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Cover trees association changed bacterial diversity in coffee production systems

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Abstract

Traditional coffee agroforestry systems often involve shade trees, which play a crucial role in maintaining soil fertility and biodiversity. In contrast, monoculture systems negatively influence soil chemistry, microbial diversity, and overall soil health over time. Although the use of cover trees such as mango (*Mangifera indica L.*) and banana (*Musa paradisiaca, var. Cavendish*.) has been shown to have beneficial effects on the soil chemical properties, little is known about their influence on microbial communities associated with coffee agricultural systems. The main objective of this study was to identify the bacteria inhabiting roots and soil of three coffee management systems via partial 16S rDNA sequencing, and to assess how coffee-shade tree associations, with different soil and plant parameters, influence the bacterial ecosystem. Results revealed that the association between coffee and shade trees improved alpha diversity, with the highest diversity found in the mango-coffee system. The dominant bacterial genera found in most of the samples, i.e., *Kribbella, Nonomuraea, Nitrospira, Sphingobium,* and *Neobacillus*, were strongly correlated with key soil chemical properties, including nitrogen content, organic matter, and available phosphorus. These correlations suggest that tree cover strategies exert beneficial effects on the bacteria microbiome. Moreover, the overall bacterial community structure was different when comparing coffee monoculture system and shade-associated systems. Our findings highlight that traditional coffee agroforestry practices involving shade trees foster more diverse and functionally enriched bacterial communities, thereby contributing to healthier soils and more sustainable coffee production.

Keywords: Bacterial community structure, Coffee agroforestry, Diversity, Shade trees, Sustainable agriculture.

Introduction

Coffee is a crop that is studied for its economic importance. After water, it is the most consumed beverage and most merchandized tropical agricultural product all around the world (Zhao et al. 2024). Mexico accounts for around 2.3% of the world's coffee production. This is related to the high production close to 2.7 million tons per year (FAO 2021; Colipse 2025). Mexico, in particular, produces around 899,000 tons per year. The state of Veracruz is the second producer with 24% of the national production (Secretaría de Agricultura y Desarrollo Rural 2022).

The primary systems for coffee production are shade-grown coffee and coffee grown under full sun (Koutouleas et al. 2022). Although the monoculture of coffee is widely distributed around the world, many of the promised benefits, such as higher seed production, lower incidence of pests and diseases, mechanization, and a reduction in human work, are now being discussed in the context of environmental resilience. Monoculture cultivation practices are commonly used; however, they often result in reduced plant growth, lower yields, and increased susceptibility to diseases associated with poor soil management (Li et al. 2016). Moreover, coffee monocultures tend to be less resilient to environmental stressors such as frost. For instance, recent events in Brazil led to an estimated 5.5% reduction in harvest production (close to 412,000 bags with 60 kg each) in comparison to previous years (Sánchez, 2025).

Given these challenges, the production of coffee should prioritize on shade-grown systems, which have been associated with improved coffee quality and enhanced environmental factors such as organic matter content, nutrient concentration in leaves, and nutritional status of the fruit (Piato et al. 2020; Getachew et al. 2023). The shade tree association is also related to an increase in pollinators, such as ants and birds, as well as associated flora like epiphytes and woody plants, playing a role in the connectivity between agroecosystems and neighboring forest patches (Philpott 2005; Buechley et al. 2015; Goodall et al. 2015; Kumsa et al. 2016).

In previous publications related to the coffee rhizosphere microbiota, an important percentage of them followed culture-dependent approaches and few studies employed a metabarcoding approach (Duong et al.

2020). Several authors have emphasized the importance of molecularly identifying soil beneficial microorganisms associated with coffee as an essential step in prospecting those that may be used as inoculants (Duong et al. 2020; Gómez-Godínez et al. 2024). These microorganisms have relevant traits such as promotion of plant growth, coffee bean production, biological control against several phytopathogens, and production of metabolites with several biotechnological applications. Moreover, soil microbial community structure is strongly linked to sensory and chemical profiles in the coffee fermentation (Duong et al. 2020; Gómez-Godínez et al. 2024; Gomes et al. 2024). However, research on soil bacteria in coffee shade systems remains scarce.

The association of coffee with other trees can be a new factor for the composition of microbial communities, as observed in grapevines, where the association with grasses had an important role in the composition of the root fungal communities. Other findings have highlighted that the cover-associated crops impact the mycorrhizal abundance and regulate the phosphorus cycle, increasing P-microbial biomass, and phosphatase activity (Vukicevich et al. 2018; Hallama et al. 2018). Concerning the microbial diversity of soils, bacterial and fungal richness decreased with continuous coffee cropping and showed a decrease in the presence of beneficial microbes such as *Nitrospira* and *Trichoderma* (Zhao et al. 2018).

Our previous research investigated the soil beneficial effects of shade-tree associations on soil quality in coffee systems, particularly the coffee-mango (CM) and coffee-banana (CB) combinations. The results showed that integrating shade trees in coffee cultivation enhances soil, plants and fruit quality. In particularly, the CM system significantly improved soil properties related to fertility and fruit production, including pH, cation exchange capacity, potassium (K) and nitrogen (N) soil concentrations, organic matter, carbon to nitrogen (C/N) ratio, microbial biomass, and the abundance of earthworms, when compared with the full-sun coffee (SC) system (Romero Fernández et al., 2023). These results indicate that the CM association has a major positive effect on soil, foliar, and grain parameters. Notably, the CM system is rarely implemented and has seldom been reported among coffee agroecosystems worldwide. In contrast, the CB system, at least in the Veracruz area in Mexico, is one of the most common and well-established shade-based coffee systems, found in both traditional or commercial plantations (Ruiz-García et al. 2021). Some of the beneficial effects observed in these systems may be linked to differences in soil and root-associated microbial communities. This possibility motivated the present study, as bacterial microbiomes play an integral role in nutrient cycling and plant health. Understanding

the complex bacterial community structure under shade or SC systems is crucial for sustainable production and soil health.

Although numerous studies have examined bacterial diversity and activity in the rhizosphere of several coffee systems, this analysis is novel in that it focuses on systems incorporating mango, a rarely used agroforestry shade tree. Moreover, the influence of soil and plant chemical parameters in the coffee systems on bacterial community structure also has received little attention. Therefore, this study focused on: a) the molecular identification of bacteria inhabiting roots and rhizosphere soil of three coffee management systems, such as coffee-banana (CB), coffee-mango (CM), and full sun-coffee (CS) systems, and the trees involved (banana and mango); b) To understand how the coffee association impacts soil and plant parameters and the bacterial ecosystem in which they grow. The hypotheses are: 1) there are differences in bacterial communities between the three coffee systems, 2) there are correlations between bacterial diversity, and soil and plant chemical properties, and 3) the bacterial communities in the rhizosphere soil differ from those found in roots. The study shows information on *silica* bacteria associated in roots and soil of coffee plants from three different agroecosystems.

Materials and methods

Sampling

The study was conducted in coffee plantations located in “La Tinaja” village, Municipality of Emiliano Zapata, Veracruz, Mexico (19º 30’ 54" N, 96º 44’ 20" W, and 810 amsl). The three coffee systems evaluated were 25 years old and included two shade-grown plantations and one coffee monoculture. One shaded system (CM) had manila mango trees (*Mangifera indica* L.), while the other (CB) included banana trees (*Musa paradisiaca* var. *Cavendish*). Coffee varieties (*Coffea arabica* L. cv. *Caturra, Catimor*, Mundo Novo, and Costa Rica) were randomly distributed across all systems. The total study area comprised 2.5 ha, with 0.7 ha allocated to each shaded system and 0.9 ha for the full-sun system (CS).

A stratified randomized soil sampling was conducted in the dry season (August 2020). At each site, soil samples containing roots were collected from four points, manually homogenized, and combined into a single

composite sample for each of the 15 sampling points per plant species. In total, 75 composite samples were obtained: 15 from CM, 15 from CB, 15 from CS, 15 from mango, and 15 from banana trees (Romero Fernández et al., 2023). From these, three biological replicates per coffee production system were selected for molecular analyses.

DNA extraction

For DNA extraction of roots (20 fragments) and rhizosphere soil (500 mg) samples, the FastDNA Spin Kit for soil (MP Biomedicals, Santa Ana, CA, USA) was used following the manufacturer's instructions with the exception that for root samples the lysing matrix type A was supplemented with one extra ¼ inch ceramic bead to assure complete rupture of the roots (Senés-Guerrero et al., 2014).

The DNA extracted from the samples was quantified using a NanoDrop ND-1000 UV-Vis spectrophotometer (NanoDrop Technologies, Wilmington, DE). DNA extracts were stored at -80°C until further analysis. High-throughput sequencing of the V3-V4 regions of the 16S rRNA gene was performed by Novogene Corporation Inc. (Chaoyang District, Beijing, China) using an Illumina NovaSeq 6000 PE250 (paired-end to generate 465 base paired-end raw reads), obtaining at least 100k raw reads per sample employing the 341F (CCTAYGGGRBGCASCAG) and 806R (GGACTACNNGGGTATCTAAT) primers.

Data processing and taxonomic association

QIIME (Quantitative Insights into Microbial Ecology) 2.0 v.2022.11 (Bolyen et al. 2019) was used to analyze raw 16S rRNA gene sequence data using the following pipeline: Firstly, chimeric, marginal sequence errors, and noisy sequences were filtered out and the errors in the sequences were corrected using DADA2 before selecting ASVs (Callahan et al., 2016). Subsequently, two characteristic tables [FeatureData(Sequence) and FeatureData(Taxonomy)] were generated by aligning sequences at a 99% identity level against the Greengenes2 database, version 2024.09 (McDonald et al. 2023). The q2-feature-classifier plugin, along with a trained Naive Bayes classifier for the 16S rRNA V3-V4 hypervariable region, were used to assign taxonomy to representative ASVs. Finally, taxonomy classification was conducted using classify-sklearn, and taxon bar charts were created and downloaded in CVS format from view.qiime2.org. The 16S rRNA gene sequences used for this study were deposited in the Sequence Read Archive of the public NCBI database under BioProject PRJNA1314311.

Diversity and statistical analysis

The ASVs were used to analyze the α and β-diversity of soils and roots associated with the cultivar trees. The R v4.2.2 was used along with the Phyloseq (McMurdie and Holmes 2013), ggplot2 (Wickham 2016), vegan (Oksanen et al. 2022) packages. To assess the α-diversity, Chao1, Shannon and Simpson diversity indices were used. For the evaluation of the ß-diversity, Bray-Curtis distance matrix and the PcoA ordination method were performed. The resulting matrix was evaluated using the ANalysis Of SIMilarity (ANOSIM) statistical function (Varsos et al. 2016). Differential ASVs abundance was estimated using R's package DESeq2 (Love et al. 2014; Halwachs et al. 2017; Jara-Servin et al. 2025).

For the correlation analysis between rhizosphere soil and plant parameters and the taxonomic assignments, a non-metric multidimensional scaling (NMDS) analysis based on Bray-Curtis distances was performed using the vegan package in R. Subsequently, redundancy analysis (RDA) was applied to explore the relationships between the microbial community composition and the chemical parameters of both soil and plants. To test the correlations between the relative abundance of taxa and soil or plant variables, Spearman´s rank correlation analyses were performed using the corrplot package (v0.84). This approach allowed the identification of ASVs most strongly associated with the environmental parameters (Contreras-Negrete et al., 2024).

Results

Bacterial composition in soil and roots

A total of 6,057,114 reads were obtained from sequencing, after the round with DADA2 the number was reduced to 3,917,582, being 2,202,494 classified at the genus and species level. The prokaryotic communities of the systems were predominantly composed of *Neobacillus, Gottfrieda, Streptomyces, Sphingomicrobium, Mycobacterium,* and *Cyanobacteria* (Fig. 1a). The cyanobacteria *Symploca* are particularly present in root samples of all coffee systems, but with a lower proportion in roots of banana and mango. Table 1 presents the core genera present in at least 80% of all samples analysed. The genera observed are *Kribellia, Nonomuraea, Nitrospira, Sphingobium*, and *Neobacillus.*

Most genera (147) are common in the three coffee systems, trees, and rhizosphere soil/root compartment. However, some bacterial genera are specific to the system and compartments. Roots showed a higher diversity

of genera in banana (46), CM (39), CB (31), and mango (22) compared to those in the rhizosphere soil in the same systems. The results also highlight that the roots of the CS system have less endemism than this in the shade tree systems (Fig. 1b).

Shade-grown coffee systems exhibited a higher number of bacterial genera compared with the CS system (Fig. 2), demonstrating that the association with cover trees increases bacterial diversity within the system. In the CS system, 476 genera were identified, of which 53% (254) were shared between rhizosphere soil and roots, 28% were only found in rhizosphere soil and 19% are exclusive of roots. In the CM association, 614 genera were detected, representing 29% increase relative to CS. Of these, 57% (348) were shared between rhizosphere soil and roots, while 21% and 23% were unique to roots and rhizosphere soil, respectively. Similarly, the CB system presented 643 bacterial genera, corresponding to a 35% increase compared with CS. In this system, 66% of genera were shared between rhizosphere soil and roots, 21% were exclusive to rhizosphere soil, and 12% were unique to roots (Fig. 2).

Table S1 shows the fifty most biologically relevant genera which were selected based on three criteria: magnitude of differential abundance (absolute log2FoldChange), statistical significance (adjusted *p*-value, *padj*), and baseline relative abundance (*baseMean*). The ten more representative genera from the significant analysis were *Symploca*, *Achromobacter, Lysinimonas, Catellatospora, Sinorhizobium, Gp1.AA122*, *Angustibacter, Burkholderia,* and *Granulicella*. The cyanobacteria *Symploca* exhibit the strongest statistical significance, followed by an unclassified Xanthobacteraceae, *Burkholderia*, and *Bacillus.* Another notable downregulated genus included *Achromobacter* and *Sinorhizobium*. In contrast, *Gp1.AA122,* an unclassified *Xanthobacteraceae*, *Granulicella*, and *Oceanobacillus* were among the most strongly upregulated genera (Table S1).

The most prevalent genera for the mango and CM are *Bacillus*, *Brevundimonas*, *Nannocystis*, *Sinorhizobium, Bacillus, Mesobacillus*, and *Micromonospora*. In contrast, for banana and CB, these are UBA4765, *Alkalihalobacillus*, Steroidobacteraceae. A big group of genera (20) is common from CB and banana tree. In another hand, *Achromobacter, Pedobacter, Pseudoxanthomonas* are strongly related with soils of CM system (Fig. S1).

α and β diversity

186 The lowest α-diversity was obtained in CS systems in both roots and rhizosphere soil (represented by Shannon,
187 Evenness, Simpson and Chao1 indexes), (Fig. 3a-d). Regarding the coffee systems and trees, there is high
188 significance in these indexes (Shannon; p=0.004, Simpson; p=0.032, Evenness; p= 0.041 and Chao1; p=0.080).

189 Among rhizosphere soil and roots samples, there are no statistical differences in the indexes; except in Chao
190 1 for banana (Fig. 3c). The increase of the *α* diversity is related to the association with the shade trees. Shannon
191 index and the Pielou´s evenness is statistically different in CM system compared to this in CS (p=0.014). In
192 contrast, CB is different to CS in the indexes Chao1, Shannon and evenness (p= 0.024). Bananas have the
193 highest value in all indices that coffee systems and mango. At the same time, it has more bacterial diversity than
194 CS.

195 On average, the richness is 335 ASVs at the genera level and 1438 at species level (data not shown). Chao1
196 richness average is 300; this gives an idea of the total information covered by the sequencing. The average
197 Shannon, Simpsons and Evenness diversity indexes across coffee systems and trees are 3.466, 0.867, and 0.607
198 respectively (Fig. 3b-d).

199 PCoA shows a clear separation between the bacterial communities associated with coffee roots from the
200 rhizosphere soil and roots have different bacterial communities' rhizosphere soil samples and trees (Fig. 4). The
201 PERMANOVA results revealed a significant difference between the two coffee shade systems and CS (R2 =
202 0.054, p = 0.001).

203 Correlation between diversity, soil and plant chemical parameters

204 The chemical properties of soils (Fig. 5a) and plants (Fig. 5b) were used for a redundancy analysis (RDA). In
205 the first case, soil chemical parameters, particularly pH, electrical conductivity (EC), organic matter (OM),
206 nitrogen content (Ns), concentration available of phosphorus (Ps), potassium (Ks), and soil micronutrients such
207 as zinc (Zns), iron (Fes), and copper (Cus) explain approximately 88% of the total variation in the bacterial
208 community structure (RDA1: 66.17%, RDA2: 22.19%).

209 All soil chemical parameters had a strong influence on the bacterial communities; except for Cus, C:N, and
210 soil moisture (SM), which had less effects, but were still significant. Along the first axis (RDA1), a clear
211 separation is observed between bacterial microbiomes from CS- soils and roots, which cluster on the far right.

Similarly, root-associated samples from CM and CB systems occupy distinct positions from their corresponding soils. *Mezorhizobium*, Cyanobacteria and Actinobacteria were prevalent in the CM and mango. These soil samples were more associated with soil OM. On the other hand, *Mycobacterium* and *Tumebacillus*_A were prevalent in banana related environments. These soils more related with parameters like Ns and EC, respectively (Table S2).

In the case of plant composition parameters, the redundancy analysis (RDA), performed between sampling sites and the chemical composition of plant tissues (Fig. 5b), explained approximately 91% of the total variation in the bacterial communities (RDA1: 76.1%; RDA2: 14.9%). The analysis revealed clear differentiation among crop systems, in terms of their association with nutrient profiles in plants.

Samples from associated coffee systems, such as CB and CM, particularly in the root compartment, clustered in the upper-central portion of the plot and showed moderate association with plant micronutrients like copper (Cup) and chlorophyll b (Clb). Meanwhile, mango and banana tress grouped in the lower-right quadrant and were positively associated with zinc (Znp), iron (Fep), and calcium (Cap). In contrast, CS samples appeared separated along the RDA1 axis.

Spearman correlation analysis revealed distinct associations between soil chemical parameters and the principal bacterial taxa (Fig. 6a). Micronutrients such as phosphorus (Ps) and nitrogen (Ns) display strong correlations with *Streptomyces* (positive) and *Peribacillus* (negative) with Ns. Zinc soil concentration (Zns) showed a marked negative relationship with *Bacillus* A, while calcium soil concentration (Cas) was positively associated with *Neocardioides* and *Fictibacillus*. Meanwhile, *Tumebacillus* appeared negatively correlated with SM.

The Spearman correlation between bacterial communities and plant nutrient content reveals specific associations (Fig. 6b). A strong negative relationship was observed between *Tumebacillus* and *Geodermatophilus* with calcium (Cap) in plant tissue, suggesting a potential role in calcium mobilization or uptake. In contrast, *Peribacillus* showed a positive correlation with Cap. Phosphorus plant concentration (Pp) correlated positively with *Actinoplanes*, *Nocardioides*, and *Geodermatophilus*, hinting at their possible contribution to phosphorus availability or solubilization. Additionally, *Sphingomicrobium,* and *Caballeronia* were negatively associated with magnesium plant concentration (Mgp). While micronutrients such as Cup and

Znp displayed mostly weak correlations, the overall pattern suggests specific interactions between root or soil bacteria and nutrient accumulation in plants.

Discussion

Bacterial composition of coffee agrosystems is diverse and shaped by plant interactions

This study is the first to characterize bacterial communities present in the roots and soils of Mexican coffee plantations in Veracruz grown under two agroforestry systems (CM and CB) compared to a full-sun monoculture system (SC), as well as their relationships with soil and leaf chemical properties across these production systems. In addition, bacterial diversity was also analysed in the roots and rhizosphere soils of mango and banana trees that provide shade in the coffee systems. This new information offers insights on the functional roles of bacteria and their potential to establish more sustainable and resilient coffee plantations based on shade-tree systems instead of full-sun monocultures. Therefore, this study provides scientific evidence supporting management strategies that incorporate the bacterial communities associated with rhizosphere soils and roots in coffee cultivation.

Across all systems, the core bacterial microbiome included phyla commonly reported in coffee agrosystems (Actinobacteria, Nitrospirae, Cyanobacteriota, Bacteroidota, Bacteriodetes, Bacillota, Pseudomonadota, Firmicutes), except Thermoproteota, which had not previously been reported in coffee soils (Table 1). Previous reports on the bacterial microbiome of coffee plantations in three regions of Colombia indicate that Firmicutes and then Chloroflexi and Acidobacteria were the most abundant phyla in soil samples from coffee cultivation at Cauca (Duong et al., 2020; Gómez-Godínez et al., 2024). While Acidobacteria, Nitrospirae and Proteobacteria were, in this order, the most abundant phyla in soils from Risalda. In soils from Magdalena, Colombia, the most abundant phyla were Planctomyces, Acidobacteria, and Verrucomicrobia (Gómez-Godínez et al., 2024). These findings highlight the importance of environmental conditions and plant associations on bacterial diversity.

Regarding Thermoproteota, this archaeal phylum commonly found in rhizosphere soils, as well as in marine and freshwater ecosystems, demonstrating its wide ecological adaptability (Taffner et al., 2018; Jung et al.,

2020). Its detection in coffee soils represents the first report of this group in this type of environment. Soils enriched with Thermoproteota members have been associated with roles in the nitrogen cycle, fixing carbon dioxide, and traits influencing plant growth promotion (Jung et al. 2020). For example, members of *Creanarcheota,* a lineage within Thermoprotetota, were found in olive orchards and suggested to play roles in soil-plant interactions (Thenappan et al., 2024). Therefore, its importance as core species in the bacterial microbiome of coffee is interesting and demands further research.

Members of Proteobacteria identified in the core microbiome of soils cultivated with *C. arabica* and *C. canephora* have also been identified in this study, including Xanthobacteraceae, *Rhizobium multhospitiium*, *R. mososinicum* and *Bradyrhizobium* sp., all of which were present across samples and are known to form central components of the coffee rhizosphere bacteriome (Fig. 1a) (Bullergahn et al., 2024). Families such as *Xanthobacteraceae*, *Nitrosomonodaceae*, and *Beijerinckiaceae*, as well as the genera *Burkholderia*, *Afipia*, *Allorhizobium*, *Ideonella*, *Mesorhizobium*, and *Pseudoaminobacter*, and the species *Clostridium magnum,* were identified exclusively in the *C. arabica* soils in previous studies. These taxa have been proposed as important for enhancing soil nitrogen availability, highlighting the relevance of maintaining and promoting them through sustainable management practices.

Coffee rhizosphere are enriched with plant-beneficial bacteria

The rhizosphere microbiota has received most attention through culture-dependent approaches, while fewer studies have used metabarcoding analysis, and even less have analysed coffee roots. A recent study isolated Vietnamese endophytic bacteria from roots and seeds of *Coffea canephora* and *C. liberica*, identifying members of the Actinobacteria, Firmicutes, and Proteobacteria phyla (Duong et al., 2021). Other studies around the world have reported Protobacteria as the dominant phylum (55%) in the rhizosphere microbiome of coffee, followed by Actinobacteria (13%), Bacteroidetes (9%), Acidobacteria (8%), Chloroflexi (5%), Patescibacteria (3%), Planctomycetota (3%), Verrucomicrobia (3), and other phyla accounting for less than 0.1% (Bez et al., 2023). Through 16S rRNA gene sequencing, the present study described the bacterial communities associated with coffee plant roots and identified the core microbiome, represented mainly by *Kribbella, Nonomuraea, Nitrospira, Sphingobium* and *Neobacillus* (Table 1), along with clear patterns of distribution across the coffee agricultural systems.

293 The results obtained in the present study are consistent with genera previously reported by de Sousa et al.,
294 (2022), such as *Streptomyces*, *Bradyrhizobium*, and *Mycobacterium* as predominant taxa in the coffee
295 rhizosphere (Fig. 1a). These genera are proposed as members of the core rhizosphere microbiome with potential
296 plant-growth-promoting functions, such as nitrogen fixation associated with *Bradyrhizobium*. The detection of
297 these genera in the present work points to their fundamental ecological role and stable association with the
298 coffee plant, regardless of the host species.
299 One of the core bacterial members identified here, *Nitrospira*, was also reported in Brazil, China, Honduras
300 (Costa et al. 2024) and Colombia (Gómez-Godínez et al., 2024). S*treptomyces* was also found in Brazil,
301 Honduras, Colombia and China (Duong et al., 2021; Gómez-Godínez et al., 2024; Costa et al., 2024). Similarly,
302 *Caballeronia* was also observed in coffee soils of China (Duong et al., 2021). Genera such as *Bacillus,*
303 *Bradyrhizobium, Mycobactrium*, and *Rhodococcus*, which were among the most abundant across all sites in this
304 study, have been also found in Colombia (Gómez-Godínez et al., 2024).

305 Some bacteria associated with coffee cultivars, such as *Sphingomonas,* have been reported to promote plant
306 growth by secreting gibberellins and modulating stress-induced ethylene through the production of 1-
307 aminocyclopropane-1-carboxylic acid (ACC) deaminase (Shi et al., 2022; Bez et al., 2023). This supports the
308 idea that bacterial communities influence plant health and plant-plant interactions. Interestingly, results from
309 this study showed the presence of Cyanobacteria particularly in the roots of associated systems, suggesting
310 potential relevance for sustainable coffee development (Fig. 1a).

311 The type of coffee cultivation modifies bacterial diversity
312 Results from the present study show that bacterial diversity and richness are influenced by the association
313 between coffee plants and shade trees such as mango and banana~~,~~ with clear differences between the SC and
314 the shade-grown systems (Fig. 3). As has been reported previously, bacterial diversity and richness are shaped
315 by cultivation type (Bez et al., 2023). Those authors compared community richness in samples from greenhouse
316 and field conditions, highlighting that microbiome composition was mainly driven by cultivation systems. The
317 common core microbiome across multiple conditions was dominated by Actinobacteria, consistent with reports
318 from other authors (Fulthorpe et al. 2020; de Sousa et al. 2022).

In relation to ß-diversity, the bacterial microbiome is strongly shaped by the presence of coffee roots (Fig. 4). Other reports also highlight the coffee roots to assemble specialized microbial communities (Fulthorpe et al., 2020). One factor proposed to influence coffee plant microbiomes is that several of the main coffee growing regions are characterised by acidic soils, which are poor in OH^- ions and present high saturation of H^+ and Mn (Romero Fernández et al., 2023). Under these conditions, acidophilic bacteria such as strains from the genus *Acidibacter* are enriched, this genus was observed in the present study particularly in the roots of the CS and CB systems. Members of *Acidibacter* include extremophiles capable of reducing ferric iron and have been identified as part of the "common-core microbiome" of coffee, suggesting that they can play important roles such as Fe acquisition (Bez et al., 2023).

Chemical profile of soil and plant characteristics influence bacterial communities

The patterns observed in the Spearman correlation analysis suggest that specific soil nutrient conditions, particularly micronutrients and plant-available elements, selectively influence different microbial taxa. This aligns with to Partelli et al. (2012) and Jurburg et al. (2020), who indicated that soil use, coffee management, and chemical parameters can act as strong selective forces on the soil microbiome. In the present results, relationships between bacterial diversity and soil chemical parameters such as N, OM and P, explained an important part of the bacterial diversity (Fig. 5a). There parameters are strongly influenced by agricultural management practices. At the same time, six bacterial taxa namely *Sphingobium, Rhizobium*, *Sphingomonas, Burkholderia* and *Amycolatopsis* showed a higher correlation with those chemical parameters (Fig. 6a). More heterogeneous environmental conditions and greater plant diversity in shade-grown coffee systems promote favorable conditions to induce a diverse and specialized bacterial community (Villarreyna et al., 2020).

A few studies have contributed insights into the principal determinants of the coffee microbial communities (both fungi and bacteria). For example, Oliveira et al. (2013) described the microbiome of coffee beans; Vilanova et al. (2015) identified the bacteriome of the coffee machine leach waste; de Sousa et al. (2018) characterised the leaf-associated microbiome of coffee and its correlation to Mn and Ca; and later de Sousa et al. (2022) studied effects of coffee plant genotype on microbial community structure. Moreover, Jurburg et al. (2020) and Fulthorpe et al. (2020) reported variation in the coffee endospheric microbiome across climatic gradient and plant age. Previously, microbiome composition has also been associated with chemical and

346 physiological changes in the plant host (Barnes et al., 2025). In the present study, the separation of bacterial
347 microbiomes from CS, CM and CB systems indicates that plant interactions and cropping systems strongly
348 shape the bacterial microbiome, with the soil chemical context (especially nutrient availability) playing a key
349 role. The principal soil parameters influencing root-associated bacterial communities were pH, SM and
350 concentrations of P, Zn, Fe and Cu. The soil microbiome also correlated with EC, OM and OC (Fig. 5a).
351 Previous studies have found that pH, OM and Cu and Fe soil concentrations had an important effect on the
352 bacterial profile (de Sousa et al., 2022; Wang et al., 2025). For plant parameters (Fig. 5b), the root- associated
353 microbiome correlated with Cla, Ca and Cu.

354 Correlations and interactions were also mapped between the most prevalent members of the coffee
355 microbiome and soil characteristics (Fig. 6a). Strains of the *Sphingobium* and *Streptomyces*, as well as members
356 of the *Sphingobium* and *Rhizobium* group, showed potential cooperative associations. Previously, Bez et al.
357 (2023) found the presence of *Sphingobium and Rhizobium* as members of a core microbiome shared across all
358 their samples, demonstrating the wide distribution of these organisms in coffee cultivars grown under different
359 soil types. Tapaça et al. (2024) also found a prevalence of *Sphingobium* and *Streptomyces* at medium altitudes
360 (~600 m), and under shade trees, again highlighting their relationship with soil health and altitude.

361 The identification of organisms related to coffee plants and soil characteristics can be also used in the
362 development of products for coffee health. In Brazil, there are commercial biological products formulated with
363 *Bacillus* species for biocontrol of coffee leaf rust and nematodes (De Souza et al., 2025). These authors observed
364 that *Pseudomonas gozinkensis* (Mn1F), *P. cariewnsis* (BEca88) and *Enterobacter cloacae* (IAC-RBca5)
365 improved plant fitness and controlled coffee leaf rust caused by *Hemileia vastatrix*, brown eye spot caused by
366 *Cercospora coffeicola* and leaf blight by *Boeremia coffeae*. The present study contributes to the bioprospecting
367 of new bacterial agents that may enhance coffee growth, production and protection. Romero Fernández (2024)
368 isolated and characterised several bacterial, filamentous and mycorrhizal fungi with beneficial traits relevant to
369 sustainable production of coffee.

370

371 **Conclusions**

Results from this research provide a comprehensive overview of the bacterial diversity in three coffee production systems, signaling important differences both among coffee production systems and between soil and root compartments. Regarding α diversity, the association of coffee with mango and banana showed higher diversity index values and greater taxon richness in Chao1, signaling diverse bacterial communities. Interestingly, ß diversity showed a clear separation of the bacterial communities associated with coffee roots, highlighting the coffee root compartment as a distinct microbial environment. The RDA analysis found that soil chemical properties such as EC, water holding capacity (WHC), C:Ns ratio, as well plant chemical parameters including Zn, Mn, Fe and P influenced the structure of the bacterial microbiome. The patterns observed, particularly in the root compartment, suggest an influence of the coffee production systems on nutrient accumulation in plant tissues. The differences observed in the RDA analysis between shade-grown coffee systems and the CS system, along with their relationships to plant nutrient variables, suggest distinct nutrient uptake patterns. Notably, roots from the CS system showed minimal association with the analysed plant nutrients and clustered far from the nutrient vectors, suggesting possible nutrient depletion or reduced nutrient translocation to plants under CS conditions. Overall, these patterns suggest that agroforestry systems may promote more balanced or enhanced nutrient uptake in plants, while in CS systems access to certain essential elements appears more limited. The association of cover trees with coffee cultivars creates favorable conditions for plant success, not only under the chemical standpoint, but also from microbiological and ecological perspectives.

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Author contributions Conceptualization: MCGC, RCG, CSG; investigation: CSG and MCT; visualization and data analysis: MCT, writing-original draft preparation: MCT, MCGC; writing-review and editing: MCT, MCGC, RCG, and CSG; supervision: MCGC. All authors have read and agreed to the final version of the manuscript.

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Declarations

Conflict of interest: The authors declare no conflict of interest.

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545 **Table 1** Bacterial core microbiome of the three coffee systems

Phylum	Bacterial genus	% Sample Sites
Actinomycetota (Actinobacteria)	*Baekduia*	90.00
Actinomycetota	*Kribbella*	100.00
(Actinobacteria)	*Arthrobacter*	93.33
(Actinobacteria)	*Solirubrobacter*	93.33
	CF.154	90.00
(Actinobacteria)	*Nonomuraea*	100.00
(Actinobacteria)	*Jatrophihabitans*	96.67
Archea	*Nitrosocosmicus*	96.67
Nitrospirae	*Nitrospira*	100.00
Cianobacteriota	*Symploca*	83.33
Bacteroidota	*Parafilimonas*	90.00
Bacteriodetes	*Flavisolibacter*	86.67
Bacteroidota	*Niastella*	86.67
	UTBCD1	80.00
Pseodomonadota	*Sphingobium*	100.00
Bacillota	*Neobacillus*	100.00
Actinobacteria	*Kurthia*	83.33
Bacillota	*Cohnella*	86.67
Bacillota	*Lysinibacillus*	93.33
Firmicutes	*Tumebacillus*	93.33

546

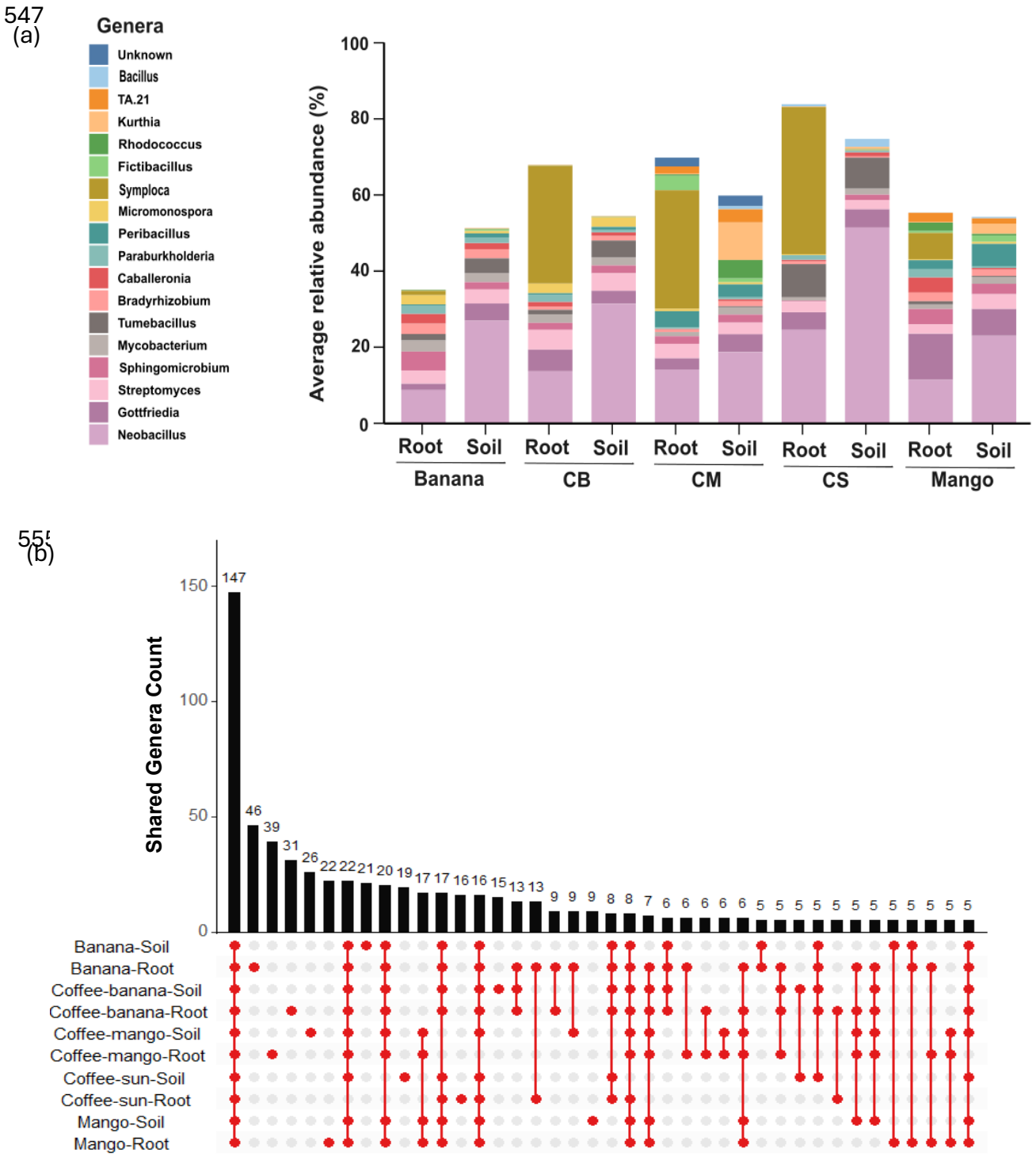

Fig. 1 Bacterial diversity in compartments of the two shade coffee systems and trees. (a) Relative abundance of representing genera (2%), (b) Shared genera between the trees involved in the production systems and compartments (root and soil).

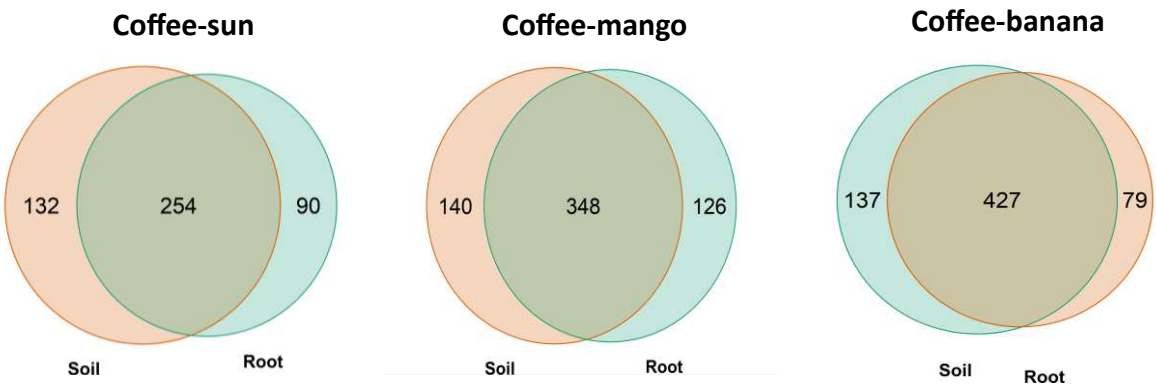

Fig. 2 Bacterial diversity of genera shared between soil and roots compartments across the three coffee systems.

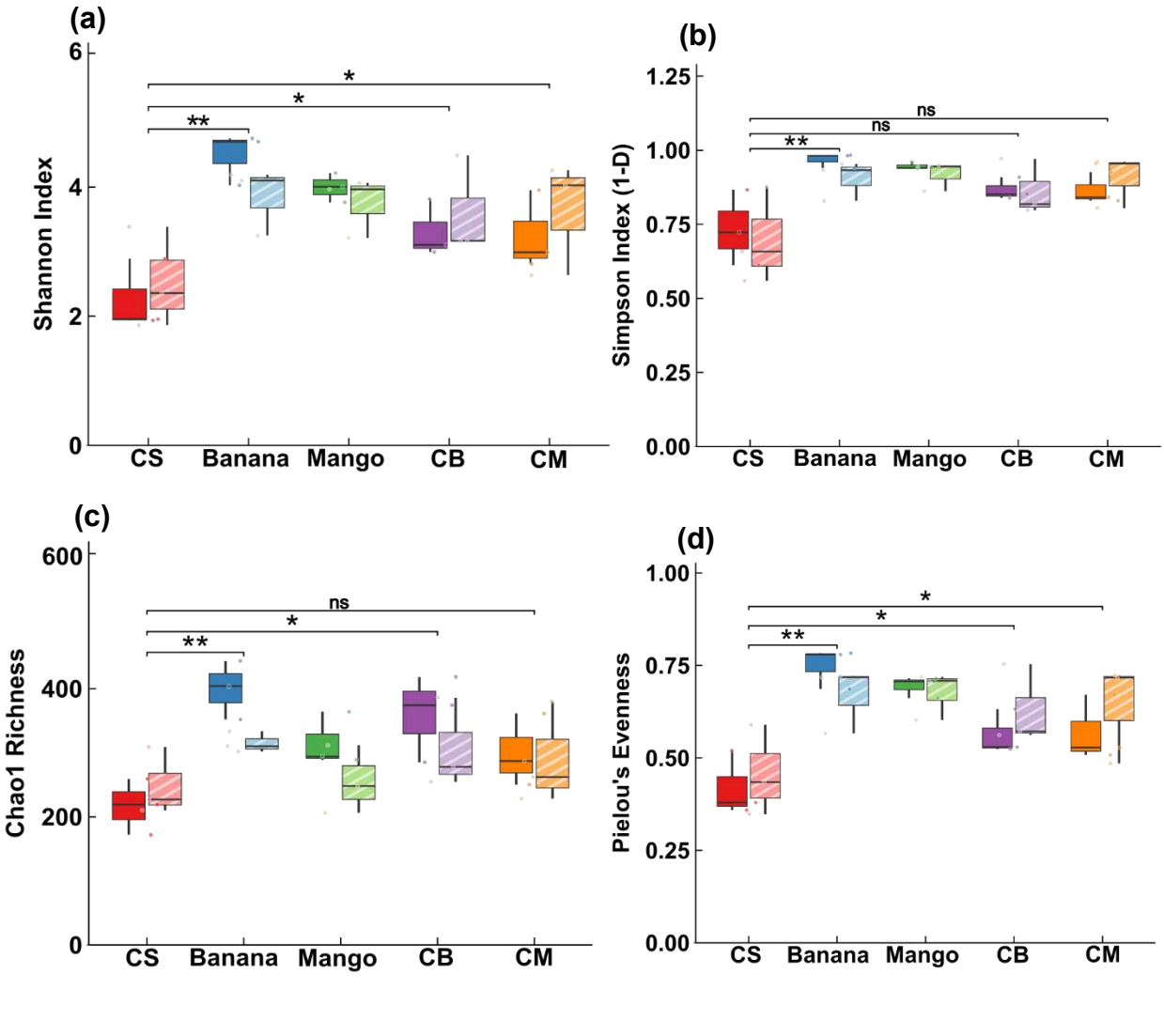

Fig. 3 Diversity indices of the systems, diversity obtained across the systems, bold color represents roots diversity and soft colors the soil diversity; chao1, Simpson, Shannon and Evenness indexes, the lateral lines represent the result of the Krustall-Wallis test between systems * represents if there's a significant difference between them or not (ns).

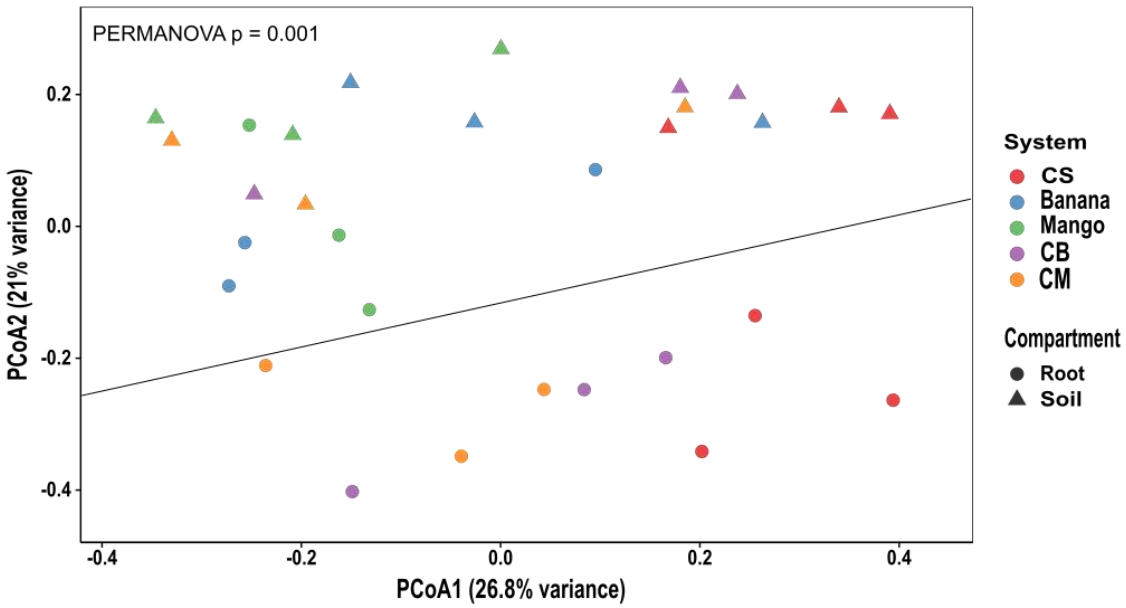

Fig. 4 Beta bacterial diversity among coffee system, trees and compartments.

CS=coffee full sun, CB=coffee banana, CM=coffee mango systems.

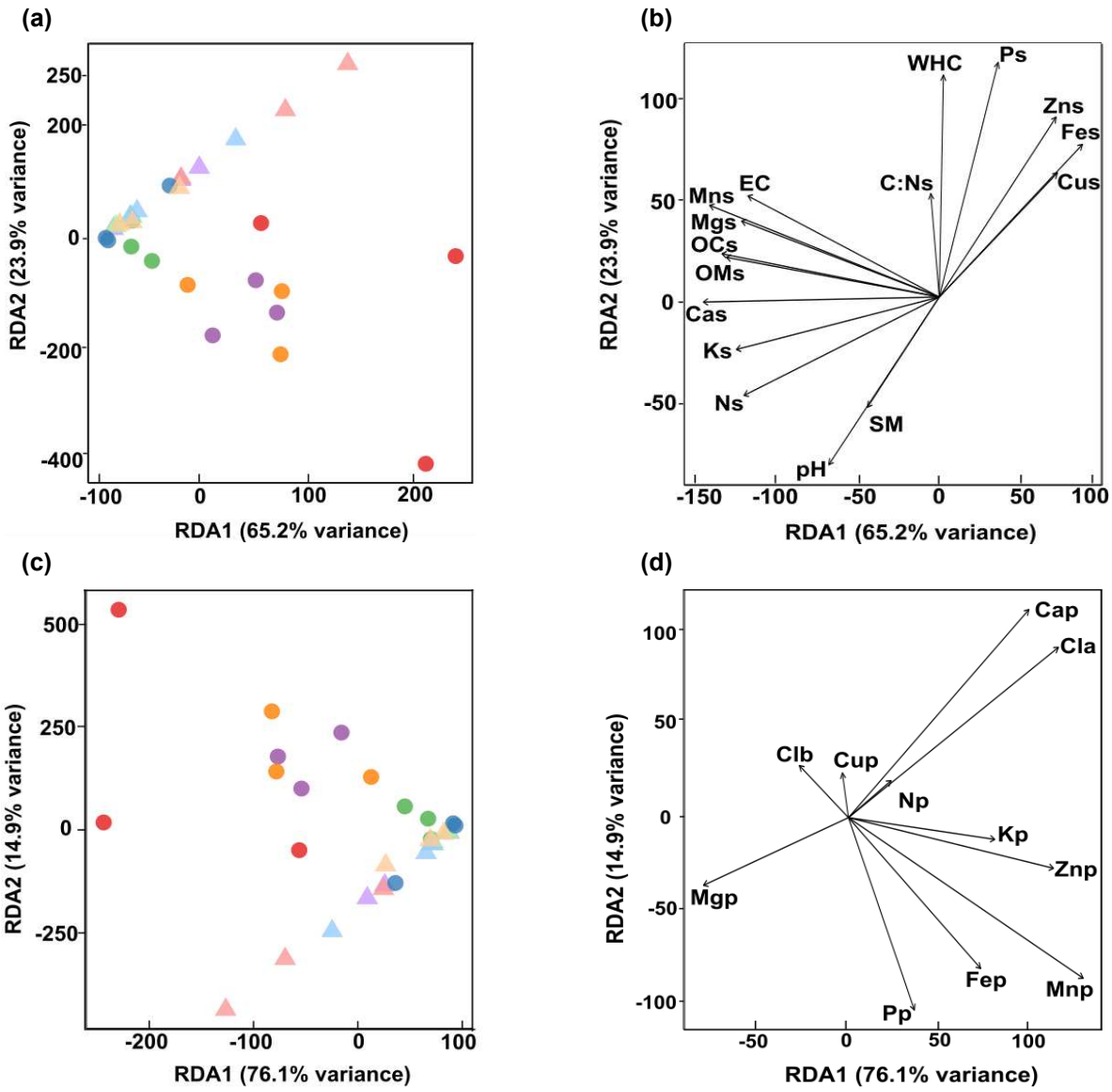

Fig. 5 Correlation plots of soil and plant parameters with root and soil samples from the three coffee systems. **a-b:** RDA NMDS plot represents the correlation linking soil chemical parameters and sample sites. **c-d:** RDA NMDS plot represents the correlation relating plant chemical parameters and sample sites.

Chemical soil parameters include; EC= electric conductivity, Mns=manganese, Mgs= magnesium, OCs= Organic carbon, OMs= Organic matter, Cas=Calcium, Ks=Potassium, Ns=Nitrogen, pH, SM=Soil moisture, Cus=Copper, Fes=Iron, Zns=Zinc, Ps=Phosphorus, WHC= Water holding capacity, C:Ns=Carbon Nitrogen ratio,

636 Chemical plant parameters include: Cap=Calcium, Cla=Chlorophyl a, Clb=Chlorophyl b, Np=Nitrogen,
637 Cup=Copper, Mnp=Manganese, Mgs= Magnesium, Kp=Potassium, Znp=Zinc, Fep=Iron.
638 CS=full-sun coffee, CB=coffee banana, CM=coffee mango systems.
639

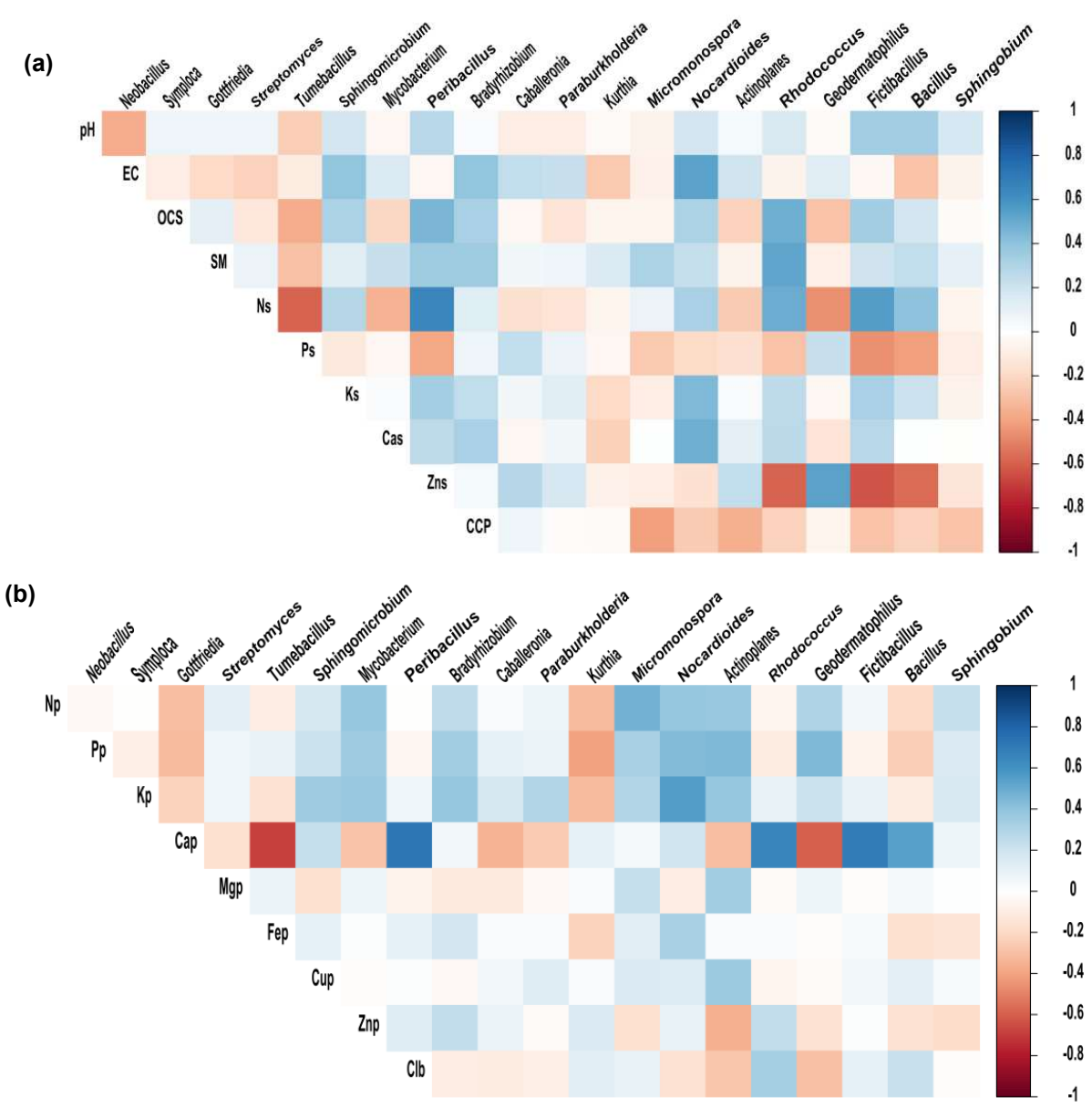

Fig. 6 Spearman correlation between top genera across all sites with the principal (a) soil chemical parameters and (b) plant chemical parameters that explain diversity.

Please, see abbreviations parameters in Fig. 5.

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