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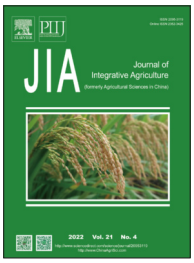

RESEARCH ARTICLE

# The rhizospheric microbiome becomes more diverse with maize domestication and genetic improvement

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**Abstract**

Domestication and genetic improvement of maize improve yield and stress tolerance due to changes in morphological and physiological properties, which likely alter rhizosphere microbial diversity. Understanding how the evolution of maize germplasm impacts its rhizobacterial traits during the growth stage is important for optimizing plant–microbe associations and obtaining yield gain in domesticated germplasms. In this study, a total of nine accessions representing domestication and subsequent genetic improvement were selected. We then sequenced the plant DNA and rhizobacterial DNA of teosinte, landraces and inbred lines at the seedling, flowering and maturity stages in a field trial. Moreover, the soil chemical properties were determined at the respective stages to explore the associations of soil characteristics with bacterial community structures. The results showed that domestication and genetic improvement increased the rhizobacterial diversity and substantially altered the rhizobacterial community composition. The core microbiome in the rhizosphere differed among germplasm groups. The co-occurrence network analysis demonstrated that the modularity in the bacterial network of the inbred lines was greater than those of teosinte and the landraces. In conclusion, the increased diversity of the rhizobacterial community with domestication and genetic improvement may improve maize resilience to biotic stresses and soil nutrient availability to plants.

**Keywords:** teosinte, landraces, inbred lines, domestication and improvement, core microbiome, network

## 1. Introduction

In agricultural systems, rhizosphere microbiota are associated with crop growth and health due to their functions in accessing nonlabile nutrients, mitigating abiotic and biotic stresses and preventing pathogen infection (Mendes *et al.* 2011; Bulgarelli *et al.* 2013). These benefits induced by rhizospheric microorganisms depend on the genetic variation of crop genotypes (Turner

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*et al.* 2013; Ofek *et al.* 2014; Pérez-Jaramillo *et al.* 2017). The genotype-specific microorganisms in the rhizosphere are mainly attributed to the quality and quantity of root secretions which are manipulated by genotype-specific gene expression (Lakshmanan *et al.* 2012; Badri *et al.* 2013; Lebeis *et al.* 2015).

Plant domestication may dramatically influence the microbial community in the rhizosphere (Pérez-Jaramillo *et al.* 2016; Tian *et al.* 2020). During plant domestication, not only have plant phenotypic traits been genetically improved, such as large seed size and apical dominance (Gepts *et al*. 2004; Doebley *et al.* 2006; Purugganan and Fuller 2009; Hou *et al.* 2020), but the plant–microbe interactions are also likely to be beneficial to the increase in crop yield in agricultural systems (Rodriguez *et al.* 2008; Farrar *et al.* 2014). Thus, it is necessary to clarify whether the rhizospheric microbial community has changed with the plant domestication and genetic improvement process, and whether the beneficial interactions between the plant and the rhizospheric microorganisms have been enhanced. Tackling these knowledge gaps is ultimately important to further improve crop yield by shaping the interrelationship between rhizospheric microorganisms and crop plants.

Recent studies indicated that domestication altered the assembly of rhizosphere microorganisms. Compared with wild plants, changes in the microbial community assembly in the rhizosphere of domesticated plants may facilitate an improvement in stress resistance and adaptability to some agricultural measures (such as fertilization and irrigation) for yield gain. For example, the relative abundance of putative fungal pathogens was lower in the rhizosphere of modern sunflower cultivars than that of ancient cultivars (Leff *et al.* 2017). Similarly, significant differences in the diversity and composition in the rhizosphere of barley (Bulgarelli *et al.* 2015), common bean (Pérez-Jaramillo *et al.* 2017) and sugar beet (Zachow *et al.* 2014) were found between wild and domesticated germplasms. However, all the crop species in these studies were grown in pots and examined at only one growth stage. It has been shown that the rhizobacterial community composition varies with the growth stage of many plant species, such as *Arabidopsis*, alfalfa, soybean, wheat, sugar beet and corn (Baudoin *et al.* 2003; Mougel *et al.* 2006; Houlden *et al.* 2008; Micallef *et al.* 2009; Xu *et al.* 2009). As the dynamics of rhizospheric microbes correspond with plant growth development and field experiments can realistically reflect crop yield improvement due to domestication, a field investigation of the microbial community assembly at key growth stages would be more convincing for revealing plant–microbe interactions in response to domestication and improvement processes.

Maize was domesticated from teosinte (*Zea mays* ssp. *parviglumis*), and this domestication event occurred ~9 000 years ago (Matsuoka *et al.* 2002; Doebley 2004). The domestication resulted in original maize landraces, which were spread throughout the USA by native Americans and adapted to various environments. With maize landraces, crop breeders began to select maize inbred lines with specific alleles for hybrid breeding, which ultimately increased the maize yield and enhanced stress tolerance (Duvick 1977; Duvick *et al.* 2004). Maize domestication reduces plant genetic diversity, resulting in morphological and physiological changes (Yamasaki *et al*. 2005). The potentially homogenized changes for high yield are assumed to suppress soil microbial diversity (Pérez-Jaramillo *et al.* 2017). However, limited knowledge is available on the coevolutionary process of maize domestication with microbial recruitment in the rhizosphere and whether domestication indeed leads to a change in bacterial diversity that is relevant to plant performance.

In this study, we used teosinte, landraces and inbred lines of maize to explore the association between maize accessions and microbial assembly in the rhizosphere, which would provide new insight into integrating microbial coevolution in future plant breeding. In a field trial, these selected maize accessions were subjected to genomic sequencing, and the rhizobacterial community was analysed using 16S rRNA sequencing. We explored the association of the microbiome in the rhizosphere with maize domestication and genetic improvement processes and examined whether the relationship changed at different growth stages of maize. We hypothesized that the coevolutionary trajectory between the genetic improvement of maize germplasms and the microbiomes in its rhizosphere might occur, resulting in a decrease in rhizobacterial diversity and a change in the rhizobacterial assembly.

## 2. Materials and methods

### 2.1. Plant materials

A total of nine accessions representing the full domestication and subsequent genetic improvement process were selected in this study. Three teosinte (*Zea mays* ssp. *paraviglumis*) accessions, W71-2 (CIMMYT 8781), B72-1 (CIMMYT 8784) and TEO: BALSAS (CIMMYT 9477), were from Mexico. Three landraces including NAYA36 (CIMMYT 2253), GUAN102 (CIMMYT 1526) and CHIS236 (CIMMYT 1222), represented the diversity of pre-modern cultivated lines that occurred approximately 9 000 years ago. These

landraces were derived from the wild progenitor (teosinte) in the Balsas River valley in Mexico (Matsuoka *et al.* 2002; Piperno *et al.* 2009; van Heerwaarden *et al.* 2011). The three modern inbred lines were B73 (temperate), Mo17 (temperate) and Zheng58 (temperate) (Appendix A).

### 2.2. Maize genotyping and genetic diversity analysis

Seeds from teosinte, landraces and inbred lines were separately germinated in an incubator with a 12-h dark-light cycle. The germinated seeds were sown into vermiculite media, and the plants were grown in a climate chamber for 2 weeks before leaves were sampled. Plant DNA was isolated by the cetyltrimethylammonium bromide (CTAB) method (Saghai-Maroof *et al.* 1984), and the quality and concentration of DNA were determined by agarose gel electrophoresis and NanoDrop. In this study, the target sequencing (GBTS) method was used for genotyping (Guo *et al.* 2019), and a 1K SNP panel was used for single nucleotide polymorphism (SNP) identification. All of these procedures were performed by CapitalBio Technology Corporation Co., Ltd. (Shijiazhuang, Hebei Province, China).

After filtering the loci containing missing genotypes, a total of 8 463 high-quality SNPs were used for genetic diversity analysis. A neighbor-joining phylogenetic tree was created using MEGA7.0 Software (Kumar *et al.* 2016) with 1 000 bootstrap replicates. The neighbor-joining tree was visualized with an online program of Interactive tree of life (iTOL) (Letunic and Bork 2019). To identify groups of individuals that conform to a genotypic makeup under a null model of evolution, the admixture Bayesian clustering approach was implemented in the program STRUCTURE (version 2.3.4) (Pritchard *et al.* 2000). With 20 000 replicates and 20 000 MCMC replicates with 10 iterations of each model from 1 to 6 populations (*k*), we aligned the data from different runs using CLUMPP software (Jakobsson and Rosenberg 2007). Structure Harvester online software (Earl and Vonholdt 2012) using the Evanno criterion (Evanno *et al.* 2005) was used to estimate the number of genetic groups.

### 2.3. Setup of the field experiment and rhizosphere soil sampling

A field experiment was performed at South China Agricultural University, Guangzhou, China (113°64´N, 23°24´E). The soil was classified as Ali-Udic Argosol. A completely randomized block design was deployed in this experiment. Each plot had an area of 24 $m^2$. The planting density was 57 000 plants $ha^{-1}$. Seeds from different accessions were sterilized with sodium hypochlorite and then rinsed in sterile water three times. After that, the seeds were soaked in $ddH_2O$ for 12 h for germination. The sterilized seeds were germinated on sterile vermiculite. Seedlings with consistent growth were selected and transplanted to the field after 4 d. Rhizosphere soil samples were collected at the seedling, flowering and maturity stages at 20, 50 and 80 d after sowing. In brief, most of the soil attached to the roots was removed by shaking. The roots were then immersed in sterile water, and after 10 s of vortexing, the rhizosphere soil was collected after sedimentation and stored at –80°C prior to DNA extraction.

### 2.4. Rhizosphere soil chemical analyses

A pH meter (FE20-FiveEasy™ pH, Mettler Toledo, Germany) was used to determine the soil pH in a 1:5 soil:water suspension. A TOC-5000A analyser (Shimadzu Corp, Kyoto, Japan) was used to measure the soil total carbon (SOC) and total nitrogen (Jones and Willett 2006). The available potassium (AK) was extracted in 1 mol $L^{-1}$ ammonium acetate and determined by flame photometry (FP640, INASA, China). Available phosphorus (Olsen-P) was extracted in 0.5 mol $L^{-1}$ $NaHCO_3$, $NH_4^+$ and $NO_3^-$ were extracted by 2 mol $L^{-1}$ KCl and then determined by a continuous flow analytical system (SKALAR SAN++, Netherlands) (Sun *et al.* 2015).

### 2.5. Soil DNA extraction and next-generation sequencing

Rhizobacterial DNA was extracted using the Fast DNA SPIN Kit for Soil (MP Biomedicals, Santa Ana, CA). To amplify the V3–V4 region, the 16S ribosomal RNA gene was amplified by PCR with the primers 338F (5´-barcode-ACTCCTRCGGGAGGCAGCAG-3´) and 806R (5´-GGACTACCVGGGTATCTAAT-3´) with 12 nt unique barcodes. The PCR program was as follows: 95°C for 45 s, followed by 28 cycles at 94°C for 15 s, 54°C for 45 s and 70°C for 10 s, followed by a final extension at 70°C for 3 min. The PCR products were then purified using the AxyPrep DNA Gel Extraction Kit (Axygen Biosciences, Union City, CA, USA) and paired-end sequenced on an Illumina MiSeq platform using 2×300 bp chemistry (Illumina Inc., San Diego, CA, USA).

### 2.6. Data analysis

The raw sequence in FASTQ files was processed using QIIME 1.9.1. Briefly, based on the barcodes, all the sequence reads were quality trimmed and assigned

to each sample. The chimaera of the sequence was detected and removed. The clean sequences were then clustered to operational taxonomic units (OTUs) at 97% similarity using the UPARSE pipeline (Edgar 2011), and the taxonomies were assigned to each OTU using the RDP Classifier (Cole *et al.* 2009). Shannon's diversity and Chao1 richness and index were also calculated in QIIME. Principal coordinate analysis (PCoA), redundancy analysis (RDA), and the adonis test and the Mantel test were performed in R with the "vegan" package. The differences in phyla and genera among the genotypes were analysed using STAMP with 95% confidence intervals (Parks and Beiko 2010). To acquire the biomarkers of taxa across teosinte, landrace and inbred line genotypes, we classified the relative abundances of phylum, class, order, family, genus and OTU levels against maize varieties using the package RandomForest in R (Zhang *et al.* 2018, 2019). The importance of features and the cross-validation curve were visualized in R using the "ggplot2" package. Ternary plots were constructed to show the abundance comparison of OTUs (>5‰) for teosinte, landrace and inbred line genotypes in the three growth stages using the "vcd" package (Friendly and Meyer 2015). Differences between treatments in soil properties, alpha diversity and the relative abundances of bacterial phyla and genera were assessed by one-way or two-way ANOVA in Genstat (ver. 13.0).

### 2.7. Core bacteria and co-occurrence network analyses

Core bacteria, which contain a list of OTUs observed in 60% of all the rhizosphere samples, were obtained in QIIME using MicrobiomeAnalyst (Chong *et al.* 2020). Core bacteria analyses were also performed for each germplasm group. Bacterial co-occurrence networks were analysed for each sweet corn germplasm group. In order to study the network structure of the OTUs with high abundance, we selected OTUs with more than 0.2% relative abundance to calculate Spearman's rank correlation coefficients. The correlations between OTUs were selected at $P<0.05$ and Spearman's correlation coefficient of more than 0.8 (Mendes *et al.* 2018). The nodes and edges represent bacterial OTUs and the correlations between bacterial OTUs, respectively. Statistical analyses were calculated using the "psych" package in R and then visualized in Gephi (Jiang *et al.* 2017). Keystone species were defined according to high node degree, high betweenness centrality and high closeness centrality (Berry and Widder 2014; Agler *et al.* 2016).

## 3. Results

### 3.1. Genetic relations among maize accessions

The 1K SNP panel was used to study the genetic variations among the 9 accessions. We identified 10 129 SNPs as genetic markers for further diversity analysis. After filtering the loci with missing genotypes, there were 8 463 high-quality SNPs. Using these SNPs, phylogenetic analysis showed that the teosinte, landraces and inbred lines were clearly grouped into three clusters (Fig. 1-A and B). We explored patterns of population structure in the maize accessions using STRUCTURE analysis. There was a sharp peak of $\Delta k$ at $k=3$, suggesting that the number of clusters was set to 3 germplasm groups; i.e., teosinte, landrace and inbred lines (Fig. 1-C; Appendix B).

### 3.2. Diversity of rhizobacterial communities in the rhizosphere of germplasm groups

Domestication and genetic improvement increased the alpha diversity of rhizobacterial communities across growth stages (one-way ANOVA, $P<0.05$) (Fig. 2-A). Although the alpha diversity was significantly different among germplasm groups (permutational multivariate ANOVA (PERMANOVA), $R^2=0.304$, $P=0.004$), there was no difference of the alpha diversity between growth stages (PERMANOVA, $R^2=0.051$, $P=0.371$) (Table 1). In particular, the Shannon diversity index was significantly higher in the rhizosphere of the landraces and inbred lines than teosinte at the flowering stage, but by the mature stage, the Shannon index in the rhizosphere of the inbred lines was higher than teosinte (Appendix C). Regarding beta diversity, PCoA and two-way PERMANOVA revealed that germplasm and growth stage interactively affected the rhizobacterial communities (PERMANOVA, $P=0.001$) (Fig. 2-B and C; Table 1). The rhizobacterial communities of maize germplasms were separated into three groups at every investigated growth stage (PERMANOVA, $P=0.0001$) (Fig. 2-D–F).

### 3.3. Specific microbiomes of germplasm groups

Proteobacteria, Firmicutes, Actinobacteria and Chloroflexi were the most abundant bacterial phyla living in the rhizosphere across growth stages, accounting for 78.48–82.15% of the whole community (Appendix D). The abundances of Actinobacteria, Firmicutes, Chloroflexi, Gemmatimonadete, Patescibacteria, Planctomycetes and Nitrospirae in the rhizosphere varied ($P<0.05$) among germplasms, while the relative abundances of Actinobacteria, Firmicutes, Acidobacteria,

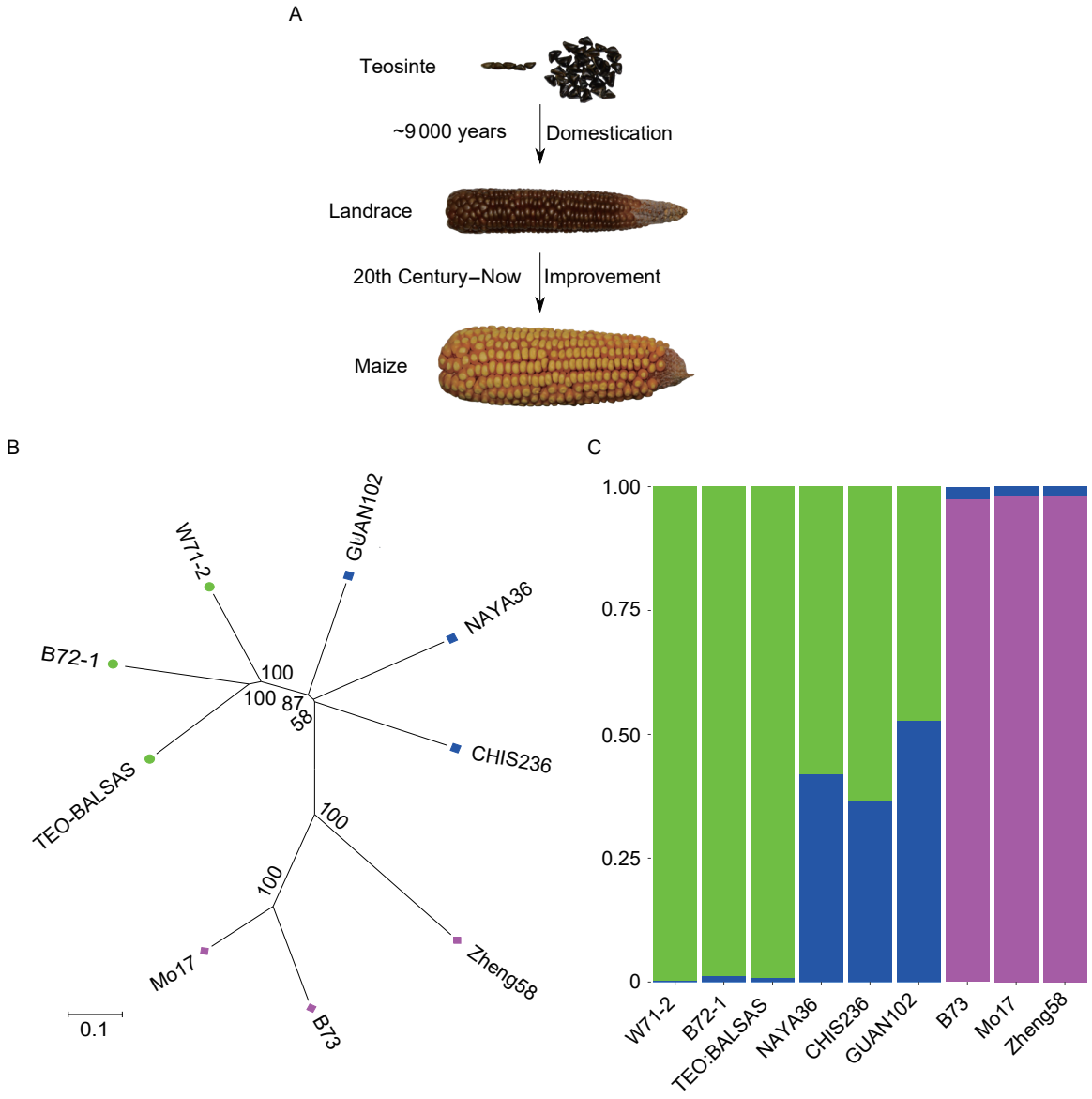


**Fig. 1** Origin and genetic structure of the maize accessions. A, maize domestication and improvement process. B, neighbor-joining phylogenetic tree constructed based on 8 463 SNPs. C, admixture plot showing clustering of different accessions into three clusters based on Bayesian-based clustering analysis.

Gemmatimonadetes, Patescibacteria and Nitrospirae changed ($P$<0.05) with growth stage (Appendix D). Moreover, six phyla were interactively affected ($P$<0.05) by germplasm and growth stage. The relative abundance of Firmicutes was greater in the inbred lines than in the landraces and teosinte (Welch's $t$-test, $P$<0.05, Bonferroni-corrected) (Fig. 3-A–C; Appendix D). Bacteroidetes had significantly greater relative abundance in the rhizosphere of inbred lines than in the landraces and teosinte at the flowering stage, while an opposite trend was observed at the maturity stage (Fig. 3-A–C).

At the genus level, 56 and 60 genera were significantly ($P$<0.05) affected by germplasm and growth stage, respectively (Appendix E). Moreover, 63 genera were interactively affected ($P$<0.05) by germplasm and growth stage. Among them, *Bacillus*, which belongs to Firmicutes, was enriched in the rhizosphere of the inbred lines at the flowering and maturity stages but not at the seedling stage. *Streptomyces* affiliated to Actinobacteria were enriched in the rhizosphere of landraces at the seedling and flower stages but enriched in the rhizosphere of teosinte at the maturity stage (Appendix E).

A linear model analysis was used to identify bacterial OTUs significantly enriched in rhizosphere soil of teosinte,

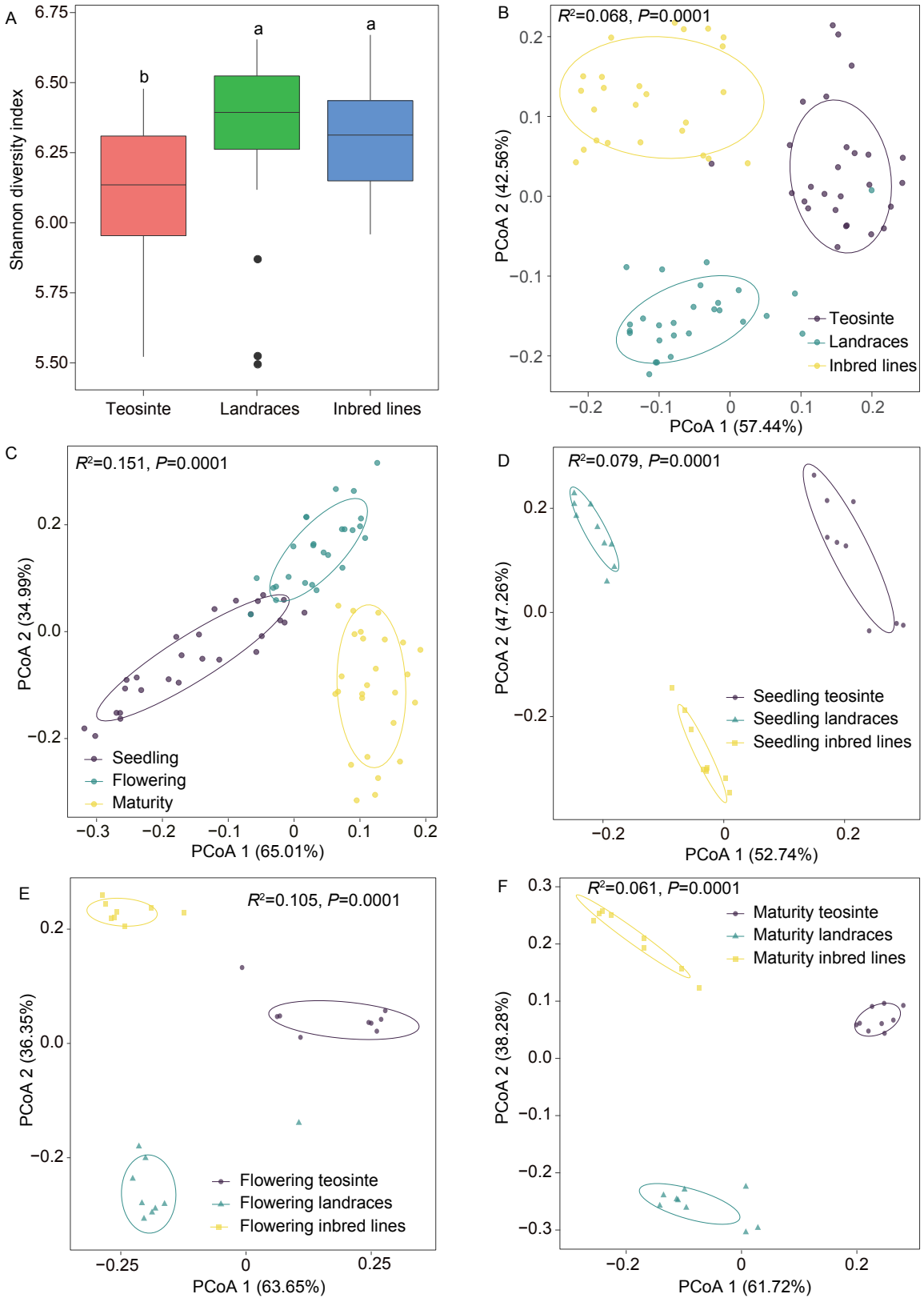


**Fig. 2** Rhizobacterial community diversity and structure of maize. A, estimated rhizobacterial Shannon diversity indexes from teosinte, landrace and inbred lines. Statistically significant differences were determined by one-way ANOVA with Student's *t*-test ($P<0.05$). B, principal coordinate analysis (PCoA) based on Bray-Curtis dissimilarities of 16S rRNA diversity in the rhizosphere of the three maize germplasms (permutational multivariate ANOVA (PERMANOVA), $P=0.001$). C, three growth stages (PERMANOVA, $P=0.001$). D–F, three germplasms in the seedling (PERMANOVA, $P=0.001$). flower (PERMANOVA, $P=0.001$), and maturity stages (PERMANOVA, $P=0.001$), respectively.

**Table 1** The effects of germplasm and growth stage of maize on the differentiation of bacterial communities based on permutational multivariate ANOVA (PERMANOVA)

| Factor | Bacterial community | | Bacterial diversity | |
|---|---|---|---|---|
| | $R^2$ | *P*-value | $R^2$ | *P*-value |
| Germplasm | 0.068 | 0.001 | 0.304 | 0.004 |
| Growth stage | 0.151 | 0.001 | 0.051 | 0.371 |
| Germplasm×Growth stage | 0.116 | 0.001 | 0.211 | 0.004 |

landraces and inbred lines. At the seedling stage, OTUs belonging to *Bacillus*, *Streptomyces* and *Sphingomonas* dominated in the rhizospheres of teosinte, landraces and inbred lines, respectively (Fig. 4). At the flowering stage, OTUs belonging to *JG30-KF-AS9*, *Sphingomonas* and *Devosia* were mainly abundant in teosinte, landraces and inbred lines, respectively. At the maturity stage, *Glycomyces*, *JG30-KF-AS9* and *Bacillus* were dominant in the rhizosphere of teosinte, landraces and inbred lines, respectively. More detailed information is available in Appendices F and G.

### 3.4. Bacterial biomarkers for germplasm groups

The random forest model based on the family level showed the highest accuracy (83.7%) within all taxonomic levels (Appendix H). The importance of indicator bacterial families was assessed by a 10-fold cross-validation of eight replicates. The cross-validation error was the lowest when the 21 most relevant families were used in the analyses. Thus, we defined these 21 families as biomarker taxa (Appendix I). Among them, five, five and four families showed the highest relative abundances in teosinte, landraces and inbred lines, respectively (FDR adjusted $P<0.05$, Wilcoxon rank sum test) (Appendix I). Microbacteriaceae and Glycomyceatceae were the highest in teosinte, Streptomycetaceae was the highest in landraces, and 0319-6G20 was the highest in the inbred line genotype (Appendix I).

### 3.5. Core microbiome for germplasm groups

Among the total of 9132 OTUs, we found that five OTUs; i.e., OTU3725 (*Bacillus*), OTU4484 (*Bacillus*), OTU4419 (*Sphingomonas*), OTU7344 (*Sphingomonas*) and OTU7265 (*Chujaibacter*), were consistently present in the rhizosphere of all germplasms across the growth stages (Fig. 5-A–E). In addition to the common core species mentioned above, OTU3955 (*norank_Gaiellales*) and OTU4054 (*Sphingobium*) were core species specific to teosinte and landraces, respectively, while OTU1750 (*Bacillus*) and OTU4054 (*unclassified_Rhizobiaceae*) were the core species specific to inbred lines (Fig. 5-F–I). The total relative abundance of OTU3725, OTU4484 and OTU1750 belonging to *Bacillus* was 6.2%, and the total relative abundance of OTU4419 and OTU7344 affiliated with *Sphingomonas* was 2.0%.

### 3.6. Higher co-occurrence network complexity in domesticated maize

Using the combined 16S rRNA data for the three stages of the three genotypes, the co-occurrence network in the rhizosphere showed marked differences in complexity among teosinte, landraces and inbred lines (Fig. 6; Table 2). Briefly, the average clustering coefficient (avgCC) and average degree (avgK) decreased with domestication and genetic improvement, while the average path length (APL), negative correlations and modularity (M) showed the opposite trend. The keystone species of the bacterial network in the rhizosphere were identified by calculating node degree, closeness centrality and betweenness centrality for all nodes in the network (Appendix J). In general, OTU6313 (*norank_JG30-KF-AS9*), OTU8602 (*WX54*) and OTU7370 (*norank_Amb-16S-1323*) were identified as keystone species for teosinte, while OTU8091 (*norank_JG30-KF-AS9*), OTU273 (*norank_IMCC26256*) and OTU6 (*norank_Elsterales*) were keystone species for the landraces. For the inbred lines, the keystone species were OTU7272 (*uncultured_JG30-KF-AS9*), OTU2948 (*uncultured_Fictibacillus*) and OTU7056 (*uncultured_FCPS473*).

Moreover, the co-occurrence network in the rhizospheres of different growth stages showed a similar trend across the growth stages (Appendix K). In general, the avgCC and avgK decreased with domestication and genetic improvement at the three growth stages, while the APL and M showed the opposite trend. However, the APL did not show a regular trend at the three growth stages (Appendix L).

### 3.7. Association of rhizobacterial community with soil chemical properties

In RDA (Fig. 7-A), the soil physical and chemical properties that were significantly correlated with the bacterial community were selected by the mantel test. The direction and length of the arrow shows the effect of environmental factors on the bacterial community, indicating the relationship between soil chemical characteristics and bacterial community structures. For the first two axes of RDA, the variances explained were 39.9 and 20.3% of the total

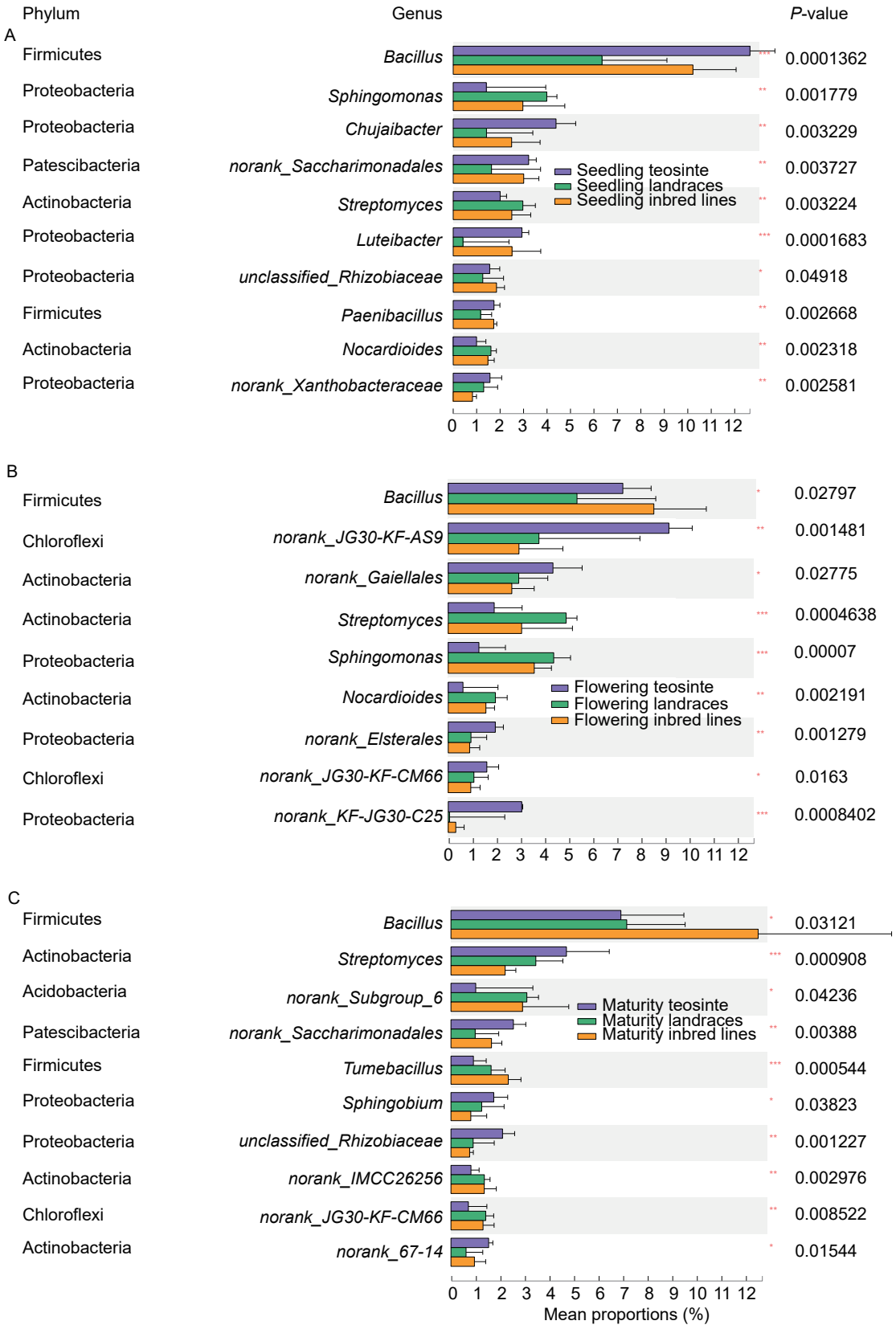


**Fig. 3** Analysis of the differences in relative abundance at the genus level among teosinte, landraces and inbred lines at the seedling (A), flowering (B) and maturity (C) stages. Statistically significant differences were determined by Welch's *t*-tests followed by Bonferroni corrections ($P<0.05$). The purple, green and yellow bars represent teosinte, landrace and inbred line genotypes, respectively. *, $P<0.05$; **, $P<0.01$; ***, $P<0.001$.

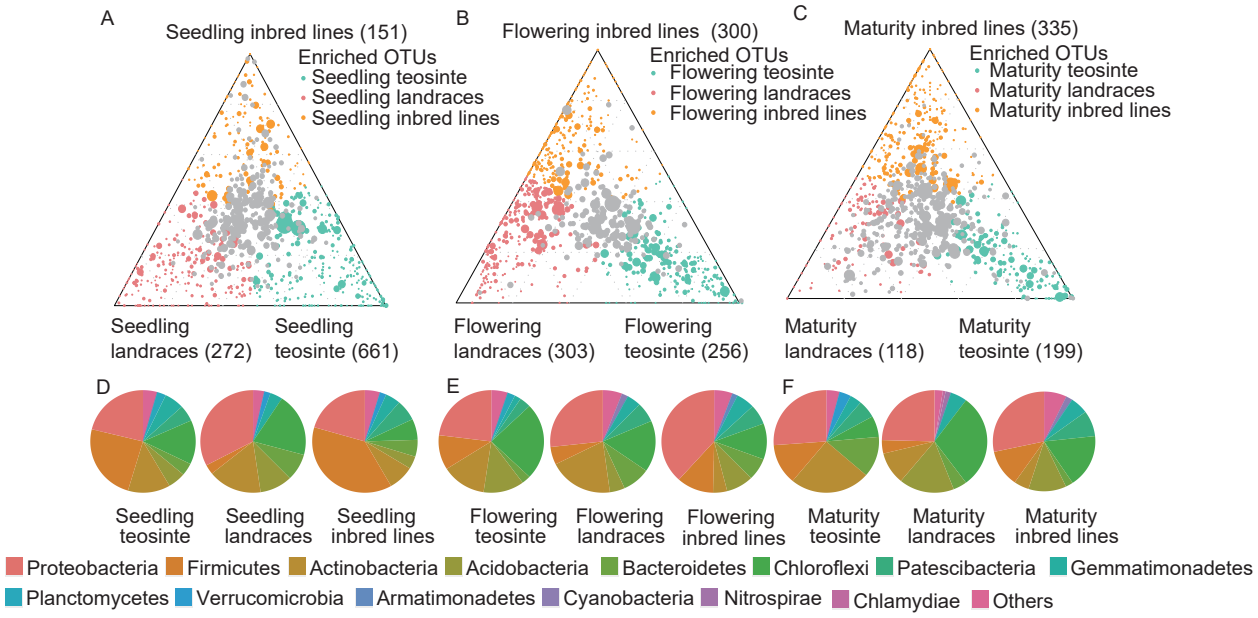


**Fig. 4** Taxonomic distribution of bacterial taxa among different maize accessions at each growth stage. A–C, ternary plots depicting compartments showing the distributions of community differentiation among different germplasm groups at each growth stage. Each circle represents an operational taxonomic unit (OTU). The size of each circle represents its relative abundance. The position of each circle is determined by its contribution to the total relative abundance. Colored circles represent germplasm groups in one compartment; i.e., green for teosinte, red for landraces, and orange for inbred lines, whereas grey circles represent OTUs that are not significantly enriched in a specific compartment. The numbers of differentiated OTUs are displayed in brackets at the vertex of the ternary plots. D–F, the pie charts show the relative abundance (%) of enriched OTUs in different phyla in each compartment.

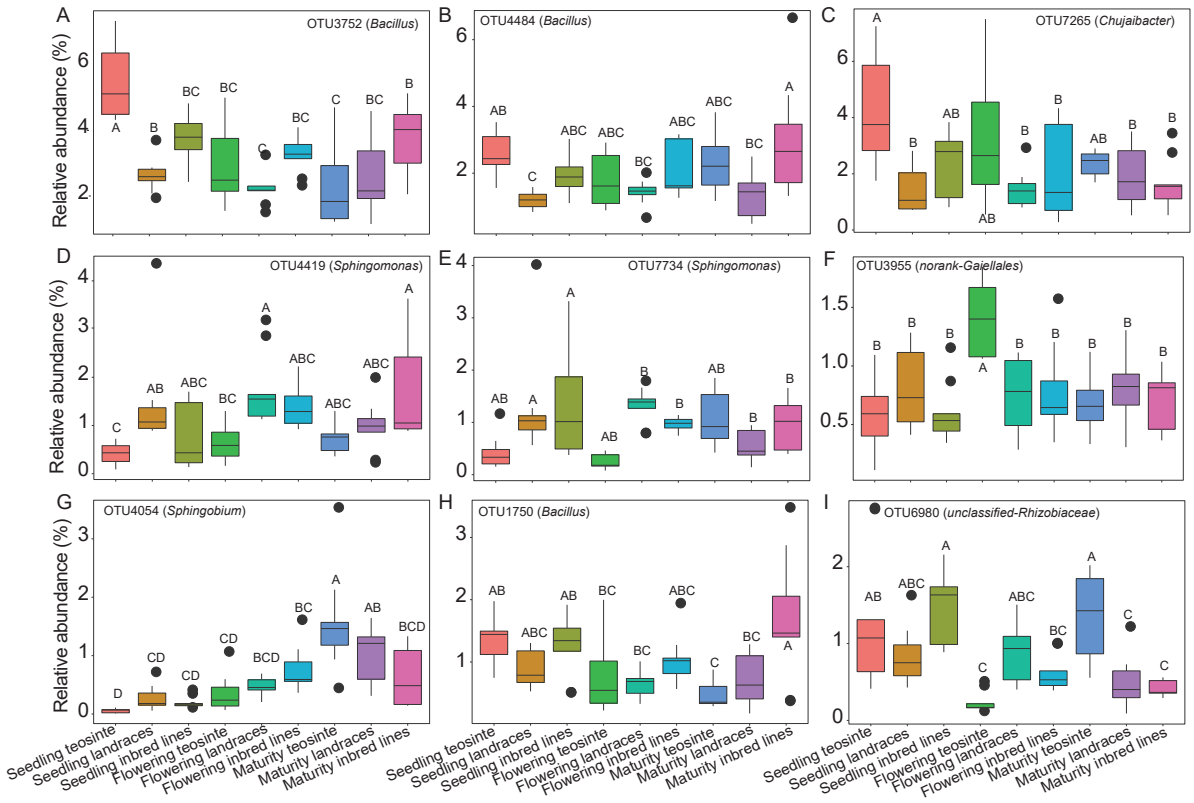


**Fig. 5** The relative abundance of the core microbiome for different maize accessions. A–E, the core microbiome for all the maize accessions. F and G, the core microbiome specific to teosinte. H, the core microbiome specific to landraces. I, the core microbiome specific to inbred lines.

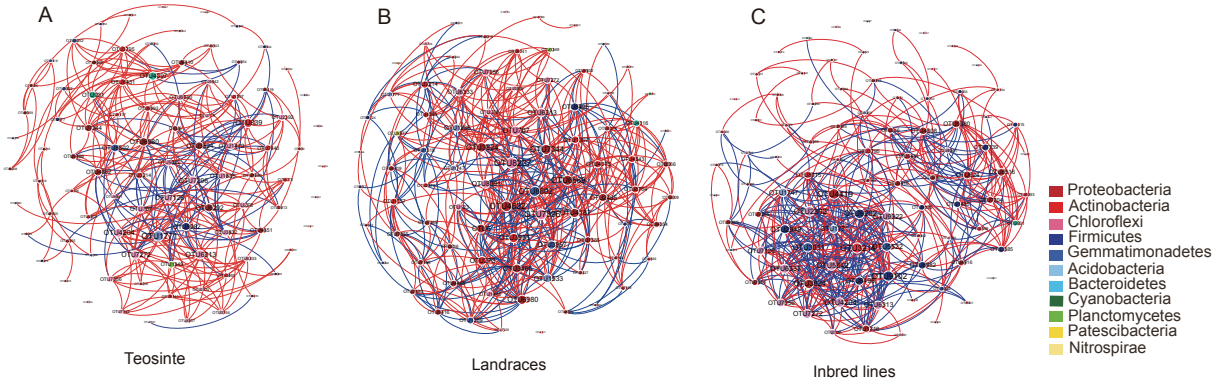


**Fig. 6** Co-occurrence network of the rhizobacterial community for teosinte (A), landraces (B) and inbred lines (C). Nodes represent operational taxonomic units (OTUs) colour-coded by phyla and scaled proportionally to the number of connections (node degree). Connection lines were drawn at $r>0.8$ (positive correlations, red) or $r<-0.8$ (negative correlations, blue) and $P<0.05$.

**Table 2** Topological characteristics of rhizobacterial networks for teosinte, landraces and inbred lines

| Network metrics | Teosinte | Landraces | Inbred lines |
|---|---|---|---|
| Number of nodes | 94 | 85 | 100 |
| Number of edges | 401 | 569 | 643 |
| Number of positive correlations | 326 (81.30%) | 393 (68.89%) | 392 (60.96%) |
| Number of negative correlations | 75 (18.70%) | 176 (31.11%) | 251 (39.04%) |
| Average path length (APL) | 3.18 | 2.515 | 2.75 |
| Graph density | 0.092 | 0.16 | 0.13 |
| Network diameter | 8 | 6 | 7 |
| Average clustering coefficient (avgCC) | 0.61 | 0.64 | 0.66 |
| Average degree (avgK) | 8.53 | 13.38 | 12.86 |
| Modularity (M) | 1.05 | 1.665 | 5.21 |

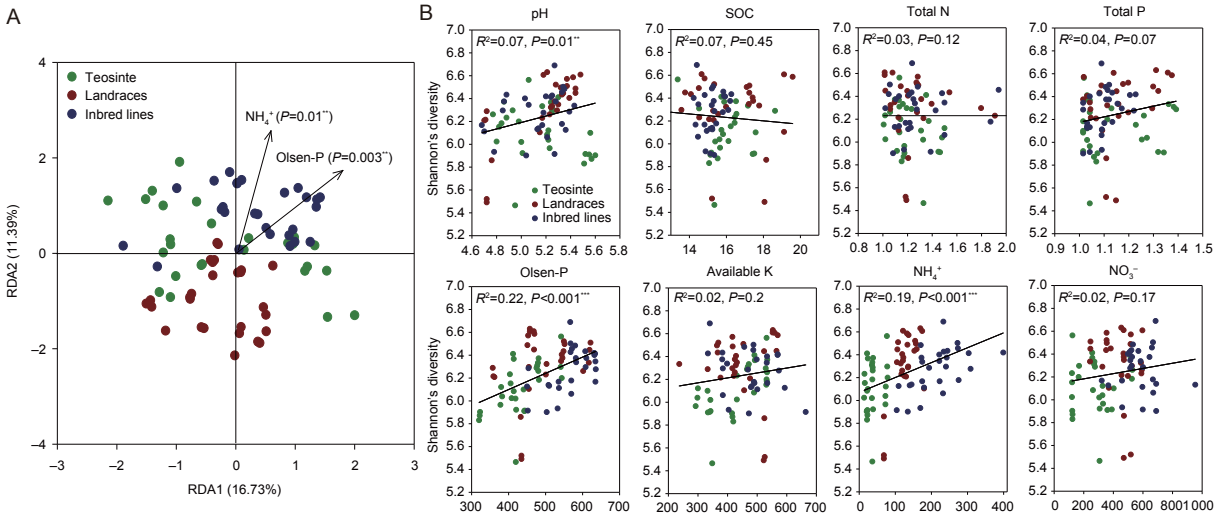


**Fig. 7** The correlations between microorganisms and environmental factors. A, redundancy analysis (RDA) constraining rhizobacterial community structure by soil chemical properties across all samples. B, linear regression relationships between soil chemical properties and Shannon's diversity. SOC, soil organic carbon; Olsen-P, available phosphorus; $NH_4^+$, ammonium nitrogen; $NO_3^-$, nitrate nitrogen.

variation, respectively. The bacterial communities in the rhizosphere were significantly correlated with Olsen-P and $NH_4^+$ (Fig. 7-A). Moreover, the Shannon index was positively correlated with pH, Olsen-P and $NH_4^+$ (Fig. 7-B). The soil chemical characteristics are shown in Appendix M.

## 4. Discussion

Domestication could change the root architecture, such as root length and branching, as well as root exudation, which likely affects rhizobacterial community diversity and structure (Pérez-Jaramillo *et al.* 2017). The maize domestication and genetic improvement process increased the rhizobacterial community diversity (Fig. 2-A), which was consistent with previous findings (Shenton *et al.* 2016) that domesticated accessions of rice displayed higher alpha diversity than their wild accessions. However, this result was against our hypothesis, and Pérez-Jaramillo *et al.* (2017, 2019) found that there were no significant differences in the alpha diversity between wild and modern accessions of *Phaseolus vulgaris*. Moreover, bacterial diversities were even lower in other modern crops, such as soybean and sunflower, when compared with their wild genotypes (Jeff *et al.* 2017; Liu *et al.* 2019). The different compositions of root exudates among crop species may contribute to these discrepancies. In addition, the experiments were conducted under different soil conditions, which may lead to different results, as soil heterogeneity is one of the main factors affecting rhizosphere microorganisms (Garcia-Palacios *et al.* 2012; Hartman *et al.* 2018). Future experiments in different soils could help to elucidate the general trend of the influence of domestication on the rhizosphere microorganisms.

A positive correlation of the Shannon index with labile nutrient concentrations indicates that inbred lines did not suppress microbial diversity, as enriched nutrients promote certain taxa and thus lower diversity (Lian *et al.* 2019). Therefore, in this study, organic compounds released from roots played a major role in their influence on microbial diversity in the rhizosphere. In addition, fertilization likely imposed a greater impact on the microbial diversity in the rhizosphere of teosinte than inbred lines, as modern accessions are adapted to a high input of fertilizer (Pérez-Jaramillo *et al.* 2019). However, these assumptions warrant further investigation of the microbial community metabolizing plant-derived C compounds under different fertilization conditions.

A previous study has found that the core microbiomes of teosinte and landrace seed endophytes were identified as belonging to *Paenibacillus*, *Enterobacter*, *Methylobacterium*, *Pantoea* and *Pseudomonas*, while *Stenotrophomonas* were only found in seeds of the wild ancestors (Johnston-Monje and Raizada 2011). In this study, a common set of five core microbiomes was found in rhizosphere soil of wild and domesticated genotypes, indicating that some microbe affinities were retained after the domestication and genetic improvement processes both in seed endophytes and the rhizosphere soil. However, these core microbiomes showed various relative abundances in the rhizosphere of different genotypes.

The domestication and genetic improvement processes altered the core microbiome in the rhizosphere, which was likely associated with plant adaptability to farming environments. The core OTU3955 (*norank_Gaiellales*) was specific to teosinte in comparison to OTU4054 (*Sphingobium*) for landraces. These core OTUs were different from the OTU1750 (*Bacillus*) and OTU4054 (*unclassified_Rhizobiaceae*) of inbred lines (Fig. 5-F–I). The change in core OTUs over the domestication and improvement processes was likely relevant to the improvement of biotic stress resilience and soil nutrient availability to the plants. Some *Sphingomonas* strains could protect plants by producing some antibiotic compounds, which may be partially responsible for the control of some soil-borne fungal pathogens present in domesticated maize (Chagas *et al.* 2018). These bacteria probably responded more efficiently to root signals, such as alkaloids, terpenoids and lipids released by the roots of domesticated maize (Chagas *et al.* 2018; Xu *et al.* 2019). In addition, *Sphingomonas* were also reported to be able to degrade lignin and pectin (Hashimoto and Murata 1998; de Gonzalo *et al.* 2016), which may be associated with the mineralization of organic matter that facilitates the transformation of nutrients making them available to plants as well.

As a core OTU in the rhizosphere inbred lines belonged to *Bacillus*, a number of studies have demonstrated that species of *Bacillus* have been identified as plant growth promoters (Canbolat *et al.* 2006) and biocontrol agents for some pathogenic species (Kolton *et al.* 2011). Some species were also considered phosphate-solubilizing bacteria (Zaidi *et al.* 2009), which can mobilize insoluble phosphorus making it available to plants (Oteino *et al.* 2015). Moreover, OTU6980 (*unclassified_Rhizobiaceae*) was increased in the maize demonstrating the seedling and flowering stages (Fig. 5-I), and this result was partly consistent with Aymé *et al.* (2020)´s research in which the abundance of *Rhizobiales* significantly increased with the demonstration of tetraploid wheat. *Rhizobiales* are considered nitrogen-fixing bacteria (Wang and Bai 2019), implying that inbred lines in this study might facilitate a rhizobacterial function in $N_2$ fixation. However, some researchers speculate that modern maize may have lost or weakened genes related to the production of aerial root-associated mucilage to decrease the diazotrophic activity on $N_2$ fixation (Van Deynze *et al.* 2018; Wang and Bai 2019). Considering these different findings, we assume that the modern accessions may uniquely interact with the aboriginal community composition in specific soils to maximize the nutrient availability in the rhizosphere. Regarding *Gaiellales*, this genus was only recently identified and remains poorly

understood (Albuquerque *et al.* 2011; Ma *et al.* 2016).

In addition to these core microbiomes, the genus *Streptomyces* was enriched in the rhizosphere of domesticated maize at the flowering stage. Streptomycin, an antibiotic produced by *Streptomyces*, is antagonistic to gram-positive and gram-negative bacteria and has been shown to enhance plant defenses and trigger plant systemic resistance (Schatz *et al.* 2005; Chaparro *et al.* 2014). Therefore, a higher relative abundance of *Streptomyces* indicates that domesticated maize might have more advantages in resisting stresses. Interestingly, Chloroflexi and Acidobacteria were enriched in the teosinte rhizosphere at the flowering stage (Fig. 3-A). These two phyla were reported to be able to survive under nutrient-deficient or suboptimal abiotic conditions (Fierer 2017), which may enhance teosinte adaptability to abiotic stress environments (Szoboszlay *et al.* 2015; Fierer 2017; Xu *et al.* 2019). However, the extent to which these enriched bacterial taxa may improve the plant adaptability to biotic and abiotic stresses remains unknown, requiring more mechanistic experiments in the future. These experiments also need to be carried out in different soil types and under different climatic conditions in order to evaluate the universality of the findings in this study.

The complexity of the rhizobacterial network increased with the domestication and improvement processes. The greater modularity in the bacterial network of modern germplasm than wild germplasm could be attributed to increased interspecies competition (Saavedra *et al.* 2011; Fan *et al.* 2018). Highly connected and modular microbial communities in domesticated maize can activate the plant immune system to accelerate the activation of pathogen defenses (Dodds and Rathjen 2010; Hu *et al.* 2020). In this sense, the process of domestication and genetic improvement has a positive feedback on the rhizosphere soil microbial community structure, which may enhance the host competitiveness. Moreover, the keystone species in the rhizosphere varied among teosinte, landraces and inbred lines, which would be a critical determinant of the other community compositions in the rhizosphere (Ma *et al.* 2016; Jiang *et al.* 2017). The root architectures and metabolomes differ between wild and modern maize (Xu *et al.* 2019), which could influence microhabitats in the rhizosphere and consequently the network structure of the bacterial community (Pérez-Jaramillo *et al.* 2017).

The large production of sugar-rich mucus secreted from aerial roots of modern maize genotypes provides a habitat for nitrogen-fixing microorganisms, such as *Rhizobium* and *Burkholderia* species (Van Deynze *et al.* 2018). The potential function of nitrogen fixation in modern maize increases the cycle of nitrogen, which may explain why the concentrations of $NO_3^-$ and $NH_4^+$ increased in the rhizosphere of modern maize (Van Deynze *et al.* 2018). It is worth noting that although $NH_4^+$ was analyzed as the main factor affecting the microbial community structure in this study, other soil chemical properties did not change significantly in the rhizosphere of those genotypes, since all genotypes were cultivated in the same soil with the same field management. Root exudates and root morphology are expected to play a more important role in affecting the structure of the rhizosphere microbial community (Pérez-Jaramillo *et al.* 2017). Therefore, future research should focus on the root exudates and root phenotypic traits associated with microorganisms.

## 5. Conclusion

Domestication and the genetic improvement of maize from teosinte to inbred lines led to an increase in rhizobacterial diversity. The core microbiome in the rhizosphere of domesticated germplasms differed from wild germplasm and might increase the biotic stress resilience of plants and soil nutrient availability to plants. The co-occurrence network structure was more complicated with domestication, which might enhance the competitiveness of domesticated maize in biotically stressed environments. More information on microbial functions linking plant gene expression should be considered in the future to better understand the impact of the domestication and genetic improvement processes on feature-based microbiome assembly. Moreover, more soil types should be considered for exploring general trends in rhizobacterial shifts during the domestication and genetic improvement processes.

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## Declaration of competing interest

The authors declare that they have no conflict of interest.

**Appendices** associated with this paper are available on http://www.ChinaAgriSci.com/V2/En/appendix.htm

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