxa which have considerable increase or decrease in relative abundance over the variation in plant and the soil they grow. To highlight the shift in community dynamics at family level, we have estimated the fold increase or decrease within eight major families associated with each of the samples. The family Xanthomonadaceae has 387.46-fold higher abundance in PRN than PRS, whereas Anaerolinaceae, Chloroflexi, Nocardiodiaceae are dominant in PRS than in PRN (Fig. 4a, b). Family Anaerolinaceae has 44.14-fold higher abundance in PRS over PRN (Table S6). Likewise, the abundance of Chloroflexi, Nocardiodiaceae, Solirubrobacteraceae, Streptomycetaceae, Thermoleophilaceae, Thermomonosporaceae families in RRN are much higher than in RRS (Fig. 4c). Thermoleophilaceae has 18.62-fold higher abundance in RRN than in RRS. Acetobacter and Gemmatimonadaceae have the highest fold increase in their abundance in RRN over RRS (Fig. 4d; Table S6).

Similarly, we found that the genus Actinocorallia, Hydrogenedens, Kaistia, Kibdelosporangium, Koribacter, Marmorica, Nakamuraella, Nitriliruptor, Plantactinospora, Prauserella, Pseudonocardiaceae, Solirubrobacterales, Sphingomonas, Sphingopyxis, Stella, Xanthomonadaceae are many folds higher abundant in PRN over PRS (Fig. 5a; Table S7). Relative abundance of Xanthomonadaceae is higher in the PRN rhizospheric soil than in the PRS. Xanthomonadaceae are found to have the highest fold increase (710.89). Bellilinea, Chloroflexaceae, Longilinea, Nocardiodioides, Nocardiosis, Pelolinea are shown to have a dominant
fold increase in PRS than that of the PRN (Fig. 5b). *Lon-gilinea* has the highest fold increase in abundance in PRS sample. *Actinocorallia, Aminicenantes, Chloroflexaceae, Marmoricola, Nocardioales, Nocardiosis, Plantactinospora, Prasereilla, Solirubrobacterales, Streptomycetaceae, Thermoleophilum*, were found to have a higher fold increase in RRN over RRS (Fig. 5c). *Hydrogenedens, Koribacter, Paludibaculum, Telmatobacter* are having a higher fold increase in RRS than the same of RRN (Fig. 5d; Table S7).

We have further confirmed the bacterial community dynamics among tested samples in phylum level through circus plot as well as venn diagram. Both these analyses not only confirm the above results but also clarify the shift in abundance of certain bacterial taxa. The circus plot represents the
switching in number of OTUs in phylum level (Fig. 6a) and family level (Fig. S3) among low and high salt grown peanut and rice rhizosphere. The same pattern has also been found when a total of 61 abundant genera present in all samples were plotted in a venn diagram (Fig. 6b). There were 8.6% of the total genera present in all rhizosphere, while 20, 5.7, 22.9, and 5.7% genera were found exclusively in PRN, PRS, RRN and RRS, respectively (Fig. 6b). The detailed distribution of major genera present in all kinds of rhizosphere is mentioned in Fig. 6b.

Analysis of the relationship between environmental factors and the rhizospheric microbial community

A beta-diversity analysis based on PCoA plot was performed to compare the bacterial compositions among the four different samples (p value < 0.05). The bacterial taxa of PRN and RRN were clustered into the same group. Although PRS and RRS were situated distantly (Fig. 7). Canonical correspondence analysis (CCA) was used to establish the relationship between the environmental factors and the bacterial phylum (p value < 0.05) (Fig. 8). CCA plot was carried out using OTUs data together with environmental factors (pH, EC, salinity, coarse sand, Al, Cd, Cr, Fe, Ni, Pb and K), which might influence the bacterial community structure, to highlight the relative abundance of different phyla among these samples. According to Tukey’s post-hoc test (999 permutations), the significant relationship between environmental variables and canonical axes was analyzed using the paleontological statistics package version 3.01 (PAST Software 1). Based on Tukey’s post-hoc test, the bacterial phylum was significantly linked (p ≤ 0.05) to the rhizosphere environmental factors (Fig. 8). Factors corresponding to the differences in the bacterial phylum were pH, EC, salinity of the sample, and presence of coarse sand, Al, Cd, Cr, Fe, Ni, Pb and K along with the first axis CCA1 explaining 69.2% and the second axis CCA2 (28.57%) of the variation (Fig. 8). The plot obtained by CCA visualizing the different habitat preferences of the phyla. The pH, EC, salinity, coarse sand, Al, Cr, Fe, Ni, Pb were the most important environmental factors to influence the rhizosphere bacterial phylum abundance and were positively correlated with CCA1 axis (Table 3). CCA2 axis had a positive correlation with pH, EC, salinity, coarse sand, Al, Cr, Fe, Ni, Pb but was negatively correlated with Cd and K.
Fig. 5  Pie chart representing the comparative abundance of the most common Genera of sample PRN (a), PRS (b), RRN (c), RRS (d). 1. Pseudonocardiaceae 2. Nocardiodes 3. Nitriliruptor 4. Hydrogenedens 5. Bellilinea 6. Actinopolysporaceae 7. Actinocorallia 8. Sphingopyxis 9. Marmoricola 10. Koribacter 11. Telmatobactor 12. Streptomyctaceae 13. Paludibaculum

Fig. 6  Distribution of the bacterial community among rice and peanut rhizosphere.  a Circos plot showing the distribution of bacterial communities present in different rhizospheric soils.  b Venn diagram of the percentages of shared and unique bacterial genera present in four different samples
Discussion

The rhizosphere is the region which is biologically active and enriched with microbes. The chemical, biological and physical characteristics of this area have great significance on the plant roots. We noticed that the rhizosphere region has a significant effect on soil physicochemical properties and rhizospheric bacterial dynamicity and diversity. Previous study is shown that soil bacterial communities have a great contribution to nutrient cycling. Carbon metabolites secreted by plant roots promote the growth and activities of microbes inhabited in the soil surrounding the roots (Hussain et al. 2011). Parallelly rhizosphere microbes benefit plants by supplying nutrient and growth-stimulating hormones phytopathogen and enhancing tolerance to environmental stress (Mendes et al. 2013). Physical and chemical properties indicate the health of the agricultural soil. Soil collected from the RRS and PRS indicates slight alkaline in nature due to prevalence of the soil belt in the intertidal region of Sundarbans, India, but the soil samples from RRN and PRN are neutral. The experimental results are in good agreement with previously published results observed by different researchers (Ghosh et al. 2019; Karak et al. 2013; Ponnamperuma 1972). The high conductivity, organic carbon content and fair distribution of the metals such as Ca, Na, Mg and K for the entire soil sample give us insight into the availability of the essential nutrient in the rhizosphere environment which helps in proliferation of microbial population in this area (Karak et al. 2013). The salinity of the PRS and RRS was found to be higher than PRN and RRN, which indicates the presence of soluble salt which essentially increases the conductivity of the soil. In general, the soil salinity is
Table 3 Correlation matrix of phylum, sampling sites and environment factors with CCA axis

| Phylum                  | Axis 1    | Axis 2    | Axis 3    |
|------------------------|-----------|-----------|-----------|
| Acidobacteria          | 2.48559   | 0.060397  | −0.23246  |
| Actinobacteria         | −0.51468  | −0.09792  | −0.34334  |
| Chloroflexi            | −0.22366  | 2.3638    | 1.08999   |
| Cyanobacteria          | −0.94508  | 1.99688   | −0.85971  |
| Firmicutes             | −0.03565  | −0.87308  | 0.076458  |
| Gemmatimonadetes       | 0.0104    | −2.70731  | 6.84472   |
| Proteobacteria         | −0.15786  | −1.11075  | −0.1061   |
| Sampling sites         |           |           |           |
| RRN                    | −0.31307  | −0.03629  | −0.15341  |
| RRS                    | 1.00534   | 0.022587  | −0.00477  |
| PRN                    | −0.25591  | −0.44394  | 0.086508  |
| PRS                    | −0.3098   | 0.527683  | 0.07222   |
| Environmental factors  |           |           |           |
| pH                     | 0.517672  | 0.820354  | 0.226273  |
| EC                     | 0.545552  | 0.665969  | 0.514376  |
| Salinity               | 0.391096  | 0.851018  | 0.357954  |
| Coarse Sand            | 0.443493  | 0.506949  | 0.748845  |
| Al                     | 0.344927  | 0.913177  | 0.212671  |
| Cd                     | −0.38441  | −0.86764  | 0.256688  |
| Cr                     | 0.490065  | 0.782779  | 0.386734  |
| Fe                     | 0.753271  | 0.545006  | 0.3578    |
| Ni                     | 0.360087  | 0.879326  | 0.31856   |
| Pb                     | 0.646596  | 0.746688  | −0.01185  |
| K                      | −0.6742   | −0.71621  | −0.12223  |

influenced by multiple ions. The overall salinity index has been found to be higher in sample of coastal region than the others. However, the concentration of Na + does not fit with the salinity index. Furthermore, the fold increase in Na + over different samples are less significant that those mentioned and analyzed through correlation plots. Salinity of the soil affected the agricultural production, economy and quality of life along with significant changes in the health of the environment (Kumar and Sharma 2020). Soil salinity can directly or indirectly affect both growth and reproduction of crop plants. (Otlewska et al. 2020). Clay content for all the soil was found to be higher with respect to the coarse sand, fine sand and silt that in turn might also provide a better condition for the microbial growth in the rhizospheric region (Biesgen et al. 2020).

The distribution of the metal content in the soil considerably varies as per the sampling locations. Few factors such as (a) soil characteristics such as grain size of the soil, organic carbon content, Mn or Fe oxygenated hydroxides, chelating agent as well as ligands (Banerjee et al. 2012); (b) substrate variation due to natural weathering of the soil (Zhang and Gao 2015); and (c) discharge of pollutants and anthropogenic pressure determines the distribution of the elements in the soil (Ghosh et al. 2020). The gradient of distribution of elements indicates presence of high concentration of Fe and Al which generally occurs due to natural weathering or due to presence of basaltic and lateritic rocks present in the soil (Nath et al. 2013). The enriched prevalence of heavy metals such as Cd, Co, Cr, Cu, Ni, Pb and Zn might occur due to natural factors or anthropogenic pressure, such as uneven use of pesticides, insecticides, and chemical fertilizers (Ghosh et al. 2019). The level of K might occur due to presence of granodiorites and granites in the soil (Ghosh et al. 2019). High occurrence of Fe might occur due to hydrological fluctuation e.g., alternate period of wet and dry season in the crop cultivated agricultural land (Dohrmann et al. 2013).

In our study, we have found total 29 phyla, 85 classes, 315 families and 639 genera from the tested samples (Tables S8–S11). The total OTUs of four different samples of PRN, PRS, RRN and RRS are 7353, 7172, 9038 and 6391, respectively. Rhizospheric bacterial alpha-diversity were higher in both monocot and dicot grown in normal soil than the saline soil. Beta-diversity shows random distribution of bacterial population in all the four samples. We have identified total 29 phyla in all four samples. Among them Actinobacteria, Acidobacteria, Chloroflexi, Cyanobacteria, Firmicutes, Gemmatimonadetes, and Proteobacteria were higher in abundance than other 22 phyla. Previous research has shown that Proteobacteria, Acidobacteria, Actinobacteria, Bacteroidetes and Firmicutes were dominant phyla in the rhizosphere soil of Arabidopsis and cotton (Lundberg et al. 2012; Qiao et al. 2017). Total 85 bacterial classes were identified across four samples. Actinobacteria, Acidobacteria, Thermoleophilia, Anaerolineae, Chloroflexia, Bacilli, Clostridia, Gemmatimonadetes, Alpha-proteobacteria, Betaproteobacteria, Deltaproteobacteria, Gamma-proteobacteria were the higher relative abundance classes in four sampling sites. Different species of Actinobacteria were responsible for recycling of nutrient in a great extent of rhizosphere soil (Bhatchariya et al. 2016; Connon and Giovannoni 2002; Handelsman 2004) and this Actinobacteria is the most abundant phylum in the rhizospheric soil PRN, PRS and RRN. However, the rhizospheric soil of RRS showed Acidobacteria as most abundant but they have quite high abundance of Actinobacteria as well. Previous study showed that Acidobacteria could grow in environment which is nutrient less and also shows higher abundance in poor soil (Zou et al. 2005). Acidobacteria and Actinobacteria were found to be abundant in disease-suppressive soils and reported to be responsible to suppress disease-causing microbes and triggering the enhancement of beneficial microbes that have potential to promote crop health (Sanguin et al. 2009). Pseudonocardiaceae is the most dominant families in the sample PRN, whereas Nocardioidaeae (33.99%) in PRS relative abundance. Actinomycetales is the most dominant in the RRN but Acidobacteria in the RRS sample. The relative abundances...
of the bacterial communities at the genus level in four rhizospheric soil were significantly different. Although Actinopolysporaceae group of genera was the most dominant bacteria in the sample PRN. Nocardioides was the enriched bacteria in the sample PRS. Telmatobacter was the most dominant genus in the sample RRS. Proteobacteria, Acidobacteria, Actinobacteria, Firmicutes and Planctomycetes were most dominant bacteria among all bacterial community found in the rice rhizosphere soil (Bhattacharyya et al. 2016). The Proteobacteria, Acidobacteria, Actinobacteria, Chloroflexi, and Firmicutes are dominant taxonomic group in most of the soil samples. Actinobacteria and proteobacteria have also been reported dominant taxonomic group found in rhizospheres soil of Maize (Dohrmann et al. 2013). Decomposition of organic matters are performed by the Chloroflexi. PGPR activity such as siderophore production, IAA production, nitrogen fixation and prevention of different phytopathogens are fascinated by the group of Firmicutes and Proteobacteria (Felestrino et al. 2017; Yamada et al. 2005).

Analysis of the rhizospheric microbiome of peanut grown in normal and saline soil delineates that the Actinobacteria, Bacillaceae, Gaiellaceae, Gemmatimonadaceae, Micromonosporaceae, Mycobacteriaceae, Pseudonocardiales, Solirubrobacteraceae, Sphingomonadaceae, Thermomonosporaceae, Xanthomonadaceae are the most dominant family in PRN. And among these, Xanthomonadaceae shows higher fold shift in PRN than PRS, whereas Anaerolineaceae, Chloroflexi, Nocardioides are found to be the dominant family in PRS than in PRN. The genus of Actinocorallia, Hydrogenedenes, Kaistia, Kibdelosporangium, Koribacter, Marmoricola, Nakamuraella, Nitriliruptor, Planctomycetaceae, Prauserella, Pseudonocardiaceae, Solirubrobacteraceae, Sphingomonadaceae, Sphingopyxis, Stella, Xanthomonadaceae were higher abundant in normal soil in respect to saline soil, as well as Bellilinea, Chloroflexaceae, Longilinea, Nocardioides, Nocardiopsis, Pelolinea were dominant genus in saline soil in compare to normal soil. Similarly, rhizospheric microbiome of rice between normal and saline soil condition, the families Chloroflexi, Nocardioides, Solirubrobacteraceae, Streptomycetaeaceae, Thermoleophilaceae, Thermomonosporaceae were dominant fold increase values in normal rhizospheric soil than the saline condition, whereas Acetobacter and Gemmatimonadaceae were the highest fold increase in saline rhizosphere soil compared to normal soil. It has been found that Xanthomonadaceae shows highest level of dynamicity in normal soil-grown peanut rhizospheric soil compared to higher saline soil-grown peanut rhizosphere, as it cannot tolerate high salt stress. It was reported that Xanthomonadaceae shows shift in community structure growing under piglet with plant litter treatment in different time frame (Olakanye et al. 2018). Similarly, Thermoleophilaceae shows much more community shift in rice rhizosphere normal soil compared to rice rhizosphere saline soil, which might be saline sensitive so that their relative abundance was less (Znój et al. 2021). The genus Actinocorallia, Aminicenantes, Chloroflexaceae, Marmoricola, Nocardioides, Nocardiopsis, Planctomycetaceae, Prauserella, Solirubrobacteraceae, Streptomycetaeaceae, Thermoleophilum, were the higher fold increase in normal rhizosphere than saline soil. Hydrogenedenes, Koribacter, Paludibaculum, Telmatobacter were showed a higher fold increase in saline rhizosphere than the normal soil. Several studies reported Sphingomonadaceae, Chitinophagaceae, Nocardioidaceae, Solibacteraceae, Bacillaceae, Cytophagaceae and Methylbacteriaceae were predominant families (>2% relative abundance) consists of genera such as Sphingomonas, Microvirga, Bacillus, Nocardioides, Marmoricola, Bryobacter, Flavisolibacter were the dominant (>1% relative abundance) of T. aestivum L rhizosphere (Rousk et al. 2010; Latif et al. 2020). Whereas Bacillus nealsnii, Rhodospirillales_bacterium_WX36 and Bacillus niacinini were prominent (>0.5% relative abundance) bacterial species (Latif et al. 2020). Sphingomonas, Kaistia, Xanthomonadaceae under the phylum Proteobacteria and Nakamuraella, Planctomycetaceae, Thermomonosporaceae under Actinobacteria and Stella present only in the rhizosphere of PRN, whereas genus Pelolinea, Longilinea (Chloroflexi) were found only in PRS. It was interesting that phylum Chloroflexi has been found only in the rhizosphere of PRS. Similarly, the genus Thermoleophilum, Prauserella, Solirubrobacterales, Rhodococcus, Marmoricola from phylum Actinobacteria; Methylloceaniibacter, Rhodospirillales from Proteobacteria and Aminicenantes has been found distinctively only in the rhizosphere RRN, whereas genus Paludibaculum, Koribacter from Acidobacteria were found only in the rhizosphere of RRS. The predominance of bacterial taxa in any given rhizosphere exclusively depends on the soil compositions and the influence of the plant roots. Though it is very important to understand the community specificity of particular rhizosphere but it is very complex to find the factors responsible behind.

The influence of different environmental factors describing the microbial community is like the finding of beta diversity analysis due to differences of rhizospheric community to the monocot and dicot types (Fig. 7). Factors corresponding to the differences in the bacterial communities were pH, EC, salinity, coarse sand, Al, Cd, Cr, Fe, Ni, Pb and K along with the first axis explaining 69.2% and the second axis (28.57%) of the variation (Fig. 8). CCA plot shows that pH, EC, salinity, coarse sand, Al, Cr, Fe, Ni, Pb were the most important environmental factors to significantly influence the rhizosphere bacterial phylum abundance (Fig. 8). Previous study has shown bacterial community structure were influenced by pH, Cr, Sb, As, Zn and moisture content, but pH was the most dominant factor (Guo et al. 2019).

The clustering of PCoA and CCA analysis signify PRN and RRN were clustered into the same group, while PRS and
RRS were situated distantly. The CCA result in our study indicates pH, EC, salinity, coarse sand, Al, Cr, Fe, Ni, Pb is positively correlated with rhizospheric community structure. Thus, pH, EC, salinity, coarse sand, Al, Cr, Fe, Ni, Pb appeared to be an important factor that influences microbial communities and dynamics.

**Conclusion**

In summary, this study illustrated the rhizospheric bacterial community of rice and peanut growing in normal soil and saline soil of West Bengal, India. Along with comment on the relative abundance of bacterial taxa present in different rhizospheric soil of peanut and rice, we also highlighted the shift in community dynamics in phylum, class, family and genus level. The normal rhizospheric soil in both monocot and dicot shows more diverse compare to saline rhizospheric soil in monocot and dicot. Alpha-diversity such as Shannon Index was higher in both monocot and dicot normal rhizospheric soil with high diversity in respect to saline rhizospheric soil. Once again it has been proved that the rice being a monocot and the peanut being a dicot has their own choice to contain preferable bacterial representative around their roots. The decreased abundance and variation of bacterial population in the rice and peanut rhizosphere of high saline zone might be one of the reasons behind the significant reduction in the vigor and yield of the crop cultivated in high salt containing region. Finally, the shift in community dynamics has been shown as a factor of soil parameters as well as the choice of the associated plants.

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**Data availability** The raw sequences are publicly available on NCBI SRA database with project identification number PRJNA660114.

**Declarations**

**Conflict of interest** The authors declare that they have no competing interests.

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