Microbial footprints of tomato domestication

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Chapter 3

Changes in taxonomic diversity and functional traits of the tomato root microbiome along a domestication trajectory

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Abstract

Domestication and breeding have substantially altered the genetic and phenotypic traits of multiple plant species. To date, however, the impact of domestication on the taxonomic and functional diversity of microorganisms colonizing plant tissues remains largely unexplored for the majority of plant species. Here, we examined the bacterial microbiome associated with roots of eight wild and domesticated tomato genotypes grown in three distinct soil management gradients, ranging from native and agricultural soils from the tomato's center of origin in Ecuador to a soil from a tomato greenhouse in The Netherlands. Our findings revealed a higher taxonomic diversity in Ecuadorean agricultural soils than in native and greenhouse soils. Soil was the primary factor governing tomato microbiome assembly, followed by the root compartment and plant genotype. Root microbiomes of tomato grown in native Ecuadorian soils had a higher abundance in Acidobacteriota, Proteobacteria, Bacteroidota, Chloroflexi, and Myxococcota, whereas Actinobacteriota, Cyanobacteria, Firmicutes, and Patescibacteria dominated the root microbiome of tomato grown in agricultural and greenhouse soils. Also, we found significant differences in the root microbiome of the different tomato genotypes, with enhanced abundance in Bacteroidota, Proteobacteria and Chloroflexi on roots of wild tomato genotypes, and Actinobacteriota, Firmicutes and Cyanobacteria on roots of domesticated tomato genotypes. Representative metagenome assembled genomes (MAGs) of bacterial taxa of wild tomato genotypes grown in native Ecuadorean soil were enriched in genes associated with motility and chemotaxis, carbon metabolism, and stress response, while MAGs from the microbiome of domesticated tomatoes grown in agricultural and greenhouse soils were enriched for genes involved in metabolism of nitrogen, iron, amino acids and vitamins. This study highlights the pivotal role of habitat domestication and genetic changes of tomato in microbiome assembly, with alterations in the abundance of functional microbial traits associated with plant growth and health.

Introduction

Plant domestication represents an evolutionary process where wild ancestral species were adapted to human needs, ultimately leading to our modern-day crop cultivars (Purugganan & Fuller, 2009). For most crops, this process was targeted at desirable traits such as larger fruit size, palatability, nutritional quality, reproductive timing or stress resistance (Bergougnoux, 2014). While favoring certain alleles during this process of artificial selection and breeding for these desired traits, many modern crop cultivars show a reduced genetic diversity as other (overlooked) genes were lost (Fernie & Yan, 2019). This phenomenon is referred to as the "domestication syndrome" and was first described for cereals in the 1970s by Harlan et al. (1973). The domestication syndrome not only comprises genetic changes caused by human artificial selection but also unintentional effects arising from agricultural practices to grow the domesticated crops, also referred to as habitat domestication (Barnes et al., 2024; Fernie & Yan, 2019; Soldan et al., 2021). Thus, domesticated species are notably different from their wild relatives, with altered morphology, physiology and ecological interactions, including those affecting microbiome assembly (Barnes et al., 2024; Cordovez et al., 2019; Hassani et al., 2020; Martínez-Romero et al., 2020; Sarango Flores et al., 2023).

Plant-associated microbiomes play essential roles in plant growth and health due to their contribution to nutrient acquisition and stress tolerance, thereby supporting and expanding the host plant's functional capabilities (Adedayo et al., 2023; Ling et al., 2022; Pérez-Rodriguez et al., 2020; Santhanam et al., 2015; Shivega & Aldrich-Wolfe, 2017; Zuluaga et al., 2021). Several factors influence the assembly of the plant microbiome, including abiotic factors (e.g. soil types, climatic conditions, agricultural management practices), plant genotype, and the diversity of local microbial pools in the surrounding habitat (Abdullaeva et al., 2022; Berg & Smalla, 2009; Hewitt et al., 2023; Ofek-Lalzar et al., 2014). Traits such as root architecture, exudate composition and nutritional requirements in domesticated plants significantly affect the composition and diversity of their microbiomes, which in turn may affect their functional benefits to the plant host (Abbamondi et al., 2016; Dennis et al., 2010; Gutierrez & Grillo, 2022; Soldan et al., 2021). Plants recruit specific microbial taxa by specific constituents in root exudates that act as chemical signals and orchestrate the surrounding microbial communities to take advantage of the outsourced functions (Barnes et al., 2024; Nakayasu et al., 2023; Walker et al., 2003; Wen et al., 2023). Furthermore, prevailing soil types, changing climatic conditions and agricultural management practices, also modulate plant microbiome assembly (Cao et al., 2024; Flemer et al., 2022; Wang et al., 2022; Xue et al., 2018). For instance, domesticated plants rely on fertilizers and pesticides and much less on their microbial alliances, which may also limit crop adaptability to future adverse environmental conditions such as drought. This network of

different factors driving microbiome assembly creates complex dynamics that can vary across plant genotypes and growth conditions (Mo et al., 2024; Pérez-Jaramillo et al., 2018; Soldan et al., 2021).

Tomato (*Solanum lycopersicum* L.) is an iconic example of plant domestication, which started in the center of origin in the Andean region in South America (Knapp & Peralta, 2016; Razifard et al., 2020). The domestication journey of tomato began with the wild tomato relative *S. pimpinellifolium,* which provided the early traits selected and crossed by indigenous people into the landrace *S. lycopersicum* var. *cerasiforme.* This variety eventually spread beyond its center of origin and continued its domestication process in Central America (Blanca et al., 2012, 2022; Razifard et al., 2020). This process has continued for thousands of years outside of the native tomato habitat, to meet regional phenotypic preferences and cultivation management practices worldwide, which in turn resulted in many modern cultivated tomato varieties of *S. lycopersicum* (Mata-Nicolás et al., 2020; Sarango Flores et al., 2023; Sim et al., 2011).

Examples of notable phenotypic changes in domesticated tomato cultivars include larger fruits with a reduced seed number, uniform shapes and colors, as well as specific metabolic pathways to prioritize sweetness (or reduce bitterness) that are linked to changes in secondary metabolite composition (Bai & Lindhout, 2007; Bergougnoux, 2014). As a consequence of the domestication syndrome, modern cultivated tomatoes suffered a genetic bottleneck which caused a narrowed gene pool compared to their closest relatives, making them more vulnerable to pests, diseases and abiotic stresses (Aflitos et al., 2014; Gao et al., 2019; Kahlon et al., 2020). This loss of genetic variation may also have reduced the modern tomato's ability to effectively select for and interact with the microbial communities surrounding the plants tissues, which in turn can reflect on plant performance (Chen et al., 2022; Huang et al., 2022; Malacrinò et al., 2022; Nerva et al., 2022; Yue et al., 2023). This was exemplified in our previous elaborate analysis of the microbiome of a tomato recombinant inbred line (RIL) population by Oyserman et al. (2022), which revealed significant differences in microbiome assembly across 100 tomato lines and identified specific genetic associations between loci in the tomato genome and in the microbiome metagenome. Additionally, work by Smulders et al. (2021) suggested that tomato wild relatives establish more beneficial interactions with their rhizosphere microbiome than domesticated cultivars.

Building on the findings of Chapter 2, which explored the rhizosphere microbiome of wild tomato *Solanum pimpinellifolium* in its native Andean habitats, we identified a conserved microbial signature dominated by Proteobacteria. While these results revealed how wild tomatoes interact with their native microbiome, they did not address how tomato domestication process and agricultural management may have impacted plant-microbiome associations. To further explore the taxonomic and functional changes in tomato rhizosphere and endosphere microbiomes, we cultivated eight tomato genotypes, representing different stages of the tomato domestication trajectory, in native and agricultural soils from the center of origin in the South of Ecuador, and in a contrasting greenhouse production soil from The Netherlands. In this chapter, we analyzed the bacterial community composition of the rhizosphere and root endosphere by 16S rRNA gene amplicon sequencing and by shotgun metagenomics. We hypothesized that habitat domestication has the largest impact on microbiome assembly, influencing both the taxonomic and functional diversity of the root microbiome.

Results

Soil and genotype drive the taxonomic diversity of the tomato rhizosphere microbiome

No significant differences (Kruskal-Wallis test, $p > 0.05$) were found in alpha diversity, represented by Shannon's diversity index, for the rhizosphere bacterial communities from the tomato genotypes grown on the different soil types (Figure 1). However, the beta diversity revealed significant differences among soil origin (PERMANOVA, $p = 0.0001$), soil type (PERMANOVA, $p = 0.0001$) and tomato domestication degree (PERMANOVA, $p = 0.024$) (Figure 2a). Soil origin and type explained 64% and 39% of the total variability in the rhizobacterial community composition, respectively.

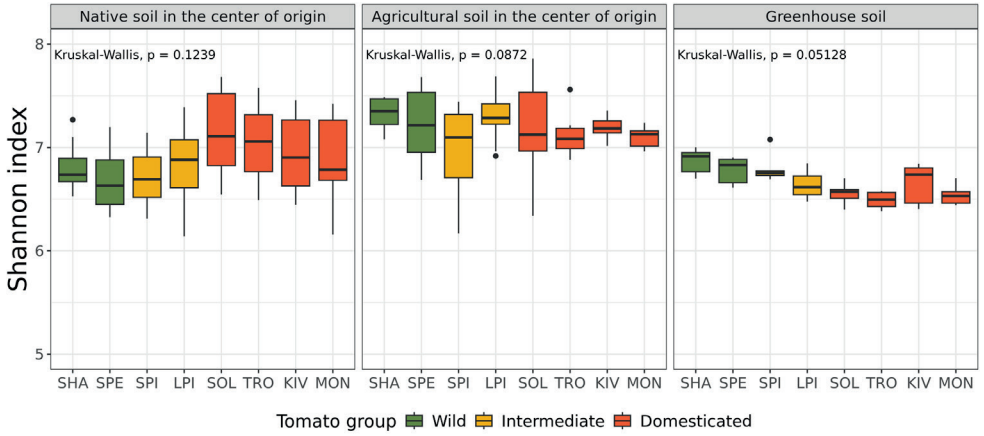

Figure 1. Shannon diversity index of the rhizosphere microbiome of tomato plants grown in Ecuadorian native and agricultural soils, and Dutch greenhouse soil. Boxplots show no significant difference (Kruskal-Wallis test, $p < 0.05$, $n = 10$) of Shannon diversity index between tomato genotypes. SHA: *S. habrochaites;* SPE: *S. peruvianum;* SPI and LPI: *S. pimpinellifolium;* and tomato varieties of *S. lycopersicum:* SOL: Solarino; TRO: Trovanzo; KIV: Kivu; MON: Moneymaker.

More detailed analysis by soil origin showed significant effects of the eight different tomato genotypes, ranging from 37% of the total variation in Ceiba and Limones native soils from the center of origin, 37-38% in the Ceiba and Limones agricultural soils from the center of origin, and 44% in the Dutch greenhouse production soil (Figure 2b–f). Significant differences were not observed between the wild and intermediate groups but were significant between the four intermediate-wild and four domesticated tomato genotypes (Adonis test, $p < 0.05$, Supplementary Table S4).

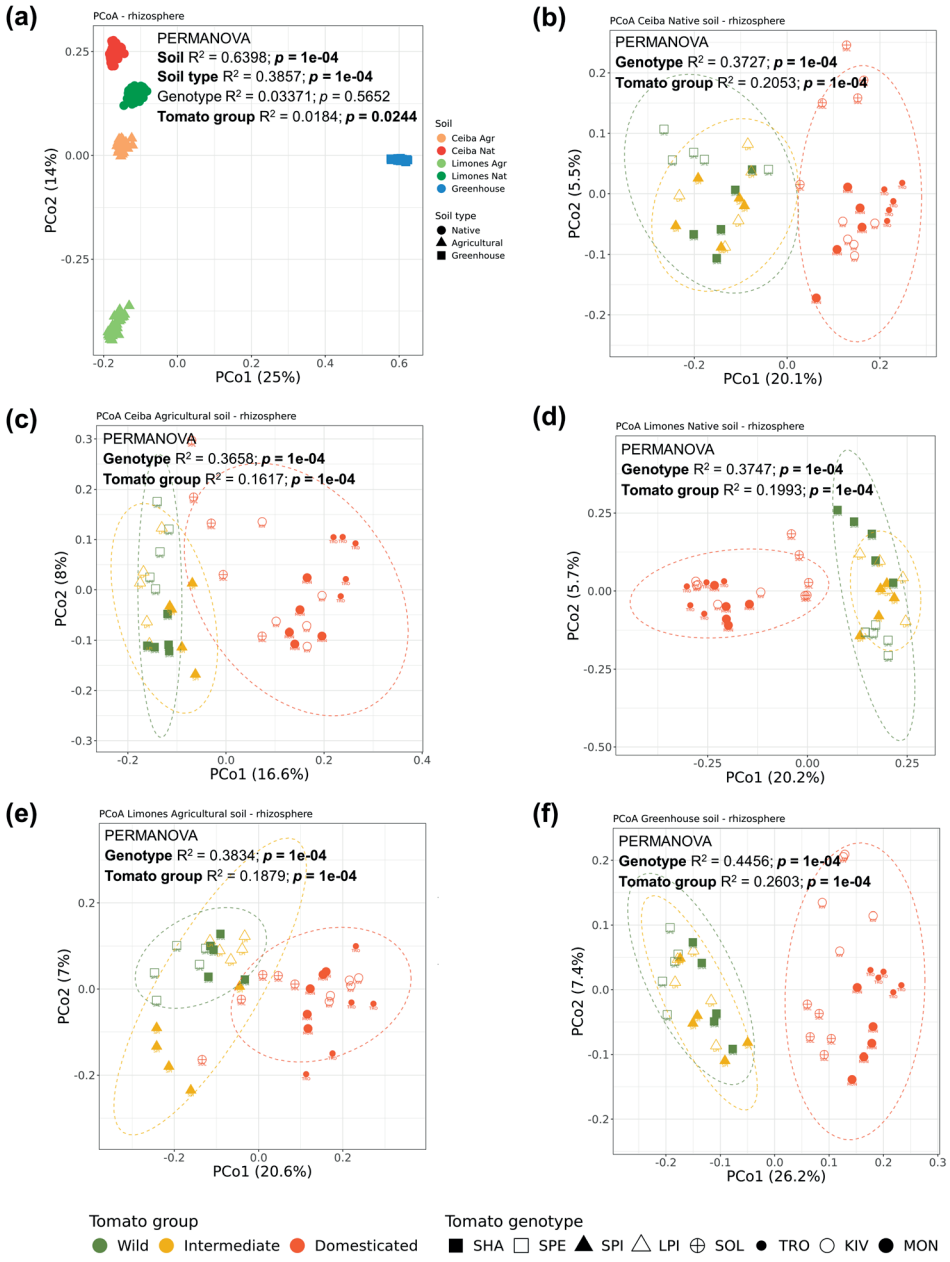

Figure 2. Rhizosphere bacterial community structure of different tomato genotypes grown in Ecuadorian native and agricultural soils, and Dutch greenhouse soil. Principal Coordinate Analysis (PCoA) of rhizosphere bacterial communities of wild (n = 2), intermediate (n = *2*) and domesticated (n = 4) tomato genotypes **(a)** PCoA by soil type; **(b) – (f)** PCoA by tomato genotype per soil type. (Agr = agricultural soil, Nat = native soil).

Subsequent differential abundance analysis revealed that soil type impacted the differential enrichment and depletion of ASVs in the rhizosphere of tomato. We first compared ASV abundance in the rhizosphere of tomatoes grown in native and agricultural soils from the South Andes in Ecuador. In native soils, a total of 490 ASVs were significantly more abundant in wild-intermediate tomato genotypes (cluster C3) and 1028 ASVs in the four domesticated tomato genotypes (cluster C4); in the agricultural soils, 1279 ASVs were significantly more abundant in wild-intermediate tomato genotypes (cluster C1) and 1121 ASVs in domesticated tomato genotypes (cluster C2) (Figure 3a). We next compared the differential abundance in the rhizosphere of tomato between the Ecuadorean agricultural soils and the Dutch greenhouse soil. In the Ecuadorean agricultural soils, 1286 ASVs were significantly more abundant in wild-intermediate tomato genotypes (cluster C5), and 2296 ASVs in domesticated tomato genotypes (cluster C4). In the Dutch greenhouse soil, 1148 ASVs showed higher abundance in wild and intermediate tomatoes (cluster C3), but only 109 ASVs were more abundant in domesticated tomatoes (cluster C2) (Figure 3b).

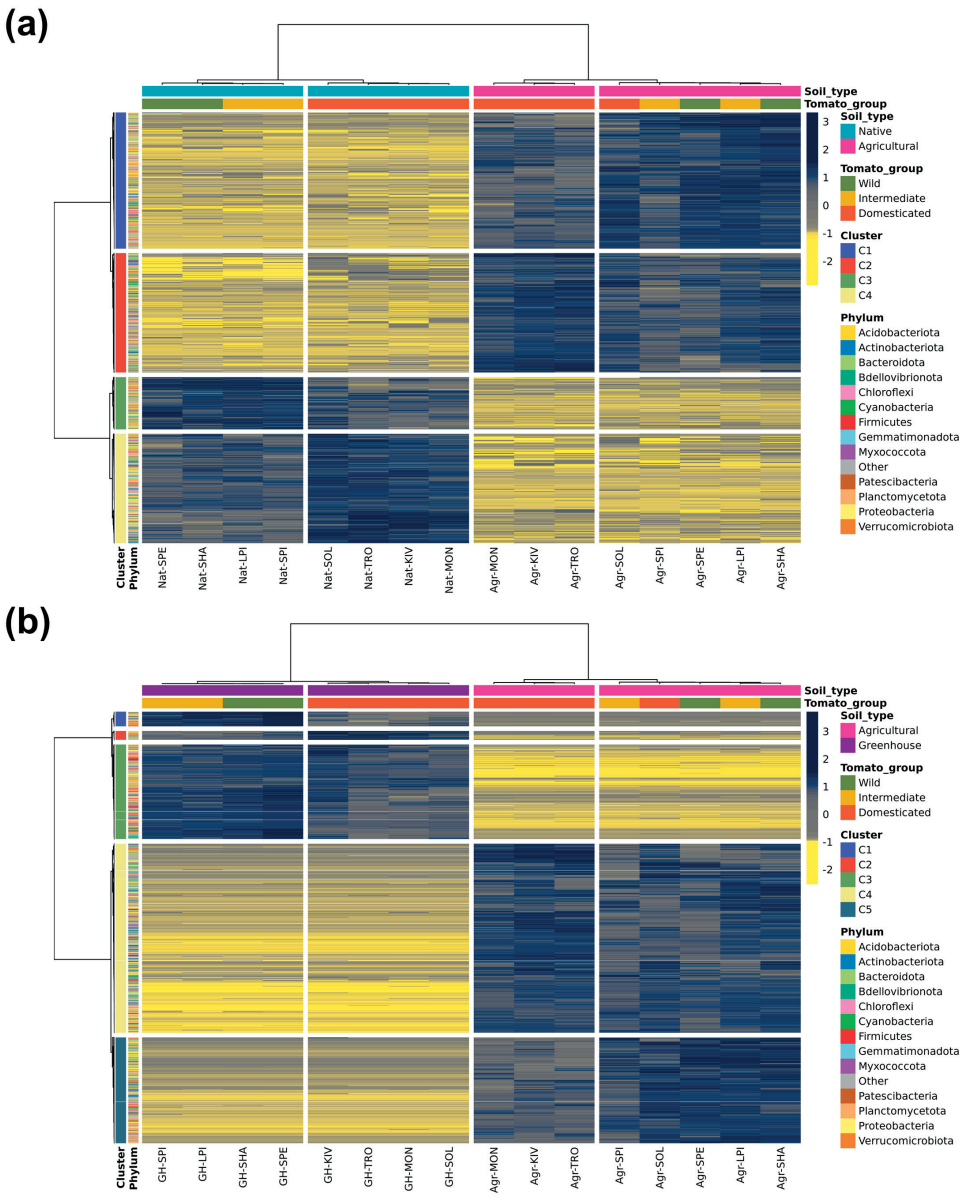

Figure 3. Differential abundance of the tomato rhizosphere amplicon sequence variants (ASVs) in pairwise comparisons of different soil types. **(a)** Heatmap of ASVs in the rhizosphere of tomatoes grown in Ecuadorian native and agricultural soils; clusters C1 = 1279; C2 = 1121; C3 = 490; C4 = 1028 ASVs. **(b)** Heatmap of ASVs in the rhizosphere of tomatoes grown in Ecuadorian agricultural and Dutch greenhouse soils; clusters C1 = 178; C2 = 109; C3 = 1148; C4 = 2296; C5 = 1286 ASVs. Significant ASVs identified from the DESeq differential abundance analysis were hierarchically clustered using Ward's method as the clustering algorithm. SHA: *S. habrochaites;* SPE: *S. peruvianum;* SPI and LPI: *S. pimpinellifolium;* and tomato varieties of *S. lycopersicum:* SOL: Solarino; TRO: Trovanzo; KIV: Kivu; MON: Moneymaker.

By grouping the significantly abundant rhizosphere ASVs from each cluster at phylum and genus level (Figure 4), we observed that the rhizosphere of tomato plants grown in soils from the center of origin, i.e. native and agricultural soils, had a higher relative abundance of Actinobacteriota, Bacteroidota, Cyanobacteria and Proteobacteria when compared with tomato plants grown in the Dutch greenhouse soil, which were more abundant in Chloroflexi, Firmicutes, Gemmatimonadota, Myxococcota, Patescibacteria and Planctomycetota (Figure 4a). At genus level, the rhizosphere of tomatoes grown in native soils from the center of origin had a higher relative abundance of *Brevundimonas, Cellvibrio, Dyadobacter, Ohtaekwangia, Pseudomonas, Rhizobacter and Sphingomonas*. In contrast, tomatoes grown in agricultural soils had an increased relative abundance of *Actinoplanes, Allorhizobium-Neorhizobium-Pararhizobium-Rhizobium, Massilia, Nostoc* and *Streptomyces*, whereas tomatoes grown in the Dutch greenhouse soil showed greater abundance of *Bacillus, Devosia, Edaphobaculum, Mesorhizobium, Paenibacillus* and *Sericytochromatia.*

The tomato domestication degree was also linked to changes in specific rhizobacterial taxa. For instance, in native soils, wild and intermediate tomato genotypes had higher relative abundances of *Chitinophaga, Dyadobacter, Ohtaekwangia* (Bacteroidota) as well as *Cellvibrio* and *Rhizobacter* (Proteobacteria). In contrast, *Nocardioides* (Actinobacteriota) were enriched in the rhizosphere of domesticated tomato genotypes grown in the Ecuadorean native soils. In the two Ecuadorean agricultural soils, wild and intermediate tomato genotypes showed higher relative abundance of *Allorhizobium-Neorhizobium-Pararhizobium-Rhizobium* (Proteobacteria) whereas domesticated tomatoes harbored more *Actinoplanes* (Actinobacteriota). In the Dutch greenhouse soil, differences among tomato genotypes were observed in *Bacillus* and *Paenibacillus* (Firmicutes), which were more abundant in wild and intermediate tomatoes, while *Devosia* (Proteobacteria), *Mesorhizobium* (Proteobacteria) and *Sericytochromatia* (Cyanobacteria) were more abundant in domesticated tomatoes. In all three soil types, *Pseudomonas* and *Massilia* had higher abundance in wild-intermediate tomatoes, whereas members of the genera *Sphingomonas* (Proteobacteria) and *Streptomyces* (Actinobacteriota) showed greater relative abundance in domesticated tomatoes in all five soils (Figure 4b).

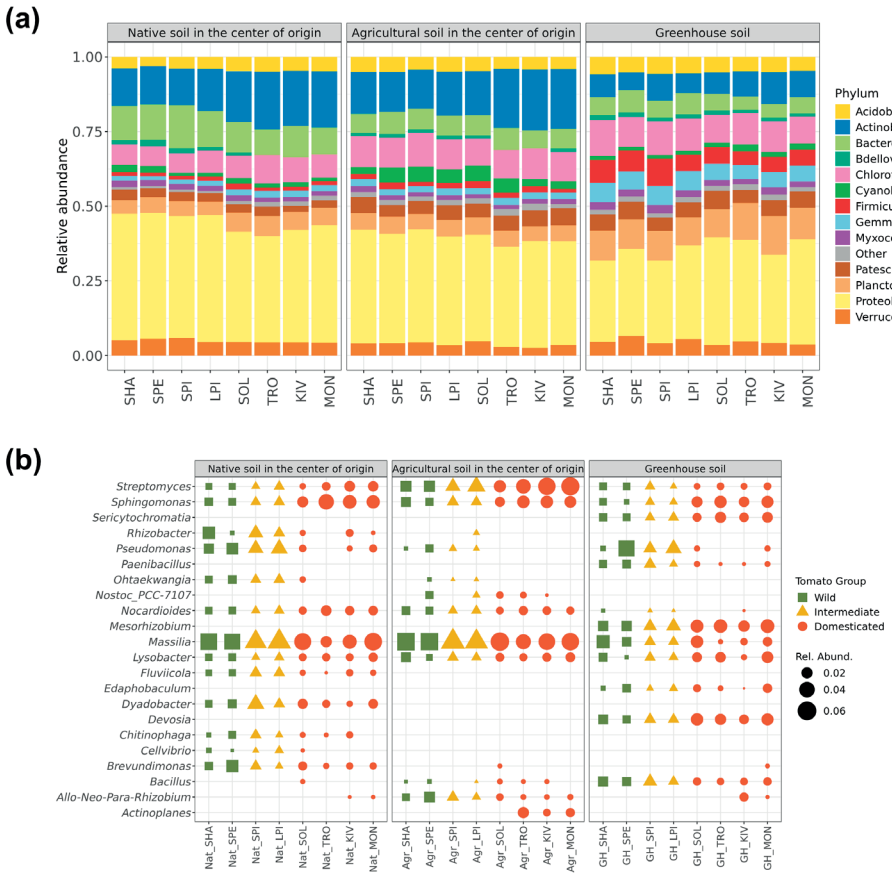

Figure 4. Rhizosphere bacterial community composition of tomato genotypes grown in native and agricultural soils. **(a)** Relative abundance of bacterial phyla in rhizosphere of different tomato genotypes grown in Ecuadorian native and agricultural soils and Dutch greenhouse soil; "Other" category corresponds to grouped phyla with relative abundance < 0.01; **(b)** Relative abundance of most abundant genera found in rhizosphere of different tomato genotypes. ASVs with significant differential abundance between soils and tomato genotypes were grouped according to their phylum or genus level and plotted as stacked bar and bubble charts, respectively. SHA: *S. habrochaites;* SPE: *S. peruvianum;* SPI and LPI: *S. pimpinellifolium;* and tomato varieties of *S. lycopersicum:* SOL: Solarino; TRO: Trovanzo; KIV: Kivu; MON: Moneymaker.

Effects of domestication on functional traits of the tomato rhizosphere microbiome

Following shotgun metagenomics of the rhizosphere samples, 127 MAGs (high quality bins completeness >70%, contamination <10%) were obtained. Of these, 12 MAGs with the highest quality were selected for functional analysis based on their taxonomic consistency with amplicon sequencing results. Thus, functions annotated by SEED Subsystems from selected MAGs related to habitat and the domestication degree of the tomato genotypes revealed significant shifts in microbial functionality. For example, MAGs taxonomically delineated as Bacteroidota (*Chitinophaga, Fluviicola*) or Proteobacteria (*Cellvibrio, Pseudomonas, Rhizobacter* and Rhizobiaceae) were more abundant in wild-intermediate tomatoes in native and agricultural soils, showed a higher abundance of genes associated with motility and chemotaxis, as well as metabolism of carbohydrates and stress response. On the other hand, MAGs taxonomically delineated as Micromonosporaceae, Bacillaceae, Cyanobacteria, *Sphingomonas* and *Streptomyces,* representative taxa of domesticated tomatoes grown in agricultural and greenhouse soils, exhibited a higher number of genes associated with iron acquisition and metabolism of nitrogen, amino acids and derivatives; and cofactors, vitamins, prosthetic groups, pigments (Figure 5).

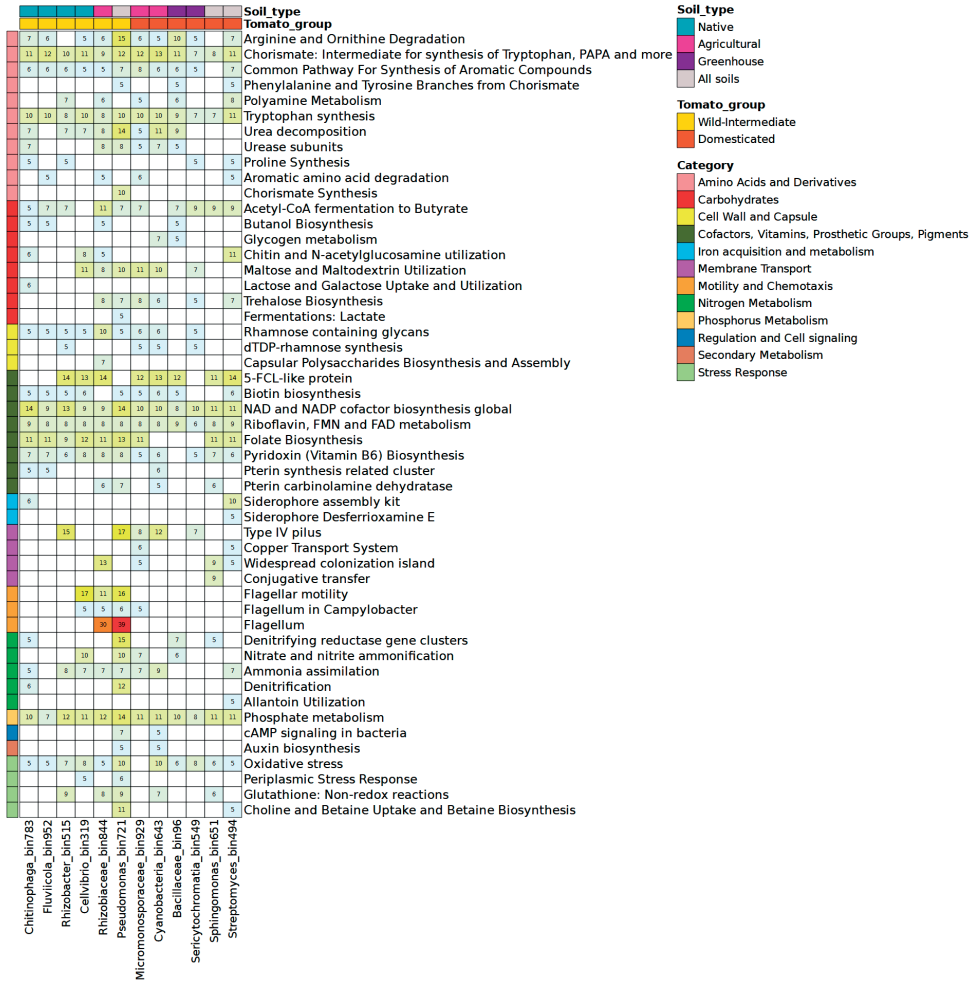

Figure 5. Heatmap of SEED Subsystems with the highest gene abundance (≥ 5 genes) in rhizosphere bacterial MAGs selected from tomato genotypes across different soil types. The number of protein-encoding genes present in each Subsystem per MAG is shown within the cells. *Chitinophaga*_bin783, *Fluviicola*_bin952, *Rhizobacter*_bin515 and *Cellvibrio*_bin319 belong to wild-intermediate tomatoes grown in native soils; Rhizobiaceae_bin844 belongs to wild-intermediate tomatoes grown in agricultural soils; *Pseudomonas*_bin721 belongs to wild-intermediate tomatoes grown in any soil type. Micromonosporaceae_bin929 and Cyanobacteria_bin643 were representatives of domesticated tomatoes in agricultural soils; Bacillaceae_bin96 and Sericytochromatia_bin549 correspond to domesticated tomatoes grown in greenhouse soil. *Sphingomonas*_bin651 and *Streptomyces*_bin494 belong to domesticated tomatoes grown in any soil type.

Tomato endosphere microbiome assembly is soil type dependent

The bacterial communities detected in the root endosphere displayed a similar Shannon diversity index across tomato genotypes and soils, differing only among the eight tomato genotypes grown in native Ecuadorean soil (Kruskal-Wallis test, $p = 0.0044$). A higher diversity index was observed for domesticated tomato genotypes compared to wild-intermediate tomato genotypes. Interestingly, a same yet statistically insignificant trend was observed for agricultural and greenhouse soils, i.e. a minor yet progressive increase of bacterial alpha diversity along the tomato domestication trajectory (Figure 6).

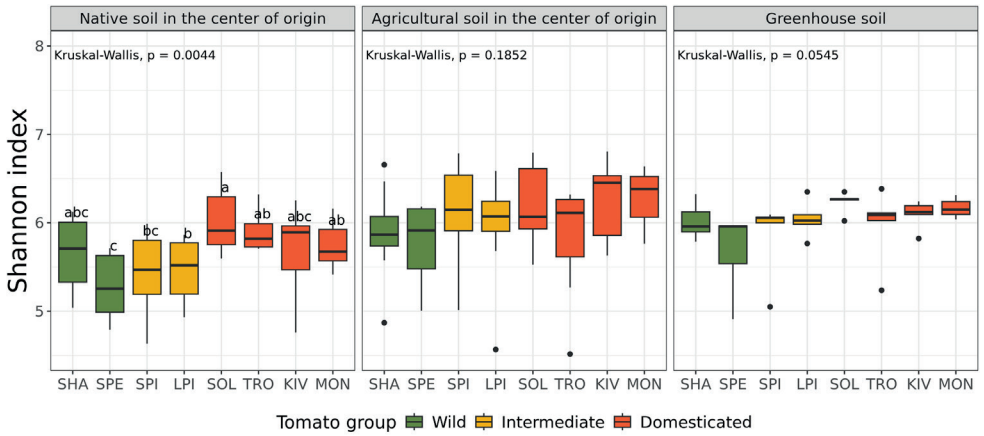

Figure 6. Shannon diversity index in tomato root endosphere grown in Ecuadorian native and agricultural soils and Dutch greenhouse soil. Different letters above boxplots show significant difference (Wilcoxon test, $p < 0.05$, $n = 10$) of Shannon diversity index between tomato genotypes. SHA: *S. habrochaites;* SPE: *S. peruvianum;* SPI and LPI: *S. pimpinellifolium;* and tomato varieties of *S. lycopersicum:* SOL: Solarino; TRO: Trovanzo; KIV: Kivu; MON: Moneymaker.

Overall, PCoA of the root endosphere showed significant differences between soil origin and soil types (PERMANOVA, $p = 0.0001$), but surprisingly there were no significant differences between tomato genotypes or domestication groups (PERMANOVA, $p > 0.05$) (Figure 7a). When the tomato endosphere microbiome composition was analyzed per soil type (i.e. native, agricultural, greenhouse), significant differences were observed between tomato genotypes and domestication degree. This variation observed in the PCoA plot appeared to be primarily driven by the broader dispersion of wild tomato genotypes across the different soils. Although some dispersion is observed in domesticated tomato genotypes, wild genotypes exhibited greater variability. This variation likely contributed to the significant differences found between domesticated tomatoes and both intermediate and wild tomato genotypes (Adonis test, $p < 0.05$, Supplementary Table S4). Specifically, tomato genotype showed 21% of the total variation in

Ceiba agricultural and native soils and in Limones native soil, while 22% was observed in Limones agricultural and greenhouse soils. The domestication effect, i.e. variation in endosphere microbiome composition between wild, intermediate and domesticated tomato groups, showed 7% of the total variation per soil. This percentage of variation represents a marked decrease compared to the variation observed in the rhizosphere microbiome of 20% (Figure 7b–f).

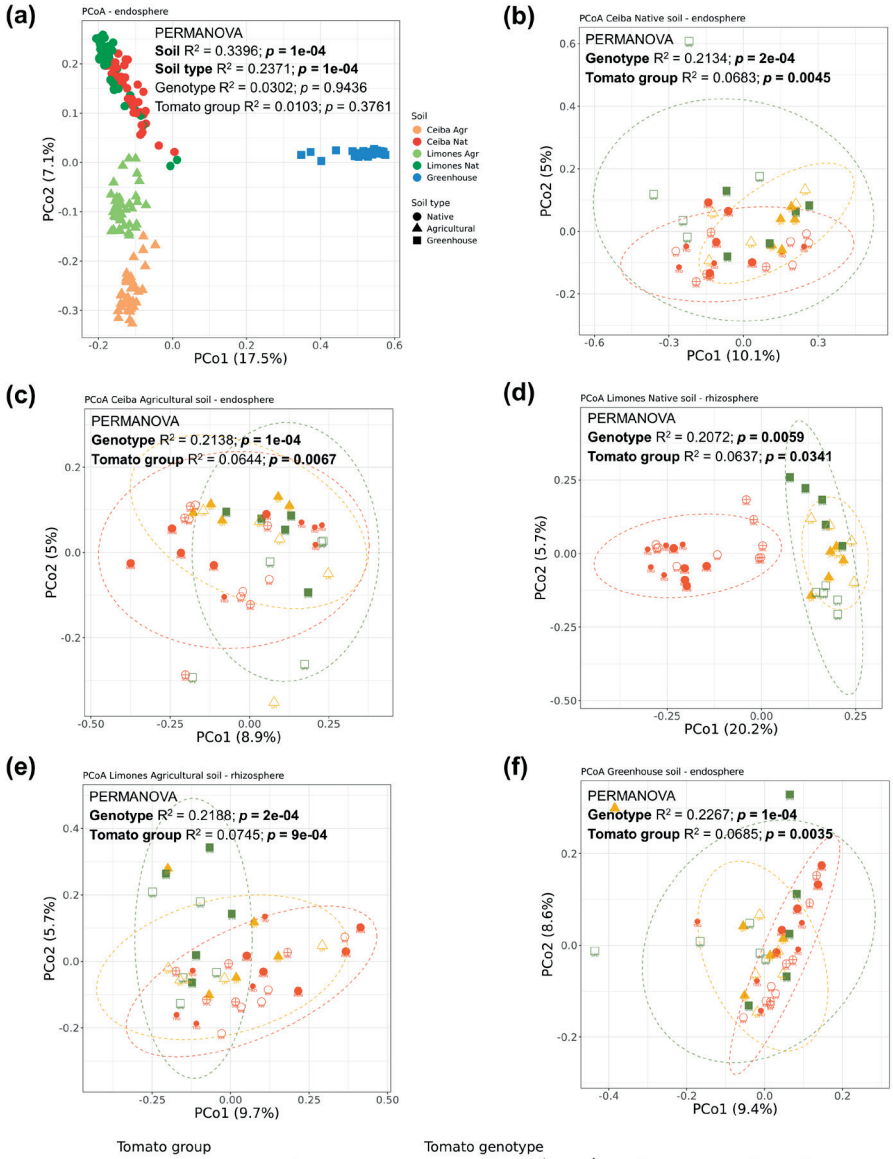

Figure 7. Principal Coordinate Analysis (PCoA) of bacterial communities in tomato root endosphere grown in different soil types. **(a)** PCoA by soil type and **(b) – (f)** PCoA by tomato genotype in each soil.

Furthermore, the differential abundance analysis of bacterial ASVs by DESeq (Wald test) through pairwise comparison between native and agricultural soils revealed no significant differences between the tomato domestication groups. The observed ASV clusters (Figure 8a) also suggest that the differences were mainly attributed to the soil type in which the tomato genotypes were grown. Similar results were found when agricultural and greenhouse soils were compared (Figure 8b).

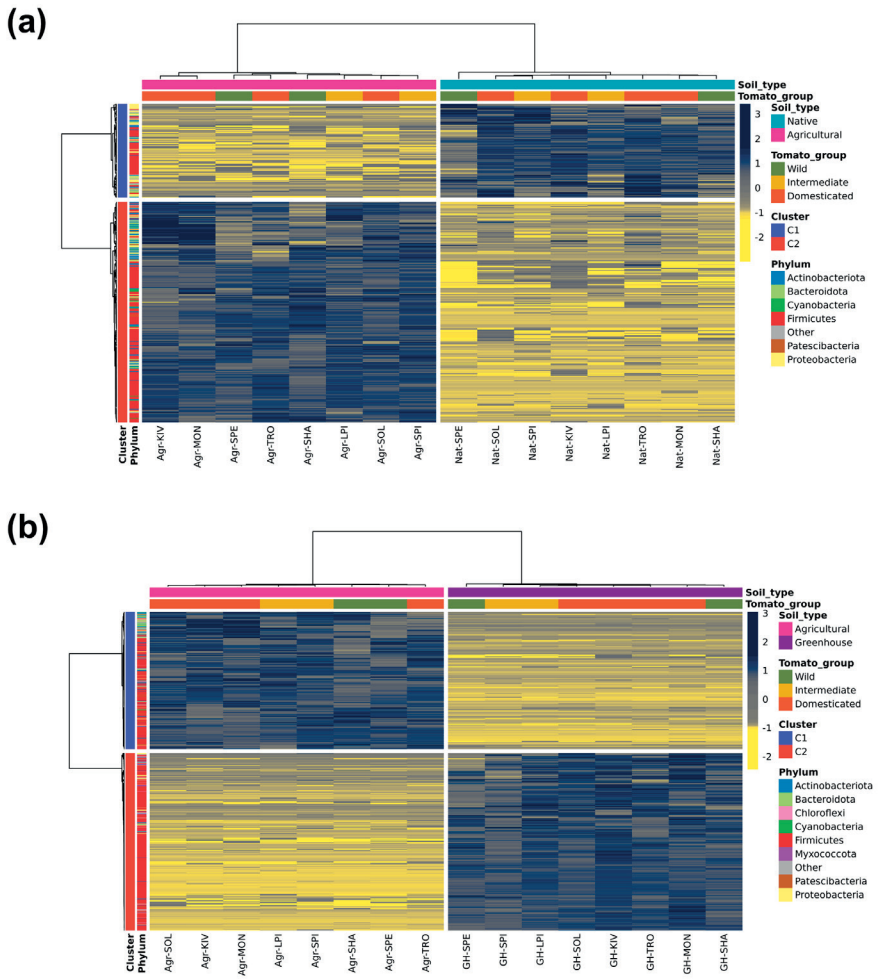

Figure 8. Differential abundance of the tomato root endosphere amplicon sequence variants (ASVs) in pairwise comparisons of different soil types. **(a)** Heatmap of ASVs in the endosphere of tomatoes grown in Ecuadorian native and agricultural soils; clusters C1 = 129; C2 = 304 ASVs. **(b)** Heatmap of ASVs in the endosphere of tomatoes grown in Ecuadorian agricultural soils and Dutch greenhouse soil; clusters C1 = 466; C2 = 602 ASVs. Significant ASVs identified from the DESeq differential abundance analysis were hierarchically clustered using Ward's method as the clustering algorithm. SHA: *S. habrochaites*; SPE*: S. peruvianum*; SPI and LPI: *S. pimpinellifolium*; and tomato varieties of *S. lycopersicum*: SOL: Solarino; TRO: Trovanzo; KIV: Kivu; MON: Moneymaker.

The significantly different ASV clusters in the tomato root endosphere from native and agricultural Ecuadorean soils showed increased abundance of the phyla Actinobacteriota, Bacterioidota, Cyanobacteria, Firmicutes and Proteobacteria. In contrast, Actinobacteriota and Firmicutes were predominantly more abundant in the endosphere of tomato plants grown in Dutch greenhouse soil (Figure 9a). At genus level, the endosphere microbiome of tomato plants grown in native soils showed higher abundance of *Ammoniphilus, Bacillus, Domibacillus, Fictibacillus, Lysinibacillus, Pseudomonas* and *Rhizobacter*, than that of plants grown in agricultural and greenhouse soils. On the other hand, agricultural and greenhouse soils, i.e. managed soils, showed higher abundance of *Clostridium, Cohnella, Massilia, Paenibacillus, Streptomyces* and *Tumebacillus.* Particularly, greenhouse soil increased the abundance of *Tumebacillus, Paenibacillus* and *Cohnella* in tomato endosphere. Although soil was shown to be the main driver of the root endosphere microbiome composition, domestication appeared to impact the abundance of *Actinoplanes, Cohnella, Massilia* and *Streptomyces,* which had higher abundance in the root endosphere of domesticated than of wild-intermediate tomato genotypes, especially when grown in agricultural soil (Figure 9b). Considering the substantial interference of plant DNA in shotgun metagenomic sequencing of endosphere samples, no data on functional genes and traits of the endophytic tomato microbiome were obtained.

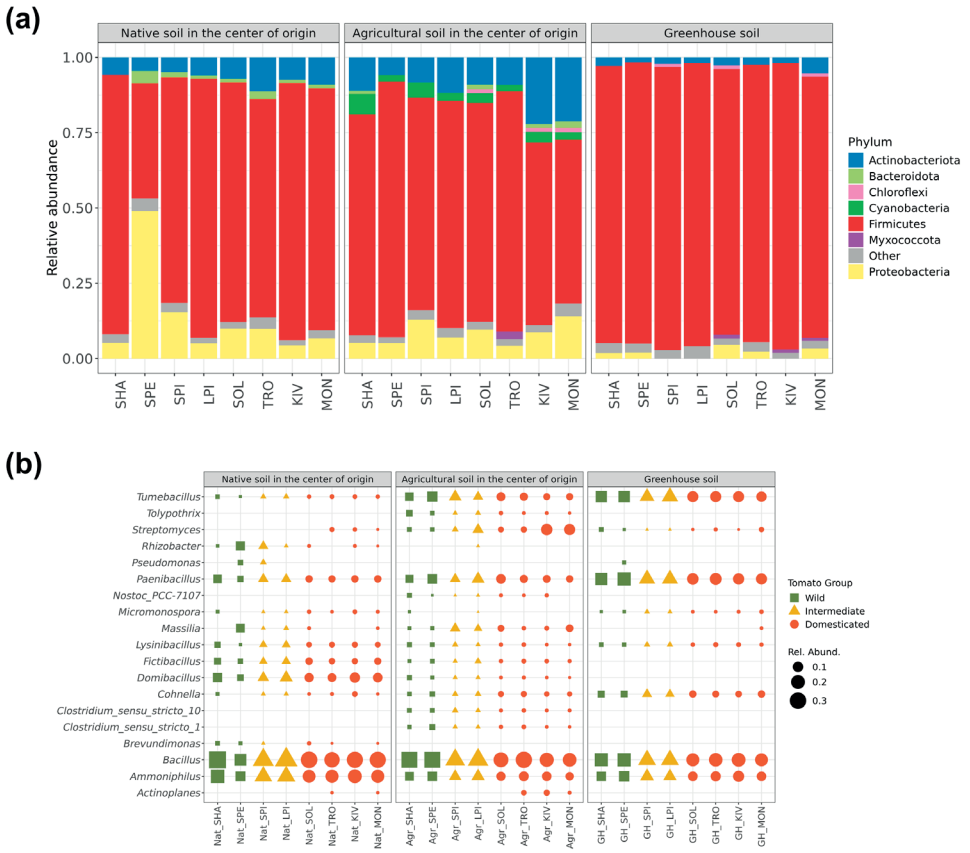

Figure 9. Root endosphere bacterial community composition at phylum and genus level of tomato genotypes in different soil types. **(a)** Relative abundance of bacterial phyla in root endosphere of different tomato genotypes grown in Ecuadorian native and agricultural soils and Dutch greenhouse soil; "Other" category corresponds to grouped phyla with relative abundance < 0.01; **(b)** Relative abundance of highest abundant genera found in root endosphere of different tomato genotypes. ASVs with significant differential abundance between soils and tomato genotypes were grouped according to their phylum or genus level and plotted as stacked bar and bubble charts, respectively. SHA: *S. habrochaites*; SPE: *S. peruvianum*; SPI and LPI: *S. pimpinellifolium*; and tomato varieties of *S. lycopersicum*: SOL: Solarino; TRO: Trovanzo; KIV: Kivu; MON: Moneymaker.

Discussion

Domestication not only evolved specific traits of wild plant species to favor human needs, it also led to substantial changes in their habitats, moving from environmentally harsh, native ecosystems to heavily managed agricultural soils. Additionally, human migration and extensive exchanges of plant germplasm worldwide have further contributed to the vast genetic variation seen in modern tomatoes (Blanca et al., 2022). Agricultural environments can also deplete putative plant growth-promoting rhizobacteria in modern crop accessions (Reid et al., 2024). In this study, we used tomato as a 'model' plant to decipher the impact of domestication on microbiome assembly. To this end, we selected different genotypes and soils, including wild and domesticated tomato genotypes and native and managed soils from the center of origin (Ecuador), as well as greenhouse soil from the center of production (Netherlands) (Supplementary material Tables S1, S2). In this study, we used the same two parental tomato lines (*S. pimpinellifolium* and *S. lycopersicum* cv. Moneymaker) and greenhouse tomato soil as used in our earlier study on microbiome assembly of a tomato RIL population with approximately 100 genotypes (Oyserman et al., 2022). It should be noted that the number of tomato genotypes (n = 8) and soils (n = 5) used in this study is limited to make solid conclusions on the impact of domestication on microbiome assembly. However, the results obtained can serve as a stepping stone for more elaborate screenings and to generate hypotheses that can be experimentally validated on larger sets of plant genotypes and soils.

Our findings revealed that selective filtering of the soil microbiome was stronger in the tomato rhizosphere than in the endosphere (Figures 2, 7). Significant variations in rhizosphere microbiome composition were observed per soil, with wild-intermediate tomato genotypes clustering separately from the domesticated tomatoes (Figure 2). This was further supported by the differential abundance analysis which revealed a similar clustering pattern of the ASVs and whose separation was driven by soil type and the degree of tomato domestication (Figure 3). Soil plays a predominant role in plant microbiome assembly due to its properties, especially nutrient content and the diversity of the microbial 'seed bank' (Cordovez et al., 2019; Ling et al., 2022; Philippot et al., 2024). Particularly, soil amendments such as organic matter, N, P and K, have been shown in several studies to considerably alter the tomato bacterial community assembly in the rhizosphere (Cheng et al., 2020; Dixon et al., 2024; Garcia et al., 2024; Naumova et al., 2022; Zhang et al., 2022). On the other hand, plant genotype can act as a microbiome filter due to the quantitative and/or qualitative differences in root exudation composition, which selects for and enhances the proliferation of specific taxa within the microbiome, as reported in previous studies (French et al., 2020; Poudel et al., 2019). Our results suggest that the differentiation in rhizosphere microbiome

assembly occurred later in the domestication trajectory, likely during breeding and genetic improvement. Based on this, further examination of the differences in tomato root exudate composition per tomato genotype and the effect of soil amendments on the rhizosphere microbiome will be needed to decipher genotype-specific signatures in rhizosphere microbiome assembly.

When summarizing the impact of tomato and habitat domestication on rhizosphere assembly (Figure 4), our results show that: i) Bacteroidota and Proteobacteria had a higher relative abundance in the rhizosphere microbiome of tomatoes grown in native Ecuadorian soils, ii) Actinobacteriota and Cyanobacteria were more abundant in the rhizosphere microbiome of tomatoes grown in Ecuadorean agricultural soils, and iii) Firmicutes were more abundant in the rhizosphere of tomatoes grown in the Dutch greenhouse soil. At genus level, *Chitinophaga, Dyadobacter, Fluviicola, Ohtaekwangia* (Bacteroidota), as well as *Brevundimonas, Cellvibrio* and *Rhizobacter* (Proteobacteria) were more abundant in wild-intermediate tomato genotypes, while *Lysobacter* (Proteobacteria) and *Nocardioides* (Actinobacteriota) were more abundant in domesticated tomato genotypes grown in native soil. In contrast, in agricultural soil, wild-intermediate tomatoes were more abundant in *Allorhizobium-Neorhizobium-Pararhizobium-Rhizobium* (Proteobacteria), while domesticated tomatoes showed increased genera such as *Actinoplanes, Nocardioides* (Actinobacteriota) and *Nostoc* (Cyanobacteria). For greenhouse soil, *Bacillus, Paenibacillus* (Firmicutes) were significantly more abundant in wild-intermediate tomatoes, while *Sericytochromatia* (Cyanobacteria) was more abundant in domesticated tomato genotypes. Interestingly, across all soils, *Pseudomonas* and *Massilia* (Proteobacteria) were more abundant in wild-intermediate tomato genotypes, while *Streptomyces* (Actinobacteriota) and *Sphingomonas* (Proteobacteria) progressively increased along the tomato domestication trajectory (Figure 4).

Several *Pseudomonas* species are known as plant growth-promoting rhizobacteria (PGPR) due their versatile abilities in root colonization, nutrient acquisition, antioxidant activities, pathogen suppression, and stress adaptation (Alattas et al., 2024; Mekureyaw et al., 2022; Sah et al., 2021; Zboralski & Filion, 2020). *Massilia* exhibits copiotrophic behavior and effective attachment to biological surfaces, including fungal hyphae, filamentous algae and Cyanobacteria (Ofek et al., 2012; Salomon et al., 2003; Scheublin et al., 2010), which can make it a successful root colonizer. In our earlier studies, *Massilia* together with *Rhizobium* was also abundant in successively planted wild tomato (Cordovez et al., 2021). Whether these beneficial traits are also prominent for the *Pseudomonas* and *Massilia* species we detected in wild-intermediate tomato genotypes remains to be further investigated.

Our results on the enrichment of *Streptomyces* in the rhizosphere of domesticated tomatoes are consistent with findings from other studies. First and foremost, our results confirm and extend the results of our earlier study on the microbiome of a tomato RIL population, conducted with the same Dutch greenhouse soil and the same parental lines *S. pimpinellifolium* and *S. lycopersicum* cv. Moneymaker (Oyserman et al., 2022). We observed similar patterns of abundance of specific rhizosphere bacteria, especially the significant abundance of *Streptomyces* in the rhizosphere of domesticated tomatoes in any soil type. In our previous study, the increased abundance of *Streptomyces* was associated with a 'modern allele' on chromosome 6 (Oyserman et al., 2022). Also in other studies, similar patterns were reported. For example, Allard (2016) observed higher abundance of members of the Streptomycetaceae family in domesticated tomato (*S. lycopersicum* BHN602) grown in greenhouse conditions. Similarly, Dixon et al. (2024) found that modern (ca. 2020) and traditional tomatoes (ca. 1900) had a greater relative abundance of Actinobacteriota than wild tomatoes, especially in P-fertilized soil. In addition, Chen et al. (2022) demonstrated differential recruitment of rhizobacteria based on tomato fruit color phenotype, with Actinobacteriota being more abundant in tomatoes with yellow fruit compared to those with red fruit. Furthermore, Actinobacteriota can be competitive for root exudates and micronutrients, such as iron, as well as for antibiotic production (Nazari et al., 2023; Oyserman et al., 2022; Pérez-Jaramillo et al., 2016, 2018; Zhao et al., 2018), which may facilitate the successful colonization of *Streptomyces* in domesticated tomato rhizosphere. The observed enrichment of *Sphingomonas* in the rhizosphere of domesticated tomatoes is also confirms and extends the study by Lee et al. (2019) who proposed *Sphingomonas* as one of the indicators of the rhizosphere of domesticated tomato genotypes sampled from different greenhouses. Interestingly, we also observed an increase in Cyanobacteria genera, such as *Nostoc* and *Sericytochromatia* in domesticated tomato genotypes grown in agricultural and in greenhouse soils, respectively. This suggests that these bacterial genera are likely responding to nutrient availability, particularly N and P (Xu et al., 2017), and possibly to the reduced use of organic fertilization in agricultural soils, as observed by Zou et al. (2024).

Our profiling of the microbial traits of key tomato rhizosphere bacteria, in relation to genotype and habitat domestication, provided a better understanding of the interactions between these bacteria, their different tomato hosts, and the soil types (Figure 5; Supplementary Table S6). Unfortunately, we did not find MAGs assigned as *Massilia* or the Oxalobacteraceae family, which were abundant taxa in the rhizosphere of wild tomatoes across the soil types tested. We found a higher number of genes associated with the SEED subsystems Motility and Chemotaxis in rhizosphere MAGs of wild tomato genotypes grown in native soil and taxonomically delineated as Bacteroidetes, Cellvibrionales, Pseudomonadales and Rhizobiales. This observation aligns with find-

ings by Sun et al. (2021), who found that the root microbiome of wild rice accessions exhibited a greater abundance of bacterial chemotaxis genes than the microbiomes of their domesticated counterparts. Moreover, abundance of these bacterial taxonomic lineages was associated by Yin et al. (2020) with plant protection against pathogens. They found a higher abundance of Bacteroidetes, Pseudomonadales and Rhizobiales in tomato cultivars that resisted bacterial canker caused by *Clavibacter michiganensis*. In addition, the higher number of genes associated with flagellar motility observed in these MAGs, particularly in *Pseudomonas, Cellvibrio* and Rhizobiacea, can be linked to enhanced rhizosphere colonization and increased carbohydrate metabolism as revealed in other studies (Barajas et al., 2020; de Weert et al., 2002; Liu et al., 2024; Ramoneda et al., 2024; Zuluaga et al., 2021). Moreover, carbohydrate metabolism also showed a higher number of genes in MAGs associated with the microbiomes of the wild tomato genotypes, consistent with findings by Zboralski & Filion (2020). Additionally, the higher abundance of microbial functions associated with stress response found here may align with the observation that the wild tomato rhizosphere has a greater capacity to adapt to environmental challenges, such as oxidative or osmotic stress, as reported in several studies (Alzate Zuluaga et al., 2021; Anjum et al., 2025; Schmitz et al., 2022).

MAGs associated with the rhizosphere of domesticated tomato genotypes, especially in agricultural and greenhouse soils, exhibited a higher abundance of genes involved in amino acid metabolism, cofactors and vitamins, as well as genes related to N, P and Fe metabolism. Specifically, the increased abundance of genes related to ammonification, allantoin utilization, and siderophore biosynthesis, suggests that the microbiome associated with domesticated tomatoes may respond to fertilizer inputs with both macro- and micronutrients, as indicated in other studies (Adedayo et al., 2022; Dixon et al., 2024; Garcia et al., 2024; Smulders et al., 2021; Terra et al., 2021; Zhang et al., 2022).

With respect to the endosphere tomato microbiome, soil type was the primary determinant of the community assembly (Figures 8, 9). This effect was particularly pronounced in the phylum Firmicutes with *Bacillus* remaining consistent across soils, while *Ammoniphilus, Domibacillus, Fictibacillus* and *Lysinibacillus* showed a progressive decline in abundance from Ecuadorean native to Dutch greenhouse soil. Conversely, *Cohnella, Paenibacillus* and *Tumebacillus* exhibited a progressive increase in abundance from Ecuadorean native to Dutch greenhouse soil. Collectively, these results suggest that soil management influenced microbiome assembly of the tomato root endosphere. Other taxa exhibited genotype-specific differences for Ecuadorean native and agricultural soils. For example, *Brevundimonas, Pseudomonas, Rhizobacter* (Proteobacteria) were more abundant in the endosphere of wild-intermediate tomatoes grown in native soils, while *Actinoplanes, Streptomyces* (Actinobacteriota) and *Tolypotrix* (Cyanobacteria) were more abundant in the endosphere of domesticated tomatoes grown in agricultural soil.

Further investigation is needed to understand how root exudates and soil management practices influence the selective enrichment of these endosphere taxa and their ability to withstand plant defense responses, as well as to adapt to the specific environmental conditions associated with different tomato genotypes and soil types.

In conclusion, our results highlight the significant impact of the tomato domestication process on its microbiome, with habitat domestication playing a pronounced role in root microbiome assembly. Our results suggest that the major differentiation in rhizosphere microbiome assembly occurred later in the domestication process, i.e. during the breeding and genetic improvement stages. Additionally, we observed that wild tomatoes grown in native soils exert strong selective pressure on the rhizosphere microbiome, favoring bacteria enriched in genes associated with motility, chemotaxis and stress response. In contrast, domesticated tomatoes establish microbiome associations with bacteria that exhibit functional adaptations to agricultural and greenhouse environments, presumably fertilizer inputs. Our study emphasizes the importance of understanding microbiome shifts driven by both genotype and habitat domestication. These insights are essential for integrating microbiome management strategies into tomato cultivation and considering the microbiome as a complementary feature in breeding programs. Future research should focus on the identity and role of specific root exudates in microbial assembly for both wild and domesticated tomatoes. Additionally, the effects of soil amendments (organic and synthetic fertilizers) and other agricultural practices on tomato genotypes should be further explored. It is also important to assess the phenotypic response of tomatoes to rhizobacterial inoculation, specifically in terms of plant growth, resistance to (a)biotic stresses, and yield, with an emphasis on the genetic background of different tomato cultivars to maximize the efficiency of microbial interventions. Such studies could provide valuable insights to promote sustainable farming practices through the integration of agricultural techniques with microbial management.

Materials and Methods

Greenhouse experiment

Native and agricultural soils from the tomato's center of origin were collected in June 2021 from two locations in the province of Loja in Southern Ecuador (Ceiba 4°18'07.6"S, 80°13'16.7"W and Limones 4°23'09.2"S, 80°20'50.7"W, Zapotillo, Loja, Ecuador). Native soils were collected from a natural vegetation close to the agricultural locations. Agricultural soil from Ceiba was sampled from a field that was cultivated with onion (vegetative growth stage), whereas the agricultural soil in Limones was sampled from a local rice field (grain filling stage). All four soils were air dried at room

temperature and subsequently sieved (2 mm diameter sieve mesh) and shipped to the greenhouse facility at the Netherlands Institute of Ecology (NIOO-KNAW) in Wageningen, The Netherlands in compliance to the permit approved by the Ecuadorian Ministry of Environment. A Dutch greenhouse used for tomato seed production in South-Holland, (51°57'47"N, 4°12'16"E, collected in June 2017), provided the greenhouse soil from the center of production (Supplementary material Table S1). The five soils of interest were coded as follows: Ceiba native (CN), Ceiba agricultural (CA), Limones native (LN), Limones agricultural (LA) and, Dutch greenhouse soil (GH) (Figure 10).

A total of 8 tomato genotypes were selected and included in this experiment, and given the following abbreviations: two wild tomato species *S. peruvianum* (SPE), and *S. habrochaites* (SHA); two accessions of the closest ancestor *S. pimpinellifolium* (LPI and SPI); and four modern *S. lycopersicum* tomato varieties Solarino (SOL), Trovanzo (TRO), Kivu (KIV) and Moneymaker (MON) (Supplementary material Table S2).

To facilitate the analysis of soils and tomato genotypes, they were grouped in soil types and tomato domestication degree. Hence, Ceiba and Limones native soils were catalogued as "native soil", and Ceiba and Limones agricultural soils were named as "agricultural soil". Also, tomatoes *S. peruvianum* and *S. habrochaites* were considered as "wild", the two *S. pimpinellifolium* accessions were named as "intermediate", and varieties of *S. lycopersicum* (Solarino, Trovanzo, Kivu and Moneymaker) were termed as "domesticated" tomatoes (Figure 10).

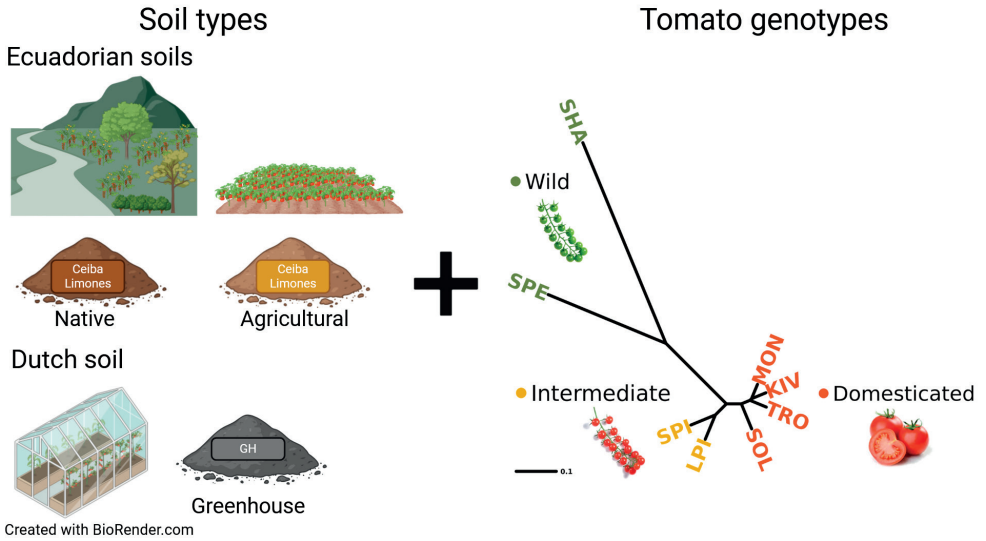

Figure 10. Soil origin (left panel) and genetic diversity of tomato genotypes (right panel) used in the experiment. Genetic diversity of the eight selected tomato genotypes was based on DArT genotyping data (17,855 SNP). The scale bar indicates the Jaccard distance to measure the dissimilarity between tomato genotypes based on SNP presence/absence. Hierarchical clustering was performed by unweighted pair group method with arithmetic mean (UPGMA). Tomato genotypes were grouped according to the domestication trajectory in wild, intermediate, and domesticated tomatoes. SHA: *S. habrochaites;* SPE: *S. peruvianum;* SPI and LPI: *S. pimpinellifolium;* and tomato varieties of *S. lycopersicum:* SOL: Solarino; TRO: Trovanzo; KIV: Kivu; MON: Moneymaker.

Prior to the greenhouse experiment, the soil samples were conditioned during seven days by adding 20% (v/w) of sterile demi-water to the soil bags. The bags were then kept under greenhouse conditions in the shade (25 ºC day; 18 ºC night). After the conditioning phase, 5% (w/w) of each soil was mixed with 95% moistened sterile fine sand (0.4–0.8 mm), and 500 g of the mixture was transferred into polyethylene pots (10 × 10 × 11 cm).

Tomato seeds were surface sterilized by adding 5 ml of 80% ethanol and shaking for 2 min. The ethanol was then removed, and 5 ml of 1.5% (v/v) sodium hypochlorite was added. The seeds were shaken for 10 min, after which the solution was discarded. To remove any residual solution, seeds were rinsed five times with 5 ml of sterile demi-water, vortexing for 2 min during each cycle and discarding the water after each rinse. Following the sterilization, seeds were placed on a wet filter paper in a Petri dish containing 5 ml of sterile demi-water and incubated at 25 ºC for three days. One pre-germinated tomato seed (radicle length ~1 cm) was sown in the center of the pot. Pots were covered with a plastic film for three days to maintain the humidity until the cotyledons emerged. The experiment consisted of eight tomato genotypes (SPE, SHA, SPI, LPI,

SOL, TRO, KIV, MON) and five soils (four Ecuadorian soils: CA, LA, CN, LN, and one Dutch tomato greenhouse soil GH), with a total of 239 pots [5 soils × 8 tomatoes × 5 replicates + 24 control (8 tomatoes in sand × 3 replicates) + 15 bulk soil (5 soil-sand mix × 3 replicates)] randomly distributed.

Plants were grown under greenhouse conditions set at 25 °C/18 °C (±1 °C) day/night; with 16 h light and 60% relative humidity. The watering regime was adjusted to the plant's requirements during the growth period, starting with 5 ml of sterile demi-water per day and gradually increasing to 100 ml per day. Additionally, a 50% Hoagland nutrient solution was applied twice per week throughout the growth period (Supplementary material Table S3).

Rhizosphere sampling

Plants were sampled at their 6th true leaf stage (25–35 days after planting the germinated seeds). The shoots were cut and the root was carefully removed from the pot. Loosely attached soil was shaken off, leaving the tightly attached soil (i.e. rhizosphere soil). A 5 g sample of each root system and 5 g of each bulk soil sample were collected in 15 ml-tubes, immediately frozen in liquid nitrogen and stored at -80 °C until further processing.

Before DNA extraction, samples were defrosted at 4 °C and 5 ml of sterile demi-water was added and vortexed at maximum speed to remove the soil particles attached to the roots (rhizosphere). The roots were transferred to a new 15 ml-tube. Both rhizosphere soil suspension and frozen bulk soil samples were freeze-dried to remove the excess water. The roots were surface sterilized by vortexing with 5 ml of 75% ethanol at medium speed (~2000 rpm) for 2 min. The ethanol solution was discarded and 5 ml of 1.5% (v/v) sodium hypochlorite were added. The roots were vortexed at medium speed for 5 min and after that, the hypochlorite solution was removed, followed by addition of 5 ml of sterile demi-water. Tubes were vortexed for 2 min, after which the water was carefully discarded. This washing process was repeated five times. Finally, the surface-sterilized roots were freeze dried to remove any remaining water.

Soil and root DNA isolation and sequencing

The rhizosphere soil samples were prepared by weighing 0.5 g of freeze-dried soil. For roots, 30 mg of freeze-dried roots were transferred into 2 ml-microtubes and the roots were homogenized with three metal beads (⌀ ⅛ inch) in the TissueLyser (Qiagen) at maximum speed (30 Hz, 1800 oscillations per minute) for 2 min. The resulting root powder was used for endosphere DNA isolation.

The Qiagen DNeasy® PowerSoil® Pro Kit was used to extract genomic DNA from soil and roots according to the manufacture's protocol. DNA samples were sent to Genome Québec (Canada) for amplicon library preparation and subsequent sequencing of the V3-V4 regions of the 16S rRNA gene using the universal bacterial primers 341F (CCTACGGGNGGCWGCAG) and 805R (GACTACHVGGGTATCTAATCC). Paired-end sequence reads (300 bp length) were generated using the Illumina NovaSeqX Plus platform. In addition, 24 rhizosphere samples corresponding to two genotypes (LPI and MON) grown in three soils (LA, LN and GH) representing four replicates were subjected to library preparation and shotgun sequencing by Novogene Co, Ltd. (Canada) to provide pair-end reads of 150 bp by Illumina NovaSeq 6000.

Amplicon data analysis

The compressed sequence reads contained in FASTQ format files were processed by the DADA2 v1.16.0 pipeline (Callahan et al., 2016) in RStudio environment (RStudio Team, 2020) to obtain the ASV abundance and taxonomy tables. The modeling of error rates associated with the sequencing process was adjusted to appropriately process NovaSeq data using the DADA2 pipeline, as suggested by Holland-Moritz (2021). The SILVA 16S ribosomal RNA gene reference database (v138) (Quast et al., 2013) was used for bacterial taxonomy assignment. ASVs present in control samples, i.e., plants grown in pure sand, were filtered out from all the samples before the analysis. The statistical analyses were performed using R software version 4.3.1 (R Core Team, 2023). Packages such as vegan (Oksanen et al., 2020), phyloseq (McMurdie & Holmes, 2013), DESeq2 (Love et al., 2014) and ggplot2 (Wickham, 2016) were used for alpha diversity, beta diversity (Bray–Curtis distance, PERMANOVA with 9,999 permutations), and differential abundance analyses, while the tidyverse package (Wickham et al., 2019) was used for formatting and visualization. Significant differences in the Shannon diversity index were determined by Kruskal-Wallis test and Wilcoxon post hoc test, while differences of beta diversity between tomato groups in pairwise comparisons were evaluated using the Adonis test. The abundance data were normalized by CSS (Cumulative Sum Scaling) for Principal Coordinates Analysis (PCoA) which was performed with the *cmdscale* function from the vegan package and the Bray–Curtis distance calculated previously. Differential abundance analyses were performed using the model "Soil_class + Tom_gen", specified in the design formula of the *DESeq* function, where Soil_class refers to the soil type, i.e. Native, Agricultural, or Greenhouse and Tom_gen represents the tomato genotype (eight genotypes). Pairwise contrasts were tested between Native vs. Agricultural soil, and Agricultural vs. Greenhouse soil. To account for varying sequencing depths, size factors were estimated using a geometric mean approach from the counts data. ASVs resulted from differential abundance analysis were visualized in a heatmap using the R package pheatmap (Kolde, 2018). Clusters

were identified through hierarchical clustering, using correlation as the distance metric and Ward's method for the clustering algorithm.

Metagenome data analysis

To gain knowledge about the potential functionality of specific members of the rhizosphere tomato microbiome, bins were produced to be annotated further. First co-assembly of all samples was done using Megahit (Li et al., 2015). Read mapping against contigs was performed using Bowtie2 (Langmead & Salzberg, 2012) and binning was done using MaxBin2 (Wu et al., 2016) and Metabat2 (Kang et al., 2019). Results from both binning approaches were processed with DAS Tool to obtain refined bins (Sieber et al., 2018). Bins were taxonomically annotated using GTDB-tk (v2.4.0) (Chaumeil et al., 2020).

The quality of the resulting bins was assessed using CheckM (Parks et al., 2015). Afterwards, 11 out of 127 bins with completeness higher than 70% and contamination less than 10%, were considered representative metagenome-assembled genomes (MAGs) of the bacteria associated with tomato and soils, consistent with the amplicon results (Supplementary Table S5). These MAGs were submitted to the RAST server (Rapid Annotation using Subsystems Technology) (Aziz et al., 2008) for annotation of functional genes (Supplementary Table S6).

Acknowledgements

We thank Dr. Sonia Zapata and Juan Mosquera (Universidad San Francisco de Quito–USFQ) for their support with the research permit procedures. We would also like to express our gratitude to Junnior Lalangui, José Luis Solano and Pablo Arévalo for their significant assistance with the collection of native and agricultural soils in Loja, Ecuador.

Author contributions

SSF: methodology, investigation, data curation; writing - original draft, review & editing; VC: supervision, writing - review & editing; data curation; BOO: review & editing; LMAG: metagenomic data analysis; review & editing; NS: conceptualization; methodology; supervision; data curation; JMR: conceptualization; supervision; funding acquisition, writing - review & editing; PVTH: supervision; review & editing. All authors contributed critically to the drafts and gave final approval for publication.

Funding

This research was supported by the Dutch Research Council Grant/Award Number: 024.004.014, the Ecuadorian National Secretary of Higher Education, Science, Technology and Innovation–SENESCYT with scholarship number: CZ07-000440-2018. Universidad San Francisco de Quito–USFQ supported this work through Chancellor Grant and COCIBA research funds to the HUBI project ID: 10093 entitled "Going back to the roots: Root microbiomes of tomato relatives". The funders had no role in the study design, data collection, analysis, decision to publish, or preparation of the manuscript. This work was performed, in part, in collaboration with the MiCRop Consortium program, Harnessing the second genome of plants (grant number 024.004.014), funded by the Dutch Research Council (NWO/OCW), using its network and infrastructure.

Plant research permit

This study was carried out under the Genetic Resource Permit N° MAE-DNB-CM-2018-0085, issued by the Ministry of Environment of Ecuador to USFQ.

Supplementary material

Supplementary Figures

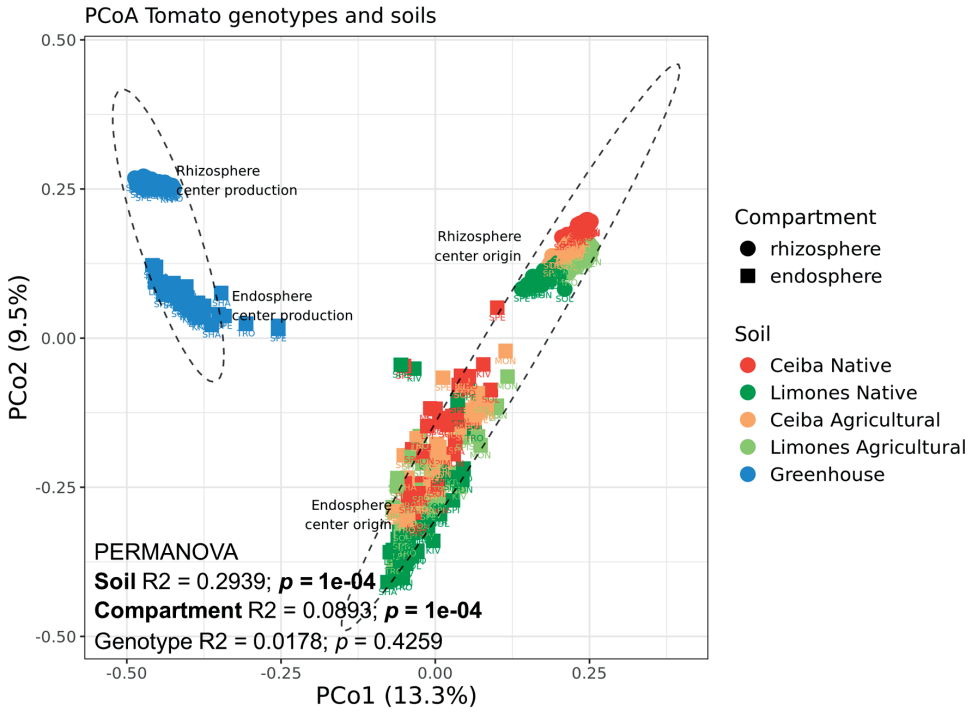

Figure S1. Bacterial community structure of tomato genotypes grown in native, agricultural and greenhouse soils. Principal Coordinate Analysis (PCoA) of rhizosphere bacterial communities showing distinct separation between soils from center of origin and the center of production, as well as differentiation of bacterial communities between tomato rhizosphere and endosphere.

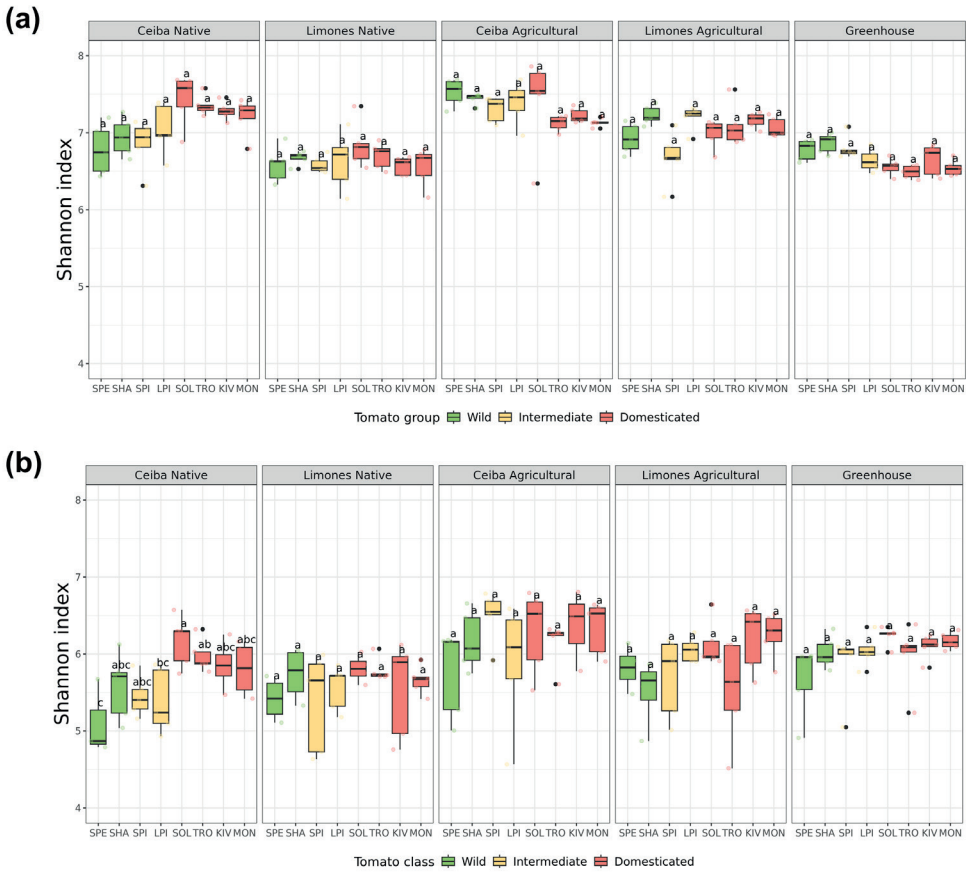

Figure S2. Shannon diversity index in tomato **(a)** rhizosphere and **(b)** endosphere grown in native, agricultural and greenhouse soils. Different letters above boxplots show significant difference (Wilcoxon test $p < 0.05$) of Shannon diversity index between tomato genotypes ($n = 5$). SPE: *S. peruvianum;* SHA: *S. habrochaites;* SPI and LPI: *S. pimpinellifolium;* and tomato varieties of *S. lycopersicum:* SOL: Solarino; TRO: Trovanzo; KIV: Kivu; MON: Moneymaker.

Table S1. Physicochemical properties of soils employed in the experiment.

Soil	pH	OM (g/kg)	N (mg/kg)	P (mg/kg)	K (mg/kg)	Ca (mg/kg)	Mg (mg/kg)	Fe (mg/kg)	Mn (mg/kg)	Cu (mg/kg)	Zn (mg/kg)	CIC (cmol/kg)	Sand (%)	Silt (%)	Clay (%)	Texture
Ceiba_Agr	7,46	13,10	700,00	19,10	50,80	2957,90	473,00	78,90	6,48	4,28	2,30	15,62	38	36	26	Loam
Ceiba_Nat	7,29	15,10	800,00	29,60	62,60	3266,50	555,70	29,60	5,48	2,56	2,29	16,01	24	50	26	Silt loam
Limones_Agr	7,19	6,20	300,00	66,80	160,30	2154,30	340,50	56,80	6,07	3,67	3,29	9,24	52	32	16	Sandy loam
Limones_Nat	7,83	2,90	100,00	47,70	215,10	2709,40	345,30	50,50	2,97	2,17	2,06	7,58	68	18	14	Sandy loam
Green-house	7,10	24,00	1040,00	15,60	309,00	156,31	196,00	2,01	1,88	0,04	0,39	7,90	85	8	3	Loamy sand

Table S2. Tomato accessions used for DArT genotyping.

Code	Species	Accession number	Origin	Passport
SPE	*Solanum peruvianum*	CGN23955	Perú	https://cgngenis.wur.nl/accessiondetails/CGN23955
SHA	*Solanum habrochaites*	CGN15792	Ecuador	https://cgngenis.wur.nl/accessiondetails/CGN15792
LPI	*Solanum pimpinellifolium*	CGN14498	NA	https://cgngenis.wur.nl/accessiondetails/CGN14498
SPI	*Solanum pimpinellifolium*	CGN23957	Perú	https://cgngenis.wur.nl/accessiondetails/CGN23957
MON	*Solanum lycopersicum* cv Money-maker	CGN14330	Netherlands	https://cgngenis.wur.nl/accessiondetails/CGN14330
KIV	*Solanum lycopersicum* cv Kivu	NA	© Rijk Zwaan	https://www.rijkzwaanusa.com/tomato/KIVU-RZ-F1-72-629-prdSL11187-ctgCrops.tomato
TRO	*Solanum lycopersicum* cv Trovanzo	NA	© Rijk Zwaan	https://rijkzwaan.it/pomodoro/TROVANZO-RZ-F1-72-762-prdSL11225-ctgCrops.tomato
SOL	*Solanum lycopersicum* cv Solarino	NA	© Rijk Zwaan	https://www.rijkzwaan.de/tomate/SOLARINO-F1-72-150-prdSL11078-ctgCrops.tomato

Table S3. Hoagland solution composition.

Hoagland solution stock	M (g/mol)	Molarity	g/l Stock	1 liter 1/2X
Macroelements:				
Calcium nitrate Ca(NO3)2.4H2O	236.16	0.5 M	118.08	5 ml
Potassium nitrate KNO3	101.11	1.0 M	101.11	2.5 ml
Potassium phosphate KH2PO4	136.09	1.0 M	136.09	0.5 ml
Magnesium sulfate MgSO4.7H2O	246.47	0.5 M	123.24	2 ml
Microelements:				1 ml
Boric acid H3BO3	61.83	46.3 mM	2.86	
Manganese chloride MnCl2.4H2O	197.91	9.1 mM	1.81	
Zinc sulfate ZnSO4.7H2O	287.54	0.77 mM	0.22	
Copper sulfate CuSO4.5H2O	249.68	0.32 mM	0.08	
Sodium molybdate Na2MoO4.2H2O	241.95	0.52 mM	0.126	
EDTA ferric salt C10H12FeN2NaO8.3H2O	421.1	98.6 mM	41.52	

Note. For preparing 1000 ml of Hoagland solution stock: Dissolve the components (g/l Stock) in 1000 ml of sterile demi water and store at room temperature in the shade. Stock solution of microelements can be prepared in 500 ml in an amber bottle or covered with aluminum foil to protect it against light.

For preparing 1000 ml of Hoagland 1/2X concentration: Autoclave 989 ml of demi water and add the volume of each Hoagland component by filtration (Whatman cellulose syringe filter 0,2 μm).

Table S4. Pairwise analysis by Adonis test in tomato rhizosphere and endosphere.

Plant Compartment	Soil	Pairs	R^2	p.adj	sig.
Rhizosphere	Ceiba_Agr	W × I	0,0653	0,0615	
Rhizosphere	Ceiba_Agr	W × D	0,1366	0,00015	*
Rhizosphere	Ceiba_Agr	I × D	0,1283	0,00015	*
Rhizosphere	Ceiba_Nat	W × I	0,0633	0,0742	
Rhizosphere	Ceiba_Nat	W × D	0,1818	0,00015	*
Rhizosphere	Ceiba_Nat	I × D	0,1737	0,00015	*
Rhizosphere	Limones_Agr	W × I	0,0698	0,0442	*
Rhizosphere	Limones_Agr	W × D	0,1693	0,00015	*
Rhizosphere	Limones_Agr	I × D	0,1491	0,00015	*
Rhizosphere	Limones_Nat	W × I	0,0662	0,0605	
Rhizosphere	Limones_Nat	W × D	0,1554	0,00015	*
Rhizosphere	Limones_Nat	I × D	0,1799	0,00015	*
Rhizosphere	Greenhouse	W × I	0,0608	0,1914	
Rhizosphere	Greenhouse	W × D	0,2344	0,00015	*
Rhizosphere	Greenhouse	I × D	0,2104	0,00015	*
Endosphere	Ceiba_Agr	W × I	0,0558	0,1893	
Endosphere	Ceiba_Agr	W × D	0,0509	0,0123	*
Endosphere	Ceiba_Agr	I × D	0,0403	0,12	
Endosphere	Ceiba_Nat	W × I	0,064	0,0506	
Endosphere	Ceiba_Nat	W × D	0,0468	0,0306	*
Endosphere	Ceiba_Nat	I × D	0,0485	0,0306	*
Endosphere	Limones_Agr	W × I	0,0585	0,0966	
Endosphere	Limones_Agr	W × D	0,0631	0,0021	*
Endosphere	Limones_Agr	I × D	0,0458	0,0461	*
Endosphere	Limones_Nat	W × I	0,0583	0,1749	
Endosphere	Limones_Nat	W × D	0,0506	0,0663	
Endosphere	Limones_Nat	I × D	0,0381	0,1749	
Endosphere	Greenhouse	W × I	0,0542	0,3477	
Endosphere	Greenhouse	W × D	0,0545	0,0108	*
Endosphere	Greenhouse	I × D	0,0459	0,0402	*

Table S5. High quality-bins assembled from rhizosphere tomato grown in different soils

Bin_Id	Marker_lineage	Completeness	Contamination	Kingdom	Phylum	Class	Order	Family	Genus	Species
bin.555	p__Bacteroidetes (UID2605)	99.87	0.48	Bacteria	Bacteroidota	Bacteroidia	Sphingobacteriales	Sphingobacteriaceae		
bin.732	o__Cytophagales (UID2936)	99.7	1.07	Bacteria	Bacteroidota	Bacteroidia	Cytophagales	Spirosomaceae	Emticicia	
bin.204	p__Bacteroidetes (UID2605)	99.52	1.9	Bacteria	Bacteroidota	Bacteroidia	AKYH767	b-17BO		
bin.895	p__Bacteroidetes (UID2591)	99.51	2.4	Bacteria	Bacteroidota	Bacteroidia	Chitinophagales	Chitinophagaceae		
bin.601	o__Cytophagales (UID2936)	99.03	5.7	Bacteria	Bacteroidota	Bacteroidia	Cytophagales	Cyclobacteriaceae		
bin.795	f__Xanthomonadaceae (UID4214)	98.85	6.98	Bacteria	Proteobacteria	Gammaproteobacteria	Xanthomonadales	Rhodanobacteraceae	Dyella	
bin.952	k__Bacteria (UID2569)	98.76	0	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales	Crocinitomicaceae	Fluviicola	
bin.745	o__Actinomycetales (UID1808)	98.54	3.73	Bacteria	Actinobacteriota	Actinobacteria	Mycobacteriales	Mycobacteriaceae	Mycolicibacterium	
bin.518	o__Sphingomonadales (UID3310)	98.3	4.66	Bacteria	Proteobacteria	Alphaproteobacteria	Sphingomonadales	Sphingomonadaceae	Sphingopyxis	
bin.714	k__Bacteria (UID203)	98.28	9.87	Bacteria	Proteobacteria	Gammaproteobacteria	Legionellales	Legionellaceae	Legionella	
bin.747	k__Bacteria (UID3187)	98.16	0.89	Bacteria	Bdellovibrionota	Bdellovibrionia	Bdellovibrionales	Bdellovibrionaceae	Ga0074139	
bin.224	o__Actinomycetales (UID2012)	97.82	8.06	Bacteria	Actinobacteriota	Actinobacteria	Mycobacteriales	Pseudonocardiaceae	Pseudonocardia	
bin.572	p__Bacteroidetes (UID2605)	97.6	1.94	Bacteria	Bacteroidota	Bacteroidia	Sphingobacteriales	Sphingobacteriaceae		

Table S5. High quality-bins assembled from rhizosphere tomato grown in different soils (*continued*)

Bin_Id	Marker_lineage	Completeness	Contamination	Kingdom	Phylum	Class	Order	Family	Genus	Species
bin.53	k__Bacteria (UID2569)	97.57	1.4	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales	Crocinitomicaceae	Fluviicola	
bin.643	p__Cyanobacteria (UID2182)	97.56	1.66	Bacteria	Cyanobacteria	Cyanobacteriia	Elainellales	Elainellaceae	Leptolyngbya_A	
bin.761	o__Sphingomonadales (UID3310)	97.4	6.14	Bacteria	Proteobacteria	Alphaproteobacteria	Sphingomonadales	Sphingomonadaceae	Sphingopyxis	
bin.929	o__Actinomycetales (UID1696)	97.25	2.54	Bacteria	Actinobacteriota	Actinobacteria	Mycobacteriales	Micromonosporaceae		
bin.918	p__Bacteroidetes (UID2605)	96.87	1.22	Bacteria	Bacteroidota	Bacteroidia	Sphingobacteriales	Sphingobacteriaceae	Mucilaginibacter	
bin.215	k__Bacteria (UID3187)	96.37	2.68	Bacteria	Bdellovibrionota	Bdellovibrionia	Bdellovibrionales	Bdellovibrionaceae	21-14-0-10-47-8	
bin.296	c__Deltaproteobacteria (UID3216)	96.13	6.45	Bacteria	Myxococcota	Polyangia	Polyangiales	Sandaracinaceae		
bin.111	p__Actinobacteria (UID1454)	96.07	1.95	Bacteria	Actinobacteriota	Thermoleophilia	Solirubrobacterales	Solirubrobacteraceae		
bin.690	k__Bacteria (UID2982)	95.95	5.41	Bacteria	Verrucomicrobiota	Verrucomicrobiae	Pedosphaerales	AV2		
bin.890	c__Gammaproteobacteria (UID4202)	95.86	6.02	Bacteria	Proteobacteria	Gammaproteobacteria	Nevskiales	Nevskiaceae	Fontimonas	
bin.721	o__Pseudomonadales (UID4488)	95.73	5.18	Bacteria	Proteobacteria	Gammaproteobacteria	Pseudomonadales	Pseudomonadaceae	Pseudomonas_E	
bin.485	p__Bacteroidetes (UID2591)	95.71	7.51	Bacteria	Bacteroidota	Bacteroidia	Chitinophagales	Chitinophagaceae	Taibaiella_B	
bin.188	o__Burkholderiales (UID4000)	95.53	7.18	Bacteria	Proteobacteria	Gammaproteobacteria	Burkholderiales	Burkholderiaceae	Herminiimonas	

Table S5. High quality-bins assembled from rhizosphere tomato grown in different soils (*continued*)

Bin_Id	Marker_lineage	Completeness	Contamination	Kingdom	Phylum	Class	Order	Family	Genus	Species
bin.591	k__Bacteria (UID3187)	95.5	1.8	Bacteria	Bdellovibrionota	Bdellovibrionia	Bdellovibrionales	Bdellovibrionaceae	Bdellovibrio_A	
bin.844	o__Rhizobiales (UID3450)	95.41	2.21	Bacteria	Proteobacteria	Alphaproteobacteria	Rhizobiales	Rhizobiaceae	Chelativorans	Chelativorans sp000014245
bin.257	k__Bacteria (UID3187)	95.39	5.73	Bacteria	Acidobacteriota	Thermoanaerobaculia	Gp7-AA8	Gp7-AA8	QHVT01	
bin.324	k__Bacteria (UID2982)	95.35	2.86	Bacteria	Verrucomicrobiota	Verrucomicrobiae	Verrucomicrobiales	Akkermansiaceae	Haloferula	
bin.633	k__Bacteria (UID2569)	95.26	1.62	Bacteria	Bacteroidota	Bacteroidia	Flavobacteriales	Crocinitomicaceae	Fluviicola	
bin.221	k__Bacteria (UID3187)	94.74	1.26	Bacteria	Bdellovibrionota	Bdellovibrionia	Bdellovibrionales	Bdellovibrionaceae	21-14-0-10-47-8	
bin.441	c__Deltaproteobacteria (UID3216)	94.62	3.39	Bacteria	Myxococcota	Myxococcia	Myxococcales	Myxococcaceae		
bin.177	k__Bacteria (UID3187)	94.12	0.89	Bacteria	Bdellovibrionota	Bdellovibrionia	Bdellovibrionales	Bdellovibrionaceae	21-14-0-10-47-8	
bin.329	o__Sphingomonadales (UID3310)	93.95	6.7	Bacteria	Proteobacteria	Alphaproteobacteria	Sphingomonadales	Sphingomonadaceae	Sphingobium	
bin.117	k__Bacteria (UID3187)	93.9	2.41	Bacteria	Bdellovibrionota	Bacteriovoracia	Bacteriovoracales	Bacteriovoraceae	Bacteriovorax	
bin.330	k__Bacteria (UID3187)	93.87	9.54	Bacteria	Acidobacteriota	Vicinamibacteria	Vicinamibacterales	Vicinamibacteraceae	Luteitalea	
bin.838	c__Betaproteobacteria (UID3959)	93.69	5.35	Bacteria	Proteobacteria	Gammaproteobacteria	Burkholderiales	SG8-41		
bin.664	o__Burkholderiales (UID4002)	93.57	4.3	Bacteria	Proteobacteria	Gammaproteobacteria	Burkholderiales	Burkholderiaceae	Herminiimonas	

Table S5. High quality-bins assembled from rhizosphere tomato grown in different soils (*continued*)

Bin_Id	Marker_lineage	Completeness	Contamination	Kingdom	Phylum	Class	Order	Family	Genus	Species
bin.273	k__Bacteria (UID2982)	93.34	5.14	Bacteria	Verrucomicrobiota	Verrucomicrobiae	Opitutales	Opitutaceae	Didemnitutus	
bin.737	c__Deltaproteobacteria (UID3216)	93.12	3.25	Bacteria	Myxococcota	Polyangia	Polyangiales			
bin.319	c__Gammaproteobacteria (UID4444)	92.98	2.39	Bacteria	Proteobacteria	Gammaproteobacteria	Pseudomonadales	Cellvibrionaceae	Cellvibrio	
bin.464	p__Bacteroidetes (UID2591)	92.61	6.03	Bacteria	Bacteroidota	Bacteroidia	Chitinophagales	Chitinophagaceae	Taibaiella_B	
bin.515	o__Burkholderiales (UID4000)	92.5	5.06	Bacteria	Proteobacteria	Gammaproteobacteria	Burkholderiales	Burkholderiaceae	Rhizobacter	
bin.302	p__Bacteroidetes (UID2605)	92.49	1.67	Bacteria	Bacteroidota	Bacteroidia	AKYH767	b-17BO		
bin.861	g__Burkholderia (UID4006)	92.23	0.31	Bacteria	Proteobacteria	Gammaproteobacteria	Burkholderiales	Burkholderiaceae	Paraburkholderia	Paraburkholderia sp000148685
bin.427	f__Micrococcaceae (UID1623)	92.16	4.38	Bacteria	Actinobacteriota	Actinobacteria	Actinomycetales	Micrococcaceae	Sinomonas	
bin.647	c__Gammaproteobacteria (UID4266)	92.16	1.75	Bacteria	Proteobacteria	Gammaproteobacteria	Legionellales	Legionellaceae	Legionella_C	
bin.606	o__Burkholderiales (UID4000)	91.79	2.29	Bacteria	Proteobacteria	Gammaproteobacteria	Burkholderiales	Burkholderiaceae	Noviherbaspirillum	
bin.607	c__Betaproteobacteria (UID3959)	91.71	5.08	Bacteria	Proteobacteria	Gammaproteobacteria	Burkholderiales	SG8-41	PLOWO2-02-64-14	
bin.7	p__Bacteroidetes (UID2591)	91.71	3.2	Bacteria	Bacteroidota	Bacteroidia	Chitinophagales	Chitinophagaceae	Flavisolibacter	
bin.124	o__Burkholderiales (UID4000)	91.49	6.51	Bacteria	Proteobacteria	Gammaproteobacteria	Burkholderiales	Burkholderiaceae	Noviherbaspirillum	

Table S5. High quality-bins assembled from rhizosphere tomato grown in different soils (*continued*)

Bin_Id	Marker_lineage	Completeness	Contamination	Kingdom	Phylum	Class	Order	Family	Genus	Species
bin.868	p__Proteobacteria (UID3887)	91.48	8.95	Bacteria	Proteobacteria	Gammaproteobacteria	Burkholderiales	Burkholderiaceae	Lautropia	
bin.373	c__Alphaproteobacteria (UID3422)	90.57	3.32	Bacteria	Proteobacteria	Alphaproteobacteria	Caulobacterales	Caulobacteraceae	Asticcacaulis	
bin.548	o__Burkholderiales (UID4000)	90.38	4.35	Bacteria	Proteobacteria	Gammaproteobacteria	Burkholderiales	Burkholderiaceae	Noviherbaspirillum	
bin.915	c__Gammaproteobacteria (UID4445)	90.04	5.96	Bacteria	Proteobacteria	Gammaproteobacteria	Pseudomonadales	Pseudomonadaceae	Pseudomonas_A	Pseudomonas_A stutzeri_AI
bin.808	f__Micrococcaceae (UID1623)	89.55	2.18	Bacteria	Actinobacteriota	Actinobacteria	Actinomycetales	Micrococcaceae	Arthrobacter_D	Arthrobacter_D sp001428435
bin.472	o__Burkholderiales (UID4002)	89.5	6.46	Bacteria	Proteobacteria	Gammaproteobacteria	Burkholderiales	Burkholderiaceae	Noviherbaspirillum	
bin.96	f__Bacillaceae (UID830)	89.34	4.14	Bacteria	Firmicutes	Bacilli	Bacillales	Anoxybacillaceae	Parageobacillus	
bin.494	g__Streptomyces (UID2052)	89.32	2.72	Bacteria	Actinobacteriota	Actinobacteria	Streptomycetales	Streptomycetaceae	Streptomyces	
bin.734	o__Rhizobiales (UID3450)	89.14	2.98	Bacteria	Proteobacteria	Alphaproteobacteria	Rhizobiales	Rhizobiaceae	UBA1059	
bin.716	c__Gammaproteobacteria (UID4266)	89.1	0.81	Bacteria	Proteobacteria	Gammaproteobacteria	Legionellales	Legionellaceae	Legionella	
bin.610	o__Burkholderiales (UID4002)	88.51	5.86	Bacteria	Proteobacteria	Gammaproteobacteria	Burkholderiales	Burkholderiaceae	Herbaspirillum	Herbaspirillum aquaticum
bin.827	c__Betaproteobacteria (UID3888)	88.47	8.33	Bacteria	Proteobacteria	Gammaproteobacteria	Burkholderiales	Methylophilaceae		
bin.577	c__Alphaproteobacteria (UID3422)	88.27	3.8	Bacteria	Proteobacteria	Alphaproteobacteria	Caulobacterales	Caulobacteraceae	Asticcacaulis	

Table S5. High quality-bins assembled from rhizosphere tomato grown in different soils (*continued*)

Bin_Id	Marker_lineage	Completeness	Contamination	Kingdom	Phylum	Class	Order	Family	Genus	Species
bin.628	k__Bacteria (UID3187)	88.24	3.3	Bacteria	Bdellovibrionota	Bdellovibrionia	Bdellovibrionales	Bdellovibrionaceae	Ga0074137	
bin.499	o__Burkholderiales (UID4000)	87.98	4.95	Bacteria	Proteobacteria	Gammaproteobacteria	Burkholderiales	Burkholderiaceae	Noviherbaspirillum	
bin.505	k__Bacteria (UID3187)	87.89	5.13	Bacteria	Acidobacteriota	Blastocatellia	Pyrinomonadales	Pyrinomonadaceae	OLB17	
bin.248	o__Burkholderiales (UID4001)	86.66	4.57	Bacteria	Proteobacteria	Gammaproteobacteria	Burkholderiales	Burkholderiaceae	Paraburkholderia_E	
bin.280	k__Bacteria (UID2982)	86.36	1.5	Bacteria	Verrucomicrobiota	Verrucomicrobiae	Verrucomicrobiales	Akkermansiaceae	Haloferula	
bin.445	c__Betaproteobacteria (UID3888)	86.09	3.75	Bacteria	Proteobacteria	Gammaproteobacteria	Burkholderiales	Methylophilaceae		
bin.783	p__Bacteroidetes (UID2591)	85.47	2.02	Bacteria	Bacteroidota	Bacteroidia	Chitinophagales	Chitinophagaceae	Chitinophaga	
bin.113	o__Rhizobiales (UID3449)	85.45	4.99	Bacteria	Proteobacteria	Alphaproteobacteria	Rhizobiales	Rhizobiaceae	Pseudorhizobium	
bin.8	k__Bacteria (UID2982)	84.5	1.36	Bacteria	Verrucomicrobiota	Verrucomicrobiae	Verrucomicrobiales	Akkermansiaceae	Haloferula	
bin.777	k__Bacteria (UID203)	84.48	6.03	Bacteria	Proteobacteria	Alphaproteobacteria	Rhizobiales	Rhizobiaceae	Shinella	
bin.898	p__Bacteroidetes (UID2591)	84.44	2.4	Bacteria	Bacteroidota	Bacteroidia	Chitinophagales	Chitinophagaceae	Niastella	
bin.625	f__Micrococcaceae (UID1623)	84.19	3.11	Bacteria	Actinobacteriota	Actinobacteria	Actinomycetales	Micrococcaceae	Arthrobacter_D	Arthrobacter_D subterraneus
bin.780	o__Actinomycetales (UID1663)	84.06	6.49	Bacteria	Actinobacteriota	Actinobacteria	Actinomycetales	Dermatophilaceae	Pedococcus	

Table S5. High quality-bins assembled from rhizosphere tomato grown in different soils (*continued*)

Bin_Id	Marker_lineage	Completeness	Contamination	Kingdom	Phylum	Class	Order	Family	Genus	Species
bin.854	g__Ensifer (UID3566)	84	4.67	Bacteria	Proteobacteria	Alphaproteobacteria	Rhizobiales	Rhizobiaceae	Sinorhizobium	Sinorhizobium meliloti_A
bin.651	c__Alphaproteobacteria (UID3305)	83.77	7.47	Bacteria	Proteobacteria	Alphaproteobacteria	Sphingomonadales	Sphingomonadaceae	Sphingomonas_A	
bin.225	o__Burkholderiales (UID4000)	83.32	8.76	Bacteria	Proteobacteria	Gammaproteobacteria	Burkholderiales	Burkholderiaceae	Rhizobacter	
bin.725	k__Bacteria (UID2565)	83.26	1.7	Bacteria	Planctomycetota	Phycisphaerae	Phycisphaerales	SM1A02		
bin.537	k__Bacteria (UID2570)	83.07	3.67	Bacteria	Bacteroidota	Rhodothermia	Rhodothermales	Rhodothermaceae		
bin.434	c__Alphaproteobacteria (UID3305)	82.63	5.25	Bacteria	Proteobacteria	Alphaproteobacteria	Sphingomonadales	Sphingomonadaceae	Sphingomonas_A	
bin.581	o__Cytophagales (UID2936)	82.62	1.99	Bacteria	Bacteroidota	Bacteroidia	Cytophagales	Cyclobacteriaceae		
bin.95	p__Cyanobacteria (UID2182)	82.23	0.79	Bacteria	Cyanobacteria	Cyanobacteriia	Neosynechococcales			
bin.383	c__Betaproteobacteria (UID3959)	82.01	1.03	Bacteria	Proteobacteria	Gammaproteobacteria	Burkholderiales	Nitrosomonadaceae	Nitrosospira	
bin.402	k__Bacteria (UID1452)	81.91	3.72	Bacteria	Chloroflexota	Chloroflexia	54-19			
bin.147	k__Bacteria (UID2982)	81.74	7.77	Bacteria	Verrucomicrobiota	Verrucomicrobiae	Opitutales	Opitutaceae	IMCC26134_A	
bin.500	o__Rhizobiales (UID3447)	81.47	4.95	Bacteria	Proteobacteria	Alphaproteobacteria	Rhizobiales	Anderseniellaceae	QKVK01	
bin.713	k__Bacteria (UID3187)	81.41	2.61	Bacteria	Acidobacteriota	Blastocatellia	Pyrinomonadales	Pyrinomonadaceae	OLB17	

Table S5. High quality-bins assembled from rhizosphere tomato grown in different soils (*continued*)

Bin_Id	Marker_lineage	Completeness	Contamination	Kingdom	Phylum	Class	Order	Family	Genus	Species
bin.634	k__Bacteria (UID203)	81.4	3.45	Bacteria	Patescibacteria	Paceibacteria	UBA9983_A	UBA2163	C7867-001	
bin.14	p__Euryarchaeota (UID3)	81.36	2.67	NA	NA	NA	NA	NA	NA	NA
bin.708	k__Bacteria (UID2495)	81.29	8.79	Bacteria	Gemmatimonadota	Gemmatimonadetes	Gemmatimonadales	Gemmatimonadaceae		
bin.585	p__Cyanobacteria (UID2182)	81.24	1.57	Bacteria	Cyanobacteria	Cyanobacteriia	Neosynechococcales			
bin.35	c__Alphaproteobacteria (UID3305)	81.05	6.81	Bacteria	Proteobacteria	Alphaproteobacteria	Sphingomonadales	Sphingomonadaceae	Sphingomonas_F	
bin.202	k__Bacteria (UID203)	80.88	5.33	Bacteria	Patescibacteria	Saccharimonadia	Saccharimonadales	UBA4665		
bin.843	p__Actinobacteria (UID1454)	80.85	7.98	Bacteria	Actinobacteriota	Thermoleophilia	Solirubrobacterales	Solirubrobacteraceae		
bin.560	o__Burkholderiales (UID4001)	80.7	0.91	Bacteria	Proteobacteria	Gammaproteobacteria	Burkholderiales	Burkholderiaceae	Paraburkholderia_E	
bin.602	p__Euryarchaeota (UID3)	80.49	3.64	NA	NA	NA	NA	NA	NA	NA
bin.84	p__Actinobacteria (UID1454)	79.31	5.03	Bacteria	Actinobacteriota	Thermoleophilia	20CM-4-69-9			
bin.759	k__Bacteria (UID203)	79.28	0	Bacteria	Patescibacteria	Paceibacteria	UBA9983_A	UBA1006		
bin.462	o__Sphingomonadales (UID3310)	79.04	6	Bacteria	Proteobacteria	Alphaproteobacteria	Sphingomonadales	Sphingomonadaceae	Sphingomonas	
bin.549	k__Bacteria (UID1453)	78.89	4.91	Bacteria	Cyanobacteria	Sericytochromatia				

Table S5. High quality-bins assembled from rhizosphere tomato grown in different soils (*continued*)

Bin_Id	Marker_lineage	Completeness	Contamination	Kingdom	Phylum	Class	Order	Family	Genus	Species
bin.688	k__Bacteria (UID2495)	78.61	3.3	Bacteria	Gemmatimonadota	Gemmatimonadetes	Gemmatimonadales	GWC2-71-9		
bin.449	k__Bacteria (UID203)	77.01	1.72	Bacteria	Patescibacteria	Paceibacteria	UBA9983_A	UBA2163	C7867-001	
bin.416	k__Bacteria (UID203)	76.72	0.86	Bacteria	Bacteroidota	Bacteroidia	AKYH767	Palsa-965	GCA-2737665	
bin.604	k__Bacteria (UID3187)	75.33	2.94	Bacteria	Bdellovibrionota	Bdellovibrionia	Bdellovibrionales	Bdellovibrionaceae	21-14-0-10-47-8	
bin.180	k__Bacteria (UID2982)	75.1	2.7	Bacteria	Verrucomicrobiota	Verrucomicrobiae	Chthoniobacterales	Terrimicrobiaceae		
bin.355	o__Burkholderiales (UID4000)	74.96	7.97	Bacteria	Proteobacteria	Gammaproteobacteria	Burkholderiales	Burkholderiaceae	Vitreoscilla_A	
bin.419	k__Bacteria (UID3187)	74.6	4.35	Bacteria	Bdellovibrionota	Bdellovibrionia	Bdellovibrionales	Bdellovibrionaceae		
bin.640	k__Bacteria (UID203)	74.57	9.48	Bacteria	Actinobacteriota	Actinobacteria	Frankiales	Frankiaceae		
bin.769	k__Bacteria (UID203)	74.22	7.99	Bacteria	Gemmatimonadota	Gemmatimonadetes				
bin.276	k__Bacteria (UID2982)	74.19	0.04	Bacteria	Verrucomicrobiota	Verrucomicrobiae	Pedosphaerales			
bin.652	k__Bacteria (UID203)	74.14	6.9	Bacteria	Proteobacteria	Gammaproteobacteria	Xanthomonadales	Rhodanobacteraceae	Dyella	
bin.368	c__Betaproteobacteria (UID3888)	73.87	5.85	Bacteria	Proteobacteria	Gammaproteobacteria	Burkholderiales	Leeiaceae	Leeia	
bin.934	k__Bacteria (UID2495)	73.08	6.66	Bacteria	Gemmatimonadota	Gemmatimonadetes	Gemmatimonadales	GWC2-71-9		

Table S5. High quality-bins assembled from rhizosphere tomato grown in different soils (*continued*)

Bin_Id	Marker_lineage	Completeness	Contamination	Kingdom	Phylum	Class	Order	Family	Genus	Species
bin.770	o__Rhizobiales (UID3654)	72.31	3.92	Bacteria	Proteobacteria	Alphaproteobacteria	Rhizobiales	Beijerinckiaceae	Microvirga	
bin.110	k__Bacteria (UID203)	71.9	2.59	Bacteria	Bacteroidota	Bacteroidia	AKYH767	Palsa-965	GCA-2737665	
bin.209	k__Bacteria (UID203)	71.9	9.48	Bacteria	Proteobacteria	Gammaproteobacteria	Xanthomonadales	Rhodanobacteraceae	Dyella	
bin.803	k__Bacteria (UID2495)	71.52	0	Bacteria	Patescibacteria	Paceibacteria	UBA9983_A	UBA5272	UBA11704	
bin.163	k__Bacteria (UID3187)	70.86	4.97	Bacteria	Bdellovibrionota	Bdellovibrionia	Bdellovibrionales	UBA1609		
bin.125	k__Bacteria (UID203)	70.33	1.75	Bacteria	Bdellovibrionota	Bdellovibrionia	Bdellovibrionales	Bdellovibrionaceae	UBA2316	
bin.297	o__Cytophagales (UID2936)	70.2	3.92	Bacteria	Bacteroidota	Bacteroidia	Cytophagales	Cytophagaceae		
bin.437	k__Bacteria (UID203)	70.19	1.72	Bacteria	Patescibacteria	Paceibacteria	UBA9983_A	UBA2163	1-14-0-10-47-16	
bin.469	k__Bacteria (UID203)	70.17	3.45	Bacteria	Proteobacteria	Gammaproteobacteria	Burkholderiales	Burkholderiaceae	Vitreoscilla_A	
bin.848	k__Bacteria (UID203)	70	1.72	Bacteria	Proteobacteria	Gammaproteobacteria	Burkholderiales	Burkholderiaceae	Roseateles	

Table S6. Annotated protein encoding genes by RAST server using the SEED Subsystem database from bacterial assembled bins from different tomato genotypes grown in different soils.

bin_name	Category	Subcategory	Subsystem	Role	Features
Chitinophaga_bin783	Nitrogen Metabolism	Denitrification	Denitrifying reductase gene clusters	Nitrous oxide reductase maturation protein NosF (ATPase)	fig|6666666.1425568.peg.2979
Chitinophaga_bin783	Nitrogen Metabolism	Denitrification	Denitrifying reductase gene clusters	Copper-containing nitrite reductase (EC 1.7.2.1)	fig|6666666.1425568.peg.2169
Chitinophaga_bin783	Nitrogen Metabolism	Denitrification	Denitrifying reductase gene clusters	Nitrous oxide reductase maturation transmembrane protein NosY	fig|6666666.1425568.peg.2978
Chitinophaga_bin783	Nitrogen Metabolism	Denitrification	Denitrifying reductase gene clusters	Nitrous oxide reductase maturation protein NosD	fig|6666666.1425568.peg.2980
Chitinophaga_bin783	Nitrogen Metabolism	Denitrification	Denitrifying reductase gene clusters	Nitrous-oxide reductase (EC 1.7.99.6)	fig|6666666.1425568.peg.2982
Chitinophaga_bin783	Nitrogen Metabolism	Denitrification	Denitrification	Copper-containing nitrite reductase (EC 1.7.2.1)	fig|6666666.1425568.peg.2169
Chitinophaga_bin783	Nitrogen Metabolism	Denitrification	Denitrification	Nitrous oxide reductase maturation protein NosF (ATPase)	fig|6666666.1425568.peg.2979
Chitinophaga_bin783	Nitrogen Metabolism	Denitrification	Denitrification	Nitrous oxide reductase maturation protein NosD	fig|6666666.1425568.peg.2980
Chitinophaga_bin783	Nitrogen Metabolism	Denitrification	Denitrification	Nitrous-oxide reductase (EC 1.7.99.6)	fig|6666666.1425568.peg.2982
Chitinophaga_bin783	Nitrogen Metabolism	Denitrification	Denitrification	Nitrous oxide reductase maturation transmembrane protein NosY	fig|6666666.1425568.peg.2978
Chitinophaga_bin783	Nitrogen Metabolism	Denitrification	Denitrification	Nitric-oxide reductase (EC 1.7.99.7), quinol-dependent	fig|6666666.1425568.peg.1512
Chitinophaga_bin783	Nitrogen Metabolism	Nitrogen Metabolism - no subcategory	Ammonia assimilation	Glutamine synthetase type III, GlnN (EC 6.3.1.2)	fig|6666666.1425568.peg.4262
Chitinophaga_bin783	Nitrogen Metabolism	Nitrogen Metabolism - no subcategory	Ammonia assimilation	Glutamate synthase [NADPH] large chain (EC 1.4.1.13)	fig|6666666.1425568.peg.1009

Table S6. Annotated protein encoding genes by RAST server using the SEED Subsystem database from bacterial assembled bins from different tomato genotypes grown in different soils. (*continued*)

bin_name	Category	Subcategory	Subsystem	Role	Features
Chitinophaga_bin783	Nitrogen Metabolism	Nitrogen Metabolism - no subcategory	Ammonia assimilation	Glutamate synthase [NADPH] small chain (EC 1.4.1.13)	fig|6666666.1425568.peg.1008
Chitinophaga_bin783	Nitrogen Metabolism	Nitrogen Metabolism - no subcategory	Ammonia assimilation	Ammonium transporter	fig|6666666.1425568.peg.4388
Chitinophaga_bin783	Nitrogen Metabolism	Nitrogen Metabolism - no subcategory	Ammonia assimilation	Ferredoxin-dependent glutamate synthase (EC 1.4.7.1)	fig|6666666.1425568.peg.242
Chitinophaga_bin783	Nitrogen Metabolism	Nitrogen Metabolism - no subcategory	Nitrosative stress	Nitric-oxide reductase (EC 1.7.99.7), quinol-dependent	fig|6666666.1425568.peg.1512
Chitinophaga_bin783	Potassium metabolism	Potassium metabolism - no subcategory	Potassium homeostasis	FKBP-type peptidyl-prolyl cis-trans isomerase SlyD (EC 5.2.1.8)	fig|6666666.1425568.peg.838
Chitinophaga_bin783	Potassium metabolism	Potassium metabolism - no subcategory	Potassium homeostasis	Potassium-transporting ATPase C chain (EC 3.6.3.12) (TC 3.A.3.7.1)	fig|6666666.1425568.peg.2163
Chitinophaga_bin783	Potassium metabolism	Potassium metabolism - no subcategory	Potassium homeostasis	Potassium efflux system KefA protein	fig|6666666.1425568.peg.3042
Chitinophaga_bin783	Potassium metabolism	Potassium metabolism - no subcategory	Potassium homeostasis	Potassium-transporting ATPase B chain (EC 3.6.3.12) (TC 3.A.3.7.1)	fig|6666666.1425568.peg.2162
Chitinophaga_bin783	Potassium metabolism	Potassium metabolism - no subcategory	Potassium homeostasis	Potassium-transporting ATPase A chain (EC 3.6.3.12) (TC 3.A.3.7.1)	fig|6666666.1425568.peg.1077
Chitinophaga_bin783	Potassium metabolism	Potassium metabolism - no subcategory	Potassium homeostasis	Large-conductance mechanosensitive channel	fig|6666666.1425568.peg.1787
Chitinophaga_bin783	Potassium metabolism	Potassium metabolism - no subcategory	Potassium homeostasis	POTASSIUM/PROTON ANTIPORTER ROSB	fig|6666666.1425568.peg.398
Chitinophaga_bin783	Protein Metabolism	Protein degradation	Serine endopeptidase (EC 3.4.21.-)	Prolyl endopeptidase (EC 3.4.21.26)	fig|6666666.1425568.peg.446, fig|6666666.1425568.peg.1370
Chitinophaga_bin783	Nitrogen Metabolism	Denitrification	Denitrifying reductase gene clusters	Nitrous oxide reductase maturation protein NosF (ATPase)	fig|6666666.1425568.peg.2979

Note. The full Table S6 is available online at https://doi.org/10.5281/zenodo.15725106