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Assessing Bacterial Communities in Bulk Soil and Rhizosphere Associated with NPK Fertilizer in Oil Palm Seedlings via Amplicon Sequencing

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Abstract: Malaysia's palm oil industry relies heavily on chemical fertilizers, leading to significant environmental concerns such as nutrient loss and declining biodiversity. This study aims to evaluate the impact of post-fertilizer application on bacterial communities in soil, particularly focusing on bulk soil and rhizosphere. Through amplicon sequencing, we investigated the response of bacterial diversity to unfertilized and NPK-fertilized soil treatments. Fertilizer application increased soil phosphorus, potassium, and magnesium levels, enhancing seedlings' growth but reducing bacterial diversity, particularly sensitive groups such as Acidobacteria and Verrucomicrobia. *Candidatus Solibacter* and *Acidothermus* were consistent biomarkers for unfertilized soil, while *Mizugakiibacter* and *Castellaniella* were for fertilized treatment. For the inferred bacterial community functions, the unfertilized bulk soil demonstrated enhanced function related to carbohydrate metabolism, and the unfertilized rhizosphere exhibited functions related to energy metabolism, stress tolerance, bioremediation, and plant defense. During fertilized treatment, functions related to secondary metabolites were enriched in the bulk soil, and bacterial colonization functions were enriched in both compartments. For network analysis, the fertilizer application reduced bacterial network interactions and complexity. Environmental drivers, namely, pH and soil total phosphorus (TP), influenced the bacterial biomarkers' abundance in the bulk soil and rhizosphere. These findings demonstrate the need to optimize chemical fertilizer applications and identify beneficial bacterial taxa to foster sustainable agricultural practices in the palm oil industry.

Keywords: *Palm oil, fertilizer, bacterial communities, amplicon sequencing, oil palm seedlings.*

1. Introduction

Oil palm (*Elaeis guineensis*) is Malaysia's most cultivated agricultural crop and has been among the country's top economic contributors. This crop is cultivated on 5.73 million hectares as of 2021, with Sarawak having the second-largest area (1.61 million hectares) and Peninsular Malaysia having the biggest oil palm plantations (2.61 million hectares) (MPOB, 2022a). The Malaysian palm oil industry generated an average of RM 108.52 billion in export earnings in 2021, making it Malaysia's most profitable agricultural crop (MPOB, 2022b). The demand for palm oil is projected to increase as the world's population grows, and it is estimated that between 93 and 156 million tonnes of palm oil might be needed by 2050 (Pirker et al., 2016; Murphy et al., 2021). Previous studies have shown that the use of NPK (nitrogen, phosphorus, potassium) chemical fertilizer increased nutrient availability in both soil and leaves which subsequently improved the production of commercialized crops (Kavvadias et al., 2023; Wang et al., 2023). Thus, optimized fertilizer usage and strategic production techniques can accomplish a higher yield.

Bulk soil is termed an area not penetrated by plant roots. In contrast, the rhizosphere is a zone of soil immediately surrounding the root of plants since plants may secrete root exudates to encourage the growth of microbes that can improve plant nutrient uptake (Vives-Peris et al., 2020; Jamil et al., 2022). The response of the bacterial community in soil-and-plant root systems, including bulk soil and rhizosphere, can vary depending on the amount of fertilizer applied, soil type, and plant species. Proteobacteria became increasingly dominant in both bulk soil and rhizosphere of *Larix* seed orchard over time after initial fertilization (Wang et al., 2024). After phosphorus-potassium (PK) fertilization, Actinobacteria demonstrated increased relative abundance in the bulk soil of buckwheat fields compared to post-fertilization (Morigasaki et al., 2024). While short-term effects may vary, the development of plants, the makeup of the

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microbiome, and the agricultural management practices can be intertwined and have long-term detrimental effects on the ecosystem. Prior studies via the amplicon approach have demonstrated that the chemical fertilizer application decreased bacterial diversity in the roots of wheat and rice, suggesting rational rate fertilizer application for environmental and sustainable development (Liu et al., 2020a; Sinong et al., 2021). NPK fertilization was also found to reduce microbial connections based on network analysis (Ji et al., 2023; Yang et al., 2023).

NPK fertilization led to the enrichment of genera such as *Dyella*, *Thermomonas*, *Massilia*, and *Devosia*, known for promoting plant growth (Zhao et al., 2013; Zheng et al., 2017; O'Brien et al., 2018). This contradicts Sinong et al. (2021), who found that low nutrient input is preferable for optimizing beneficial bacterial population structure and promoting plant health and growth. The application of chemical fertilizer also enhanced the specialized functions of soil and root-associated bacterial communities, potentially impacting plant growth and health (Caradonia et al., 2019). Tang et al. (2023) demonstrated that soil physicochemical parameters drove the microbial community succession in response to the NPK fertilizer. However, there remains a lack of studies concentrated on how chemical fertilizer application influences the bacterial changes in the compartments of oil palm seedlings.

Therefore, we hypothesize that: (i) post-NPK fertilizer application will potentially lead to increased availability of soil nutrients, resulting in enhanced foliar nutrient content of oil palm seedlings and a shift towards enrichment of bacterial populations and functions associated with plant growth promotion within soil-plant compartments; (ii) the fertilizer application will induce a reduction in bacterial diversity in both bulk soil and rhizosphere, possibly due to altered nutrient availability and shifts in microbial interactions within soil-plant compartments. The primary objectives of this study were: (i) to analyze the effects of post-NPK fertilizer application on soil and foliar nutrient availability, bulk soil and rhizosphere bacterial diversity and co-occurrence network, and microbial functions associated with plant growth promotion; and (ii) to understand the role of environmental drivers, such as soil physicochemical properties and foliar nutrient contents, in shaping the abundance and composition of bacterial populations within soil-plant compartments.

2. Materials and Methods

Experimental Design and Sample Collection

The experimental design and sample collection were conducted by Sime Darby Plantation Technology Centre (SDPTC) Sdn. Bhd. The crossing type of oil palm germinated seeds (*Dura* x *Pisifera*, Calix 600) were sown in polybags (10 × 12 inches) and grew in a controlled nursery environment. The polybag contained inland soil, which was perceived to be less fertile than coastal soil, but the encroachment of oil palm cultivation land has been extended to inland soil (Tarmizi & Tayeb, 2006; Arifin et al., 2022). The study was conducted in a randomized block pattern, and the germinated seedlings were subjected to unfertilized soil (control) and a fertilized treatment using commercial NPK chemical fertilizer (CCM25, N:P:K: Mg-14:13:9:2.5). Each type of soil had five replicates. According to standard agronomic practice, the chemical fertilizer was applied once every two weeks until the 30th week (approximately seven months). The seedlings were watered daily. Destructive sampling was carried out following the completion of NPK fertilization at the oil palm seedlings' ideal development stage of the eighth month. The seedling phenotypes, including height and biomass, were recorded during sampling. All the soil samples were flash-frozen in liquid nitrogen and stored at -80°C before DNA extraction. The soil and plant samples were homogenized and sent to an accredited MS ISO/IEC 17025 certified laboratory (Estate Research and Advisory Services RISDA Estates, ERAS Lab) for further analysis, as described below.

Soil Physicochemical Properties

For soil physicochemical analysis, soil samples underwent air drying until constant readings were achieved. About 150 g of soil was used for the analysis. pH, electrical conductivity (EC), total carbon (TC), organic carbon (OC), total nitrogen (TN), carbon-to-nitrogen (C/N) ratio, total phosphorus (TP), available phosphorus (AP), potassium (K), calcium (Ca), magnesium (Mg), sodium (Na), cation exchange capacity (CEC), base saturation (BS), and mechanical analysis (clay, silt, coarse, fine sand) were evaluated for the soil samples.

The soil was suspended in distilled water (1:2.5 WV^{-1}) to determine soil pH using a pH meter. By using the same ratio of 1:2.5 WV^{-1}, the soil-water suspension was mixed and allowed to stand for 30 minutes before measuring the EC using an EC meter. Approximately 100 grams of soil samples were subjected to combustion, converting them into gases, before being analyzed for carbon (C), nitrogen (N), and the C/N ratio using the dry combustion method (Matejovic, 1993) with an Elemental Analyzer (EA, Thermo Fisher). Total phosphorus (TP) and available phosphorus (AP) concentrations were analyzed using the vanadate-molybdate method, as described by Tandon et al. in 1968. Soil samples, weighing approximately 10 g, underwent treatment with specific extractant solutions to dissolve the phosphorus compounds. Subsequently, the TP and AP levels were quantified by measuring the absorbance of colored complexes formed during the chemical reactions, utilizing an Ultraviolet-Visible Spectrometer (UV-Vis, Thermo Fisher). CEC and exchangeable cations (Ca, Mg, K, Na) were then determined using ammonium acetate solution (David, 1960). Approximately 10 g of soil was treated with ammonium acetate solution to release the cations, which were then quantitatively measured using Inductively Coupled Plasma Optical Emission Spectrometry (ICP-EOS, Thermo Fisher). The soil texture, including clay, silt, coarse, and fine sand, was estimated using a soil hydrometer. A minimum of 100 g of soil was used to observe the settling rate over time in water before comparing it to standard classifications. All the parameters were evaluated using three biological replicates. The analyses were performed by ERAS Laboratory, adhering to the M.S 678 (soil) method outlined by the Standard and Industrial Research Institute of Malaysia (Malaysian Standard [MS], 1980).

Foliar Nutrient Content Analysis

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The leaf samples also underwent air drying until constant readings were achieved, and an approximation of 5 g of dried leaves was used for the analysis. The samples were subjected to the same method mentioned in the soil physicochemical analysis for TN, TC, C/N, P, K, Mg, and Ca. Moreover, trace elements such as boron (B), copper (Cu), manganese (Mn), iron (Fe), and zinc (Zn) were quantified. Plant tissue samples underwent preparation via dry ashing, following the method outlined by Heanes in 1981, utilizing a muffle furnace, and were determined using Inductively Coupled Plasma-Optical Emission Spectrometry (ICP-EOS, Thermo Fisher). All the above parameters were tested with three biological replicates.

Soil-Root Fraction and DNA Extraction

Bacterial DNA for the bulk soil and rhizosphere was extracted as described (Wieland et al., 2001). For the bulk soil fraction, 100 g of non-adhering soil was collected after the seedling was removed from the polybag. For the rhizosphere fraction, 50 g of the primary roots with loosely attached soil were cut into smaller pieces (1-2 cm length) to increase surface area and enhance DNA extraction efficiency, followed by mixing in 500 ml of 0.85% NaCl in a shaker incubator (15 mins, 150 rpm). The washing solutions were centrifuged (10 mins, 10,000 rpm, 4°C) to obtain rhizosphere pellets. All processed samples were kept at -20°C before DNA extraction. According to the manufacturer's protocols, two hundred fifty milligrams of soil-processed samples were utilized to extract the genomic DNA using the FastDNA SPIN Kit for Soil (MP Bio, USA). The quality of DNA was determined by 1% agarose gel electrophoresis and a Nanodrop 1000 spectrophotometer according to the manufacturer’s protocols (Thermo Scientific, USA).

Amplicon Sequencing and Amplicon Data Pre-Processing

A final concentration of 1 ng/µl was used for subsequent analysis. The amplification of the V3–V4 region of the 16S rRNA gene employed forward primer 341 F (5’-CCTACGGGNGGCWGCAG-3’) and reverse primer 805R (5’-GACTACHVGGGTATCTAATCC-3’), both barcoded. PCR reactions utilized Phusion® High-Fidelity PCR Master Mix (New England Biolabs) with a composition of Phusion Master Mix (1X), primers (0.5 µM), genomic DNA (250 ng), and dd H2O to reach a final volume of 25 µl. The PCR program involved an initial denaturation at 98°C for 1 min, followed by 30 cycles at 98°C for 10 s, 50°C for 30 s, and 72°C for 30 s, with a final extension at 72°C for 5 min. Sequencing libraries were prepared with TruSeq® DNA PCR-Free Sample Preparation Kit (Illumina, USA) and assessed for quality using Qubit@ 2.0 Fluorometer (Thermo Scientific) and Agilent Bioanalyzer 2100 system. Sequencing was performed on a Novaseq PE250 platform, generating 250 bp paired-end reads.

Paired-end reads were assigned to samples based on unique barcodes. The barcode and primer sequences were removed. Paired reads were then merged using FLASH (V 1.2.7) (Magoč & Salzberg, 2011). Quality filtering followed specific filtering conditions in QIIME (V1.7.0) (Bolyen et al., 2019) to achieve high-quality clean tags. Chimeric sequences were removed using the UCHIME algorithm (Quast et al., 2013). Clean amplicon data were then clustered into operational taxonomic units (OTUs) with Uparse (V 7.0.1001) (Edgar, 2013) at a similarity threshold of ≥97%. A representative sequence was selected for each OTU, and taxonomic affiliations were determined by aligning them against the Greengenes database (V.05/2013) for 16S rRNA sequences (DeSantis et al., 2006; McDonald et al., 2012).

Statistical and Bioinformatic Analysis

Operational taxonomic units (OTUs) assigned to the chloroplasts and mitochondria were removed. Bacterial relative abundance (>2%), and alpha and beta diversities were performed using the phyloseq R package V 1.4.1106 (McMurdie & Holmes, 2013). The significant difference of taxa was analyzed with Statistical Analysis of Metagenomic Profile (STAMP) V2.1.3 using a two-sided Welch’s t-test (Parks et al., 2014). The alpha diversity of the microbiome was evaluated using richness (Chao1) and diversity (Shannon and Simpson) indices. The Wilcoxon rank sum test was employed to perform statistical comparisons between the treatments. Beta diversity was visualized using Principal Coordinate Analysis (PCoA) based on Bray-Curtis dissimilarity. Analysis of Similarities (ANOSIM) was used to determine the significant differences between the groups (Legendre & Gallagher, 2001).

The Kruskal-Wallis sum rank test and linear discriminant analysis size effect (LEfSe) were used to identify discriminatory taxa and functions in the soil-plant compartments. The LEfSe analysis was used with default parameters (LDA>2, $p < 0.05$) in the Galaxy server (V. 1.0) (Goecks et al., 2010; Segata et al., 2011). The predictive functional analysis based on an operational taxonomic unit (OTU) was performed using Tax4Fun as described (Chong et al., 2020). For network analysis, correlations between bacterial genera (LDA>2) were calculated based on Spearman rank coefficient ($r > \pm 0.7$, $p < 0.01$) using the iGraph R package (Csardi & Nepusz, 2006). The network was then visualized in Cytoscape V 3.8.3 (Shannon et al., 2003). The network analysis identified the bacterial keystone within the community based on high mean degree, high closeness centrality, and low betweenness centrality (Banerjee et al., 2018). Canonical correspondence analysis (CCA) was used to investigate the relationship between significant physicochemical parameters and biomarker taxa using the vegan R package (V 2.6-2). A variance inflation factor (VIF) of less than 10 was set to avoid multicollinearity between variables (Oksanen, 2015).

3. Results and Discussion

The Chemical Fertilizer Application Increased Soil Nutrient Availability Yet Not Directly Proportionate to Foliar Nutrient Contents

Tables 1 and 2 show the impact of fertilizer application on soil physicochemical properties and foliar nutrient content. The fertilized soil showed higher levels of TP, K, and Mg, indicating increased nutrient availability (Table 1). Prior work also demonstrates the positive impact of fertilizer application on soil nutrients, such as TP level (Mao et al., 2015; Ahmed et al., 2019). The fertilized soil also showed higher levels of acidity, EC, and BS (Table 1). The release of hydrogen ions (H+) during fertilizer reactions and the use of ammonium-based fertilizers, which may cause soil acidification (Gu et al., 2017; Tkaczyk et al., 2020), are responsible for the increase in EC (Aizat et al., 2014). Consequently, the fertilized soil had a lower soil pH than the unfertilized soil. The higher base cations (K+, Mg2+) and base saturation in the fertilized soil are likely a response to mitigate soil acidification caused by the fertilizer application (Havlin, 2005; Goulding, 2016). These buffering effects aid to maintain soil fertility and nutrient availability for plant uptake (Ng et al., 2022).

Table 1. Soil physicochemical properties

Parameter	Unit	Unfertilized		Fertilized	
		Mean	S.D.	Mean	S.D.
pH*		4.66	0.18	4.13	0.21
EC*	%	49.67	1.53	217.67	39.40
TC		0.59	0.03	0.58	0.05
TOC		0.45	0.02	0.45	0.04
TN		0.22	0.03	0.24	0.02
C/N		2.67	0.58	2.33	0.58
BS*		2.50	0.01	3.39	0.22
Clay		65.33	7.57	62.67	1.15
Slit		13.67	2.08	13.67	1.15
Coarse Sand		13.00	1.73	14.67	0.58
Fine Sand		8.00	5.29	9.00	1.00
TP*	ppm	318.33	45.06	1029.00	377.13
AP		3.00	0.00	120.33	80.09
K*	meq/ 100g	0.08	0.02	0.25	0.05
Ca		0.80	0.10	0.79	0.04
Mg*		0.14	0.02	0.40	0.05
Na		0.06	0.01	0.01	0.03
CEC		41.06	4.29	42.62	1.71

Data are presented as mean and standard deviation (n = 3). An asterisk within the parameter column indicates a significant difference ($p < 0.05$) between treatments for two independent means. EC – electrical conductivity; TC – total carbon; TOC – total organic carbon; TN – total nitrogen; C/N – carbon to nitrogen ratio; BS – base saturation; TP – total phosphorus (P); AP – available P; K – potassium; Ca – calcium; Mg – magnesium; Na – Sodium; CEC – cation exchange capacity.

Despite increased soil nutrient availability, the foliar nutrient analysis (Table 2) revealed that the fertilized soil did not significantly ($p < 0.05$) reflect higher foliar nutrient concentrations of P, K, Ca, Mn, Fe, and Zn. These findings suggest that the increased soil nutrient content did not translate into proportional increases in foliar nutrient concentrations. This discrepancy is likely due to the complex nutrient uptake, translocation, and utilization processes within plants. The absorption and distribution of nutrients in plant tissues are regulated based on the demands of the plants (Han et al., 2016). Nutrients in leaves are mobile and can be rapidly transferred from leaves to other plant parts, such as the stems and roots, to promote the development of new tissues (Kim et al., 2018). Despite the increased availability of soil nutrients due to fertilizer application, there was minimal effect on the leaf nutrient concentrations.

Table 2. Foliar nutrient contents

Parameter	Unit	Unfertilized		Fertilized	
		Mean	S.D.	Mean	S.D.
TN	%	3.06	0.14	2.98	0.35
TC*		43.86	0.20	45.65	1.39
C/N		14.33	0.58	15.46	1.49
P*		0.20	0.01	0.11	0.01
K*		3.01	0.13	2.06	0.21
Mg		0.26	0.02	0.28	0.04
Ca*		1.02	0.10	0.31	0.05
B	ppm	21.33	4.16	13.33	6.51
Cu		9.79	1.50	9.54	1.80
Mn*		173.00	11.53	73.67	8.39
Fe*		371.19	50.47	198.41	46.13
Zn*		35.89	6.04	24.87	0.21
Plant dry weight (DW)*	g	442.32	77.62	576.16	74.92
Plant height*	cm	50.67	3.06	70.33	6.81

Data are presented as mean and standard deviation (n = 3). An asterisk within the parameter column indicates a significant difference ($p < 0.05$) between treatments for two independent means. TN – total nitrogen; TC – total carbon; C/N – carbon to nitrogen ratio; P – phosphorus; K – exchangeable potassium (K+); Mg – exchangeable magnesium (Mg2+); Ca – exchangeable calcium (Ca2+); B – boron; Cu – copper; Mn – manganese; Fe – Iron; Zn – Zinc.

Beneficial Phyla for Plant Growth in Response to Soil Nutrient Availability

Proteobacteria constituted the top predominant taxon up to 43.15% of the total bacterial community, followed by Acidobacteria (18.79%), Chloroflexi (12.51%), Actinobacteria (9.34%), and Firmicutes (4.20%) (Figure 1A). The fertilizer application significantly increased the abundance of Proteobacteria in the bulk soil (Figure 1A, S1A), consistent with prior studies (Xu et al., 2022; Bai et al., 2022). Proteobacteria, particularly copiotrophic members like Pseudomonas and Bacillus, thrive in nutrient-rich environments such as agricultural soils and around plant roots (Wei et al., 2018; Angelina et al., 2020). The flourishing of these bacteria in the fertilized soil is likely attributed to the nitrogen-containing fertilizers used, as genes associated with nitrogen metabolism were linked to the Proteobacteria phylum (Ren et al., 2018). This proposes that the current use of chemical fertilizers that contain nitrogen stimulates Proteobacteria to thrive in the soil. The significant increase in

Proteobacteria abundance (Figure 1A, S1A) in response to substantially higher K (Table 1) in the fertilizer bulk soil may promote the growth of the seedlings. Proteobacteria aid crop growth by producing organic acids, siderophores, biofilms, and plant growth hormones, enhancing yield and quality through improved nutrient availability and stress resistance (Bright et al., 2022). Conversely, the chemical fertilizer substantially reduced the abundance of Acidobacteria in the bulk soil (Figure 1A, S1A), in line with other studies (Dai et al., 2018; Shi et al., 2020). This could be because Acidobacteria genera such as Terriglobus and Granulicella are oligotrophs that enable them to flourish in low-nutrient soil (Tebo et al., 2015; Dedysh & Damsté, 2018; Noble et al., 2020). Given that Acidobacteria prefer oligotrophic environments, this suggests that fertilizing soil might harm their abundance.

Whereas for the rhizosphere, the average abundance of phyla Proteobacteria constituted the top predominant taxon by 54% of the total bacterial community, followed by Actinobacteria (10.73%), Acidobacteria (10.39%), Chloroflexi (6.28%), and Bacteroidetes (5.33%) (Figure 1B). Moreover, the fertilizer application caused a noticeably greater abundance of Saccharibacteria and Actinobacteria (Figure 1B, S1B) and aligns with earlier research (Shen et al., 2018; Liu et al., 2020b). These phyla likely grew and proliferated because of the increasing availability of nutrients, particularly nitrogen and phosphorus (Figueroa-Gonzalez et al., 2020; Boubekri et al., 2021). As a source of carbon and energy for these bacteria in the rhizosphere, N-containing fertilizer can also encourage plant root development, resulting in larger production of root exudates (Zhu et al., 2016). Therefore, this implies that the fertilizer application increases the abundance of Saccharibacteria and Actinobacteria in the rhizosphere because of improved nutrient availability and root exudation. In contrast, the abundance of Verrucomicrobia and Acidobacteria were significantly reduced in the fertilized soil (Figure 1B, S1B) and the pattern was similarly found in several other crops including wheat, corn, soybeans, and rice (Wang et al., 2015; Singh et al., 2018; Kandel et al., 2019). These phyla thrive in low-nutrient environments, playing crucial roles in nutrient cycling, plant development, and health (Feng et al., 2019; Kalam et al., 2020; Bünger et al., 2020). Their ability to efficiently use limited nutrients suggests they are oligotrophs, potentially enhancing plant growth in nutrient-poor soil, as seen in their prevalent abundance in the unfertilized treatment (Figure 1B, S1B).

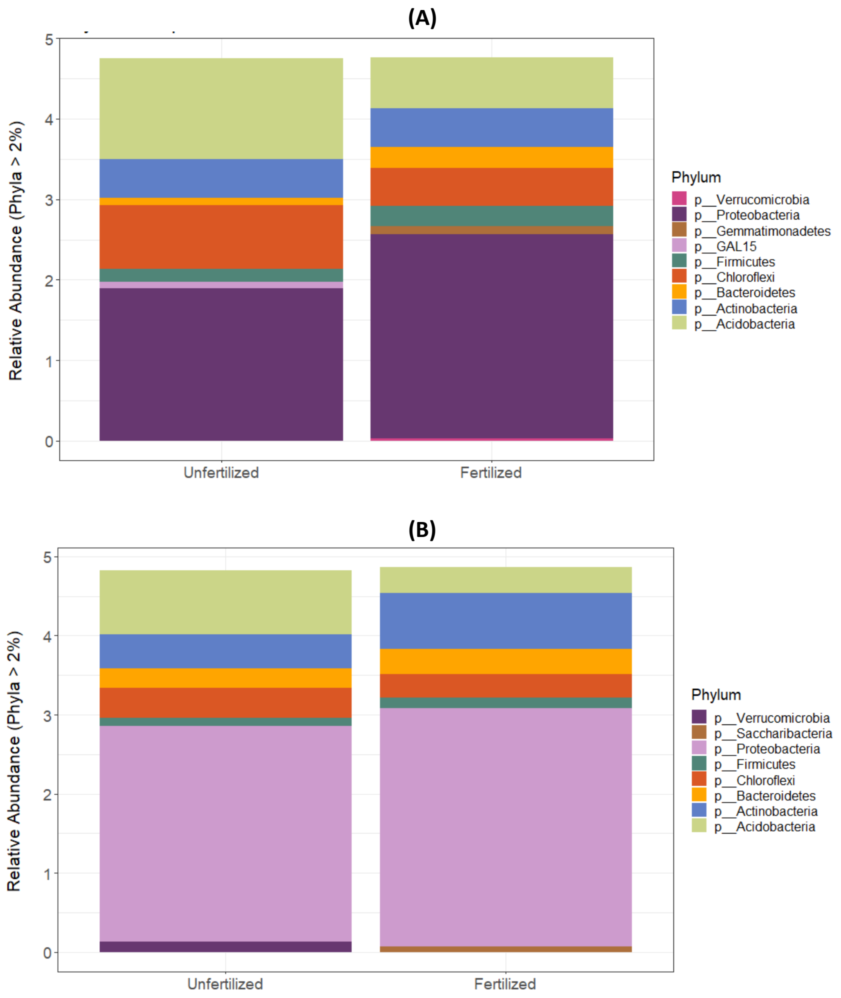

Figure 1. Relative abundance of bacterial phyla (> 2%) between unfertilized and fertilized soil in the (A) bulk soil and (B) rhizosphere

Reduced Bacterial Diversity Following the Chemical Fertilizer Application

The chemical fertilizer application significantly reduced the bacterial richness and diversity in the bulk soil and rhizosphere (Figure 2A, B) aligning with previous studies (Wang et al., 2018; Liu et al., 2020a; Chen et al., 2020; Semenov et al., 2020; Xu et al., 2020). This adverse impact, particularly on sensitive oligotrophs like Acidobacteria, suggests a potential early indicator of declining soil fertility due to agricultural activities (Feng et al., 2022). The fertilizer application also reduces soil organic matter, hindering bacterial growth while favoring antibiotic-producing bacteria and compromising community diversity and richness (Lin et al., 2019). Additionally, root exudates such as phenols and flavonoids also contribute to the rhizosphere's declining bacterial richness and diversity, as they contain allelopathic properties, releasing antibacterial chemicals that reduce microbial diversity (Wen et al., 2022; Kakar et al., 2023). Therefore, applying fertilizer can decrease bacterial richness and diversity in both bulk soil and the rhizosphere, signaling potential early signs of declining soil fertility. Root exudates, with allelopathic compounds, may contribute to reducing microbial diversity in this context.

Diversity loss due to nitrogen addition could also be due to the Resource Competition theory (Eliot, 2011). The existing evidence suggests that, similar to its impact on plant communities, the enhancement of dominant microbial species, possibly due to nitrogen additions, may contribute to diversity losses of subservient species through competitive exclusion for the resource (Wu et al., 2022). While the theory has been extensively investigated with plant diversity (Farrer et al., 2016; Wu et al., 2022), its application to microbial diversity requires further exploration to alleviate the species loss caused by nutrient enrichment and maintain the diversity of ecosystems.

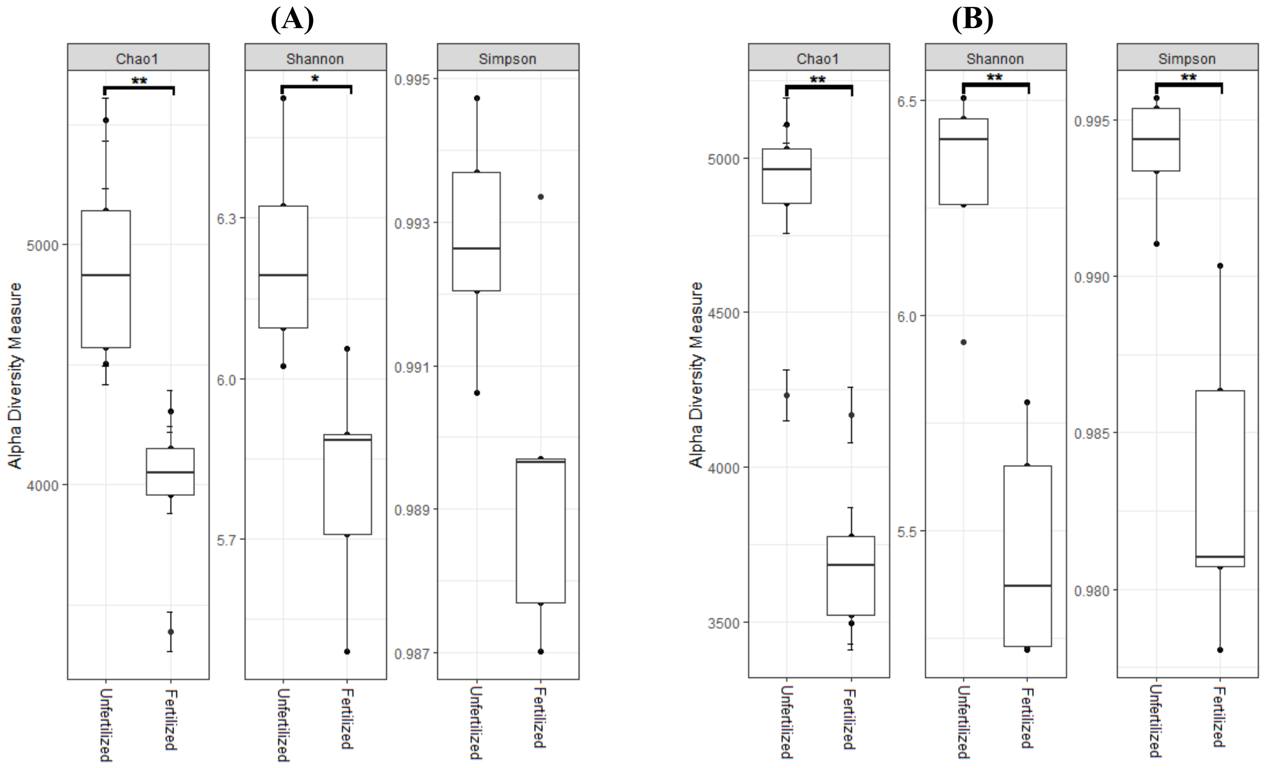

Figure 2. Box-whisker plots depicting bacterial richness (Chao1) and alpha diversity (Shannon and Simpson) between unfertilized and fertilized soil in the (A) bulk soil and (B) rhizosphere at the feature level. Statistical significance *p*-values were assessed by the Wilcoxon rank sum test. $*p < 0.05$, $**p < 0.01$, $***p < 0.001$

The PCoA analysis revealed no clear grouping between the soil types in the bulk soil, indicating that the treatment likely did not affect the bacterial composition (Figure 3A). Previous research has suggested that soil bacteria can be resilient to disturbances caused by chemical fertilizers (Čuhel et al., 2019). In contrast, a distinct, clear separation between the soil types was found in the rhizosphere, suggesting that the fertilizer application may have significantly impacted the bacterial community (Figure 3B). Exposure to nitrogen fertilizer has been observed to stimulate the growth of microbial genera possessing identifiable pathogenic characteristics (Zhou et al., 2016). Consequently, plant roots may actively choose certain microorganisms to inhabit the rhizosphere (Berendsen et al., 2012). This selective process ultimately attracts and supports beneficial microorganisms, enhancing nutrient absorption and counteracting potentially harmful taxa (Dennis et al., 2010). These findings support previous research indicating that chemical fertilizer can selectively affect bacterial populations in the rhizosphere (Zhao et al., 2022).

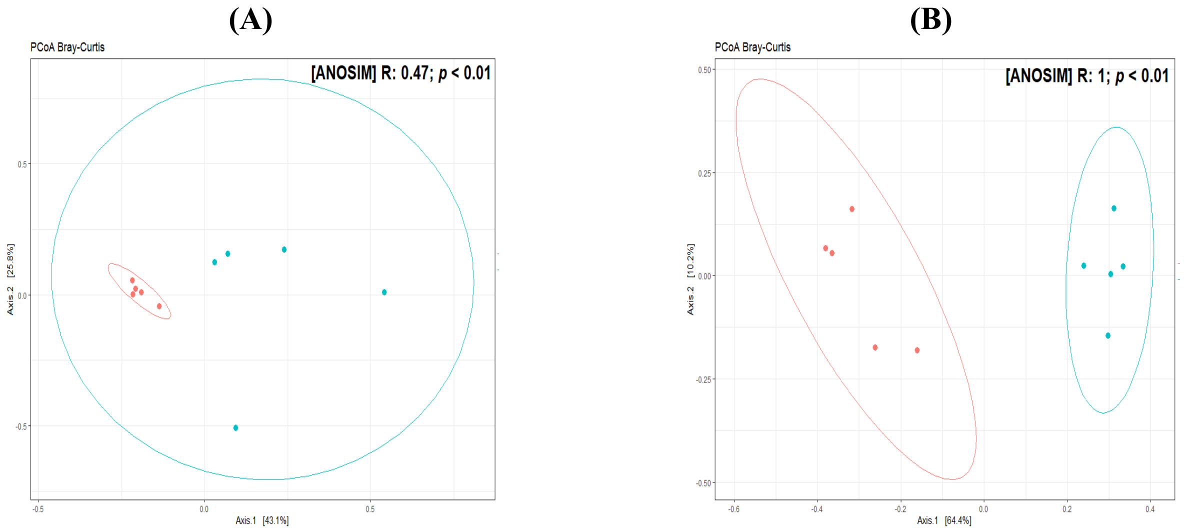

Figure 3. Principal Coordinate Analysis (PCoA) ordination based on the Bray-Curtis dissimilarity matrix of taxonomic bacterial community between the unfertilized and fertilized soil in the (A) bulk soil and (B) rhizosphere. Red indicates unfertilized soil whereas blue indicates NPK-treated soil

Potential Bacterial Biomarkers and Their Role in Soil Fertility and Plant Growth

The research findings suggest that Bryobacter, Candidatus Solibacter, and Acidothermus were more abundant in the unfertilized bulk soil (Figure 4A). Bryobacter and Candidatus Solibacter are known to play a role in mobilizing phosphate and reducing nitrite and nitrate, respectively, which are essential for plant development in nutrient-poor soil (Ward et al., 2009; Zhao et al., 2019; Zhang et al., 2019a). The prevalence of Acidothermus may indicate its potential role in combating pathogens, as suggested by research in tobacco and oil palm crops with limited nutrients (Barabote et al., 2009; Svenningsen et al., 2018; Gao et al., 2019; Goh et al., 2020). These findings could justify the prevalence of these bacteria in unfertilized soil, indicating their potential beneficial roles in promoting nutrient cycling and plant defense under nutrient limitations. In contrast, Mizugakiibacter and Castellaniella were found to be more abundant in the fertilized bulk soil (Figure 4A). These bacteria are involved in nitrogen cycling and can act as biocontrol agents by competing with harmful pathogens for nutrients (Kojima et al., 2014; Lin et al., 2018; Yin et al., 2022). Additionally, a previous study has shown that Castellaniella has the potential to degrade harmful pollutants like polychlorinated biphenyls (PCBs) (Su et al., 2019), suggesting they could be useful for bioremediation. These findings suggest that Mizugakiibacter and Castellaniella may be important in promoting plant growth, defending against pathogens, and maintaining a healthy soil ecosystem.

Meanwhile, in the rhizosphere, Rhizomicrobium, Acidibacter, Bradyrhizobium, Candidatus Solibacter, and Acidothermus were more abundant in the unfertilized soil (Figure 4B). These genera have been reported to symbiotically interact and promote plant growth by fixing nitrogen, producing plant hormones, and converting ammonium to nitrate (Antoun et al., 1998; Bárta et al., 2017; Arocha-Garza et al., 2017; Bei et al., 2018; Halifu et al., 2019; Liu et al., 2019). Thus, these beneficial bacteria could suggest a mutually beneficial relationship with the plant roots to support plant survival in a nutrient-limited environment. Applying chemical fertilizer in the rhizosphere enriched Proteobacteria members, including Mizugakiibacter, unidentified Xanthomonadaceae, and Castellaniella (Figure 4B). Previous studies have linked Mizugakiibacter and Castellaniella with nitrification and denitrification (Lin et al., 2018), while Xanthomonadaceae is recognized for its significant contribution to nitrogen, phosphorus, and carbon transformation in the soil (Li et al., 2017). Granulicella was also enriched by the fertilizer application (Figure 4B). Granulicella boosts plant growth by producing indole-3-acetic acid and siderophores (Kalam et al., 2020). Additionally, it carries genes involved in exopolysaccharide synthesis, enhancing soil structure and water retention (Rawat et al., 2012; Kalam et al., 2020; Morcillo & Manzanera, 2021). These findings demonstrate that the enriched genera may play important roles in maintaining soil fertility, nutrient cycling, and promoting plant development.

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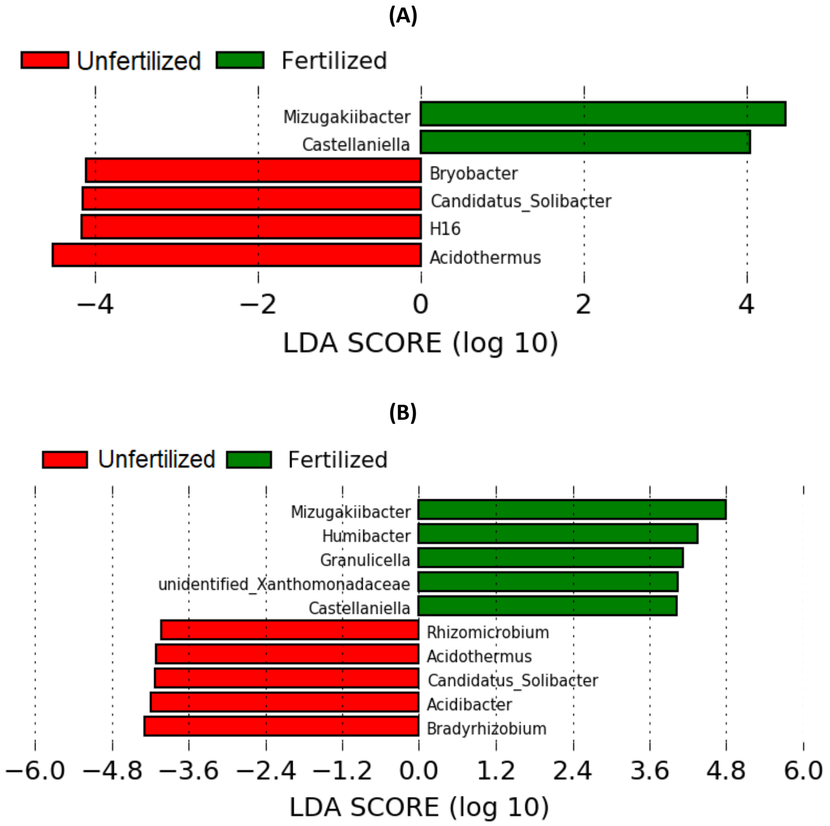

Figure 4. Linear discriminant analysis effect size (LEfSe) (LDA > 4) in the (A) bulk soil and (B) rhizosphere. Red indicates unfertilized soil-enriched taxa while green indicates fertilized soil-enriched taxa

Inferred Functional Responses of Bacterial Community Associated with Soil Fertility and Plant Growth

The fertilizer application enriched glycan biosynthesis and metabolism in the bulk soil and rhizosphere (Figure 5), which may suggest beneficial plant-microbe interactions. Rhizobacteria produce lipochitooligosaccharides, a glycan group, to distinguish between harmful pathogens and beneficial microorganisms in the plant-microbe relationship (Wanke et al., 2021). The enrichment of other secondary metabolites in the fertilized bulk soil and rhizosphere (Figure 5) may be linked to the increased abundance of Proteobacteria and Actinobacteria (Figure S1A) as these phyla produce various secondary metabolites such as siderophores, which help plants acquire iron, and indole acetic acid (IAA), a hormone that promotes root growth and enhances plant tolerance to stress (Duncan et al., 2021; Chhetri et al., 2021; Selim et al., 2021). These enhanced functions in response to the fertilizer application may improve the growth of oil palm seedlings, as evidenced by higher dry weight and height measurements (Table 2). Moreover, the constant enrichment of these functions in the bulk soil and rhizosphere may suggest a successful association between plants and beneficial microbes in the fertilized soil.

Carbohydrate metabolism was enriched in the unfertilized bulk soil (Figure 5A). Bacteria produce extracellular enzymes such as phosphatase and nitrate reductase to promote plant growth as part of carbohydrate metabolism (Ndabankulu et al., 2022). However, carbohydrate metabolism enrichment was shifted from the unfertilized bulk soil to the fertilized rhizosphere (Figure 5). It may be attributed to fertilization's increased availability of nutrients and root exudates in the rhizosphere. Chemical fertilizers enhance soil microbial carbon utilization, producing carbohydrates, carboxylic acids, and amino acids (Haiming et al., 2020). These products benefit plant growth, as carbohydrates provide structural support, carboxylic acids aid in photosynthesis, and amino acids serve as building blocks for plant tissue (Mallhi et al., 2019; Guo et al., 2021). Furthermore, the enrichment of carbohydrate metabolism by plant growth-promoting bacteria has increased plant biomass and nutrient uptake (Dhawi et al., 2017), which could explain the higher total carbon content and better seedling traits (Table 2) observed in this study.

For the unfertilized soil in the rhizosphere, amino acid metabolism, xenobiotics biodegradation and metabolism, metabolism of cofactors and vitamins, and metabolism of terpenoids and polyketides were enriched (Figure 5B). These metabolisms may be important for basic cellular functioning, defense mechanisms, nutrient cycling, and plant stress tolerance (Lewis et al., 2018). Rhizospheric bacteria enhance amino acid metabolism by extracting amino groups and converting them into ammonia, providing nitrogen for plant energy and growth. The xenobiotic degradation was enriched in the unfertilized soil (Figure 5B) as a fitness response to environmental stress. Xenobiotics are toxic substances, including heavy metals, insecticides, herbicides, and naturally occurring substances such as lignin and cellulose (Arora, 2020; Kathiravan & Gnanadoss, 2021). The bacteria can degrade them through enzymatic conversion into less toxic compounds or by storing them in their cells to prevent environmental harm (Kathiravan & Gnanadoss, 2021; Verma & Rawat, 2021).

Enriching cofactors and vitamins in the unfertilized rhizosphere (Figure 5B) may mitigate adverse effects in stressful environments (Lu et al., 2020; Loutet et al., 2021; Amjad et al., 2021). Based on the foliar physicochemical result (Table 2), significantly higher Fe and Zn as cofactors and vitamins in the unfertilized soil could potentially be utilized by the bacterial community via root exudation for cellular strategies (Merchant & Helmann, 2012). Lastly, the metabolism of terpenoids and polyketides was enriched in the unfertilized rhizosphere (Figure 5B), indicating that the bacterial community may serve in antimicrobial activities, plant growth promotion, yield increase, and stress alleviation (Piccoli & Bottini, 2013). These findings highlight the functional roles of bacteria in the rhizosphere in the absence of NPK fertilizer, particularly in nutrient cycling, plant stress response, and the reduction of environmental contaminants. However, these inferred observations are speculative because of database coverage restrictions and potential variations in microbial functions across various phases of plant growth (Aßhauer et al., 2015; Breitkreuz et al., 2021). When evaluating Tax4Fun results, care should be practiced, and experimental validation is advised for more accurate functional evaluations.

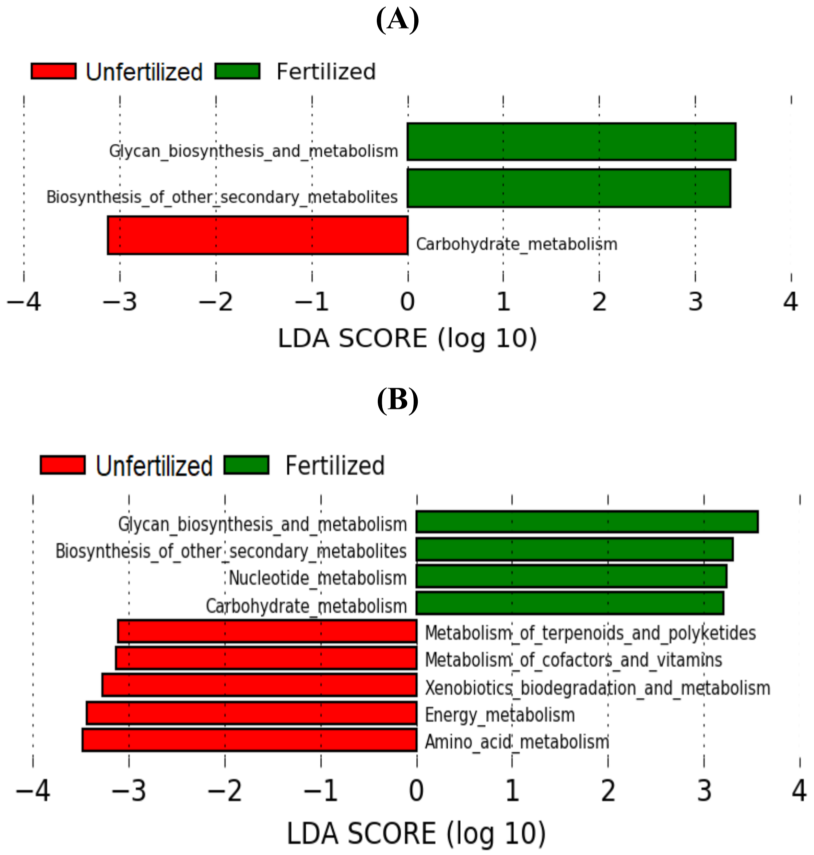

Figure 5. Linear discriminant analysis effect size (LEfSe) of inferred bacterial functions (LDA > 2) using Tax4Fun in the (A) bulk soil and (B) rhizosphere. Red indicates unfertilized soil-enriched function while green indicates the fertilized soil-enriched function

The Chemical Fertilizer Application Reduced Bacterial Network Complexity

The complexity of the bacterial networks was analyzed using topological data (Qiu et al., 2021; Price et al., 2021; Yang et al., 2021). The fertilizer application reduced the bacterial network complexity in the bulk soil and rhizosphere compared to the unfertilized soil (Table 3). Chemical fertilizer addition decreased bacterial diversity (Figure 2A), which could further simplify the complexity of species co-occurrence and redundancy of bacterial interaction (Yu et al., 2019). Bacteria may compete for available resources from fertilizer and root exudates, which causes some bacteria to thrive better than others (McNear, 2013). In contrast, the unfertilized soil encompassed more intricate bacterial networks in the bulk soil and rhizosphere (Table 3). This complexity may be linked to higher diversity (Figure 2) in nutrient-limited ecosystems through feedback processes related to nutrient recycling (Aerts & Chapin, 1999). The trend of network complexity can be supported by the Stress Gradient hypothesis, where microbial interactions become increasingly important in response to low nutrient availability and extreme environmental conditions (Bertness & Callaway, 1994; Mandakovic et al., 2023).

Table 3. The topological properties of bacterial in the bulk soil and rhizosphere

Summary Statistic	Bulk Soil		Rhizosphere	
	C	F	C	F
Number of nodes	69	23	112	47
Number of edges	68	36	267	42
Positive correlation (%)	52.94	100	73.78	52.38
Negative correlation (%)	47.06	0	26.22	47.62
Avg. number of neighbours	1.971	3.13	4.768	1.787
Network diameter	3	1	2	2
Network radius	1	1	1	1
Characteristic path length	1.284	1	1.187	1.256
Clustering coefficient	0.199	0.37	0.445	0.185
Network density	0.014	0.071	0.021	0.019
Connected components	21	7	18	16

C – Unfertilized, F – Fertilized

The potential association between the bacterial keystones and the network members is further determined in the context of plant growth-promotion. An Acidobacteria member, 11-24 was the keystone taxa in unfertilized bulk soil and formed positive correlations with Proteobacteria members (Figure 6A), yet literature on this genus (11-24) is limited. At the phylum level, Acidobacteria breaks down various complex compounds like carbohydrates, amino acids, and alcohols which are subsequently used by Proteobacteria, aiding in the cycling of nitrogen, phosphorus, and sulfur in ecosystems. (Ward et al., 2009; Belova et al., 2018; Zhou et al., 2020; Song et al., 2021; Berza et al., 2022). In the unfertilized rhizosphere, a Planctomycetes member (Gemmata) was a key player and formed positive correlations with the genera belonging to the Actinobacteria, Bacteroidetes, Proteobacteria, and Verrucomicrobia (Figure 7). These bacterial phyla thrive in chitin-rich environments, which can be found in fungal cell walls (Zegeye et al., 2019). They play a crucial role in the plant's defense system by breaking down the chitin-based cell walls of pathogenic fungi (Esperschütz et al., 2011; Ren et al., 2015; Kramer et al., 2016), thereby cooperating within the network to protect the seedlings in nutrient-poor soil.

In the fertilized bulk soil, Paenibacillus and Nitrospira formed a positive correlation (Figure 6B). Paenibacillus could convert nitrogen into ammonia, which is further converted into nitrate by Nitrospira for plant utilization (Liu et al., 2019; Sakoula et al., 2021). Nitrospira and Sporosarcina exhibited a positive correlation, suggesting a potential cooperative relationship within the nitrogen cycle. Nitrospira is involved in nitrification, whereas Sporosarcina plays a crucial role by producing urease, an enzyme essential for nitrogen cycling (Zhang et al., 2019b; Ma et al., 2020). These findings suggest that chemical fertilizers could positively impact these two genera, promoting soil health and optimizing nutrient cycling. Gordonia, a genus belonging to Actinobacteria, was found as a network keystone in the rhizosphere of fertilized treatment and formed a positive association with Lysinibacillus (Figure 8). Gordonia is involved in nitrogen fixation, converting atmospheric nitrogen into ammonia, whereas Lysinibacillus has genes related to ammonia conversion, specifically ammonia monooxygenase and ammonium transporter, suggesting its involvement in nitrification. This may imply that both bacteria likely cooperate in the nitrogen cycle, with Gordonia fixing nitrogen and Lysinibacillus converting ammonia into nitrite and nitrate for the plants' benefit (Gomez-Garzon et al., 2017).

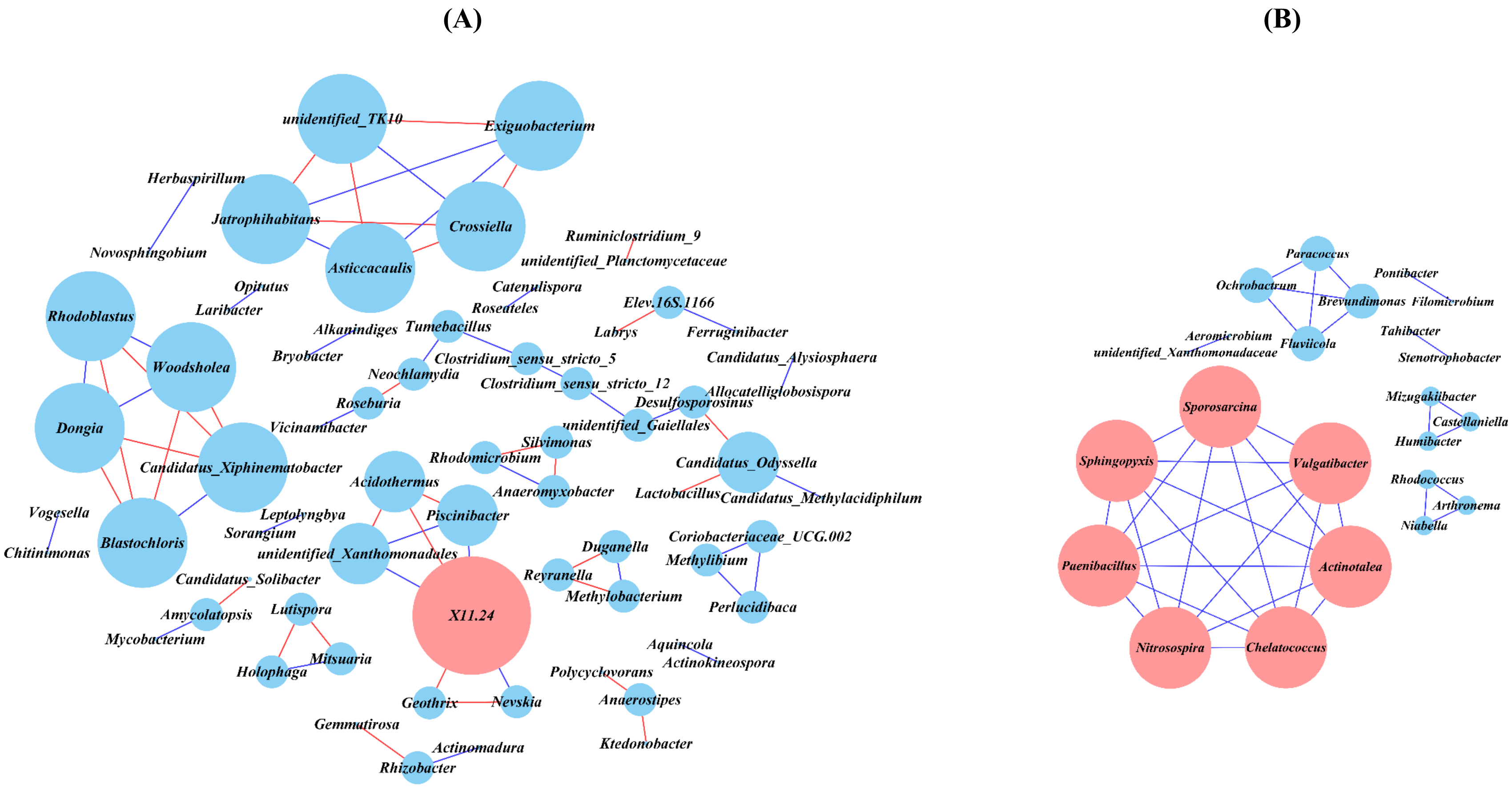

Figure 6. Bacterial co-occurrence network of (A) unfertilized and (B) fertilized soil in the bulk soil. The connection between genera (LDA > 2) is visualized based on the Spearman coefficient (r > ±0.7) and significant ($p < 0.01$) correlation. The node size is proportioned to the number of connections (degree) and the edge width (weight) is proportioned to the r-value. The edge is colored blue and red for positive and negative correlation, respectively

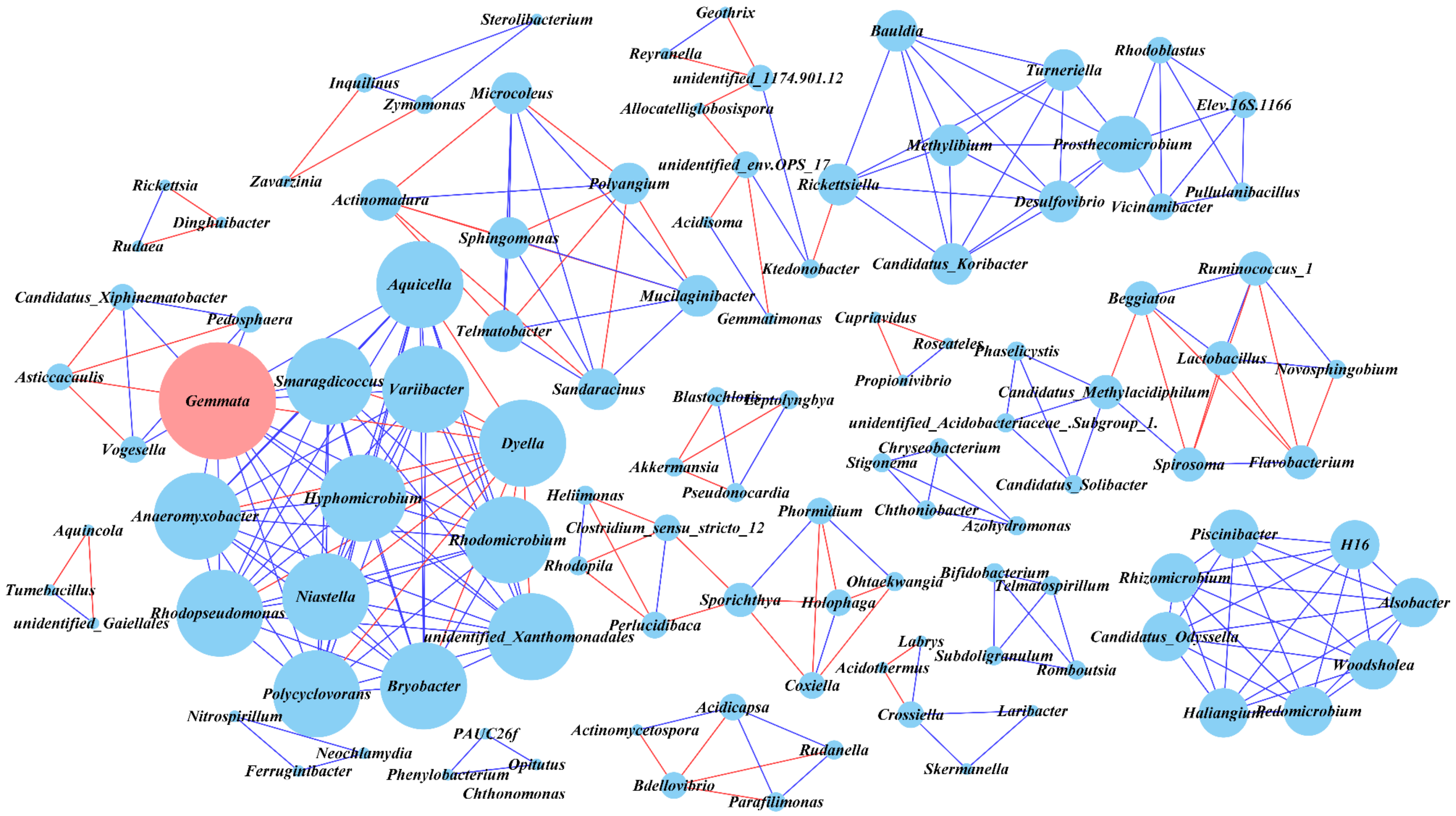

Figure 7. Bacterial co-occurrence network of the unfertilized soil in the rhizosphere. The connection between genera (LDA > 2) is visualized based on the Spearman coefficient (r > ±0.7) and significant ($p < 0.01$) correlation. The node size is proportioned to the number of connections (degree) and the edge width (weight) is proportioned to the r-value. The edge is colored blue and red for positive and negative correlation, respectively

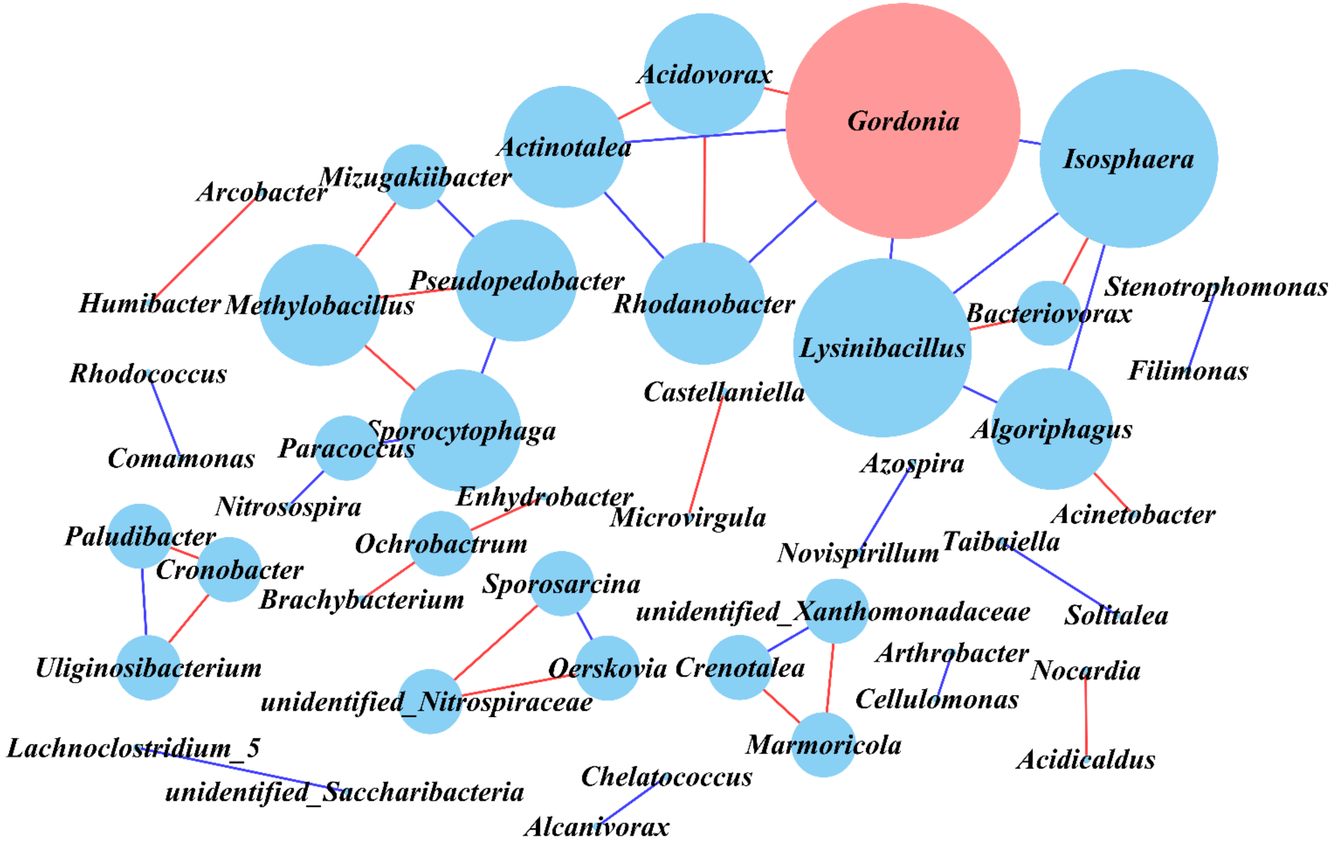

Figure 8. Bacterial co-occurrence network of the fertilized soil in the rhizosphere. The connection between genera (LDA > 2) is visualized based on the Spearman coefficient (r > ±0.7) and significant ($p < 0.01$) correlation. The node size is proportioned to the number of connections (degree) and the edge width (weight) is proportioned to the r-value. The edge is colored blue and red for positive and negative correlation, respectively

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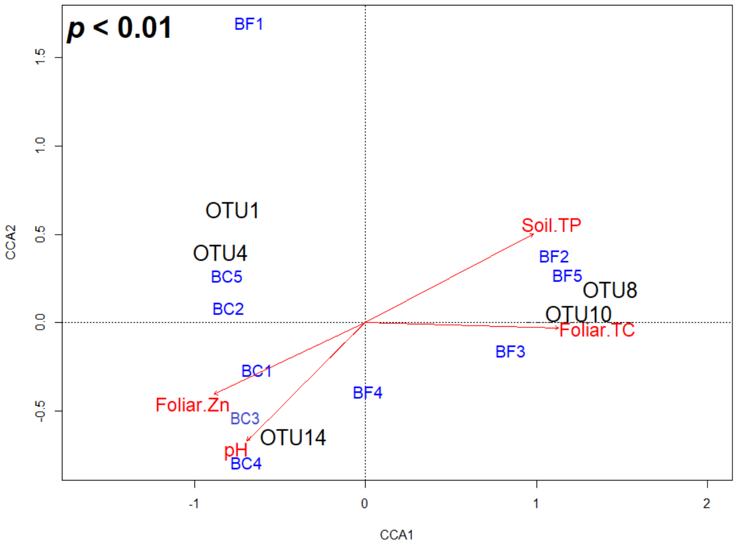
Significant Environmental Factors Drove the Abundance of Potentially Beneficial Biomarkers

The relationship between the potential biomarkers (LDA > 4) with significant soil physicochemical parameters and foliar nutrient contents was further investigated (Figure 9). In the unfertilized bulk soil, Acidothermus (OTU14) was positively correlated with pH (Figure 9A), suggesting that lower soil pH (Table 1) may drive the genus' abundance as proposed (Kim et al., 2016; Ogola et al., 2021; Ren et al., 2021). The decreased soil pH causes Mg to be more soluble, yet appears to diverge from the anticipated outcome with significantly lower Mg in the unfertilized soil (Table 1). As proposed in Liebig's Law of the Minimum, the plant's growth will be limited by the scarcest nutrient (van der Ploeg et al., 1999), hence suggesting that Mg may be further utilized by the seedlings rather than stored in the soil. Additionally, Castellaniella (OTU10) in the fertilized bulk soil was positively correlated with soil TP (Figure 9A), suggesting that soil phosphorus may influence the genus's abundance. Phosphate helps Castellaniella (OTU10), a denitrifying bacterium, by stabilizing pH, boosting their activity, causing zinc phosphate to form, and lessening the impact of ZnO nanoparticles on interactions with extracellular polymeric substances. This positively affects the abundance and activity of denitrifying bacteria (Cheng et al., 2019). This may explain its dependence on soil TP.

In terms of the rhizosphere, Acidothermus (OTU12) and Bradyrhizobium (OTU13) were strongly associated with pH in the unfertilized soil (Figure 9B). Acidothermus (OTU12) may be driven by an acidic environment and is known to break down plant tissues, leading to increased organic matter and nutrients available to plants (Ren et al., 2021; Ogola et al., 2021). Bradyrhizobium (OTU13) can adapt to acidic soil, despite generally not thriving in low pH environments (Jaiswal & Dakora, 2019), and effectively fix nitrogen (Holland et al., 2023). It also produces a siderophore that improves iron availability for plants and inhibits pathogens (Kumawat et al., 2019; Seraj et al., 2020). This may explain the higher foliar Fe content (Table 2), promoting plant growth and defense in nutrient-deficient conditions. In addition, Mizugakiibacter (OTU16) in the rhizosphere was positively correlated with fertilized soil TP (Figure 9B), and this pattern was consistent with a prior study (Li et al., 2021). During the hydrolysis of P-containing substrates, Mizugakiibacter (OTU16) produces phosphatase to release orthophosphates for utilization by soil biota and plants. (Kojima et al. 2014; Dotaniya et al. 2019). This implies that their abundance was influenced by the availability of phosphate and may aid to solubilize phosphate for plant development.

(A)



(B)

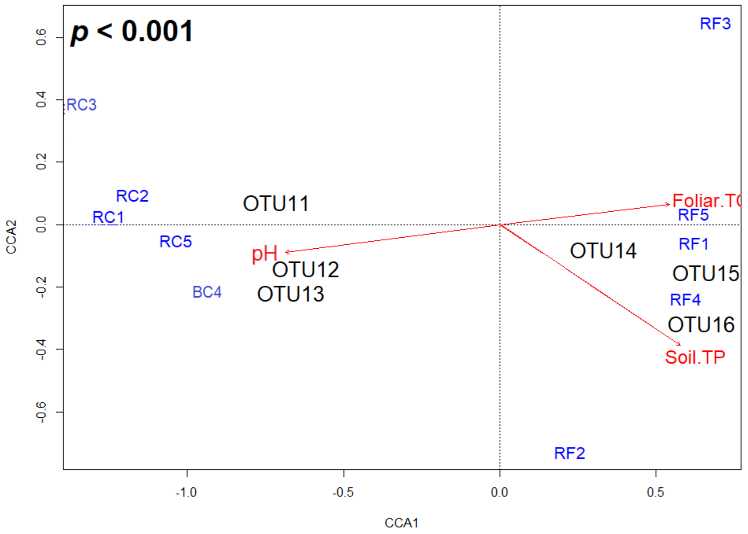


Figure 9. Canonical correspondence analysis (CCA) shows a correlation between significant physicochemical parameters and bacterial biomarkers (LDA > 4) for (A) bulk soil and (B) rhizosphere. The closeness of the points indicates the similarity of the samples, the arrowhead of variables shows a degree of association, and the length represents strength that explains the biomarker dispersion observed. B – Bulk soil, R – Rhizosphere, C – Unfertilized, F – Fertilized

4. Conclusion

While fertilizer application increased soil nutrient availability, it did not necessarily produce proportional increases in foliar nutrient concentrations. The abundance of Proteobacteria, Saccharibacteria, and Actinobacteria significantly increased in response to the fertilizer application, suggesting their succession as dominant phyla due to the nutrient-rich conditions. However, the fertilizer application also reduced bacterial diversity in the soil and root systems, especially in sensitive bacterial groups like Acidobacteria, indicating potential early indicators of declining soil fertility due to agricultural activities. The consistent enrichment of *Mizugakiibacter* and *Castellaniella* in the fertilized bulk soil and rhizosphere may suggest potential capabilities to utilize the nutrients present in the fertilizer. Current findings also revealed a higher number of genera belonging to Proteobacteria (*Rhizomicrobium*, *Bradyrhizobium*), Actinobacteria (*Acidothermus*), and Acidobacteria (*Candidatus Solibacter*, *Bryobacter*) compared to the fertilized soil, suggesting that the unfertilized soil may represent an early successional stage in bacterial community development in the absence of fertilizer application. Moreover, the fertilizer application enhanced the enrichment of specific metabolic processes in bacteria, such as glycan biosynthesis, nucleotide metabolism, and carbohydrate metabolism, which likely contribute to improved plant-microbe interactions and plant growth in the fertilized treatment. Alternatively, the enriched bacterial functions in the unfertilized soil may suggest cellular functioning strategies.

Regarding network analysis, the fertilizer application resulted in a simpler bacterial network. However, it can also promote positive interactions and contribute to nutrient cycling. In contrast, the unfertilized soil exhibits more complex networks, potentially associated with nutrient limitation and the recruitment of beneficial bacteria for growth support. The CCA demonstrated that the presence of *Acidothermus* and *Castellaniella* was positively associated with specific nutrient levels in the unfertilized soil, suggesting their potential role in nutrient cycling and plant health. Acidothermus, Bradyrhizobium, and Mizugakiibacter also showed associations with different nutrient conditions in the fertilized treatment, indicating their potential contributions to nutrient availability and plant growth. Understanding the impact of fertilizer application on the bacterial community composition, diversity, functionality, and networks will aid in promoting the seedlings' growth. Future studies should focus on optimizing chemical fertilizer applications to address the presence of pathogens and highlight the enrichment of beneficial taxa for sustainable agriculture practices.

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6. References

Abhauer, K. P., Wemheuer, B., Daniel, R., & Meinicke, P. (2015). Tax4Fun: predicting functional profiles from metagenomic 16S rRNA data. *Bioinformatics, 31*(17), 2882-2884. https://doi.org/10.1093/bioinformatics/btv287

Aerts, R., & Chapin III, F. S. (1999). The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns.

Advances in Ecological Research, 30, 1-67. https://doi.org/10.1016/S0065-2504(08)60016-1

Ahmed, W., Jing, H., Kaillou, L., Qaswar, M., Khan, M. N., Jin, C., Geng, S., Qinghai, H., Yiren, L., Guangrong, L., Mei, S., Chao, L., Dongchu, L., Ali, S., Normatov, Y., Mehmood, S., & Zhang, H. (2019). Changes in phosphorus fractions associated with soil chemical properties under long-term organic and inorganic fertilization in paddy soils of southern China. *PloS One, 14*(5), 1-17. https://doi.org/10.1371/journal.pone.0216881

Aizat, A. M., Roslan, M. K., Sulaiman, W. N. A., & Karam, D. S. (2014). The relationship between soil pH and selected soil properties in 48 years logged-over forest. *International Journal of Environmental Sciences, 4*(6), 1129-1140. https://doi.org/10.6088/ijes.2014040600004

Amjad, S. F., Mansoora, N., Yaseen, S., Kamal, A., Butt, B., Matloob, H., Alamri, S. A. M., Alrumman, S. A., Eid, E. M., & Shahbaz, M. (2021). Combined use of endophytic bacteria and pre-sowing treatment of thiamine mitigates the adverse effects of drought stress in wheat (*Triticum aestivum* L.) cultivars. *Sustainability*, *13*(12), 6582. https://doi.org/10.3390/su13126582

Angelina, E., Papatheodorou, E. M., Demirtzoglou, T., & Monokrousos, N. (2020). Effects of *Bacillus subtilis* and *Pseudomonas fluorescens* inoculation on attributes of the lettuce (*Lactuca sativa* L.) soil rhizosphere microbial community: The role of the management system. *Agronomy*, *10*(9), 1428. https://doi.org/10.3390/agronomy10091428

Antoun, H., Beauchamp, C. J., Goussard, N., Chabot, R., & Lalande, R. (1998). Potential of *Rhizobium* and *Bradyrhizobium* species as plant growth promoting rhizobacteria on non-legumes: effect on radishes (*Raphanus sativus* L.). In *Molecular Microbial Ecology of The Soil* (pp. 57-67). Springer, Dordrecht. https://doi.org/10.1007/978-94-017-2321-3_5

Arifin, I., Hanafi, M. M., Roslan, I., Ubaydah, M. U., Abd Karim, Y., Tui, L. C., & Hamzah, S. (2022). Responses of irrigated oil palm to nitrogen, phosphorus and potassium fertilizers on clayey soil. *Agricultural Water Management, 274*, 107922. https://doi.org/10.1016/j.agwat.2022.107922

Arocha-Garza, H. F., Canales-Del Castillo, R., Eguiarte, L. E., Souza, V., & De la Torre-Zavala, S. (2017). High diversity and suggested endemicity of culturable Actinobacteria in an extremely oligotrophic desert oasis. *PeerJ, 5*, 1-21. https://doi.org/10.7717/peerj.3247

Arora, P. K. (2020). Bacilli-mediated degradation of xenobiotic compounds and heavy metals. *Frontiers in Bioengineering and Biotechnology*, *8*, 570307. https://doi.org/10.3389/fbioe.2020.570307

Bai, L., Wang, Y., Li, Y., Zhang, X., Lu, Z., Zhang, D., Sun, F., & Zhao, X. (2022). Changes in the Microbial Community in Maize (*Zea mays* L.) Root Spatial Structure Following Short-Term Nitrogen Application. *ACS Omega*, *8*(1), 208–218. https://doi.org/10.1021/acsomega.2c01711

Banerjee, S., Schlaeppi, K., & van der Heijden, M. G. (2018). Keystone taxa as drivers of microbiome structure and functioning. *Nature Reviews Microbiology, 16*(9), 567-576. https://doi.org/10.1038/s41579-018-0024-1

Barabote, R. D., Xie, G., Leu, D. H., Normand, P., Necsulea, A., Daubin, V., Médigue, C., Adney, W. S., Xu, X. C., Lapidus, A., Parales, R. E., Detter, C., Pujic, P., Bruce, D., Lavire, C., Challacombe, J. F., Brettin, T. S., & Berry, A. M. (2009). Complete genome of the cellulolytic thermophile *Acidothermus cellulolyticus* 11B provides insights into its ecophysiological and evolutionary adaptations. *Genome Research, 19*(6), 1033-1043. http://www.genome.org/cgi/doi/10.1101/gr.084848.108

Barta, J., Tahovská, K., Šantrůčková, H., & Oulehle, F. (2017). Microbial communities with distinct denitrification potential in spruce and beech soils differing in nitrate leaching. *Scientific Reports, 7*(1), 1-15. https://doi.org/10.1038/s41598-017-08554-1

Bei, S., Zhang, Y., Li, T., Christie, P., Li, X., & Zhang, J. (2018). Response of the soil microbial community to different fertilizer inputs in a wheat-maize rotation on a calcareous soil. *Agriculture, Ecosystems & Environment, 260*, 58-69. https://doi.org/10.1016/j.agee.2018.03.014

Belova, S. E., Ravin, N. V., Pankratov, T. A., Rakitin, A. L., Ivanova, A. A., Beletsky, A. V., Damste, J. S. S., & Dedysh, S. N. (2018). Hydrolytic capabilities as a key to environmental success: chitinolytic and cellulolytic Acidobacteria from acidic sub-arctic soils and boreal peatlands. *Frontiers in Microbiology*, *9*, 2775. https://doi.org/10.3389/fmicb.2018.02775

Berendsen, R. L., Pieterse, C. M., & Bakker, P. A. (2012). The rhizosphere microbiome and plant health. *Trends in plant science, 17*(8), 478-486. https://doi.org/10.1016/j.tplants.2012.04.001

Bertness, M. D., & Callaway, R. (1994). Positive interactions in communities. *Trends in Ecology & Evolution, 9*(5), 191-193.

Berza, B., Sekar, J., Vaiyapuri, P., Pagano, M. C., & Assefa, F. (2022). Evaluation of inorganic phosphate solubilizing efficiency and multiple plant growth promoting properties of endophytic bacteria isolated from root nodules *Erythrina brucei. BMC Microbiology*, *22*(1), 276. https://doi.org/10.1186/s12866-022-02688-7

Bolyen, E., Rideout, J. R., Dillon, M. R., Bokulich, N. A., Abnet, C. C., Al-Ghalith, G. A., Alexander, H., Alm, E. J., Arumugam, M., Asnicar, F., Bai, Y., Bisanz, J. E., Bittinger, K., Brejnrod, A., Brislawn, C. J., Brown, C. T., Callahan, B. J., Caraballo-Rodríguez, A. M., Chase, J., Cope, E. K., Da Silva, R., Diener, C., Dorrestein, P. C., Douglas, G. M., Durall, D. M., Duvallet, C., Edwardson, C. F., Ernst, M., Estaki, M., Fouquier, J., Gauglitz, J. M., Gibbon, S. M., Gibson, D. L., Gonzalez, A., Gorlick, K., Guo, J., Hillman, B., Holmes, S., Holste, H., Huttenhower, C., Huttley, G. A., Janssen, S., Jarmusch, A. K., Jiang, L., Kaehler, B. D., Kang, K. B., Keefe, C. R., Keim, P., Kelley, S. T., Knights, D., Koester, I., Kosciolek, T., Kreps, J., Langille, M. G. I., Lee, J., Ley, R., Liu, Y. X., Loftfield, E., Lazupone, C., Maher, M., Marotz, C., Martin, B. D., McDonald, D., Mclver, L. J., Melnik, A. V., Metcalf, J. L., Morgan, S. C., Morton, J. T., Naimey, A. T., Navas-Molina, J. A., Nothias, L. F., Orchanian, S. B., Pearson, T., Peoples, S. L., Petras, D., Preuss, M. L., Pruesse, E., Rasmussen, L. B., Rivers, A., Robeson II, M. S., Rosenthal, P., Segata, N., Shaffer, M., Shiffer, A., Sinha, R., Song, S. J., Spear, J. R., Swafford, A. D., Thompson, L. R., Torres, P. J., Trinh, P., Tripathi, A., Turnbaugh, P., J., Ul-Hasan, S., van der Hooft, J. J. J., Vargas, F., Vázquez-Baeza, Y., Vogtmann, E., von Hippel, M., Walters, W., Wan, Y., Wang, M., Warren, J., Weber, K. C., Williamson, C. H. D., Willis, A. D., Xu, Z., Z., Zaneveld, J. R., Zhang, Y., Zhu, Q., Knight, R., & Caporaso, J. G. (2019). Reproducible, interactive, scalable and extensible microbiome data science using QIIME 2. *Nature Biotechnology, 37*(8), 852-857. https://doi.org/10.1038/s41587-019-0252-6

Boubekri, K., Soumare, A., Mardad, I., Lyamlouli, K., Hafidi, M., Ouhdouch, Y., & Kouisni, L. (2021). The screening of potassium- and phosphate-solubilizing actinobacteria and the assessment of their ability to promote wheat growth parameters. *Microorganisms, 9*(3), 470. https://doi.org/10.3390/microorganisms9030470

Breitkreuz, C., Heintz-Buschart, A., Buscot, F., Wahdan, S. F. M., Tarkka, M., & Reitz, T. (2021). Can we estimate functionality of soil microbial communities from structure-derived predictions? A reality test in agricultural soils. *Microbiology Spectrum, 9*(1), 10-1128. https://doi.org/10.1128/Spectrum.00278-21

Bright, J. P., Baby, A. S., Thankappan, S., George, A. S., Maheshwari, H. S., Nataraj, R., Judson, S., & Binodh, A. K. (2022). Potassium releasing bacteria for unlocking soil potassium-a way forward for judicious use of chemical fertilizers. *International Journal of Plant & Soil Science, 34*, 49-61. https://doi.org/10.9734/IJPSS/2022/v34i1931088

Bunger, W., Jiang, X., Müller, J., Hurek, T., & Reinhold-Hurek, B. (2020). Novel cultivated endophytic Verrucomicrobia reveal deep-rooting traits of bacteria to associate with plants. *Scientific Reports, 10*(1), 8692. https://doi.org/10.1038/s41598-020-65277-6

Caradonia, F., Ronga, D., Catellani, M., Giaretta Azevedo, C. V., Terrazas, R. A., Robertson-Albertyn, S., Francia, E., & Bulgarelli, D. (2019). Nitrogen fertilizers shape the composition and predicted functions of the microbiota of field-grown tomato plants. *Phytobiomes Journal, 3*(4), 315-325. https://doi.org/10.1094/PBIOMES-06-19-0028-R

Chen, L., Li, F., Li, W., Ning, Q., Li, J., Zhang, J., Ma, D., & Zhang, C. (2020). Organic amendment mitigates the negative impacts of mineral fertilization on bacterial communities in Shajiang black soil. *Applied Soil Ecology*, *150*, 103457. https://doi.org/10.1016/j.apsoil.2019.103457

Cheng, Y. F., Zhang, Z. Z., Li, G. F., Zhu, B. Q., Zhang, Q., Liu, Y. Y., Zhu, W. Q., Fan, N. S., & Jin, R. C. (2019). Effects of ZnO nanoparticles on high-rate denitrifying granular sludge and the role of phosphate in toxicity attenuation. *Environmental Pollution*, *251*, 166-174. https://doi.org/10.1016/j.envpol.2019.04.138

Chhetri, G., Kang, M., Kim, J., Kim, I., So, Y., & Seo, T. (2021). *Sphingosinicella flava* sp. nov., indole acetic acid producing bacteria isolated from maize field soil. *International Journal of Systematic and Evolutionary Microbiology, 71*(10), 005038. https://doi.org/10.1099/ijsem.0.005038

Chong, J., Liu, P., Zhou, G., & Xia, J. (2020). Using MicrobiomeAnalyst for comprehensive statistical, functional, and meta-analysis of microbiome data. *Nature Protocols, 15*(3), 799-821. https://doi.org/10.1038/s41596-019-0264-1

Csardi, G., & Nepusz, T. (2006). The igraph software package for complex network research. *InterJournal Complex Systems, 1695*(5), 1–9. http://igraph.sf.net

Cuhel, J., Malý, S., & Královec, J. (2019). Shifts and recovery of soil microbial communities in a 40-year field trial under mineral fertilization. Pedobiologia, 77, 150575. https://doi.org/10.1016/j.pedobi.2019.150575

Dai, Z., Su, W., Chen, H., Barberán, A., Zhao, H., Yu, M., Yu, L., Brookes, P. C., Schadt, C. W., Chang, S. X., & Xu, J. (2018). Long-term nitrogen fertilization decreases bacterial diversity and favors the growth of Actinobacteria and Proteobacteria in agro-ecosystems across the globe. *Global Change Biology*, *24*(8), 3452-3461. https://doi.org/10.1111/gcb.14163

David, D. J. (1960). The determination of exchangeable sodium, potassium, calcium and magnesium in soils by atomic-absorption spectrophotometry. *Analyst, 85*(1012), 495-503.

Dedysh, S. N., & Damsté, J. S. S. (2018). Acidobacteria. *eLS*, 1-10. https://doi.org/10.1002/9780470015902.a0027685

Dennis, P. G., Miller, A. J., & Hirsch, P. R. (2010). Are root exudates more important than other sources of rhizodeposits in structuring rhizosphere bacterial communities?. *FEMS Microbiology Ecology, 72*(3), 313-327. https://doi.org/10.1111/j.1574-6941.2010.00860.x

DeSantis, T. Z., Hugenholtz, P., Larsen, N., Rojas, M., Brodie, E. L., Keller, K., Huber, T., Dalevi, D., Hu, P., & Andersen, G. L. (2006). Greengenes, a chimera-checked 16S rRNA gene database and workbench compatible with ARB. *Applied and Environmental Microbiology, 72*(7), 5069-5072. https://doi.org/10.1128/AEM.03006-05

Dhawi, F., Datta, R., & Ramakrishna, W. (2017). Proteomics provides insights into biological pathways altered by plant growth promoting bacteria and arbuscular mycorrhiza in sorghum grown in marginal soil. *Biochimica et Biophysica Acta (BBA)-Proteins and Proteomics, 1865*(2), 243-251. https://doi.org/10.1016/j.bbapap.2016.11.015

Dotaniya, M. L., Aparna, K., Dotaniya, C. K., Singh, M., & Regar, K. L. (2019). Role of soil enzymes in sustainable crop production. In *Enzymes in Food Biotechnology* (pp. 569-589). Academic Press. https://doi.org/10.1016/B978-0-12-813280-7.00033-5

Duncan, T. R., Werner-Washburne, M., & Northup, D. E. (2021). Diversity of Siderophore-Producing Bacterial Cultures From Carlsbad Caverns National Park (Ccnp) Caves, Carlsbad, New Mexico. *Journal of Cave and Karst Studies: the National Speleological Society bulletin*, *83*(1), 29-43. https://doi.org/10.4311%2F2019es0118

Edgar, R. C. (2013). UPARSE: highly accurate OTU sequences from microbial amplicon reads. *Nature Methods, 10*(10), 996-998. https://doi.org/10.1038/nmeth.2604

Eliot, C. H. (2011). Competition theory and channeling explanation. *Philosophy, Theory, and Practice in Biology, 3* (20130604), 1-16. https://doi.org/10.3998/ptb.6959004.0003.001

Esperschütz, J., Pérez-de-Mora, A., Schreiner, K., Welzl, G., Buegger, F., Zeyer, J., Hagedorn, F., Munch, J. C., & Schloter, M. (2011). Microbial food web dynamics along a soil chronosequence of a glacier forefield. *Biogeosciences, 8*(11), 3283-3294. https://doi.org/10.5194/bg-8-3283-2011

Farrer, E. C., & Suding, K. N. (2016). Teasing apart plant community responses to N enrichment: the roles of resource limitation, competition and soil microbes. Ecology letters, 19(10), 1287-1296. https://doi.org/10.1111/ele.12665

Feng, C., Jia, J., Wang, C., Han, M., Dong, C., Huo, B., Li, D., & Liu, X. (2019). Phytoplankton and bacterial community structure in two chinese lakes of different trophic status. *Microorganisms, 7*(12), 621. https://doi.org/10.3390/microorganisms7120621

Feng, Y., Delgado-Baquerizo, M., Zhu, Y., Han, X., Han, X., Xin, X., Li, W., Guo, Z., Dang, T., Li, C., Zhu, B., Cai, Z., Li, D., & Zhang, J. (2022). Responses of soil bacterial diversity to fertilization are driven by local environmental context across China. *Engineering*, *12*, 164-170. https://doi.org/10.1016/j.eng.2021.09.012

Figueroa-Gonzalez, P. A., Bornemann, T. L., Adam, P. S., Plewka, J., Révész, F., Von Hagen, C. A., Táncsics, A., & Probst, A. J. (2020). Saccharibacteria as organic carbon sinks in hydrocarbon-fueled communities. *Frontiers in Microbiology, 11*, 587782. https://doi.org/10.3389/fmicb.2020.587782

Gao, L., Wang, R., Gao, J., Li, F., Huang, G., Huo, G., Liu, Z., Tang, W., & Shen, G. (2019). Analysis of the structure of bacterial and fungal communities in disease suppressive and disease conducive tobacco-planting soils in China. *Soil Research, 58*(1), 35-40. https://doi.org/10.1071/SR19204

Goecks, J., Nekrutenko, A., Taylor, J., Afgan, E., Ananda, G., Baker, D., Blankenberg, D., Chakrabarty, R., Coraor, N., Goecks, J., Von Kuster, G., Lazarus, R., Li, K., Taylor, J., & Vincent, K. (2010). Galaxy: a comprehensive approach for supporting accessible, reproducible, and transparent computational research in the life sciences. *Genome Biology*, *11*(8), 1–13. https://doi.org/10.1186/gb-2010-11-8-r86

Goh, Y. K., Zoqratt, M. Z. H. M., Goh, Y. K., Ayub, Q., & Ting, A. S. Y. (2020). Determining soil microbial communities and their influence on *Ganoderma* disease incidences in oil palm (*Elaeis guineensis*) via high-throughput sequencing. *Biology, 9*(12), 1-21. https://doi.org/10.3390/biology9120424

Gomez-Garzon, C., Hernández-Santana, A., & Dussan, J. (2017). A genome-scale metabolic reconstruction of *Lysinibacillus sphaericus* unveils unexploited biotechnological potentials. *PLoS One, 12*(6), 1-21. https://doi.org/10.1371%2Fjournal.pone.0179666

Goulding, K. W. T. (2016). Soil acidification and the importance of liming agricultural soils with particular reference to the United Kingdom. *Soil Use and Management, 32*(3), 390-399. https://doi.org/10.1111/sum.12270

Gu, Y., Wang, Y., Lu, S. E., Xiang, Q., Yu, X., Zhao, K., Zou, L., Chen, Q., Tu, S., & Zhang, X. (2017). Long-term fertilization structures bacterial and archaeal communities along soil depth gradient in a paddy soil. *Frontiers in Microbiology, 8*, 1-15. https://doi.org/10.3389/fmicb.2017.01516

Guo, N., Zhang, S., Gu, M., & Xu, G. (2021). Function, transport, and regulation of amino acids: What is missing in rice?. *The Crop Journal*, *9*(3), 530-542. https://doi.org/10.1016/j.cj.2021.04.002

Haiming, T., Xiaoping, X., Chao, L., Xiaochen, P., Kaikai, C., Weiyan, L., & Ke, W. (2020). Microbial carbon source utilization in rice rhizosphere and nonrhizosphere soils with short-term manure N input rate in paddy field. *Scientific Reports*, *10*(1), 6487. https://doi.org/10.1038/s41598-020-63639-8

Halifu, S., Deng, X., Song, X., An, Y., & Song, R. (2019). Effects of Sphaeropsis Blight on Rhizosphere Soil Bacterial Community Structure and Soil Physicochemical Properties of *Pinus sylvestris* var. *mongolica* in Zhanggutai, China. *Forests, 10*(11), 1-18. https://doi.org/10.3390/f10110954

Han, S. H., An, J. Y., Hwang, J., Kim, S. B., & Park, B. B. (2016). The effects of organic manure and chemical fertilizer on the growth and nutrient concentrations of yellow poplar (*Liriodendron tulipifera* Lin.) in a nursery system. *Forest Science and Technology,* *12*(3), 137-143. https://doi.org/10.1080/21580103.2015.1135827

Havlin, J. L. (2005). Fertility. In *Encyclopedia of Soils in the Environmen*t (pp. 10-19). Elsevier.

Heanes, D. L. (1981). Determination of trace elements in plant materials by a dry-ashing procedure. Part II. Copper, manganese and zinc. *Analyst,* *106*(1259), 182-187. https://doi.org/10.1039/AN9810600172

Hernandez, D., Cardell, E., & Zarate, V. (2005). Antimicrobial activity of lactic acid bacteria isolated from Tenerife cheese: initial characterization of plantaricin TF711, a bacteriocin-like substance produced by *Lactobacillus plantarum* TF711. *Journal of Applied Microbiology*, *99*(1), 77-84. https://doi.org/10.1111/j.1365-2672.2005.02576.x

Holland, B. L., Matthews, M. L., Bota, P., Sweetlove, L. J., Long, S. P., & diCenzo, G. C. (2023). A genome‐scale metabolic reconstruction of soybean and Bradyrhizobium diazoefficiens reveals the cost–benefit of nitrogen fixation. *New Phytologist.* https://doi.org/10.1111/nph.19203

Jaiswal, S. K., & Dakora, F. D. (2019). Widespread distribution of highly adapted Bradyrhizobium species nodulating diverse legumes in Africa. *Frontiers in microbiology*, *10*, 310. https://doi.org/10.3389/fmicb.2019.00310

Jamil, F., Mukhtar, H., Fouillaud, M., & Dufossé, L. (2022). Rhizosphere signaling: Insights into plant–rhizomicrobiome interactions for sustainable agronomy. *Microorganisms*, *10*(5), 899. https://doi.org/10.3390/microorganisms10050899

Ji, L., Xu, X., Zhang, F., Si, H., Li, L., & Mao, G. (2023). The Preliminary Research on Shifts in Maize Rhizosphere Soil Microbial Communities and Symbiotic Networks under Different Fertilizer Sources. *Agronomy*, *13*(8), 2111. https://doi.org/10.3390/agronomy13082111

Kakar, K., Xuan, T. D., & Khanh, T. D. (2023). Allelopathic Potential of Sweet Sorghum Root Exudates and Identification of the Relevant Allelochemicals. *Agrochemicals*, *2*(1), 96-105. https://doi.org/10.3390/agrochemicals2010007

Kalam, S., Basu, A., Ahmad, I., Sayyed, R. Z., El Enshasy, H. A., Dailin, D. J., & Suriani, N. (2020). Recent understanding of soil Acidobacteria and their ecological significance: A critical review. *Frontiers in Microbiology,* *11*, 1-15. https://doi.org/10.3389/fmicb.2020.580024

Kandel, S., Kim, Y., Park, J., & Lee, J. (2019). Nitrogen and phosphorus fertilization effects on bacterial community structure and functional gene diversity of the rice rhizosphere. Frontiers in Microbiology, 10, 1498.

Kathiravan, A., & Gnanadoss, J. J. (2021). White-rot fungi-mediated bioremediation as a sustainable method for xenobiotic degradation. *Environmental and Experimental Biology, 19*(3), 103-119. https://doi.org/10.22364/eeb.19.11

Kavvadias, V., Ioannou, Z., Vavoulidou, E., & Paschalidis, C. (2023). Short Term Effects of Chemical Fertilizer, Compost and Zeolite on Yield of Lettuce, Nutrient Composition and Soil Properties. *Agriculture, 13(5), 1022.* https://doi.org/10.3390/agriculture13051022

Kim, C., Baek, G., Yoo, B. O., Jung, S. Y., & Lee, K. S. (2018). Regular fertilization effects on the nutrient distribution of bamboo components in a moso bamboo (*Phyllostachys pubescens* (Mazel) Ohwi) stand in South Korea. *Forests, 9*(11), 1-12. https://doi.org/10.3390/f9110671

Kim, S. K., Chung, D., Himmel, M. E., Bomble, Y. J., & Westpheling, J. (2016). Heterologous expression of family 10 xylanases from *Acidothermus cellulolyticus* enhances the exoproteome of *Caldicellulosiruptor bescii* and growth on xylan substrates. *Biotechnology for Biofuels*, *9*, 1-10. https://doi.org/10.1186/s13068-016-0588-9

Kojima, H., Tokizawa, R., & Fukui, M. (2014). *Mizugakiibacter sediminis* gen. nov., sp. nov., isolated from a freshwater lake. *International Journal of Systematic and Evolutionary Microbiology*, *64*(Pt_12), 3983-3987. https://doi.org/10.1099/ijs.0.064659-0

Kramer, S., Dibbern, D., Moll, J., Huenninghaus, M., Koller, R., Krueger, D., Marhan, S., Urich, T., Wubet, T., Bonkowski, M., Buscot, F., Leuders, T., & Kandeler, E. (2016). Resource partitioning between bacteria, fungi, and protists in the detritusphere of an agricultural soil. *Frontiers in Microbiology, 7*, 1-12. https://doi.org/10.3389/fmicb.2016.01524

Kumawat, K. C., Sharma, P., Sirari, A., Singh, I., Gill, B. S., Singh, U., & Saharan, K. (2019). Synergism of *Pseudomonas aeruginosa*

(LSE-2) nodule endophyte with *Bradyrhizobium* sp. (LSBR-3) for improving plant growth, nutrient acquisition and soil health in soybean. *World Journal of Microbiology and Biotechnology, 35*(3), 1-17. https://doi.org/10.1007/s11274-019-2622-0

Legendre, P., & Gallagher, E. D. (2001). Ecologically meaningful transformations for ordination of species data. *Oecologia*, *129*, 271-280. https://doi.org/10.1007/s004420100716

Lewis, R. W., Barth, V. P., Coffey, T., McFarland, C., Huggins, D. R., & Sullivan, T. S. (2018). Altered bacterial communities in long-term no-till soils associated with stratification of soluble aluminum and soil pH. *Soil Systems, 2*(1), 1-13. https://doi.org/10.3390/soils2010007

Li, F., Chen, L., Zhang, J., Yin, J., & Huang, S. (2017). Bacterial community structure after long-term organic and inorganic fertilization reveals important associations between soil nutrients and specific taxa involved in nutrient transformations. *Frontiers in Microbiology, 8*, 1-12. https://doi.org/10.3389/fmicb.2017.00187

Li, K., Han, X., Ni, R., Shi, G., De-Miguel, S., Li, C., Shen, W., Zhang, Y., & Zhang, X. (2021). Impact of *Robinia pseudoacacia* stand conversion on soil properties and bacterial community composition in Mount Tai, China. *Forest Ecosystems, 8*(1), 1-12. https://doi.org/10.1186/s40663-021-00296-x

Lin, S. Y., Hameed, A., Hsieh, Y. T., Hsu, Y. H., Lai, W. A., & Young, C. C. (2018). *Castellaniella fermenti* sp. nov., isolated from a fermented meal. *International Journal of Systematic and Evolutionary Microbiology, 68*(1), 52-57. https://doi.org/10.1099/ijsem.0.002436

Lin, W., Lin, M., Zhou, H., Wu, H., Li, Z., & Lin, W. (2019). The effects of chemical and organic fertilizer usage on rhizosphere soil in tea orchards. *PloS One, 14*(5), e0217018. https://doi.org/10.1371/journal.pone.0217018

Liu, C., Gong, X., Dang, K., Li, J., Yang, P., Gao, X., Deng, X., & Feng, B. (2020b). Linkages between nutrient ratio and the microbial community in rhizosphere soil following fertilizer management. *Environmental Research, 184*, 109261. https://doi.org/10.1016/j.envres.2020.109261

Liu, J., Ma, Q., Hui, X., Ran, J., Ma, Q., Wang, X., & Wang, Z. (2020a). Long-term high-P fertilizer input decreased the total bacterial diversity but not phoD-harboring bacteria in wheat rhizosphere soil with available-P deficiency. *Soil Biology and Biochemistry*, *149*, 107918. https://doi.org/10.1016/j.soilbio.2020.107918

Liu, K., Cai, M., Hu, C., Sun, X., Cheng, Q., Jia, W., Yang, T., Nie, M., & Zhao, X. (2019). Selenium (Se) reduces *Sclerotinia* stem rot disease incidence of oilseed rape by increasing plant Se concentration and shifting soil microbial community and functional profiles. *Environmental Pollution, 254*, 1-10. https://doi.org/10.1016/j.envpol.2019.113051

Loutet, S. A., Chan, A. C., Kobylarz, M. J., Verstraete, M. M., Pfaffen, S., Ye, B., Arrieta, A. L., & Murphy, M. E. (2021). The fate of intracellular metal ions in microbes.

Lu, X., Heal, K. R., Ingalls, A. E., Doxey, A. C., & Neufeld, J. D. (2020). Metagenomic and chemical characterization of soil cobalamin production. *The ISME Journal*, *14*(1), 53-66. https://doi.org/10.1038/s41396-019-0502-0

Ma, L., Pang, A. P., Luo, Y., Lu, X., & Lin, F. (2020). Beneficial factors for biomineralization by ureolytic bacterium *Sporosarcina pasteurii*. *Microbial Cell Factories*, *19*(1), 1-12. https://doi.org/10.1186/s12934-020-1281-z

Magoč, T., & Salzberg, S. L. (2011). FLASH: fast length adjustment of short reads to improve genome assemblies. *Bioinformatics, 27*(21), 2957-2963. https://doi.org/10.1093/bioinformatics/btr507

Malaysian Standard [MS] (1980). *MS 678–Recommended methods for soil chemical analysis: Part I–V*. Shah Alam: Standards and Industrial Research Institute of Malaysia.

Mallhi, Z. I., Rizwan, M., Mansha, A., Ali, Q., Asim, S., Ali, S., Hussain, A., Alrokayan, S. H., Khan, H. A., Alam, P., & Ahmad, P. (2019). Citric acid enhances plant growth, photosynthesis, and phytoextraction of lead by alleviating the oxidative stress in castor beans. *Plants, 8*(11), 525. https://doi.org/10.3390/plants8110525

Mandakovic, D., Aguado-Norese, C., García-Jiménez, B., Hodar, C., Maldonado, J. E., Gaete, A., Latorre, M., Wilkinson, M. D., Gutiérrez, R. A., Cavierres, L. A., Medina, J., Cambiazo, V., & Gonzalez, M. (2023). Testing the stress gradient hypothesis in soil bacterial communities associated with vegetation belts in the Andean Atacama Desert. *Environmental Microbiome, 18*(1), 1-17. https://doi.org/10.1186/s40793-023-00486-w

Mao, X., Xu, X., Lu, K., Gielen, G., Luo, J., He, L., Donnison, A., Xu, Z., Xu, J., Yang, W., Song, Z., & Wang, H. (2015). Effect of 17 years of organic and inorganic fertilizer applications on soil phosphorus dynamics in a rice–wheat rotation cropping system in eastern China. *Journal of Soils and Sediments, 15*(9), 1889-1899. https://doi.org/10.1007/s11368-015-1137-z

Matejovic, I. (1993). Determination of carbon, hydrogen, and nitrogen in soils by automated elemental analysis (dry combustion method). *Communications in Soil Science and Plant Analysis, 24*(17-18), 2213-2222. https://doi.org/10.1080/00103629309368950

McDonald, D., Price, M. N., Goodrich, J., Nawrocki, E. P., DeSantis, T. Z., Probst, A., Andersen, G. L., Knight, R., & Hugenholtz, P. (2012). An improved Greengenes taxonomy with explicit ranks for ecological and evolutionary analyses of bacteria and archaea. *The ISME Journal,* *6*(3), 610-618. https://doi.org/10.1038/ismej.2011.139

McMurdie, P. J., & Holmes, S. (2013). Phyloseq: An R Package for Reproducible Interactive Analysis and Graphics of Microbiome Census Data. *PLoS One*, *8*(4), 1–11. https://doi.org/10.1371/journal.pone.0061217

McNear Jr., D. H. (2013) The Rhizosphere - Roots, Soil and Everything In Between. Nature Education Knowledge 4(3), 1. https://www.nature.com/scitable/knowledge/library/the-rhizosphere-roots-soil-and-67500617/ (accessed 22 February 2023)

Merchant, S. S., & Helmann, J. D. (2012). Elemental economy: microbial strategies for optimizing growth in the face of nutrient limitation. *Advances in Microbial Physiology, 60*, 91-210. https://doi.org/10.1016/B978-0-12-398264-3.00002-4

Morcillo, R. J., & Manzanera, M. (2021). The effects of plant-associated bacterial exopolysaccharides on plant abiotic stress tolerance. *Metabolites*, *11*(6), 337. https://doi.org/10.3390/metabo11060337

Morigasaki, S., Matsui, M., Ohtsu, I., Doi, Y., Kawano, Y., Nakai, R., Iwasaki, W., Hayashi, H., & Takaya, N. (2024). Temporal and fertilizer-dependent dynamics of soil bacterial communities in buckwheat fields under long-term management. *Scientific Reports, 14*(1), 9896. https://doi.org/10.1038/s41598-024-60655-w

MPOB (2022a). Malaysian Oil Palm Statistics 2021. 41st edition. MPOB, Bangi

MPOB (2022b). Review of the Malaysian Oil Palm Industry 2021. MPOB, Bangi.

Murphy, D. J., Goggin, K., & Paterson, R. R. M. (2021). Oil palm in the 2020s and beyond: challenges and solutions. *CABI Agriculture and Bioscience*, *2*(1), 1–22. https://doi.org/10.1186/s43170-021-00058-3

Ndabankulu, K., Egbewale, S. O., Tsvuura, Z., & Magadlela, A. (2022). Soil microbes and associated extracellular enzymes largely impact nutrient bioavailability in acidic and nutrient poor grassland ecosystem soils. *Scientific Reports, 12(1), 12601.* https://doi.org/10.1038/s41598-022-16949-y

Ng, J. F., Ahmed, O. H., Jalloh, M. B., Omar, L., Kwan, Y. M., Musah, A. A., & Poong, K. H. (2022). Soil nutrient retention and pH buffering capacity are enhanced by calciprill and sodium silicate. *Agronomy,* *12*(1), 219. https://doi.org/10.3390/agronomy12010219

Noble, A. S., Noe, S., Clearwater, M. J., & Lee, C. K. (2020). A core phyllosphere microbiome exists across distant populations of a tree species indigenous to New Zealand. *PLoS One*, *15*(8), e0237079. https://doi.org/10.1371/journal.pone.0237079

O'Brien, F. J., Dumont, M. G., Webb, J. S., & Poppy, G. M. (2018). Rhizosphere bacterial communities differ according to fertilizer regimes and cabbage (*Brassica oleracea* var. capitata L.) harvest time, but not aphid herbivory. *Frontiers in Microbiology, 9*, 1620. https://doi.org/10.3389/fmicb.2018.01620

Ogola, H. J. O., Selvarajan, R., & Tekere, M. (2021). Local geomorphological gradients and land use patterns play key role on the soil bacterial community diversity and dynamics in the highly endemic indigenous afrotemperate coastal scarp forest biome. *Frontiers in Microbiology*, *12*, 592725. https://doi.org/10.3389/fmicb.2021.592725

Oksanen, J. (2015). Vegan: an introduction to ordination. URL http://cran. r-project. org/web/packages/vegan/vignettes/introvegan. pdf, 8, 1-19.

Parks, D. H., Tyson, G. W., Hugenholtz, P., & Beiko, R. G. (2014). STAMP: Statistical analysis of taxonomic and functional profiles. *Bioinformatics*, *30*(21), 3123–3124. https://doi.org/10.1093/bioinformatics/btu494

Piccoli, P., & Bottini, R. (2013). Terpene production by bacteria and its involvement in plant growth promotion, stress alleviation, and yield increase. *Molecular Microbial Ecology of the Rhizosphere, 1,* 335-343. https://doi.org/10.1002/9781118297674.ch31

Pirker, J., Mosnier, A., Kraxner, F., Havlík, P., & Obersteiner, M. (2016). What are the limits to oil palm expansion? *Global Environmental Change*, *40*, 73–81. https://doi.org/10.1016/j.gloenvcha.2016.06.007

Price, G. W., Langille, M. G., & Yurgel, S. N. (2021). Microbial co-occurrence network analysis of soils receiving short-and long-term applications of alkaline treated biosolids. *Science of The Total Environment, 751*, 1-11. https://doi.org/10.1016/j.scitotenv.2020.141687

Qiu, L., Zhang, Q., Zhu, H., Reich, P. B., Banerjee, S., van der Heijden, M. G. A., Sadowsky, M. J., Ishii, S., Jia, X., Shao, M., Liu, B., Jiao, H., Li, H., & Wei, X. (2021). Erosion reduces soil microbial diversity, network complexity and multifunctionality. *The ISME Journal*, *15*(8), 2474-2489. https://doi.org/10.1038/s41396-021-00913-1

Quast, C., Pruesse, E., Yilmaz, P., Gerken, J., Schweer, T., Yarza, P., Peplies, J., & Glöckner, F. O. (2012). The SILVA ribosomal RNA gene database project: improved data processing and web-based tools. *Nucleic Acids Research, 41*(D1), D590-D596. https://doi.org/10.1093/nar/gks1219

Rawat, S. R., Männistö, M. K., Bromberg, Y., & Häggblom, M. M. (2012). Comparative genomic and physiological analysis provides insights into the role of Acidobacteria in organic carbon utilization in Arctic tundra soils. *FEMS Microbiology Ecology, 82*(2), 341-355. https://doi.org/10.1111/j.1574-6941.2012.01381.x

Ren, D., Madsen, J. S., Sørensen, S. J., & Burmølle, M. (2015). High prevalence of biofilm synergy among bacterial soil isolates in cocultures indicates bacterial interspecific cooperation. *The ISME Journal, 9*(1), 81-89. https://doi.org/10.1038/ismej.2014.96

Ren, H., Wang, H., Qi, X., Yu, Z., Zheng, X., Zhang, S., Wang, Z., Zhang, M., Ahmed, T., & Li, B. (2021). The damage caused by decline disease in bayberry plants through changes in soil properties, rhizosphere microbial community structure and metabolites. *Plants*, *10*(10), 2083. https://doi.org/10.3390/plants10102083

Ren, M., Zhang, Z., Wang, X., Zhou, Z., Chen, D., Zeng, H., Zhao, S., Chen, L., Hu, Y., Zhang, C., Liang, Y., She, Q., Zhang, Y., & Peng, N. (2018). Diversity and contributions to nitrogen cycling and carbon fixation of soil salinity shaped microbial communities in Tarim Basin. *Frontiers in Microbiology, 9*, 1-14. https://doi.org/10.3389/fmicb.2018.00431

Sakoula, D., Koch, H., Frank, J., Jetten, M. S., van Kessel, M. A., & Lücker, S. (2021). Enrichment and physiological characterization of a novel comammox *Nitrospira* indicates ammonium inhibition of complete nitrification. *The ISME Journal, 15*(4), 1010-1024. https://doi.org/10.1038/s41396-020-00827-4

Segata, N., Izard, J., Waldron, L., Gevers, D., Miropolsky, L., Garrett, W. S., & Huttenhower, C. (2011). Metagenomic biomarker discovery and explanation. *Genome Biology*, *12*(6), 1–18. https://doi.org/doi.org/10.1186/gb-2011-12-6-r60

Selim, M. S. M., Abdelhamid, S. A., & Mohamed, S. S. (2021). Secondary metabolites and biodiversity of actinomycetes. *Journal of Genetic Engineering and Biotechnology*, *19*(1), 72. https://doi.org/10.1186/s43141-021-00156-9

Semenov, M. V., Krasnov, G. S., Semenov, V. M., & van Bruggen, A. H. (2020). Long-term fertilization rather than plant species shapes rhizosphere and bulk soil prokaryotic communities in agroecosystems. *Applied Soil Ecology*, *154*, 103641. https://doi.org/10.1016/j.apsoil.2020.103641

Seraj, M. F., Rahman, T., Lawrie, A. C., & Reichman, S. M. (2020). Assessing the plant growth promoting and arsenic tolerance potential of *Bradyrhizobium japonicum* CB1809. *Environmental Management, 66*(5), 930-939. https://doi.org/10.1007/s00267-020-01351-z

Shannon, P., Markiel, A., Ozier, O., Baliga, N. S., Wang, J. T., Ramage, D., Amin, N., Schwikowski, B., & Ideker, T. (2003). Cytoscape: A Software Environment for Integrated Models. *Genome Research*, *13*(11), 24980–2504. https://doi.org/10.1101/gr.1239303.metabolite

Shen, G., Zhang, S., Liu, X., Jiang, Q., & Ding, W. (2018). Soil acidification amendments change the rhizosphere bacterial community of tobacco in a bacterial wilt affected field. *Applied Microbiology and Biotechnology, 102*, 9781-9791. https://doi.org/10.1007/s00253-018-9347-0

Shi, Y., Qiu, L., Guo, L., Man, J., Shang, B., Pu, R., Ou, X., Dai, C., Liu, P., Yang, Y., & Cui, X. (2020). K fertilizers reduce the accumulation of Cd in *Panax notoginseng* (Burk.) FH by improving the quality of the microbial community. *Frontiers in Plant Science*, *11*, 888. https://doi.org/10.3389/fpls.2020.00888

Singh, B. K., Jha, B., Tripathi, S., Singh, D. K., & Trivedi, P. (2018). Impact of long-term fertilizer application on rhizosphere bacterial community structure of wheat and barley. MicrobiologyOpen, 7(5), e00637.

Sinong, G. F., Yasuda, M., Nara, Y., Lee, C. G., Dastogeer, K. M. G., Tabuchi, H., Nakai, H., Djedidi, S., & Okazaki, S. (2021). Distinct root microbial communities in nature farming rice harbor bacterial strains with plant growth-promoting traits. *Frontiers in Sustainable Food Systems*, *4*, 629942. https://doi.org/10.3389/fsufs.2020.629942

Song, J., Min, L., Wu, J., He, Q., Chen, F., & Wang, Y. (2021). Response of the microbial community to phosphate-solubilizing bacterial inoculants on *Ulmus chenmoui* Cheng in Eastern China. *Plos One,* *16*(2), e0247309. https://doi.org/10.1371/journal.pone.0247309

Su, X., Li, S., Cai, J., Xiao, Y., Tao, L., Hashmi, M. Z., Lin, H., Chen, J., Mei, R., & Sun, F. (2019). Aerobic degradation of 3, 3′, 4, 4′-tetrachlorobiphenyl by a resuscitated strain *Castellaniella* sp. SPC4: kinetics model and pathway for biodegradation. *Science of the Total Environment*, *688*, 917-925. https://doi.org/10.1016/j.scitotenv.2019.06.364

Svenningsen, N. B., Watts-Williams, S. J., Joner, E. J., Battini, F., Efthymiou, A., Cruz-Paredes, C., Nybroe, O., & Jakobsen, I. (2018). Suppression of the activity of arbuscular mycorrhizal fungi by the soil microbiota. *The ISME Journal, 12*(5), 1296-1307. https://doi.org/10.1038/s41396-018-0059-3

Tandon, H. L. S., Cescas, M. P., & Tyner, E. H. (1968). An acid-free vanadate-molybdate reagent for the determination of total phosphorus in soils. *Soil Science Society of America Journal, 32*(1), 48-51. https://doi.org/10.2136/sssaj1968.03615995003200010012x

Tang, S., Zhou, J., Pan, W., Sun, T., Liu, M., Tang, R., Li, Z., Ma, Q., & Wu, L. (2023). Effects of combined application of nitrogen, phosphorus, and potassium fertilizers on tea (*Camellia sinensis*) growth and fungal community. *Applied Soil Ecology, 181*, 104661. https://doi.org/10.1016/j.apsoil.2022.104661

Tarmizi, A. M., & Mohd Tayeb, D. (2006). Nutrient demands of *tenera* oil palm planted on inland soil of Malaysia. *Journal of Oil Palm Research, 18*, 204.

Tebo, B. M., Davis, R. E., Anitori, R. P., Connell, L. B., Schiffman, P., & Staudigel, H. (2015). Microbial communities in dark oligotrophic volcanic ice cave ecosystems of Mt. Erebus, Antarctica. *Frontiers In Microbiology*, *6*, 179. https://doi.org/10.3389/fmicb.2015.00179

Tkaczyk, P., Mocek-Płóciniak, A., Skowrońska, M., Bednarek, W., Kuśmierz, S., & Zawierucha, E. (2020). The mineral fertilizer-dependent chemical parameters of soil acidification under field conditions. *Sustainability,* *12*(17), 1-11. https://doi.org/10.3390/su12177165

van der Ploeg, R. R., Böhm, W., & Kirkham, M. B. (1999). On the origin of the theory of mineral nutrition of plants and the law of the minimum. *Soil Science Society of America Journal*, *63*(5), 1055-1062. https://doi.org/10.2136/sssaj1999.6351055x

Verma, P., & Rawat, S. (2021). Rhizoremediation of heavy metal- and xenobiotic-contaminated soil: an eco-friendly approach. *Removal of Emerging Contaminants Through Microbial Processes*, 95-113. https://doi.org/10.1007/978-981-15-5901-3_5

Vives-Peris, V., De Ollas, C., Gómez-Cadenas, A., & Pérez-Clemente, R. M. (2020). Root exudates: from plant to rhizosphere and beyond. *Plant Cell Reports, 39*, 3-17. https://doi.org/10.1007/s00299-019-02447-5

Wang, M., Xu, Y., Ni, H., Ren, S., Li, N., Wu, Y., Yang, Y., Liu, Y., Liu, Z., Liu, Y., Shi, J., Zhang, Y., Jiang, L., & Tu, Q. (2023). Effect of fertilization combination on cucumber quality and soil microbial community. *Frontiers in Microbiology*, *14*, 1122278. https://doi.org/10.3389/fmicb.2023.1122278

Wang, Q., Jiang, X., Guan, D., Wei, D., Zhao, B., Ma, M., Chen, S., Li, L., Cao, F., & Li, J. (2018). Long-term fertilization changes bacterial diversity and bacterial communities in the maize rhizosphere of Chinese Mollisols. *Applied Soil Ecology, 125*, 88-96. https://doi.org/10.1016/j.apsoil.2017.12.007

Wang, W., Yang, Y., Li, J., Bu, P., Lu, A., Wang, H., He, W., Bermudez, R. S., & Feng, J. (2024). Consecutive Fertilization-Promoted Soil Nutrient Availability and Altered Rhizosphere Bacterial and Bulk Fungal Community Composition. *Forests, 15*(3), 514. https://doi.org/10.3390/f15030514

Wang, Y., Zhang, L., Zhang, X., Wang, S., & Zhou, J. (2015). Nitrogen fertilization alters bacterial community structure and diversity in the soybean rhizosphere. *Applied and Environmental Microbiology, 81*(20), 7113-7121.

Wanke, A., Malisic, M., Wawra, S., & Zuccaro, A. (2021). Unraveling the sugar code: the role of microbial extracellular glycans in plant–microbe interactions. *Journal of Experimental Botany, 72*(1), 15-35. https://doi.org/10.1093/jxb/eraa414

Ward, N. L., Challacombe, J. F., Janssen, P. H., Henrissat, B., Coutinho, P. M., Wu, M., Xie, G., Haft, D. H., Sait, M., Badger, J., Barabote, R. D., Bradley, B., Brettin, T. S., Brinkac, L. M., Bruce, D., Creasy, T., Daugherty, S. C., Davidsen, T. M., DeBoy, R. T., Detter, J. C., Dodson, R. J., Durkin, A. S., Ganapathy, A., Gwinn-Giglio, M., Han, C. S., Khouri, H., Kiss, H., Kothari, S. P., Madupu, R., Nelson, K. E., Nelson, W. C., Paulsen, I., Penn, K., Ren, Q., Rosovitz, M. J., Selengut, J. D., Shrivastava, S., Sullivan, S. A., Tapia, R., Thompson, L. S., Watkins, K. L., Yang, Q., Yu, C., Zafar, N., Zhou, L., & Kuske, C. R. (2009). Three genomes from the phylum Acidobacteria provide insight into the lifestyles of these microorganisms in soils. *Applied and Environmental Microbiology*, *75*(7), 2046-2056. https://doi.org/10.1128/AEM.02294-08

Wei, W., Yang, M., Liu, Y., Huang, H., Ye, C., Zheng, J., Guo, C., Hao, M., He, X., & Zhu, S. (2018). Fertilizer N application rate impacts plant-soil feedback in a sanqi production system. *Science of the Total Environment*, *633*, 796-807. https://doi.org/10.1016/j.scitotenv.2018.03.219

Wen, T., Yu, G. H., Hong, W. D., Yuan, J., Niu, G. Q., Xie, P. H., Sun, F. S., Guo, L. D., Kuzyakov, Y., & Shen, Q. R. (2022). Root exudate chemistry affects soil carbon mobilization via microbial community reassembly. *Fundamental Research, 2*(5), 697-707. https://doi.org/10.1016/j.fmre.2021.12.016

Wieland, G., Neumann, R., & Backhaus, H. (2001). Variation of Microbial Communities in Soil, Rhizosphere, and Rhizoplane in Response to Crop Species, Soil Type, and Crop Development. *Applied and Environmental Microbiology*, *67*(12), 5849–5854. https://doi.org/10.1128/AEM.67.12.5849-5854.2001

Wu, W., Wang, X., Ren, Z., Zhou, X., & Du, G. (2022). N-Induced Species Loss Dampened by Clipping Mainly Through Suppressing Dominant Species in an Alpine Meadow. *Frontiers in Plant Science,* *13*, 815011. https://doi.org/10.3389%2Ffpls.2022.815011

Xu, A., Li, L., Xie, J., Zhang, R., Luo, Z., Cai, L., Liu, C., Wang, L., Anwar, S., & Jiang, Y. (2022). Bacterial Diversity and Potential Functions in Response to Long-Term Nitrogen Fertilizer on the Semiarid Loess Plateau. *Microorganisms*, *10*(8), 1579. https://doi.org/10.3390/microorganisms10081579

Xu, Q., Ling, N., Chen, H., Duan, Y., Wang, S., Shen, Q., & Vandenkoornhuyse, P. (2020). Long-term chemical-only fertilization induces a diversity decline and deep selection on the soil bacteria. *Msystems*, *5*(4), e00337-20. https://doi.org/10.1128/mSystems.00337-20

Yang, L., Sun, R., Li, J., Zhai, L., Cui, H., Fan, B., Wang, H., & Liu, H. (2023). Combined organic-inorganic fertilization builds higher stability of soil and root microbial networks than exclusive mineral or organic fertilization. *Soil Ecology Letters, 5(2), 220142*. https://doi.org/10.1007/s42832-022-0142-6

Yang, L., Sun, R., Li, J., Zhai, L., Cui, H., Fan, B., Wang, H., & Liu, H. (2021). Organic-inorganic fertilization built higher stability of soil and root microbial networks than exclusive mineral or organic fertilization. *ResearchSquare*, 1-26. https://doi.org/10.21203/rs.3.rs-652488/v1

Yin, X., Li, T., Jiang, X., Tang, X., Zhang, J., Yuan, L., & Wei, Y. (2022). Suppression of grape white rot caused by *Coniella vitis* using the potential biocontrol agent *Bacillus Velezensis* GSBZ09. *Pathogens*, *11*(2), 248. https://doi.org/10.3390/pathogens11020248

Yu, Z., Hu, X., Wei, D., Liu, J., Zhou, B., Jin, J., Liu, X., & Wang, G. (2019). Long-term inorganic fertilizer use influences bacterial communities in Mollisols of Northeast China based on high-throughput sequencing and network analyses. *Archives of Agronomy and Soil Science*. 1-13. https://doi.org/10.1080/03650340.2018.1563685

Zegeye, E. K., Brislawn, C. J., Farris, Y., Fansler, S. J., Hofmockel, K. S., Jansson, J. K., Wright, A. T., Graham, E. B., Naylor, D., McClure, R. S., & Bernstein, H. C. (2019). Selection, succession, and stabilization of soil microbial consortia. *Msystems, 4*(4), 1-13. https://doi.org/10.1128/mSystems.00055-19

Zhang, C., Song, Z., Zhuang, D., Wang, J., Xie, S., & Liu, G. (2019a). Urea fertilization decreases soil bacterial diversity, but improves microbial biomass, respiration, and N-cycling potential in a semiarid grassland. *Biology and Fertility of Soils*, *55*(3), 229-242. https://doi.org/10.1007/s00374-019-01344-z

Zhang, Q., Li, Y., He, Y., Liu, H., Dumont, M. G., Brookes, P. C., & Xu, J. (2019b). *Nitrosospira* cluster 3-like bacterial ammonia oxidizers and *Nitrospira*-like nitrite oxidizers dominate nitrification activity in acidic terrace paddy soils. *Soil Biology and Biochemistry*, *131*, 229-237. https://doi.org/10.1016/j.soilbio.2019.01.006

Zhao, F., Guo, X. Q., Wang, P., He, L. Y., Huang, Z., & Sheng, X. F. (2013). *Dyella jiangningensis* sp. nov., a γ-proteobacterium isolated from the surface of potassium-bearing rock. *International Journal of Systematic and Evolutionary Microbiology, 63(Pt_9),* 3154-3157. https://doi.org/10.1099/ijs.0.048470-0

Zhao, Z., Zhao, R., Qiu, X., Wan, Y., & Lee, L. (2022). Structural Diversity of Bacterial Communities and Its Relation to Environmental Factors in the Surface Sediments from Main Stream of Qingshui River. *Water, 14*(21), 3356. https://doi.org/10.3390/w14213356

Zheng, B. X., Bi, Q. F., Hao, X. L., Zhou, G. W., & Yang, X. R. (2017). *Massilia phosphatilytica* sp. nov., a phosphate solubilizing bacteria isolated from a long-term fertilized soil. *International Journal of Systematic and Evolutionary Microbiology, 67*(8), 2514-2519. https://doi.org/10.1099/ijsem.0.001916

Zhou, J., Jiang, X., Zhou, B., Zhao, B., Ma, M., Guan, D., Li, J., Chen, S., Cao, F., Shen, D., & Qin, J. (2016). Thirty four years of nitrogen fertilization decreases fungal diversity and alters fungal community composition in black soil in northeast China. *Soil Biology and Biochemistry, 95*, 135-143. https://doi.org/10.1016/j.soilbio.2015.12.012

Zhou, Z., Tran, P. Q., Kieft, K., & Anantharaman, K. (2020). Genome diversification in globally distributed novel marine Proteobacteria is linked to environmental adaptation. *The ISME Journal, 14*(8), 2060-2077. https://doi.org/10.1038/s41396-020-0669-4

Zhou, Z., Yan, T., Zhu, Q., Bu, X., Chen, B., Xue, J., & Wu, Y. (2019). Bacterial community structure shifts induced by biochar amendment to karst calcareous soil in southwestern areas of China. *Journal of Soils and Sediments*, *19*, 356-365. https://doi.org/10.1007/s11368-018-2035-y

Zhu, S., Vivanco, J. M., & Manter, D. K. (2016). Nitrogen fertilizer rate affects root exudation, the rhizosphere microbiome and nitrogen-use-efficiency of maize. *Applied Soil Ecology, 107*, 324-333. https://doi.org/10.1016/j.apsoil.2016.07.009