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Diversity and potential function of bacteria from soil and cowpea root nodules across two agroecological zones in Tharaka Nithi, Kenya

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ABSTRACT

Cowpea (*Vigna unguiculata*) productivity is influenced by soil microbial communities; however, the effects of ecological niche, agroecological zones, and soil physicochemical properties on microbial community assembly remain poorly understood in Kenyan agroecosystems. We used 16S rRNA gene sequencing and PICRUSt2 to characterize diversity, composition, and predicted functions in soil and root nodules from semi-arid and non-arid cowpea farms. Plants were grown under standardized greenhouse conditions to examine soil-origin effects. Non-arid soils had significantly higher nutrient and moisture levels than semi-arid soils, while microbial richness did not differ between zones. Richness and diversity were significantly higher in soil than in nodules ($p < 0.05$), suggesting host-mediated selection. Community composition differed significantly between niches and zones, with soil organic carbon identified by canonical correspondence analysis (CCA) as the main variable associated with a fertility–moisture gradient. Root nodules were dominated by *Bradyrhizobium*, with *Rhodoligotrophos* detected as a nodule-associated taxon. Non-arid soils were enriched in Actinomycetes, Chloroflexota, and Acidobacteriota, whereas *Rubrobacter* and *Microvirga* were more abundant in semi-arid soils. PICRUSt2 predictions indicated higher representation of plant-growth-promoting pathways in nodules and identified microbial taxa with potential relevance to sustainable cowpea production. These findings provide a basis for future screening of native microbial communities as potential bioinoculant candidates.

1. INTRODUCTION

Cowpea (*Vigna unguiculata*) is an important legume widely grown across sub-Saharan Africa, where it contributes to food security and helps maintain soil fertility. Africa accounts for more than 80% of global cowpea production, with an estimated annual output of 8–9 million metric tons [1–3]. In Kenya specifically, cowpea serves as both an important source of dietary protein and a source of household income [4]. Despite its importance, cowpea production remains low in many areas, largely due to poor soil fertility, nutrient deficiencies, irregular rainfall, and limited access to effective rhizobial inoculants [5]. Cowpea production in Tharaka-Nithi County faces real limits: drought, poor soil fertility, and phosphorus deficiency all constrain output there [6,7]. Soil and root-nodule bacteria present a biologically plausible way to counter these constraints. Nitrogen-fixing rhizobia increase plant nitrogen supply where soil fertility is low [8]; phosphate-solubilizing bacteria increase phosphorus availability without costly fertilizer inputs [9]; and bacterial mechanisms supporting osmotic and drought stress tolerance help plants withstand water limitation [10]. Non-rhizobial endophytes associated with cowpea nodules have also been characterized in the same broader semi-arid Kenyan region, widening the pool of native bacterial resources potentially available [11]. Previous research on cowpea in Tharaka-Nithi has focused on agronomic and socioeconomic factors, leaving the soil and root-nodule bacterial communities that accompany the crop there uncharacterized. Whether these native communities possess comparable functional capacities, and whether those capacities differ between the county's semi-arid and non-arid zones, has yet to be examined. Beyond nitrogen fixation, plant growth-promoting bacteria support nutrient cycling, phytohormone production, and other plant-associated processes [12], and their composition can differ among plants and environments [13–15]. Because the soil surrounding the plant is an important source of bacteria that may become associated with roots and nodules [16,17], soil conditions can influence the bacterial pool available to the plant. Soil pH, nutrient status, and moisture are among the physicochemical properties known to affect bacterial communities in agricultural soils [18]. Since these properties often change together, it can be difficult to determine which individual factors are most closely related to shifts in bacterial community composition. Tharaka-Nithi County provides a suitable setting to examine these relationships. Cowpea is grown in both semi-arid and non-arid agroecological zones within the county. The soils in these areas differ in several physicochemical

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characteristics, particularly moisture and nutrient availability. These differences may be reflected in the bacterial communities present in the soil [19]. At the same time, the plant can influence which bacteria become established in its root nodules [20]. Thus, both soil conditions and host selection may contribute to the assembly of nodule bacterial communities. Previous studies have examined cowpea rhizosphere or nodule microbiomes separately [21,22]. Fewer studies have compared bulk soil and root-nodule communities across contrasting agroecological zones within the same production area. Such comparisons can provide a better understanding of how ecological niche, agroecological origin, and soil physicochemical conditions are related to bacterial community patterns. In this study, bacterial diversity, community composition, and predicted functional potential were examined in bulk soil and root nodules collected from cowpea farms in semi-arid and non-arid areas of Tharaka-Nithi County, Kenya. Three main hypotheses were tested. First, differences were expected between bacterial communities in soil and nodule compartments. Second, soil communities were considered a potential reservoir for bacteria associated with root nodules. Third, bacterial communities from semi-arid and non-arid soils were expected to show differences in community composition and predicted functional profiles.

2. MATERIAL AND METHODS

2.1. Study Site and Sample Collection

This study was conducted in Tharaka-Nithi County, Kenya, across two contrasting agro-ecological zones: semi-arid and non-arid (Fig. 1). Five farms were selected from each zone. In the semi-arid zone, these were Farm 1 (0.168159° S, 37.847059° E), Farm 2 (0.167259° S, 37.848310° E), Farm 3 (0.167418° S, 37.839841° E), Farm 4 (0.161146° S, 37.843680° E), and Farm 5 (0.161554° S, 37.845882° E). In the non-arid zone, the five selected farms were Farm 6 (0.380631° S, 37.617248° E), Farm 7 (0.381156° S, 37.616701° E), Farm 8 (0.380777° S, 37.596809° E), Farm 9 (0.379430° S, 37.598083° E), and Farm 10 (0.380180° S, 37.598554° E). To characterize the climatic contrast between zones, sampling coordinates were used to extract climatic variables from the WorldClim v2.1 database (30 arc-second resolution) using the geodata and terra packages in R. The semi-arid zone had a mean annual temperature (MAT) of ~22.3°C and mean annual precipitation (MAP) of 747–806 mm, whereas the non-arid zone, located on the windward slopes of Mount Kenya, had a lower MAT (~19.1°C) and markedly higher MAP (1,441–1,542 mm), confirming a genuine climatic contrast between the two zones [23].

2.2. Soil Physicochemical Properties and Greenhouse Trapping Experiment

Soil samples were collected from 10 farms, with five farms representing each agroecological zone. At each farm, 20 subsamples were collected following a zigzag pattern and pooled to form one composite sample [24]. The 10 composite samples were analyzed independently for pH, electrical conductivity (EC), moisture content (MC), organic carbon, total nitrogen, phosphorus, potassium, calcium, magnesium, iron, and zinc using standard laboratory methods [24–27]. Zone-level means ± SD are presented in Table 1 (n = 5 farms per zone), while individual farm measurements are provided in Supplementary Table S5. Differences between zones for each physicochemical variable were assessed using two-sided Mann–Whitney U (Wilcoxon rank-sum) tests, given the small per-zone sample size (n = 5); each variable was tested independently without multiple-testing correction, consistent with the exploratory, per-variable analysis presented in Table 1. Root nodules were trapped using cowpea plants grown in a greenhouse at Kenyatta University under a completely randomized design [28,29]. Each farm-level composite soil sample was treated as an independent soil-origin treatment, with three pot replicates per treatment, giving a total of 30 pots. No fertilizer was applied. All treatments were maintained under the same greenhouse conditions to allow bacterial communities associated with different soil origins to be compared under a common environment [30]. The greenhouse temperature was approximately 27°C, with a 12-hour photoperiod and relative humidity generally ranging from 75% to 85%. Surface-sterilized cowpea (*Vigna unguiculata*) seeds [31,32] were planted in a 2:1 (w/w) mixture of field soil and autoclave-sterilized sand. Plants were maintained at approximately 80% field capacity [33,34] and harvested 35 days after emergence. No drought treatment was imposed. Thus, plants from both agroecological zones were grown under the same well-watered conditions [30]. At harvest, 10 active nodules per plant, identified by their pink-red coloration [32], were collected. Nodules from the three replicate pots belonging to each farm were pooled to obtain one nodule sample per farm. This resulted in 10 nodule and 10 soil sequencing libraries, giving a total of 20 libraries.

Table 1. Soil physico-chemical parameters of samples collected from two agro-ecological zones in Tharaka-Nithi County, Kenya.

Parameters	Non-arid	Semi-arid	*p*-value
pH	5.74 ± 0.38	5.71 ± 0.17	1.00
EC (mmhos/cm)	0.13 ± 0.04	0.06 ± 0.03	0.03
MC (%)	5.04 ± 0.61	2.64 ± 0.50	0.01
N (%)	0.18 ± 0.03	0.10 ± 0.04	0.02
C (%)	1.82 ± 0.32	1.00 ± 0.35	0.02
K (mg/Kg)	58.04 ± 25.35	20.95 ± 7.63	0.01
P (mg/kg)	20.95 ± 2.96	12.08 ± 5.28	0.01
Mg (mg/Kg)	29.36 ± 3.24	21.90 ± 1.21	0.01
Ca (mg/Kg)	432.26 ± 65.55	332.88 ± 35.09	0.06
Fe (mg/Kg)	1.11 ± 0.09	0.86 ± 0.14	0.02
Zn (mg/Kg)	1.03 ± 0.19	0.81 ± 0.07	0.02

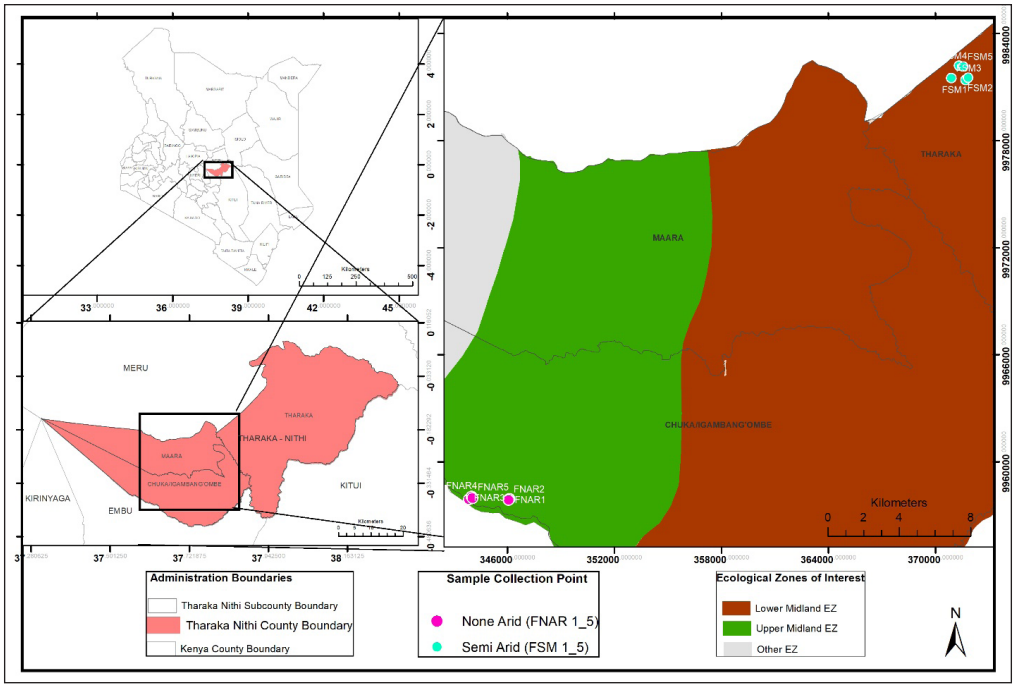

Figure 1. Map of Kenya showing the sampling sites within the study region of Tharaka-Nithi County. Source: generated using GPS coordinates, with the map produced in ArcGIS v10.8. The areas highlighted in green and red mark the two ecological zones of interest, while sample collection points appear in pink for non-arid sites and cyan for semi-arid sites. Farm labels FNAR1–5 and FSM1–5 identify the individual non-arid and semi-arid sampling farms, respectively.

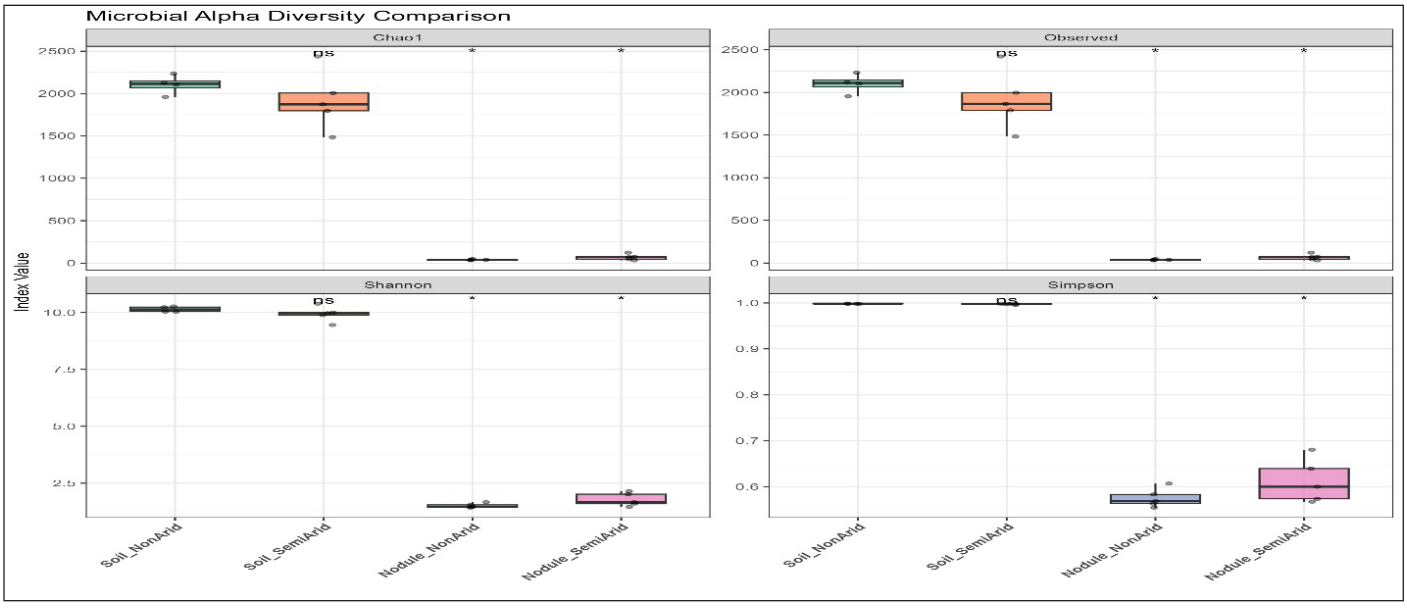

Figure 2. Microbial alpha diversity across soil and root-nodule samples, compared between aridity zones. Four panels capture this: Chao1 richness, observed ASVs, Shannon diversity, and the Gini–Simpson index. Each box marks the interquartile range (IQR), with the horizontal line inside showing the median. Individual replicates appear as jittered points scattered around each box. "ns" marks a non-significant pairwise comparison between non-arid and semi-arid soil sample replicates.

2.3. Genomic DNA Extraction, Bioinformatics, and Statistical Analysis

Pooled nodule samples were thoroughly washed with sterile distilled water to remove adhering soil particles. The nodules were then surface-sterilized with 75% ethanol and aseptically crushed in sterile distilled water using a sterile mortar and pestle. Genomic DNA was extracted from 0.5 g of homogenized bulk soil and processed nodule material using the ZymoBIOMICS™ DNA Miniprep Kit (Zymo Research, USA), following the manufacturer's instructions. Purified DNA was stored at −20°C until library preparation. DNA quality

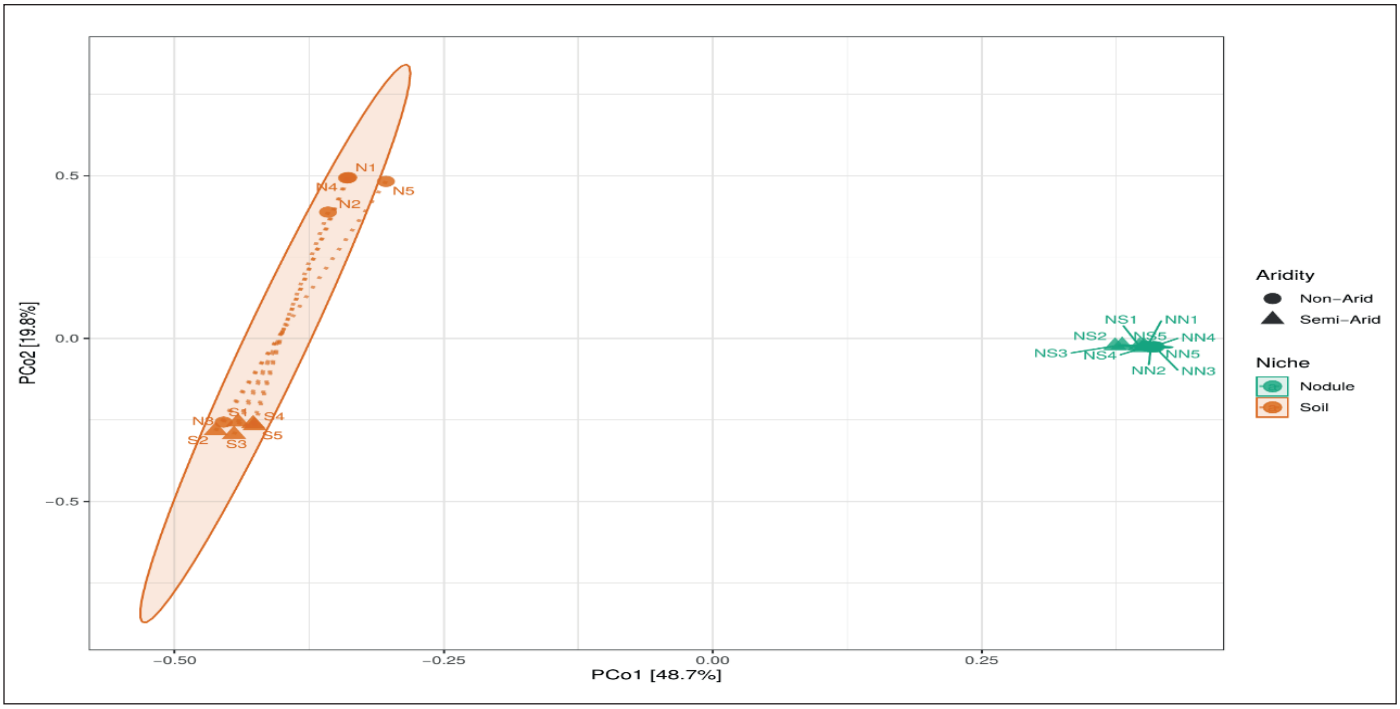

Figure 3. PCoA plot of microbial community diversity in bulk soil and root nodules from non-arid and semi-arid ecological zones, based on Bray–Curtis dissimilarities after Hellinger transformation ($n = 20$). The plot illustrates how bacterial community structure shifts across niche and aridity, with PCo1 accounting for 48.7% of total variation and PCo2 for 19.8%. Sample codes: N, non-arid soil; S, semi-arid soil; NN, non-arid nodules; NS, semi-arid nodules.

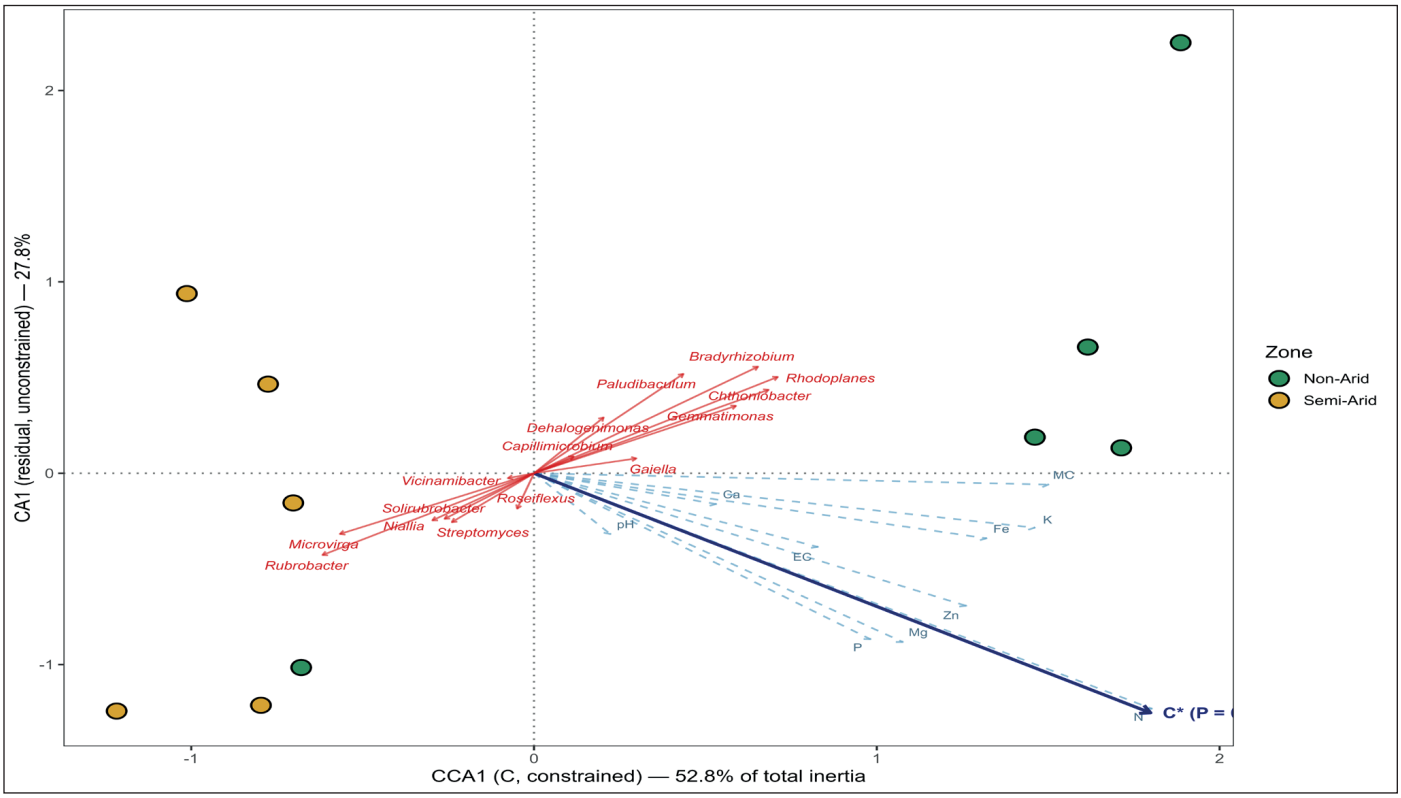

Figure 4. CCA biplot showing the relationships between the 15 most abundant soil bacterial genera and soil physicochemical properties ($n = 10$). After assessment of multicollinearity using variance inflation factors (VIFs), forward selection using ordistep with 999 permutations, organic carbon (C) was the only environmental variable retained as a statistically significant driver ($F = 8.950$, $p = 0.006$, VIF = 1 in the final single-predictor model; full-model VIF = 1.94, Supplementary Table S8), with CCA1 explaining 52.8% of the total inertia (eigenvalue = 0.220). The solid dark-blue arrow represents organic carbon, the sole variable retained in the constrained model. Light-blue dashed arrows represent the remaining physicochemical variables, plotted as passive variables for visualization, while red arrows represent the 15 most abundant bacterial genera. Full forward-selection statistics are provided in Supplementary Table S7.

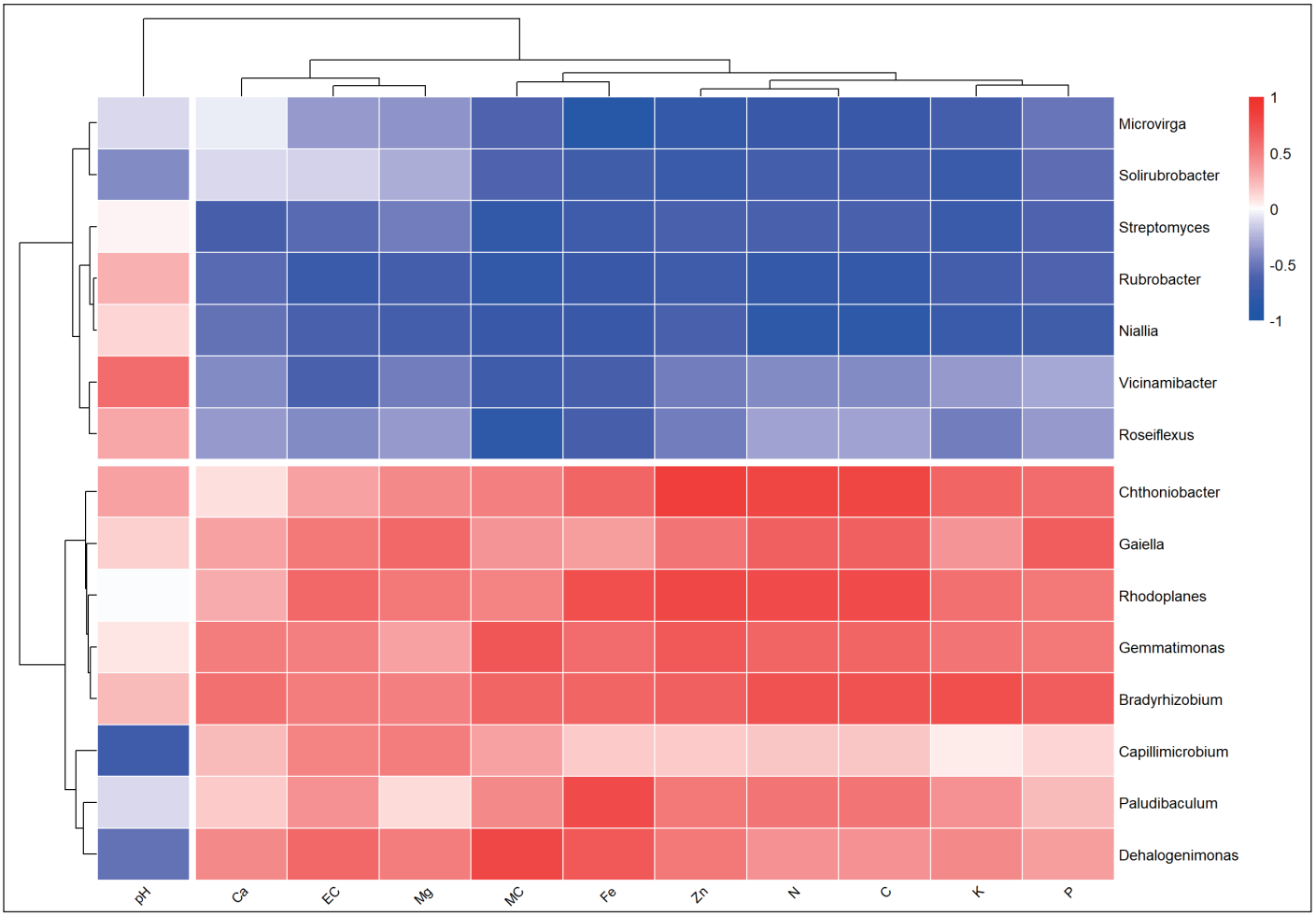

Figure 5. Spearman correlation heatmap showing the relationships between the 15 most abundant bacterial genera and 11 soil physicochemical properties across both agroecological zones (n = 10). Genera are shown as rows, while soil variables are shown as columns. The color scale ranges from blue (negative correlation) to red (positive correlation), from −1 to +1. Hierarchical clustering groups genera and soil variables with similar correlation patterns. After FDR correction for the 165 pairwise comparisons, none of the correlations remained statistically significant. The full correlation coefficients, together with the raw and FDR-adjusted p-values, are provided in Supplementary Table S10.

and integrity were assessed using NanoDrop spectrophotometry and agarose gel electrophoresis. The bacterial 16S rRNA gene V3–V4 region was amplified using the universal 341F/805R primer pair (forward: 5′-CCTACGGGNGGCWGCAG-3′; reverse: 5′-GACTACHVGGGTATCTAATCC-3′), following the Illumina metagenomic sequencing protocol. Library preparation and sequencing were performed by Macrogen using an Illumina MiSeq platform with 2 × 300 bp paired-end chemistry.

Raw sequencing reads were first assessed using FastQC [35]. Adapter sequences and low-quality reads were removed using Cutadapt [36] and fastp [37]. Denoising and amplicon sequence variant (ASV) inference were performed using DADA2 within the QIIME2 platform [38,39]. Sequencing quality metrics for all samples are presented in Supplementary Table S1. Rarefaction curves were generated using Chao1, Observed Features, and Shannon indices to assess sequencing depth and coverage of bacterial diversity (Supplementary Fig. S1). Taxonomic classification was performed using BLAST+ [40] against the NCBI reference database. Diversity and ordination analyses were conducted in R using the microeco and vegan packages [41,42]. Predictive functional profiling was performed using PICRUSt2 (v2.5.2) on the Galaxy platform, using the KEGG Orthology (KO) and MetaCyc pathway databases [43,44]. Eight functional categories related to plant growth promotion and stress tolerance were examined: nitrogen fixation (K02586, K02588, and K02591), phosphate solubilization (K01077 and K01078), siderophore production (K02013 and K02014), indole-3-acetic acid (IAA) biosynthesis (K00466 and K00817), urease subunit alpha (K01428), valine dehydrogenase (K00271), glycine betaine biosynthesis (K00128), N-acetyl-gamma-glutamyl-phosphate reductase (argC; K00145). For each sample and ASV, KO contributions were estimated by multiplying marker-gene-copy-number-normalized ASV abundance by the corresponding PICRUSt2-predicted gene copy number. The resulting contributions were summed across ASVs in R and grouped into the eight functional categories. For predicted PGP/stress-tolerance functions traced to specific taxa (Fig. 8), and for putative *Bradyrhizobium* species-level assignments (Section 3.6), ASV relative abundance (%) was averaged across biological replicates within each group (n = 5 per nodule zone; n = 5 per soil zone; n = 10 for pooled soil) in R, to generate the group-level means reported in Supplementary Tables S12–S14. Functional profiles were visualized as hierarchically clustered heatmaps using Euclidean distance and Ward.D2 linkage [45].

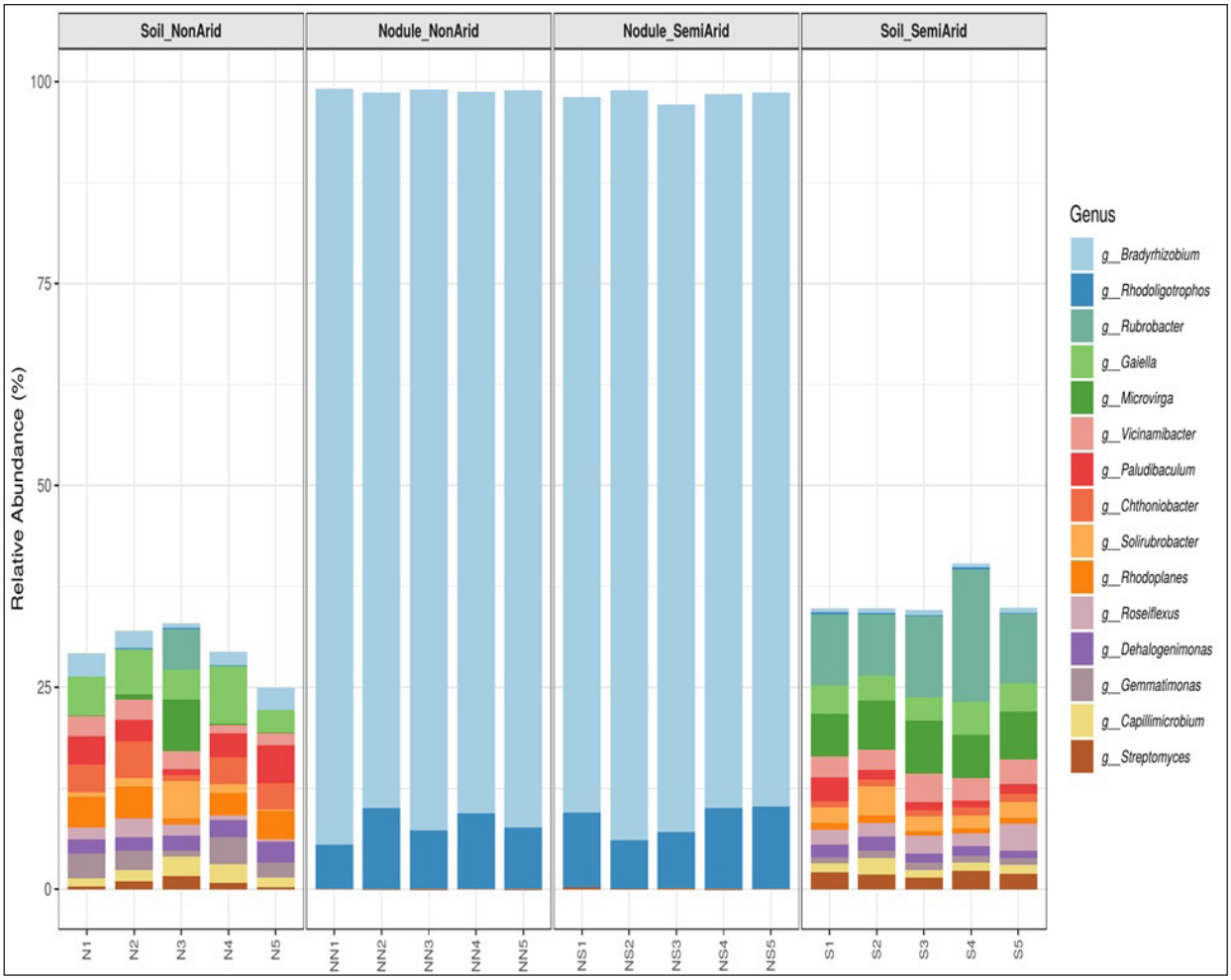

Figure 6. Bacterial community composition in cowpea bulk soil and root nodules across two ecological zones based on the 16S rRNA gene. Bar plots illustrating the taxonomic relative abundance of dominant bacterial taxa at the genus level. Samples are categorized into non-arid soil (N), semi-arid soil (S), non-arid nodules (NN), and semi-arid nodules (NS).

Heatmaps were generated with the pheatmap package [46]. Mean weighted Nearest Sequenced Taxon Index (NSTI) values were also calculated to assess prediction confidence (Supplementary Table S3). The predicted functions were interpreted as indicators of functional potential rather than confirmed biological activities. Differences in alpha diversity among the four groups were evaluated using the Kruskal–Wallis test followed by pairwise Wilcoxon rank-sum tests [47]. The four groups were defined according to niche compartment (bulk soil and root nodules) and agroecological zone (non-arid and semi-arid). The Benjamini–Hochberg method was applied to control the false discovery rate (FDR) [48]. Homogeneity of multivariate dispersion among groups was assessed using PERMDISP (betadisper) [49]. Genus-level relative abundance (%) was calculated for each sample and visualized using stacked bar plots generated with the ggplot2 package [50]. Differences in the relative abundance of the top 15 genera among the four sample groups were assessed using one-way ANOVA followed by Tukey's honestly significant difference post hoc test [51], with pairwise comparisons summarized as a compact letter display; full statistical results are provided in Supplementary Table S16. Differentially abundant taxonomic biomarkers between niche compartments and agroecological zones were identified using Linear Discriminant Analysis Effect Size (LEfSe) [52], using an LDA score threshold of 2.0 and $\alpha = 0.05$ for the Kruskal–Wallis and pairwise Wilcoxon tests; resulting p-values were further adjusted for multiple comparisons using the Benjamini–Hochberg FDR procedure [48], with adjusted $p < 0.05$ considered statistically significant (Supplementary Table S6). Differences in bacterial community composition among niches and agroecological zones were assessed using PERMANOVA with 999 permutations in the vegan package [42]. Pairwise comparisons and full F-statistics are reported in Supplementary Table S9. Predicted abundances of the eight functional categories were compared between soil and nodule communities, and between agroecological zones within each compartment, using two-sided Wilcoxon rank-sum tests in R. P-values from all 24 comparisons were jointly adjusted using the Benjamini–Hochberg FDR procedure [48], with adjusted $p \leq 0.05$ considered statistically significant (Supplementary Table S11). CCA and Spearman correlation analyses were performed on soil samples only ($n = 10$) to examine relationships between bacterial community composition and soil physicochemical properties. CCA was conducted in R using the vegan package [42] and the 15 most abundant bacterial genera. Detrended correspondence analysis was first used to determine the appropriate ordination model [53]. Full-model variance inflation factors (VIFs) were calculated for all 11 physicochemical variables to assess multicollinearity

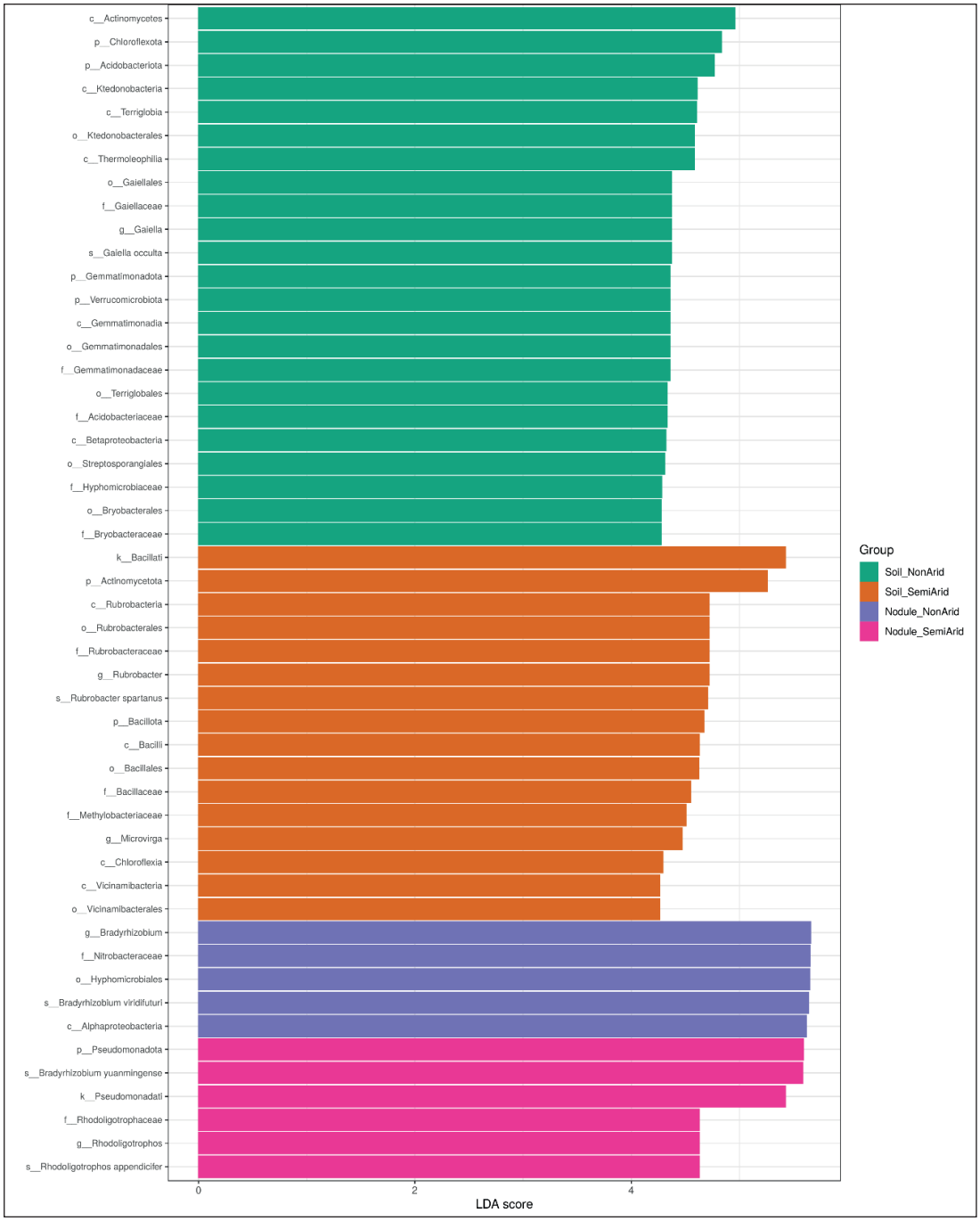

Figure 7. Linear Discriminant Analysis (LDA) Effect Size (LEfSe) identifying the top 50 microbial biomarkers (LDA score > 2.0) distinguishing bulk soil and root nodule bacterial communities across non-arid and semi-arid agroecological zones. Taxa are shown across multiple taxonomic ranks (species to phylum); bar color indicates the sample group in which each taxon was significantly enriched, and bar length represents the LDA effect size.

(Supplementary Table S8); variables were not pre-filtered based on VIF. Independent environmental drivers were identified by forward selection using the ordistep function with 999 permutations, starting from a null model and retaining variables that significantly improved model fit ($p < 0.05$). The final constrained model was assessed using permutation-based ANOVA with 999 permutations, and the VIF of the selected model was reported. Non-selected physicochemical variables were passively fitted using the envfit function with 999 permutations for visualization. Spearman rank correlations were calculated between the relative abundances of the 15 most abundant bacterial genera and the 11 measured soil physicochemical variables, resulting in 165 genus–environment comparisons. Correlations were calculated using the cor.test() function in R. *P*-values were adjusted across all 165 comparisons using the Benjamini–Hochberg FDR method [48], with adjusted $p \leq 0.05$ considered statistically significant. Correlation patterns were visualized using a hierarchically clustered heatmap generated with the pheatmap package. Genera and physicochemical variables were clustered using Euclidean distance and complete linkage.

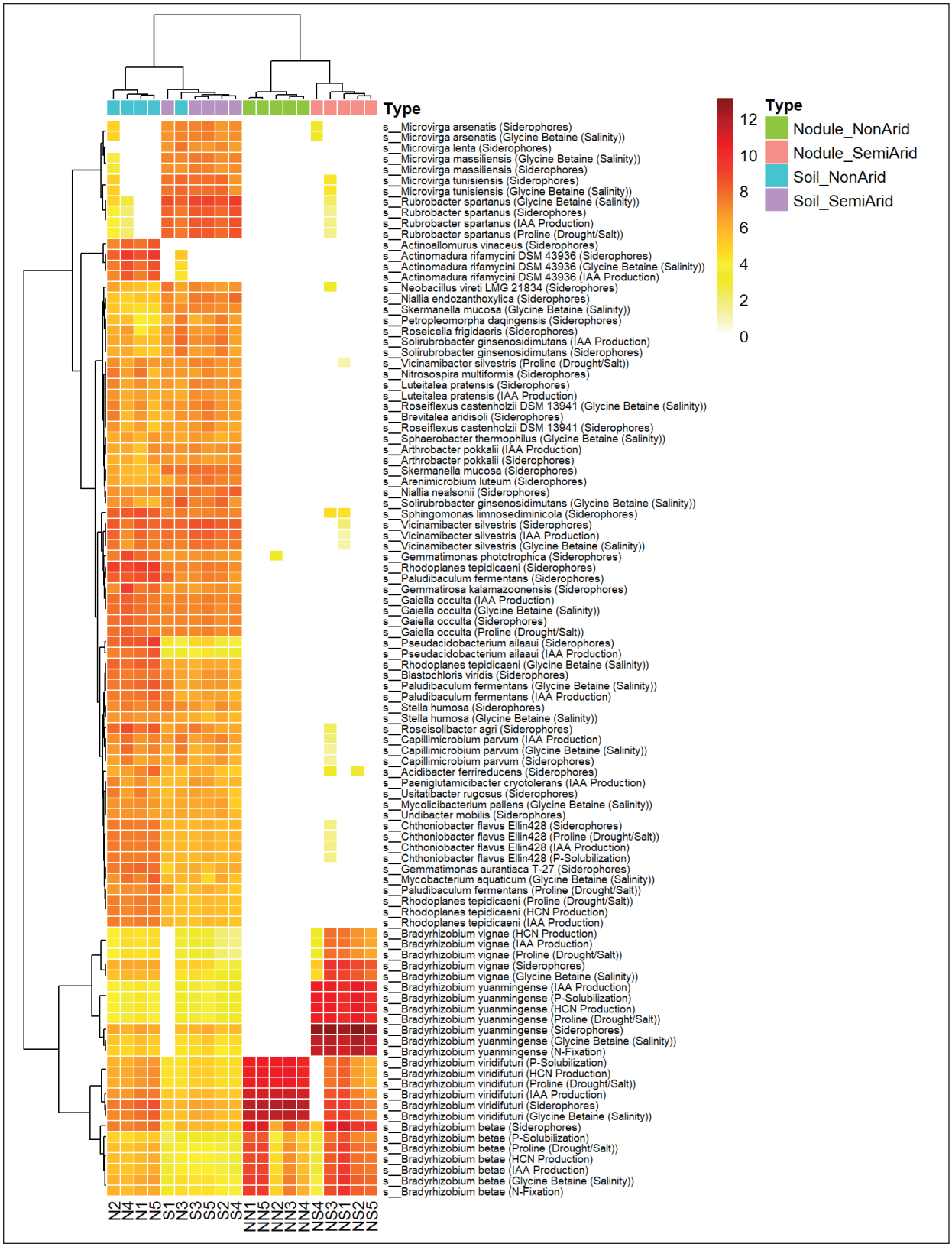

Figure 8. Clustered heatmap showing the predicted contributions of plant-growth-promoting (PGP) and stress-tolerance gene families across taxa, based on PICRUSt2 KEGG Orthology predictions. Functional intensity is shown on a log scale, with lower contributions represented by white/yellow and higher contributions by dark red. The top annotation bar indicates the four sample groups: Soil_NonArid (cyan), Soil_SemiArid (purple), Nodule_NonArid (green), and Nodule_SemiArid (pink). Genus-level dominance by *Bradyrhizobium* provides the most robust basis for interpreting the predicted functional patterns shown here; taxon-level assignments within this genus are treated with caution (see Discussion). Formal statistical comparison of the eight underlying PGP/stress-tolerance functional categories is reported in Supplementary Table S11.

3. RESULTS

3.1. Soil Physico-Chemical Properties across Agroecological Zones

Soil physico-chemical properties varied significantly among semi-arid and non-arid agro-ecological zones, as illustrated in Table 1. These variations demonstrated strong environmental heterogeneity in the study sites. The non-arid agro-ecological zone had significantly higher EC, moisture content, total nitrogen, organic carbon, phosphorus, potassium, magnesium, iron, and zinc concentrations compared with semi-arid soils ($p < 0.05$). This implies that the environment in the non-arid zone was more nutrient-rich. However, soil pH and calcium levels did not differ significantly between the two agro-ecological zones ($p > 0.05$), although calcium was nearly significant ($p = 0.056$). This shows that the two zones differed in terms of moisture content and nutrient availability.

3.2. Sequencing Quality and Microbial Coverage

The raw sequencing data exhibited mean Q20 and Q30 values of 99.4% and 97.9%, respectively, and an average GC content of 56.6%; the Q30/Q20 ratio is ≈ 0.985 (or 98.5%), reflecting high sequencing quality. Total average reads after quality filtering were 92,821. Denoised reads were 84,513, and merged reads accounted for 64,502. A total of 12,213 ASVs for 16S rRNA were identified across all samples. Good's coverage exceeded 99%, which indicates sufficient sequencing depth for downstream analyses. Across all 20 sequenced samples, non-chimeric read counts ranged from 32,635 to 87,729 reads per sample (mean = 57,827 reads), with group-level ranges of 40,723–60,745 (non-arid soil, $n = 5$), 63,901–83,377 (non-arid nodule, $n = 5$), 32,635–46,452 (semi-arid soil, $n = 5$), and 48,962–87,729 (semi-arid nodule, $n = 5$) (Supplementary Table S1). Rarefaction curves showed that most samples approached a plateau across the three alpha-diversity metrics, indicating that the sequencing depth captured the major patterns of bacterial diversity. However, several Chao1 and Observed Features curves remained slightly upward at the highest read depths, suggesting that additional sequencing could recover a limited number of rare taxa (Supplementary Fig. S1)

3.3. Microbial Diversity in Soil and Root Nodules

Alpha diversity was analyzed using Observed ASVs, Chao1, Shannon, and Gini–Simpson indices. The results revealed significantly higher microbial richness, diversity, and community evenness in soil samples compared with root nodules ($p < 0.05$), as indicated in Figure 2. Non-arid soils had the highest observed taxa richness numerically, although this difference from semi-arid soils was not statistically significant, whereas root nodules showed markedly reduced diversity relative to both soil groups. These results suggest strong host-mediated microbial selection and a more specialized microbial assemblage within nodules. Differences in alpha diversity between semi-arid and non-arid soils were not statistically significant across any of the diversity indices, indicating that aridity had a limited effect on overall microbial richness and diversity relative to ecological niche. For example, observed ASV richness averaged 2075.60 ± 114.22 in non-arid soils and 1911.00 ± 342.00 in semi-arid soils, with both groups assigned to the same compact-letter group ('a'). In contrast, root nodules exhibited markedly lower richness, with 38.20 ± 5.72 ASVs in non-arid nodules and 67.20 ± 34.52 ASVs in semi-arid nodules, both belonging to compact-letter group ('b'). The same pattern was consistently observed for the Chao1, Shannon, and Gini–Simpson indices (Supplementary Table S2). Pairwise comparisons for each index (Wilcoxon rank-sum test, FDR-corrected) are provided in full in Supplementary Table S4. This confirms that ecological niche, rather than aridity, was the dominant driver of alpha diversity, consistent with the non-significant pairwise comparisons between aridity zones within each niche.

3.4. Microbial Community Assembly of Soil and Root Nodules based on Ecological Niches and Aridity Levels

Beta diversity analysis revealed distinct shifts in microbial community composition across ecological niches and aridity levels (agroecological zones). Principal Coordinate (PCoA) showed that the first two axes explained 68.5% of the total variation, with PCo1 explaining 48.7% and PCo2 explaining 19.8%. As shown in Figure 3, a strong separation along PCo1 clearly distinguished soil and root nodule microbial communities. These findings indicate that ecological niche was the primary factor associated with differences in bacterial community structure. Soil samples displayed greater dispersion than root nodules, which suggests higher microbial heterogeneity in soils and stronger host-mediated selection within nodules; homogeneity of multivariate dispersion among groups was formally evaluated using PERMDISP (betadisper): dispersion differed significantly overall ($F = 23.63$, $p = 0.001$) and specifically between the nodule and soil compartments (pairwise permuted $p \leq 0.009$ for all niche-based comparisons), indicating that part of this compositional separation may partly reflect within-group dispersion rather than centroid location alone; critically, dispersion did not differ significantly between non-arid and semi-arid soils ($p = 0.379$), indicating that the aridity-associated separation observed within soil communities reflects genuine compositional differences rather than a dispersion artifact (complete PERMDISP results in Supplementary Table S15). Along PCo2, semi-arid and non-arid soils formed distinct clusters, demonstrating that aridity was associated with further shifts in soil microbial composition, in combination with other unmeasured, co-varying agroecological factors (see Discussion). In contrast, root nodule communities remained closely clustered despite the aridity level. Furthermore, pairwise PERMANOVA (999 permutations, Bray–Curtis dissimilarity, FDR-adjusted *p*-values) confirmed significant compositional variability among all six pairwise comparisons of the four sample groups (all padj ≤ 0.026; $F = 4.05–24.67$; $R^2 = 0.34–0.76$), with the full pairwise results reported in Supplementary Table S9.

3.5. Microbial Community Assembly of Soil and Root Nodules Related to Physicochemical Properties

CCA identified organic carbon (C) as the only statistically significant independent environmental driver of soil bacterial community composition. After assessment of multicollinearity using VIFs among the 11 physicochemical variables, forward selection with 999 permutations retained C as the sole significant variable ($F = 8.950$, $p = 0.006$, VIF = 1 in the final model; full-model VIF = 1.94, Supplementary Table S8; forward-selection statistics in Supplementary Table S7). CCA1 had an eigenvalue of 0.220 and explained 52.8% of the total inertia (Fig. 4). No other variable significantly improved the model after C was included ($p > 0.05$), although moisture content showed the closest association ($p = 0.121$). The remaining passively fitted variables (MC, Ca, Fe, K, EC, Zn, Mg, and P) were aligned with the C axis, indicating a shared fertility–moisture gradient rather than independent environmental effects. Bacterial genera and soil samples showed a clear separation along this gradient. Chthoniobacter, Rhodoplanes, Gemmatimonas, *Bradyrhizobium*, Paludibaculum, Dehalogenimonas, Capillimicrobium, and Gaiella occurred toward the C-associated end of CCA1, whereas *Rubrobacter*, *Microvirga*, Niallia, Streptomyces,

Soli*rubrobacter*, Vicinamibacter, and Roseiflexus occurred toward the opposite end. Non-arid soil samples were mainly positioned on the positive side of CCA1, while semi-arid samples were predominantly located on the negative side, corresponding to the two ends of the fertility–moisture gradient. Genera positioned toward the positive (carbon-associated) end of CCA1 were also aligned with moisture content, consistent with organic carbon capturing a broader fertility–moisture gradient rather than acting as an isolated driver. Spearman correlation analysis showed a similar overall pattern at the genus level (Fig. 5; Supplementary Table S10), but none of the 165 genus–environment comparisons remained significant after Benjamini–Hochberg correction; these patterns are therefore best regarded as descriptive and exploratory (see Discussion). The stronger statistical evidence comes from the CCA, which identified organic carbon as an independent driver of community composition. Taken together, the analyses point to a broader fertility–moisture gradient underlying soil bacterial community variation, rather than independent effects of individual nutrients or pH.

3.6. Distinct Taxonomic Composition between Soil and Root Nodules

The genus-level stacked bar plot (Fig. 6) showed pronounced variability in bacterial community composition between soil and root nodule samples. Root nodules were strongly dominated by *Bradyrhizobium*, which accounted for 90.91% and 89.67% of the bacterial community in non-arid and semi-arid nodules, respectively, compared with only 2.02% and 0.54% in the corresponding soils (Supplementary Table S16); this pattern confirms strong host-mediated selection of the genus regardless of agroecological zone. *Rhodoligotrophos* emerged as a consistent secondary component of the nodule microbiome, maintaining 7.99%–8.5% relative abundance across both zones while remaining at or below 0.18% in bulk soil. Together, these two genera accounted for approximately 98%–99% of the nodule bacterial community, leaving minimal representation for taxa otherwise abundant in soil. Semi-arid soils were characterized instead by higher abundances of stress-adapted genera: *Rubrobacter* (10.29%), *Microvirga* (5.87%), and *Vicinamibacter* (2.88%), reflecting adaptation to drought-prone and nutrient-limited conditions. Non-arid soils, by comparison, favored *Gaiella* (4.76%), *Paludibaculum* (2.91%), *Chthoniobacter* (3.05%), and *Rhodoplanes* (2.93%), consistent with more favorable conditions for organic matter decomposition, carbon turnover, and nutrient cycling. LEfSe analysis (Fig. 7) further supported these compositional differences, identifying significant taxonomic biomarkers across the four sample groups (LDA > 2.0, FDR-adjusted $p < 0.05$; full statistical results in Supplementary Table S6). *Rhodoligotrophos* (appendicifer/Rhodoligotrophaceae) emerged as the single highest-ranking biomarker by LDA score, distinguishing nodules from soil irrespective of zone and matching its niche-specific abundance pattern in the bar plot above. Actinomycetes, Chloroflexota, Acidobacteriota, and Gemmatimonadota were significantly enriched in non-arid soils, whereas semi-arid soils showed enrichment of *Rubrobacter*, Bacilli, *Microvirga*, Methylobacteriaceae, and Vicinamibacteria. Non-arid nodules were additionally characterized by biomarkers including *Bradyrhizobium viridifuturi*, Nitrobacteraceae, Hyphomicrobiales, and Alphaproteobacteria, while semi-arid nodules carried a distinct biomarker set comprising Pseudomonadota, *Bradyrhizobium yuanmingense*, Rhodoligotrophaceae, and *Rhodoligotrophos* (including *Rhodoligotrophos* appendicifer at the species level). Although both nodule zones remained dominated by the same host-selected genus, the specific taxa and phyla driving that dominance differed by zone.

3.7. Plant Growth-Promoting Functional Traits Are Enriched in Nodules

KEGG Orthology-based profiling showed differences in the predicted PGP and stress-tolerance functions between soil and nodule communities (Fig. 8). The predicted functions included nitrogen fixation, phosphate solubilization, siderophore production, IAA biosynthesis, HCN production, ACC deaminase activity, and osmoprotectant biosynthesis related to drought and salinity tolerance. Mean weighted NSTI was lower in nodules (0.031 ± 0.002) than in soil (0.237 ± 0.028), indicating higher prediction confidence for the nodule samples (Supplementary Table S3). After Benjamini–Hochberg correction, 13 of the 24 comparisons were significant (Supplementary Table S11). Compared with soil, nodules had higher predicted levels of HCN production, phosphate solubilization, glycine betaine biosynthesis, IAA biosynthesis, proline biosynthesis, and siderophore production (P_FDR ≤ 0.013). ACC deaminase showed the opposite pattern, with higher predicted abundance in soil. Among the soil samples, non-arid soils had higher predicted ACC deaminase, HCN production, and IAA biosynthesis than semi-arid soils (P_FDR ≤ 0.047). In nodules, predicted IAA production was higher in the non-arid zone, whereas predicted siderophore production and nitrogen-fixation potential were higher in semi-arid nodules (P_FDR = 0.017). *Bradyrhizobium* remained the predominant genus in root nodules across both agroecological zones. The nodule communities were also characterized by predicted functions associated with nitrogen fixation, phosphate solubilization, IAA and siderophore production, as well as stress tolerance. BLAST-based assignments suggested differences in the putative *Bradyrhizobium* species between zones. Semi-arid nodules were mainly associated with *B. yuanmingense*, *B. vignae*, and *B. betae*, while non-arid nodules were mainly associated with *B. viridifuturi* and *B. betae* (Supplementary Tables S12 and S13). Since the V3–V4 region has limited resolution for closely related *Bradyrhizobium* species, these assignments were treated as putative and were not used for strain-level interpretation. Confirmation would require higher-resolution markers such as nodC and recA or shotgun metagenomics [54–58]. Soil communities included *Rubrobacter*, Actinomadura, and Rhodoplanes, with predicted functions related to nutrient mobilization, iron acquisition, and stress tolerance (Supplementary Table S14). These taxon–function relationships are based on PICRUSt2 predictions and therefore indicate potential functions rather than measured biological activity.

4. DISCUSSION

The findings indicate that cowpea bacterial community assembly was shaped by both environmental conditions in the soil and host-associated selection within root nodules, consistent with a sequential model in which environmental conditions first structure the bacterial pool surrounding the plant, followed by more selective recruitment into root nodules. This interpretation aligns with recent evidence that rhizosphere, root, and nodule bacterial communities are shaped by host-regulated gatekeeping, in which the plant selectively permits compatible microbes to colonize the nodule niche while excluding others [59], consistent with earlier work in other crop systems showing that root-associated compartments assemble through a multistep, increasingly selective process [17]. PCoA showed a clear separation between soil and nodule communities, fitting the selective role of plant roots, which favor recruitment of a narrower subset of bacteria from the surrounding soil into the nodules [60]. PERMANOVA supported this directly. Within the soil compartment, non-arid and semi-arid communities formed distinct clusters along PCoA2, whereas nodule communities remained relatively closely grouped across both agroecological zones, indicating a stronger influence of environmental

conditions on soil communities and host-associated selection on nodule structure [61]. The absence of significant dispersion differences between non-arid and semi-arid soils confirms that this separation reflects genuine compositional differences rather than within-group variability [49]. Alpha diversity reinforced this pattern, with soil communities consistently showing greater richness, diversity, and evenness than nodule communities across all four indices (Observed ASVs, Chao1, Shannon, and Gini–Simpson), strengthening confidence in this result [62] and matching the expectation that host-mediated selection restricts which soil bacteria successfully establish within nodules [20]. This selection appeared to be independent of aridity. No significant differences in alpha diversity were observed between the two zones in either soil or nodule communities, indicating that aridity did not reduce the number of taxa present. Beta diversity, however, did differ significantly between the zones, indicating that aridity reshaped which bacteria were present rather than how many. This decoupling of composition from richness contrasts with reports of both experimentally imposed drought stress in cowpea [63] and natural aridity gradients across global drylands [64], where richness itself declined. Our pattern is instead consistent with the classical ecological principle that the environment acts as a selective filter, favoring organisms specifically adapted to local conditions, rather than as a limiting factor on total community richness [65]. The taxonomic and LEfSe results highlight the bacterial taxa involved and their potential functional roles. *Bradyrhizobium* dominance in nodules extended across its entire taxonomic lineage, from the family Nitrobacteraceae to the order Hyphomicrobiales and class Alphaproteobacteria, with no other bacterial class showing a distinct compositional pattern within this niche. This saturation from genus to class signals unusually strong host selection, showing just how tightly the host controls which organisms persist in the nodule, consistent with reports of strong host-driven selection of rhizobial partners from soil, root-surface, and nodule compartments [66]. *Rhodoligotrophos*, the highest-ranking biomarker overall (Fig. 7; Supplementary Table S6), was consistently detected in nodules across both zones. Its presence is consistent with the broader group of non-rhizobial endophytes (NREs), which can coexist with rhizobia in nodules without inducing nodulation and may contribute to plant growth promotion or support effective nodulation [20], although its specific functional role remains to be established. Among the semi-arid-associated soil genera, *Microvirga* stands out. This genus is more than just a stress-tolerant, free-living soil bacterium. One of its species, *Microvirga vignae*, was isolated directly from cowpea root nodules in semi-arid Brazil and formally described as a nitrogen-fixing rhizobial symbiont [67]. This suggests that its enrichment in semi-arid soil is not merely coincidental; it may reflect a genuine reservoir of cowpea-associated symbiotic bacteria. Streptomyces, also enriched in semi-arid soil, has been shown to increase nodulation frequency, nodule size, and nitrogenase activity when co-inoculated with rhizobia [68]. This suggests that it may contribute to nodulation under more resource-limited conditions. Among the genera associated with non-arid soils, *Rhodoplanes* has been linked to nitrogen-related processes in the rhizosphere and identified as a hub taxon in a nitrogen-metabolism co-occurrence network [69]. In addition, Actinomycetes, Chloroflexota, Acidobacteriota, and Gemmatimonadota are commonly associated with the breakdown of complex organic matter; Chloroflexota, specifically, has been linked to cellulose and lignin degradation in agricultural soils [70]. Their enrichment in the non-arid soils may therefore be related to the higher organic carbon content rather than to drought tolerance. This pattern differs from reports in other plant systems, where drought has been linked to increased abundance of Actinomycetes [71]. Notably, this class-level signal (Actinomycetes) in non-arid soils is distinct from the phylum-level Actinomycetota biomarker identified in semi-arid soils (Fig. 7), a biologically meaningful distinction. The class-level signal specifically tracks organic carbon availability, consistent with the broader role of Actinomycetes in enriching soil organic matter and nutrient cycling [72], and with a substrate-driven response, whereas the broader phylum-level signal in semi-arid soils likely reflects a more generalized stress response spanning multiple Actinomycetota lineages, consistent with reports that edaphic stress shapes Actinobacterial community structure across the phylum [73]. Beyond carbon cycling, Actinomycetes have also been specifically linked to legume productivity. By promoting nitrogen availability and the activity of key nitrogen-metabolizing enzymes, including nitrate reductase, glutamate synthase, and glutamine synthetase, they have been shown to improve seed quality and yield in legume rhizospheres [72]. Their enrichment in non-arid soils may therefore extend beyond organic matter cycling to offer a direct plant-productivity benefit. A recent shotgun metagenomic study of sorghum rhizosphere soil under different crop rotations, including cowpea–sorghum rotation, also identified Actinomycetota as a dominant bacterial phylum and reported associations between soil physicochemical properties and microbial community composition [74]. A recent study using a nearly identical approach on common bean nodules in a semi-arid region reached the same conclusion, reflected in the zone-specific *Bradyrhizobium*, *Rhodoligotrophaceae*, and *Pseudomonadota* biomarkers observed here: host-level filtering, rather than fine-scale variation within species, is what actually shapes which bacteria persist in the nodule [75]. Soil physicochemical conditions likely shape cowpea-associated bacterial communities through resource availability and environmental filtering. Moisture and fertility, in particular, determine which bacteria establish and persist in the rhizosphere. Once established, these bacterial communities contribute to nutrient cycling and other plant-associated functions, and may also include bacteria capable of colonizing root nodules [16]. Non-arid soils carried higher moisture and several nutrient-related properties than semi-arid soils, but pH and calcium told a different story. Neither varied significantly between zones (Table 1). It was moisture and nutrient status, not pH or calcium, that drove the main contrast between zones. This pH stability likely matters for *Bradyrhizobium*. Unlike many other rhizobia, which favor near-neutral to alkaline conditions, this genus tolerates more acidic soils [76], and the mildly acidic-to-neutral pH found across both zones here (Table 1) falls comfortably within that range [77]. This may help explain why *Bradyrhizobium* dominated nodules regardless of zone. Calcium works differently, but its role is just as direct. During early rhizobial infection, calcium influx and spiking in root hairs follow Nod-factor perception and are needed for the infection thread to form [78]. Because calcium levels did not shift between zones, it probably was not limiting symbiotic establishment in either one, consistent with the stable nodulation observed throughout. Beyond pH and calcium, these differences in soil resources can alter nutrient availability and the conditions supporting microbial growth and activity [18]. CCA captured this genus-level pattern directly. Organic carbon emerged as part of a broader fertility–moisture gradient rather than an isolated driver, consistent with the class-level Actinomycetes enrichment discussed above. Spearman correlations showed a similar direction of association, though caution is warranted. Of 165 genus–environment comparisons, 56 were nominally significant ($p < 0.05$), but none survived Benjamini–Hochberg correction, so these associations remain exploratory rather than confirmed. Chthoniobacter, Gemmatimonas, and Rhodoplanes tracked with higher carbon and moisture, while *Rubrobacter*, *Microvirga*, and Soli*rubrobacter* tracked with more resource-limited conditions [79–83]. Tellingly, *Rubrobacter* and the other resource-limited-associated genera were found exclusively in soil, never in nodules from either zone (Fig. 6), pointing

to environmental filtering operating within the soil compartment itself, distinct from recruitment into the host niche. This convergence across CCA and Spearman, despite the latter's exploratory status, suggests the fertility–moisture gradient may shape not just community composition but predicted functional potential too, with implications for cowpea nutrient acquisition and stress adaptation. This physicochemical link has direct agronomic relevance. In a semi-arid Kenyan cowpea system, conservation agriculture practices that improved soil moisture and organic matter retention showed potential to enhance biological nitrogen fixation [84]. Shared *Bradyrhizobium* ASVs between soil and nodules support a possible connection between the two pools, though amplicon data cannot establish direct recruitment of individual strains. The soil environment likely shapes which rhizobia are available, while host selection then determines which of these actually establish within the nodule. For semi-arid cowpea production, this suggests that maintaining sufficient soil organic carbon and moisture may help sustain microbial and rhizobial populations under water- and nutrient-limited conditions [85,86]. However, it remains uncertain whether these soil conditions would lead to greater nodulation, nitrogen fixation, or cowpea productivity. Field studies that combine soil management practices with rhizobial inoculation are needed to determine their effects.

The functional profiles point to distinct ecological roles for soil and nodule communities within the cowpea-associated microbiome, with nutrient acquisition and stress-tolerance functions in nodules particularly relevant given their close association with the host [12,13,87–89]. Siderophore production likely influences iron availability, consistent with reports that siderophore-producing bacteria can enhance host iron content [90]. This predicted function may be particularly relevant given that soil iron concentrations differed significantly between zones (Table 1). Similarly, phosphate solubilization can increase phosphorus availability for plant nutrition and nitrogen-fixation-related processes [13,91], while measured soil phosphorus also differed significantly between zones (Table 1). Because *Bradyrhizobium* accounts for approximately 90% of the nodule community in both zones (Section 3.6), this predicted enrichment of siderophore- and phosphate-related functions is plausibly attributable to this genus specifically: *Bradyrhizobium* is documented to possess molecular mechanisms for adapting to variable iron and phosphorus availability and to increase nitrogenase activity under stress conditions [92]. Glycine betaine and proline are compatible solutes that help maintain cellular osmotic balance under water-limited conditions, and IAA is associated with root development and nutrient uptake [13,89]; bacterial IAA specifically promotes root elongation and architectural changes that improve access to deeper soil moisture, offering a plausible mechanism through which the predicted IAA biosynthesis could support cowpea performance under water limitation [10]. Predicted HCN production could contribute to microbial competition in the rhizosphere, though its direct contribution to cowpea performance remains uncertain [93]. Higher predicted ACC deaminase in soil likely reflects the greater importance of stress-related functions in the rhizosphere [88]; the associated glycine betaine and proline biosynthesis functions linked to *Rubrobacter* align with genomic evidence that this genus synthesizes compatible solutes as part of its stress-resistance strategy, consistent with its enrichment under the more resource-limited semi-arid conditions [94]. Zone-level differences add a further layer. The higher predicted nitrogen-fixation potential in semi-arid nodules is consistent with lower soil nitrogen availability increasing the importance of biological nitrogen acquisition, though this remains a prediction requiring direct assays to confirm. The pattern nevertheless aligns with evidence that climate-adapted *Bradyrhizobium* strains can improve cowpea productivity and symbiotic performance under contrasting climatic conditions [85,95] and may reflect functional variation within the *Bradyrhizobium* community across zones, consistent with reports linking such variation to environmental adaptation, competitiveness, or symbiotic performance [96–98]. *Bradyrhizobium betae* was also detected in nodules from both zones at comparable, lower abundances, in contrast to the zone-specific dominance of *B. viridifuturi* and *B. yuanmingense*, suggesting a shared, minor species alongside the zone-dominant ones. These species-level assignments should be treated cautiously: the V3–V4 region provides limited resolution among closely related *Bradyrhizobium* lineages, so the genus-level dominance pattern offers a more robust basis for interpretation than any species-level claim [54–58]. This is illustrated at finer resolution in Figure 8 and Supplementary Tables S12–S14, where predicted functions cluster by compartment and zone even at the species level, though these finer-resolution labels remain exploratory. More broadly, PICRUSt2 estimates genomic potential from phylogenetic placement rather than measuring gene expression or biological activity directly [43]. The lower mean NSTI in nodules (0.031) than in soil (0.237) indicates greater prediction confidence for nodule communities, but predictions for both compartments ultimately require experimental validation. Overall, this study provides an integrated view of bacterial community assembly in cowpea-associated soil and root nodules across contrasting agroecological zones in Tharaka-Nithi. The findings highlight three linked patterns. Strong differentiation between soil and nodule communities, association of soil bacterial composition with a fertility–moisture gradient, and persistent *Bradyrhizobium* dominance within nodules despite differences in the surrounding soil environment, consistent with reports that cowpea nodules host a similar bacterial community regardless of soil properties [99]. The identification of *Rhodoligotrophos* as a consistent nodule-associated taxon, together with the predicted functional differences between compartments, provides candidate microbial features for future investigation, pending field and experimental studies to determine whether these patterns translate into measurable gains in cowpea nutrient acquisition, stress tolerance, nodulation, nitrogen fixation, and overall productivity.

5. CONCLUSION AND RECOMMENDATIONS

This study showed that ecological niche and aridity were associated with differences in cowpea-associated bacterial communities. Non-arid soils had greater moisture and nutrient availability, while bacterial richness remained similar between zones. Nodule communities were less diverse and strongly dominated by *Bradyrhizobium*, indicating host-associated selection. PCoA, PERMANOVA, and CCA identified ecological niche as an important factor in community assembly, with soil organic carbon associated with the fertility–moisture gradient. PICRUSt2 predicted functional differences, including higher nitrogen-fixation potential in semi-arid nodules. These predictions require experimental validation, and the identified taxa should therefore be considered candidates for future isolation, functional testing, and development of locally adapted bioinoculants.

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7. CONFLICTS OF INTEREST

The authors report no financial or any other conflicts of interest in this work.

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9.ETHICAL APPROVALS

This study does not involve experiments on animals or human subjects.

10. DATA AVAILABILITY

All the data is available with the authors and shall be provided upon request.

11. AUTHORS' CONTRIBUTIONS

All authors made substantial contributions to conception and design, acquisition of data, or analysis and interpretation of data; took part in drafting the article or revising it critically for important intellectual content; agreed to submit to the current journal; gave final approval of the version to be published; and agreed to be accountable for all aspects of the work. All the authors are eligible to be authors as per the International Committee of Medical Journal Editors (ICMJE) requirements/guidelines.

12. USE OF ARTIFICIAL INTELLIGENCE (AI)-ASSISTED TECHNOLOGY

During the preparation of this manuscript, the authors used Grammarly solely for language editing, including improvements to grammar, sentence structure, clarity, and readability. All suggested changes were reviewed and verified by the authors. No AI tools were used to generate, alter, or manipulate research data. The authors take full responsibility for the final content of the manuscript.

13. SUPPLEMENTARY MATERIAL

The supplementary material can be accessed at the journal's website: Link here [https://jabonline.in/admin/php/uploadss/1531_pdf.pdf]

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