Soil Biology and Biochemistry 145 (2020) 107794

Contents lists available at ScienceDirect

Soil Biology and Biochemistry

journal homepage: http://www.elsevier.com/locate/soilbio

Impacts of directed evolution and soil management legacy on the maize rhizobiome

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ARTICLE INFO

Keywords:
Agroecosystem
Breeding
Domestication
Genotype-by-environment interaction
Maize
Rhizosphere

ABSTRACT

Domestication and agricultural intensification dramatically altered maize and its cultivation environment. Changes in maize genetics (G) and environmental (E) conditions increased productivity under high-synthetic-input conditions. However, novel selective pressures on the rhizobiome may have incurred undesirable tradeoffs in organic agroecosystems, where plants obtain nutrients via microbially mediated processes including mineralization of organic matter. Using twelve maize genotypes representing an evolutionary transect (teosintes, landraces, inbred parents of modern elite germplasm, and modern hybrids) and two agricultural soils with contrasting long-term management, we integrated analyses of rhizobiome community structure, potential microbe-microbe interactions, and N-cycling functional genes to better understand the impacts of maize evolution and soil management legacy on rhizobiome recruitment.

We show complex shifts in rhizobiome communities during directed evolution of maize (defined as the transition from teosinte to modern hybrids), with a larger effect of domestication (teosinte to landraces) than modern breeding (inbreds to hybrids) on rhizobiome structure and greater impacts of modern breeding on potential microbe-microbe interactions. Rhizobiome structure was significantly correlated with plant nutrient composition. Furthermore, plant biomass and nutrient content were affected by G x E interactions in which teosinte and landrace genotypes had better relative performance in the organic legacy soil than inbred and modern genotypes. The abundance of six N-cycling genes of relevance for plant nutrition and N loss pathways did not significantly differ between teosinte and modern rhizospheres in either soil management legacy. These results provide insight into the potential for improving maize adaptation to organic systems and contribute to interdisciplinary efforts toward developing resource-efficient, biologically based agroecosystems.

1. Introduction

Natural and artificial selection have changed modern maize profoundly in comparison to its wild ancestor, teosinte (*Zea mays* ssp. *parviglumis*). Crop breeding and directed evolution led to environmental and genetic changes that dramatically increased productivity in high-input, intensively managed conventional agricultural systems. However, this process may have created undesirable tradeoffs for interactions between maize and its rhizosphere microbiome ("rhizobiome", Olanrewaju et al., 2019), which are especially crucial in organic systems that rely on microbial nutrient cycling for resource acquisition (Schmidt et al., 2016). Recent studies of maize evolution in single soil environments have revealed inadvertent effects of directed aboveground selection on root traits and rhizosphere processes (Brisson et al., 2019b;

Abbreviations: ASV, amplicon sequence variant; G x E, genotype-by-environment; GWAS, genome-wide association studies; ITS, internal transcribed spacer; N, nitrogen.

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https://doi.org/10.1016/j.soilbio.2020.107794
Received 8 December 2019; Received in revised form 19 March 2020; Accepted 25 March 2020
Available online 10 April 2020

Emmett et al., 2018; Szoboszlay et al., 2015). Nonetheless, it remains unclear whether genetic (G) and environmental (E) selective pressures that drove adaptation to conventional agricultural systems may have led to a G x E interaction in which modern maize and its rhizobiome are maladapted to organic agricultural systems.

With recent shifts toward understanding host-microbiome associations as pan-genomes (Tkacz and Poole, 2015) or holobionts (Dessaux et al., 2016; Vandenkoornhuyse et al., 2015), host genetic effects on the rhizobiome should be integrated into evolutionary studies. Improvement of aboveground traits during maize evolution had unintended belowground effects that likely impacted rhizosphere interactions. For example, both domestication and agricultural intensification affected maize root system architecture, which can affect rhizobiome composition (Corneo et al., 2016), and anatomy, which can affect pathogenic and symbiotic fungal colonization (Galindo-Castañeda et al., 2019). Domestication led to longer nodal roots, more seminal roots, more aerenchyma, and greater genetic variation for anatomical and architectural traits in landraces than teosinte (Burton et al., 2013), and reduced root branching despite equivalent root:shoot ratio (Gaudin et al., 2014). Physiological changes such as enhancement of culinary properties (e.g. via genes *su1* and *ae1*) may have altered systemic carbohydrate metabolic pathways affecting root exudation (da Fonseca et al., 2015). Furthermore, the domestication-related genetic bottleneck from teosinte to landraces (Eyre-Walker et al., 1998; C. J. Yang et al., 2019) may have correspondingly decreased diversity of the maize microbiome (Pérez-Jaramillo et al., 2016).

The genetic effects described above create differences in rhizobiome composition of various maize evolutionary stages even in a single soil environment. For instance, teosinte, landrace, and modern genotypes recruit distinct rhizosphere bacterial and fungal communities from a nutrient-depleted soil, but with no differences in diversity (Brisson et al., 2019b). Maize genotypes varying at the *su1/sh2* locus, a domestication gene affecting kernel starch and sugar content, have rhizobiomes that differ in structure and fertilization response (Aira et al., 2010). Similarly, sweet corn and popping corn have decreased rhizosphere bacterial and fungal diversity and changes in rhizobiome composition compared to teosinte (Szoboszlay et al., 2015). Studies of modern maize inbreds and hybrids have also shown effects of host genetic group on rhizobiome structure (Bouffaud et al., 2012; Walters et al., 2018) and extracellular enzyme activity (Emmett et al., 2018), although this influence is independent of host genetic distance or decade of release.

Genetic changes to improve agronomic traits went hand-in-hand with agricultural intensification: a transition from low-synthetic-input agroecosystems to increasingly managed, high-density, and input-dependent cultivation environments. Agrochemical inputs for fertility, weed management, and pest control became widespread (Duvick, 2005) and synthetic N fertilizer application rates rose rapidly, replacing organic matter as the primary source of crop nutrients (Cao et al., 2018). Today, although the diversity of modern agricultural systems is not accurately represented by a conventional-organic dichotomy, management systems that rely on inorganic inputs vs. organic matter have profoundly different consequences for soil physicochemical properties and microbial communities. Crucially, the effects of divergent management practices extend beyond a single growing season to long-term legacy impacts: Organically managed agroecosystems have distinct microbial diversity, community structure (Francioli et al., 2016; Li et al., 2017; Lupatini et al., 2017; Mader et al., 2002; Wang et al., 2016), and microbe-microbe ecological interactions (Berry and Widder, 2014; Coyte et al., 2015; Faust and Raes, 2012; Layeghifard et al., 2017) in comparison to conventionally managed systems. Plant-microbe interactions likely also have a greater impact on crop health and productivity in organic systems that depend on microbial mineralization processes to release plant-available nutrients than when inorganic fertilizers are applied.

While genetic and environmental changes during maize evolution have frequently been investigated separately, the interaction of these selective forces may have had profound impacts on the modern maize rhizobiome and microbially-mediated adaptation to organic agroecosystems. Adaptation of landrace genetic clusters to local climatic and ecological conditions appears to have been influenced by the rhizobiome (Vigouroux et al., 2008). Later, the high-density, high-nitrogen (N) environment of modern intensive agriculture led to shallower root systems with reduced branching (York et al., 2015) and potential reduction in the benefits to maize of microbial mutualisms (Kiers et al., 2002; Wissuwa et al., 2009). However, G x E interactions impacting maize acquisition of organic N and adaptation to organic agroecosystems have not been fully investigated.

We examined potential impacts of maize evolution on rhizobiome composition and plant growth in soils of contrasting agricultural management legacy. Using twelve genotypes representing an evolutionary transect (teosintes, landraces, inbred parents of modern elite germplasm, and modern hybrids) and two agricultural soils with contrasting management legacies (long-term conventional vs. organic), we determined G (maize genetic group), E (soil management legacy), and G x E effects on rhizobiome diversity and structure, potential microbe-microbe interactions, and agriculturally relevant N-cycling processes. We hypothesized that domestication and further agricultural intensification led to a) decreased rhizobiome diversity and b) caused progressive shifts in rhizobiome composition and potential microbe-microbe interactions, with a greater effect of modern breeding than domestication. Furthermore, we hypothesized that c) rhizobiome composition would be correlated with plant nutrition and productivity, and that d) G x E interactions in plant and rhizobiome metrics would reflect decreased adaptation to the organic legacy soil over evolutionary time. Addressing these questions can provide a more comprehensive understanding of the impacts of maize evolution on its rhizobiome and inform breeding efforts to develop more sustainable agroecosystems.

2. Material and methods

2.1. Soil collection

Soil for a greenhouse experiment was collected from the Century Experiment located at Russell Ranch Sustainable Agriculture Facility of the University of California, Davis (38.54°N, −121.87°W) (Wolf et al., 2018). Topsoil was collected from the upper 10 cm of soil at random locations in three replicate 0.40-ha plots per long-term management treatment (organic and conventional) of the maize-tomato rotation in September 2016 after maize harvest. Plots had been under continuous conventional or certified organic management since 1993 with the same total N rate applied but different N sources. Conventional plots received inorganic N fertilizer, whereas organic plots received organic N sources in the form of cover crops and composted poultry manure before each crop cycle. Furthermore, the organically managed plots were planted with a winter cover crop of mixed oat (Avena sativa L.), vetch (Vicia villosa) and bell bean (Vicia faba L.) that was cut and incorporated prior to tomato transplanting in the spring. Pests were controlled in both treatments using sulfur and *Bacillus thuringiensis* applications as needed. For further details of the management systems and soil properties, please refer to Wolf et al. (2018) and Li et al. (2019). After collection, soil was homogenized in a cement mixer and used to fill 5-gallon pots over a 1-week period. Pots were placed in a greenhouse and watered with individual drippers to avoid cross-contamination between experimental units. Soil physicochemical properties were analyzed at the UC Davis Analytical Laboratory (Davis, CA, USA); details and references for the analysis protocols can be found in Supplementary Table S1.

2.2. Maize growth and plant analysis

Seeds of 12 *Zea mays* genotypes representing an evolutionary transect (*sensu* Iannucci et al., 2017) of maize domestication and breeding (Supplementary Table S2) were first germinated on moist paper towels

in the dark for 4 days. Genotypes included major stages in maize evolution: teosinte, the wild ancestor; landraces, which were created through domestication, dispersal, and local adaptation; inbreds, created from the best-performing open-pollinated varieties that originated from North American landraces (Duvick et al., 2004; Smith et al., 2005); and single-cross and double-cross hybrids, created by crossing elite inbred lines. The inbreds selected were not the direct parents of the hybrids. Teosinte seeds were scarified with sterilized nail clippers on one end to enhance homogeneous germination. Six germinated seeds per genotype and soil combination were transplanted into moist soil at approximately 1.5 cm depth (n = 144). Pots were arranged in a randomized complete block design and watered daily without fertilization until harvest so that plant growth would reflect differences in the combined effect of soil management legacy and microbial communities. Weeds were controlled manually as needed. Plants were grown for 35 days without supplemental lighting or heating (temperature range 16–32 °C). The duration of the experiment was chosen to prevent pots from becoming rootbound and experiencing corresponding resource limitation that might have impacted plant-microbe interactions.

At 35 days after transplanting (growth stage V5), each plant was clipped at the base and shoots were dried at 105 °C for 72 h and weighed. The entire shoot was ground, sieved (2 mm) and three shoot samples per genotype and soil combination were analyzed for C and N content on an elemental analyzer (Costech Analytical Technologies, Inc., Valencia, California, USA) and submitted for total nutrient analysis (N, P, K, Ca, Mg, S, Cu, Mn, Zn, Na, B, Al, Fe) using the acid digest method (Huang and Schulte, 1985) at the Pennsylvania State University Agricultural Analytical Services Laboratory (University Park, Pennsylvania, USA).

2.3. Statistical analysis of plant parameters

All statistical analyses were carried out in R software v.3.4.4 (R Core Team, 2018). Data were assessed to satisfy the requirements for analysis of variance (ANOVA), including homogeneity of variance and normality of residuals, using normal QQ plots, Bartlett tests, and Shapiro-Wilk tests. Shoot dry biomass was analyzed using ANOVA with management legacy (conventional, organic), genetic group (teosinte, landrace, inbred line, modern hybrid), and their interaction as fixed effects, genotype nested within genetic group and block as random effects. Normality of residuals was assessed with the Shapiro-Wilk test. Relative performance under different management legacy for each genetic group was calculated by dividing the mean shoot biomass in the organic legacy soil by mean shoot biomass in the conventional legacy soil for all samples belonging to that genetic group. Because the same plants were not grown in both conditions and relative performance was thus calculated as the ratio of group means, lack of replication precluded the use of ANOVA for this metric. Plant tissue nutrients were ordinated using principal components analysis (PCA). Permutational multivariate analysis of variance (PERMANOVA) based on Bray-Curtis distance with 999 permutations was used to test fixed effects of soil management and genetic group as well as their interaction on plant tissue nutrients. Mantel tests were conducted on Bray-Curtis dissimilarity matrices to determine whether tissue nutrients were correlated with bacterial and fungal rhizosphere communities.

2.4. Rhizosphere soil collection

At harvest, the entire root system was immediately removed from the soil and stored at 4 °C. Rhizosphere soil adhering to roots after shaking was collected from 3 5-cm segments of roots 5 cm away from the crown within 72 h. Root subsamples with adhering soil were gently shaken (120 rpm) for 90 min in a 0.9% NaCl/0.01% Tween 80 (v/v) solution (Sigma Aldrich, St. Louis, Missouri, USA). Roots were removed and the solution was centrifuged for 10 min at 14,000 rpm. The resulting pellet was stored at −80 °C. Total DNA was extracted from rhizosphere soil using a DNeasy PowerSoil Pro kit according to manufacturer's instructions (Qiagen, Inc., Germantown, Maryland, USA) and stored at −80 °C until further use.

2.5. 16S rRNA gene sequencing

Genomic DNA was submitted to the DOE Joint Genome Institute (Walnut Creek, CA, USA) for amplicon-based sequencing of the 16S rRNA gene for bacteria and archaea (region V4–V5, Parada et al., 2016) and the internal transcribed spacer for fungi (ITS2, (White et al., 1990). An Illumina MiSeq platform was used to generate 300-bp paired-end reads. Sequencing data analyzed in this project is available in the NCBI SRA database under the project ID PRJNA593859.

Raw sequencing data were demultiplexed using the Idemp toolkit and primers were removed using Cutadapt (Martin, 2011). All further read processing was done in the Dada2 package (Callahan et al., 2016) using R v.3.4.1 (R Core Team, 2018). Based on read quality profiles, 16S rRNA gene forward reads were truncated to 210 bp and reverse reads to 160 bp; ITS reads were not truncated to a specific length because the length of this region is highly variable. 16S rRNA gene sequences were filtered and trimmed using the parameters maxEE = 2 and truncQ = 2 and forward and reverse reads merged, while ITS reads were filtered and trimmed using maxEE = 2 and truncQ = 11. Bacterial and archaeal taxonomy was assigned to the genus level using the SILVA reference database v.128 (Glöckner et al., 2017) and fungal taxonomy was assigned using the 2017 release of the UNITE database (Kõljalg et al., 2013). Sequences were rarefied to the minimum number of reads per sample (4949 for 16S rRNA gene and 71052 for ITS), leaving a total of 11062 16S rRNA amplicon sequence variants (ASVs) and 3248 fungal ITS ASVs for further analysis.

2.6. Microbial community diversity and composition

Microbial community diversity and composition were analyzed in rhizosphere soil samples. The Shannon index was calculated for each sample as a measure of alpha diversity (Spellerberg and Fedor, 2003). ANOVA was used to test the effects of soil management legacy, genetic group, and their interaction on alpha diversity as described for shoot biomass. Non-metric multidimensional scaling (NMDS) of distance matrices based on Bray-Curtis dissimilarity values was used to ordinate prokaryotic and fungal rhizosphere communities. Permutational analysis of variance (PERMANOVA) based on Bray-Curtis distance with 999 permutations was used to test the effects of soil management legacy, genetic group, and the management legacy x group interaction on rhizobiome composition. The proportion of variation corresponding to each of these factors was calculated by converting the PERMANOVA estimated components of variation to percentages. To compare between-sample (β) diversity among maize genetic groups, the distance from each rhizobiome sample to the group centroid was calculated using management-legacy-specific Bray-Curtis distance matrices with the usedist package (Bittinger, 2017). One-way ANOVA was used to test whether the distance to group centroid differed among genetic groups, with distance to centroid as the response variable and genetic group as the independent variable. Furthermore, the distance between group centroids was calculated for samples from each pair of maize genetic groups based on Bray-Curtis distances. Distance-between-centroid calculations were conducted separately for prokaryotic communities and fungi within each soil management legacy.

2.7. Differential abundance analysis

Differential abundance analysis was used to identify ASVs differing in abundance among maize genetic groups using the DESeq2 package (Love et al., 2014). Samples from different genetic groups did not differ in library size, so it was appropriate to use non-rarefied data for the DESeq2 analysis. For more detailed justification of the use of

non-rarefied data in differential abundance analysis, the reader is referred to Weiss et al. (2015, 2017). Analysis was conducted for prokaryotic and fungal communities separately using the Wald test, parametric fit, and a significance threshold of $p < 0.01$.

2.8. Indicator species analysis

Indicator ASVs associated with a genetic group or combination of two groups were identified within each soil management legacy. Taxa considered as indicators of a given environment are defined as being both more abundant in that environment than other environments and found more frequently there than in other environments (see Dufrene and Legendre (1997) for further explanation). Combinations of two genetic groups (teosinte-landrace, teosinte-inbred, teosinte-hybrid, landrace-inbred, landrace-hybrid, inbred-hybrid) were included to provide insight into shifts during domestication and breeding, as more shared indicator taxa could indicate greater similarity between rhizobiomes. To avoid bias due to rare taxa, only sequences present in at least 10 samples were included. The Indicator Value (IndVal) index, which integrates abundance and frequency of occurrence into a single metric, was calculated for each bacterial/archaeal or fungal ASV (Dufrene and Legendre, 1997). Associations of ASVs with each of the 20 environments [2 soil management legacies x (4 genetic groups + 6 combinations of two genetic groups)] were tested for significance with 999 permutations using the indicspecies package (De Cáceres and Legendre, 2009). The Bonferroni correction was used to control the family-wise error rate at $\alpha = 0.05$ for the 20 comparisons.

2.9. Network analysis

Co-occurrence network analysis was used to visualize differences in microbe-microbe interactions within rhizobiome samples. Nodes in these networks represent microbial ASVs and edges represent significant co-occurrence patterns. Only sequences present in at least 10 samples were included in network analyses to avoid bias due to rare taxa (Berry and Widder, 2014), leaving a total of 465 prokaryotic and 114 fungal ASVs. The HabitatCorrectedNetwork tool, which accounts for habitat filtering effects by centering each sample around the mean value for the respective subgroup, was used to construct correlation tables based on the Spearman's rank correlation coefficient and corrected for habitat filtering by using genotype as the subgroup variable (Brisson et al., 2019a). One network was constructed for each maize genetic group within each soil management legacy from significant positive correlations ($r > 0.75$ and $p < 0.01$). Network properties thought to be ecologically relevant according to the literature, such as number of nodes and edges, mean degree, and modularity, were calculated using the igraph package (Csárdi and Nepusz, 2006).

2.10. Quantitative PCR (qPCR) of N-cycling genes

Abundances of six microbial genes involved in N-cycling processes in the rhizosphere of teosinte and modern maize were quantified as proxies for potential alterations to the N cycle. Specifically, the genes measured were *nifH* for N_2 fixation, archaeal *amoA* and bacterial *amoA* for nitrification, and *nirK*, *nirS*, and *nosZ* for denitrification.

A microfluidics Fluidigm Gene Expression chip was used to amplify and quantify all genes simultaneously. The following primers were used: Po1F/Po1R (*nifH*) (Poly et al., 2001), CrenamoA23f/CrenamoA6161r (archaeal *amoA*) (Tourna et al., 2008), amoA-1F/amoA-2R (bacterial *amoA*) (Rotthauwe et al., 1997), nirK876/nirK1040 (*nirK*) (Henry et al., 2005), nirSCd3aF/nirSR3cd (*nirS*) (Kandeler et al., 2006), and nosZ1F/nosZ1R (*nosZ*) (Henry et al., 2006). Specific target amplification (STA) was used to increase the amount of template for each target gene prior to Fluidigm qPCR (Ishii et al., 2014). The STA pre-amplification reaction was performed in 5 μl reaction mixtures containing 2 × Taqman PreAmp Master Mix (Applied Biosystems), 0.5 μM of all primer sets listed above, and 1.25 μl of the DNA template extracted from rhizosphere soil. The STA reaction was performed on an MJ Research Tetrad thermal cycler with the following cycling program: 95 °C for 10 min followed by 14 cycles of 95 °C for 15 s and 58 °C for 4 min. Standards of each gene were derived from soil microbial communities, quantified, and mixed. A 5-fold dilution series from 1×10^5 to 3.2×10^1 copies/μl was subjected to the STA pre-amplification reaction along with the soil DNA to provide standard curves for Fluidigm qPCR. STA products were treated by exonuclease to remove excess primers. For qPCR, 5 μl of sample premix was prepared containing 2 × SsoFast Evagreen Supermix with Low Rox (BioRad), 20 × DNA Binding Dye Sample Loading Reagent (Fluidigm), and 2.25 μl exonuclease-treated STA products. Five μl of assay mix was prepared containing 2 × Assay Loading Reagent (Fluidigm), 1 × DNA Suspension Buffer (Teknova), and 50 μM each forward and reverse primer for each gene target. The sample premix and assay mix were loaded on a 96.96 chip (Fluidigm), and amplification by primer sets for individual genes was performed according to the following program: 70 °C for 40 min, 58 °C for 30 s, 95 °C for 1 min followed by 30 cycles of 96 °C for 5 s, 58 °C for 20 s, and followed by a dissociation curve. All of the samples and standards were analyzed in 12 technical replicates. The Fluidigm Real-Time PCR Analysis software version 4.1.3 and the copy number of each gene (calculated from DNA quantification in Qubit and the known length of each gene) were used to determine the C_t (cycle threshold). All Fluidigm qPCR was conducted at the Roy J. Carver Biotechnology Center (Urbana, IL, USA). Mean values and standard errors for number of copies per ng DNA (quantified by Qubit, Invitrogen, Carlsbad, CA, USA) were calculated from technical replicates with quality scores of at least 0.65.

2.11. qPCR data analysis

Data were again tested for homogeneity of variance and normality of residuals using normal QQ plots, Bartlett tests, and Shapiro-Wilk tests. Analysis of variance (ANOVA) was used to test the fixed effects of soil management legacy and genetic group on abundance of each N-cycling gene with block as a random effect. Outliers identified as greater than four times the mean value for Cook's distance were removed to meet assumptions of normality of residuals. Because both soil management legacy and genetic group significantly influenced abundance, Student's t tests were used to examine whether the abundance of each gene differed significantly between the rhizobiome of teosinte and modern maize hybrids within each soil management legacy.

3. Results

3.1. Plant biomass and nutrient content

Plant biomass was higher in the organic legacy soil, which was higher in most nutrients (Supplementary Table S1) than the conventional legacy soil, for all genetic groups (Fig. 1a). However, a significant genetic group x soil management legacy interaction showed that relative growth in the two soil treatments varied by genetic group ($p < 0.001$). Relative biomass increases in the organic legacy soil compared to the conventional legacy soil were higher for teosinte and landrace genotypes than inbred and modern hybrid genotypes (Fig. 1b).

Shoot nutrient composition was also affected by a genetic group x soil management legacy interaction ($p < 0.01$). Soil management legacy appeared to have a stronger effect than genetic group on plant nutrient profiles: PCA ordination separated samples primarily by soil management legacy along the first principal component (PC1) axis, which explained 29.8% of variation (Fig. 1c). Plant shoot nutrients with the highest factor loadings for this axis included Ca, Mg, Al, Na, Fe, Mn, and B. The second principal component (PC2), which accounted for 25.1% of variation, was most influenced by N, P, K, and Zn (Fig. 1c).

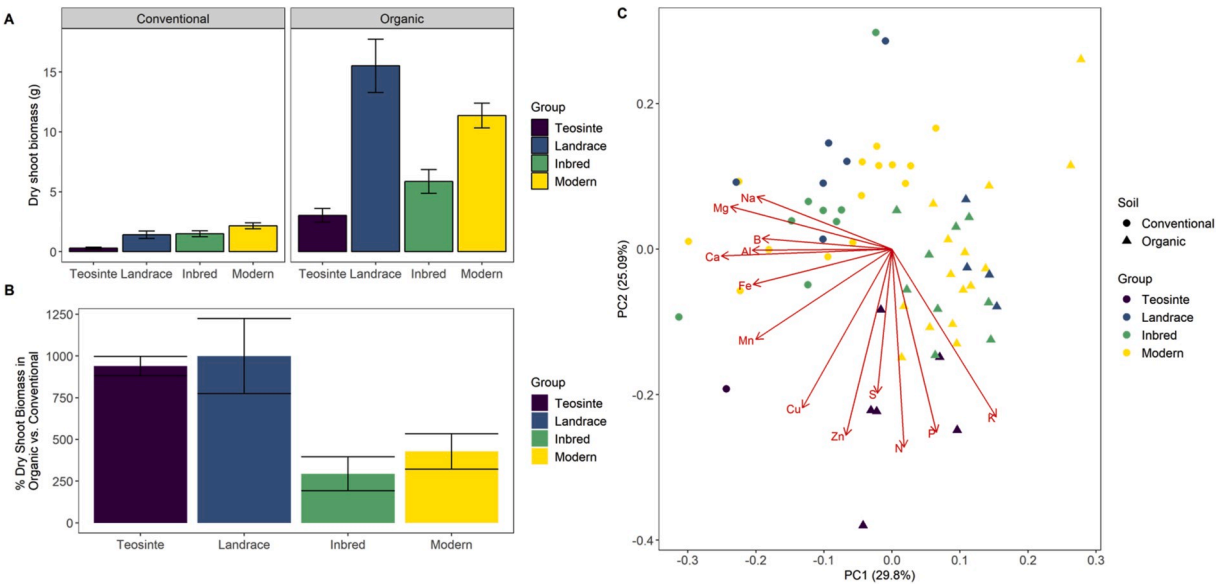

Fig. 1. Plant aboveground biomass and nutrient composition. A) Dry shoot biomass was higher in the organic legacy soil for all genetic groups. B) Relative growth, calculated as biomass in the organic legacy soil relative to biomass in the conventional legacy soil on a percentage basis, varied by genetic group ($p < 0.001$). Teosinte and landrace genotypes had higher relative growth in the organic legacy soil than inbred and modern genotypes. C) Principal components analysis (PCA) revealed that shoot nutrient composition was affected by a genetic group x soil management legacy interaction (PERMANOVA $p < 0.01$). Separation by soil management legacy occurred primarily along the PC1 axis, which explained 29.8% of variation, but genetic group effects were less clearly shown.

3.2. Rhizobiome composition and diversity

Within-sample (α) diversity of rhizosphere prokaryotic communities did not differ by soil management legacy or maize genetic group ($p > 0.05$, Supplementary Fig. S1a). Fungal alpha diversity was significantly higher ($p < 0.001$) in the rhizosphere of plants growing in the conventional legacy soil but did not differ between genetic groups (Supplementary Fig. S1b). In contrast, between-sample (β) diversity (or dispersion), calculated as the distance to the group centroid, tended to decrease along the evolutionary transect from teosinte to modern maize (Fig. 2). This trend was observed for bacteria/archaea and fungi under both soil management legacies, but the effect of maize genetic group was not statistically significant ($p > 0.05$).

The composition of prokaryotic and fungal communities varied with soil management legacy and maize genetic group (all PERMANOVA $p < 0.001$), with no significant interaction (Supplementary Fig. S2, Supplementary Table S3). Soil management legacy explained a greater proportion of variation in community composition (10% for prokaryotes, 20% for fungi) than genetic group (6.1% for prokaryotes, 5.3% for fungi).

The distance between group centroids was calculated for rhizobiome samples from each pair of maize genetic groups in each soil management legacy (Fig. 3). For prokaryotic communities, the greatest distance between centroids was observed between teosinte and inbred lines and the smallest distance was observed between inbred lines and modern maize in both soil management legacies (Fig. 3a). In contrast, the greatest distance between centroids for fungal communities was between teosinte and landraces and the smallest distance was between inbred lines and modern maize in both soil management legacies (Fig. 3b). However, distances were non-additive, i.e. the distances between genetic groups adjacent on the maize evolutionary timeline did not sum to the distance between non-adjacent groups. For prokaryotic communities, in fact, the distance between teosinte and modern maize was smaller than the distance between teosinte and inbred lines for both soil management legacies.

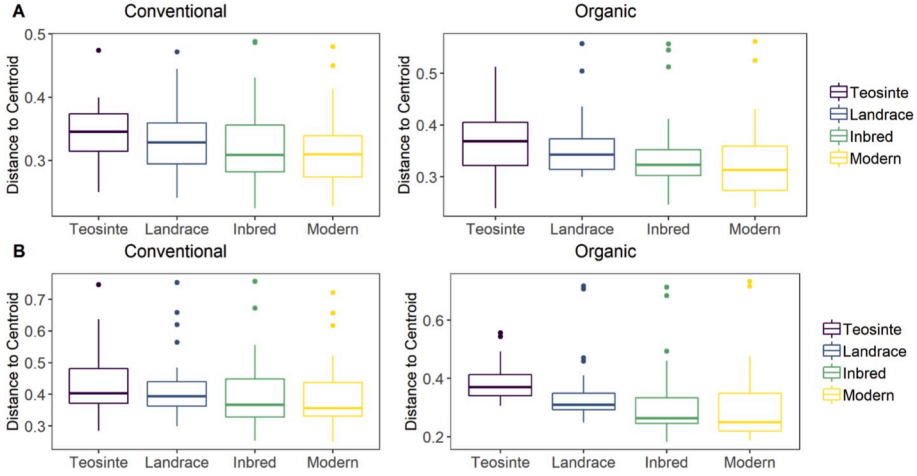

Fig. 2. Beta diversity of maize rhizobiome samples. Within-group beta diversity of A) prokaryotic and B) fungal rhizosphere communities was calculated for each combination of maize genetic group and soil management legacy as the mean distance from each rhizobiome replicate to the centroid of all replicates for that group x soil management legacy combination. A trend towards decreasing beta diversity over maize evolutionary time was observed, although it was not significantly different at the $p = 0.05$ level.

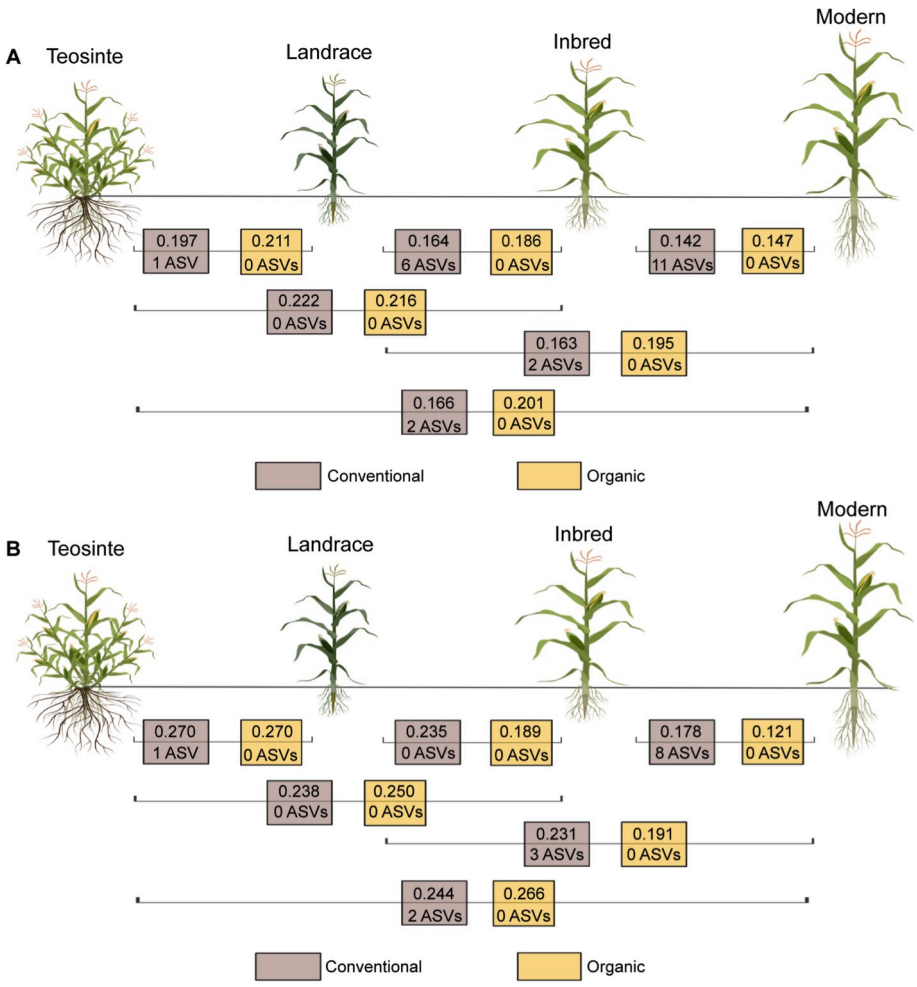

Fig. 3. Distance between centroids and shared indicator ASVs. Distance and similarity metrics were calculated to investigate the dynamics of rhizobiome shifts during maize evolution for A) prokaryotes and B) fungi in conventional and organic legacy agricultural soils. The distance between centroids of rhizobiome samples was calculated for each pair of genetic groups in each soil management legacy. Indicator species analysis identified thirty-six prokaryotic and fungal ASVs uniquely associated with a pair of genetic groups, and the number of indicator ASVs unique to each pair is shown below the corresponding connecting line. Non-additive distance between centroid values and numbers of shared indicator ASVs suggest that changes in rhizobiome structure and plant-microbe interactions during maize evolution have not been linear. Differences in distance and similarity metrics between soil management legacies show a genotype-by-environment (G x E) interaction.

3.3. Specific microbial taxa responding to different maize genetic groups

Differential abundance analysis was used to identify prokaryotic and fungal ASVs whose abundance differed among the four maize genetic groups (Supplementary Fig. S3, Supplementary Fig. S4, Supplementary Fig. S5 and Supplementary Fig. S6). Due to significant effects of soil management legacy on rhizobiome composition, organic legacy and conventional legacy soils were handled separately in differential abundance and indicator species analyses. As with the distances between centroids and indicator ASVs, shifts in the relative abundance of taxa that responded to maize genetic group were generally non-additive (Supplementary Fig. S3, Supplementary Fig. S4, Supplementary Fig. S5 and Supplementary Fig. S6).

Ninety-five prokaryotic ASVs responded to the effect of maize genetic group in the conventional legacy soil and 103 prokaryotic ASVs differed in relative abundance across maize genetic groups in the organic legacy soil. In the conventional legacy soil, differentially abundant taxa that tended to increase in abundance over evolutionary time included members of the genera *Achromobacter*, *Azohydromonas*, *Burkholderia-Paraburkholderia*, *Pseudorhodoferax*, and *Sphingomonas*, while many other taxa showed non-additive patterns of variation in relative abundance (Supplementary Fig. S3). In the organic legacy soil, members of the genera *Azotobacter*, *Pedobacter*, and *Sphingobium* tended to increase over evolutionary time, while an ASV belonging to the genus *Devosia* tended to decrease (Supplementary Fig. S4).

In the conventional legacy soil, differentially abundant fungal ASVs whose abundance increased over maize evolutionary time included members of the genera *Acremonium*, *Alternaria*, *Apodus*, *Cladosporium*, *Mortierella*, and *Preussia*, while an ASV belonging to the genus *Burgoa* decreased in relative abundance (Supplementary Fig. S5). Some of the same genera were differentially abundant in the organic legacy soil, where *Alternaria* sp., *Cercophora* sp., *Fusarium* sp., *Minimedusa* sp., and *Podospora* sp. increased while *Mycosphaerella* sp. and *Spizellomyces* sp. decreased over maize evolutionary time (Supplementary Fig. S6). Certain ASVs were present in the teosinte rhizobiome but had extremely low relative abundance in the rhizobiomes of all other genetic groups, including members of the genera *Coprinus*, *Fusarium*, *Podospora*, and *Spizellomyces* in the conventional legacy soil and *Cladosporium*, *Cystobasidium*, *Olpidium*, *Penicillium*, and *Rhizophlyctis* in the organic legacy soil (Supplementary Fig. S5 and Supplementary Fig. S6). This unique pattern among fungi associated with teosinte was not observed for other maize genetic groups or in differentially abundant prokaryotic ASVs.

Indicator species analyses identified specific microbial ASVs that responded to the influence of a specific maize genetic group in each soil management legacy and provided insight into similarities between the rhizobiomes of each pair of genetic groups. Twenty-six prokaryotic and 18 fungal ASVs were associated with an environment (combination of soil management legacy and genetic group or pair of groups), eight of which were associated with a single environment and 36 with a combination of two environments (Supplementary Table S4). Evolutionarily adjacent genetic groups tended to share greater numbers of the two-environment ASVs than more distant genetic groups across soil management legacies (Fig. 3, shared two-environment ASV numbers shown below the line). The inbred/modern groups shared the greatest number of indicator ASVs (19), followed by the landrace/inbred groups (6), while the teosinte/landrace groups shared only two indicator ASVs

(Fig. 3). However, the most distantly related maize genetic groups, teosinte/modern, still shared 4 indicator ASVs. 58% of the prokaryotic indicator ASVs belonged to the phylum Proteobacteria and 15% to the phylum Bacteroidetes (Supplementary Table S4). 67% of fungal indicator ASVs belonged to the phylum Ascomycota (Supplementary Table S4).

3.4. Co-occurrence network analysis

Co-occurrence networks (with nodes representing ASVs and edges representing positive co-occurrence relationships, as described in the Material and Methods) were constructed to investigate the effects of maize evolution and soil management legacy on potential microbe-microbe ecological interactions in the rhizosphere. Prokaryotic co-occurrence network structure varied by soil management legacy and genetic group (Fig. 4, Table 1). All rhizosphere networks had 464-465 nodes, but the number of edges differed according to soil management legacy and genetic group. Prokaryotic rhizosphere networks of plants grown in the conventional legacy soil (Fig. 4a) had 7–9% fewer edges than networks from the organic legacy soil (Fig. 4b) for all genetic groups except for modern maize. In that case, the prokaryotic rhizosphere network of modern maize in the conventional legacy soil had 5% more edges than the prokaryotic rhizosphere network of modern maize in the organic legacy soil. Teosinte networks had the highest number of edges and mean degree, and modern maize networks had the lowest values for these parameters in both soil management legacies. However, the trends did not progress in one direction along the evolutionary transect, as values for inbred networks were higher than for landraces. Teosinte networks were slightly less modular than networks from other genetic groups in both soil management legacies (Table 1).

Fungal networks were similar in size in both soil management legacies, but structural properties varied by genetic group (Fig. 5, Table 1). Number of edges and mean degree were highest in teosinte rhizosphere networks in both soil management legacies, followed by modern maize networks. Landrace and inbred networks tended to have the highest modularity values.

3.5. Relationship between rhizobiome composition and plant parameters

Mantel tests were used to test correlations between dissimilarity matrices for prokaryotic and fungal ASV abundances and dissimilarity matrices for plant shoot nutrient composition. Rhizosphere prokaryotic and fungal communities were each correlated with shoot nutrient composition (both $p < 0.05$).

3.6. Abundance of N-cycling genes

To determine whether domestication and selection have shifted rhizosphere N cycling in soils with contrasting agricultural management legacies, we quantified the abundance of microbial genes related to N_2 fixation, nitrification, and denitrification in teosinte and modern maize rhizosphere samples in both soil management legacies. Soil management legacy influenced the abundance of bacterial *amoA* and *nosZ*, with higher abundances in the organic legacy soil ($p < 0.05$), but maize genetic group did not affect the abundance of any of the genes ($p > 0.05$, Fig. 6).

4. Discussion

In partial support of our hypothesis of decreased rhizobiome diversity over the course of maize evolution, we found a trend towards decreased dispersion of rhizobiome samples within genetic groups (β diversity), but equivalent species richness and evenness within individual rhizobiome samples (α diversity).

Supporting our hypothesis of shifts in rhizobiome composition, prokaryotic and fungal rhizobiome composition differed among maize genetic groups in both soil management legacies. Genetic group explained a relatively small proportion of rhizobiome variation (5–6%), in accordance with other studies showing that effects of host genotype on the maize rhizobiome are significant but weaker than those of location or soil type (Peiffer et al., 2013; Walters et al., 2018). Substantial variation remained after accounting for the effects of soil management legacy and maize genetic group (Supplementary Table S3), as has been noted elsewhere (Edwards et al., 2015). Factors not accounted for in the model, such as variation in initial colonizing communities due to soil heterogeneity and subsequent divergence due to microbe-microbe interactions and stochastic processes (Adair and Douglas, 2017), likely contributed to the observed rhizobiome variation among genotype replicates.

Both community- and taxa-level analyses supported this hypothesis of shifts in maize rhizobiome composition. Distances between group centroids, numbers of indicator ASVs, and changes in the relative abundance of taxa responsive to maize genetic group were non-additive, showing no progressive divergence of rhizobiomes (Fig. 3, Supplementary Fig. S3, Supplementary Fig. S4, Supplementary Fig. S5 and Supplementary Fig. S6). A greater impact of domestication than modern breeding is suggested by a) a decrease in distances between group centroids for genetic groups adjacent on the evolutionary timeline (teosinte/landrace to inbred/modern), and b) more prokaryotic and fungal indicator taxa shared between the inbred and modern maize rhizobiomes than between other genetic groups (Fig. 3). This concordance between community-level analyses and taxa-level analyses could

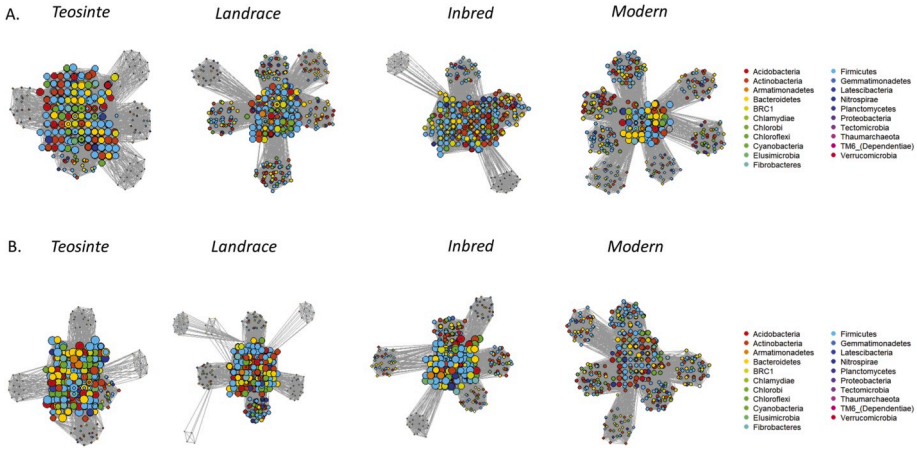

Fig. 4. Prokaryotic co-occurrence networks. Rhizosphere co-occurrence networks in A) a conventional legacy soil and B) an organic legacy soil. Nodes represent ASVs, with node size corresponding to betweenness centrality and color corresponding to phylum, and edges represent Spearman correlations between ASVs. Data were filtered to remove ASVs present in fewer than 10 samples and networks were constructed from positive significant correlations ($r \geq 0.75$ and $p \leq 0.01$). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Table 1
Selected properties of rhizosphere co-occurrence networks.

Network	Soil Management Legacy	Group	Nodes	Edges	Mean degree	Modularity
Ecological interpretation			*# of ASVs*	*Positive co-occurrence networks*	*Mean connections of one node to other nodes*	*Existence of sub-communities within the network*
CT	Conventional	Teosinte	465	18520	79.66	0.74
CL	Conventional	Landrace	465	14796	63.64	0.82
CI	Conventional	Inbred	465	15850	68.17	0.82
CM	Conventional	Modern	465	14388	61.88	0.82
OT	Organic	Teosinte	465	20119	86.53	0.71
OL	Organic	Landrace	464	15862	68.37	0.77
OI	Organic	Inbred	465	16949	72.90	0.75
OM	Organic	Modern	465	13743	59.11	0.86
CT	Conventional	Teosinte	114	1067	18.72	0.70
CL	Conventional	Landrace	114	841	14.75	0.82
CI	Conventional	Inbred	114	801	14.05	0.85
CM	Conventional	Modern	114	929	16.30	0.77
OT	Organic	Teosinte	114	1055	18.51	0.71
OL	Organic	Landrace	113	669	11.84	0.82
OI	Organic	Inbred	114	913	16.02	0.76
OM	Organic	Modern	114	937	16.44	0.79

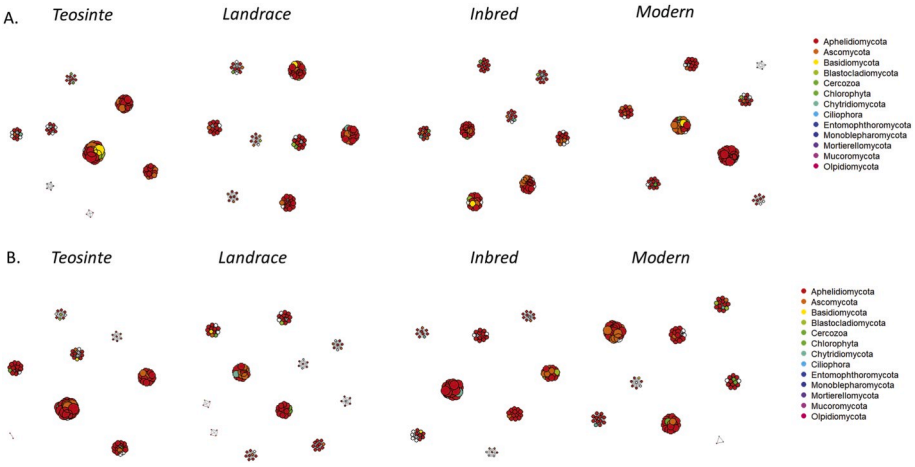

Fig. 5. Fungal co-occurrence networks. Rhizosphere co-occurrence networks in A) a conventional legacy soil and B) an organic legacy soil. Nodes represent ASVs, with node size corresponding to betweenness centrality and color corresponding to phylum, and edges represent Spearman correlations between ASVs. Data were filtered to remove ASVs present in fewer than 10 samples and networks were constructed from positive significant correlations ($r \geq 0.75$ and $p \leq 0.01$). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

suggest that maize evolution has impacted both plant root and rhizosphere traits favoring strategies for rhizosphere competence (e.g. root exudation, nutrient uptake) and taxon-specific host-microbe signaling mechanisms. Notably, while a greater impact of domestication than modern breeding was found for emmer wheat (Iannucci et al., 2017), a study of these maize genotypes in a nutrient-depleted agricultural soil found evidence for a stronger effect of breeding (Brisson et al., 2019b). This discrepancy highlights the dependence of rhizosphere recruitment on bulk soil management, which establishes the microbial pool from which the rhizobiome is selected.

Microbial co-occurrence network analysis revealed different effects of maize evolution on potential microbe-microbe interactions, represented by positive co-occurrences, than on rhizobiome composition. The number of co-occurrences, which are thought to indicate ecological relationships including mutualisms, predator-prey interactions, and niche overlap (Faust and Raes, 2012), is a form of biodiversity termed "interaction diversity" (Tylianakis et al., 2010). Decreased interaction diversity can occur even with no reduction of species richness and can affect ecosystem service provisioning and resilience (Tylianakis et al., 2010; Valiente-Banuet et al., 2015). Here, prokaryotic networks of modern hybrid rhizobiomes had far fewer co-occurrences than those of other genetic groups in both soil management legacies (Table 1), consistent with findings for these genotypes in a nutrient-depleted soil from the same experiment (Brisson et al., 2019b). The distinct structure of modern hybrid prokaryotic networks suggests that while domestication may have had more profound effects on *plant*-microbe interactions (Fig. 3), subsequent agricultural intensification has had greater impacts on potential *microbe*-microbe interactions. In fungal co-occurrence networks, in contrast, network size decreased from teosinte to landraces but increased from inbreds to hybrids (Table 1). Unique responses of bacteria/archaea and fungi were observed in most analyses of rhizobiome composition in this study, perhaps because rhizosphere recruitment of prokaryotes and fungi could be governed by distinct mechanisms that respond differently to shifts in host genotype and environment. As with prokaryotes, fungal co-occurrence networks showed different patterns than rhizobiome composition. Direct recruitment of microorganisms to the rhizosphere may thus be partially decoupled from indirect plant influence on microbe-microbe interactions through rhizodeposits and physicochemical modification of the rhizosphere. Networks were also affected by a G x E interaction: While most prokaryotic networks had more co-occurrences in the organic legacy soil, the modern hybrid network had more co-occurrences in the conventional legacy soil. In contrast, the fungal modern hybrid network had more co-occurrences in the conventional soil than fungal inbred or landrace networks (Table 1). Organic amendments such as compost have been shown elsewhere to increase positive co-occurrences (W. Yang et al., 2019), but our results show that plant adaptation to specific agricultural management systems may interact with the effects of management itself on co-occurrence network structure (Schmidt et al., 2019).

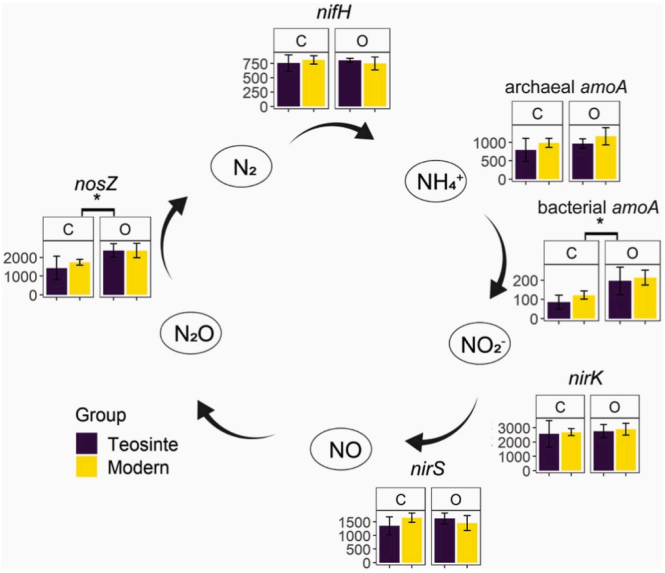

Fig. 6. Abundance of nitrogen-cycling genes. We quantified the abundance of microbial genes related to N fixation (*nifH*), ammonia oxidation (archaeal and bacterial *amoA*), and denitrification (*nirK*, *nirS*, *nosZ*) in modern maize hybrid and teosinte rhizosphere samples in both soil management legacies. The abundance of nitrification genes and some denitrification genes tended to be higher in the rhizosphere of modern maize hybrids than the teosinte rhizosphere. Soil management legacy influenced the abundance of bacterial *amoA* and *nosZ* (* indicates statistically significant difference between soil management legacies at $\alpha = 0.05$. Values are reported as copies per ng DNA and error bars represent standard error. C = conventional legacy soil; O = organic legacy soil.

In accordance with our third hypothesis, prokaryotic and fungal rhizosphere communities were significantly correlated with plant nutrient composition. Our hypothesis of decreased adaptation to organic agroecosystems seems to have been supported by the proportionally higher biomass in the organic legacy soil of teosinte/landrace than inbred/hybrid genotypes, although other interpretations are possible. This G x E interaction could suggest decreased adaptation to organic management or, alternatively, increased adaptation to lower-nutrient conditions over the maize evolutionary timeline (Fig. 1b). Whether similar G x E interactions have impacted harvest index and allocation to grain among post-domestication genotypes should be investigated, although this question was beyond the scope of the present study as the plants were not grown to maturity. Greater differences among genetic groups in rhizosphere recruitment (as quantified by number of indicator ASVs) were observed in the lower-nutrient conventional legacy soil, which may indicate increased reliance on rhizosphere interactions when resources are more limited (Kiers et al., 2002; Wissuwa et al., 2009).

To identify potential loss or gain of beneficial associations during maize evolution, we sought agriculturally relevant taxa among indicator ASVs associated with the teosinte/landrace and inbred/modern pairs. Only one prokaryotic ASV (order Bradyrhizobiales) and one fungal ASV (*Absidia koreana* sp.) were indicators of the teosinte/landrace pair, both of which were found in the conventional legacy soil (Supplementary Table S4). The Bradyrhizobiales are composed of plant-associated commensalists, some of which promote root growth and/or fix N_2 inside root nodules (Garrido-Oter et al., 2018), but evidence for benefits to non-leguminous hosts is limited (Antoun et al., 1998; Prévost et al., 2000). *Absidia koreana* was only recently isolated from soil and little is known about the physiology and ecology of this zygomycete (Ariyawansa et al., 2015). The 11 prokaryotic and 7 fungal ASVs associated with the inbred/modern pair, which could represent associations gained during modern breeding, belonged predominantly to the common soil phyla Proteobacteria and Ascomycota.

Finally, we found no difference between teosinte and modern hybrid rhizobiomes in the abundance of six genes related to N_2 fixation, nitrification, and denitrification. While maize evolution has altered rhizobiome diversity, structure, and potential microbe-microbe interactions, it appears to have had negligible impacts on these N-cycling genes.

Still, many questions remain. First, practical application of these results to the design of more sustainable agroecosystems will require improved mechanistic understanding of the genetic basis for observed shifts in the maize rhizobiome. Root traits and exudates are key drivers of rhizobiome assembly and have likely been affected by maize evolution (Schmidt et al., 2016). Direct evidence for changes in root exudates is lacking in maize, but exudate composition has been affected by domestication in other cereals (Iannucci et al., 2017). Variation in rhizobiomes associated with *su/sh* genotypes (differing in kernel sugar/-starch content) may provide support for the role of root exudates via shared carbohydrate metabolic pathways (da Fonseca et al., 2015). Exudates may also explain observed G x E interactions, in light of the plasticity of root exudate composition across soil environments (Badri and Vivanco, 2009); metabolomics would be a valuable tool in testing this hypothesis.

Significant genetic group effects were observed even in this relatively small evolutionary transect, indicating the need for future studies with a far greater number of *Zea mays* genotypes. Using genotypes for which full genomes are available would enable exploration of potential host-microbiome phylogenetic correlations and investigation of how host diversity within maize genetic groups may affect calculations of beta diversity such as those conducted here. Host-microbiome genome-wide association studies (GWAS) (Awany et al., 2019) of well-characterized maize genotypes could help pinpoint the timing of shifts in rhizobiome composition and identify genes controlling rhizobiome interactions. Finally, metagenomic sequencing could vastly improve our understanding of whether maize evolution has impacted agriculturally relevant functions that might affect plant productivity in contrasting agroecosystems. Our findings highlight the need to better understand plant adaptation to contrasting agroecosystems and integrate G x E effects into existing models of rhizobiome assembly.

4.1. Conclusions

We show significant and ecologically relevant effects of maize evolution on rhizobiome structure, with no loss of species richness and evenness but a trend towards decreased variability among rhizobiome samples within maize genetic groups. Domestication (teosinte to landraces) appears to have had greater effects than modern breeding (inbreds to hybrids) on rhizosphere recruitment and individual plant-microbe interactions, despite stronger apparent impacts of modern breeding on potential microbe-microbe interactions. Crucially, rhizobiome differences among genetic groups are strongly shaped by soil management legacy. A G x E interaction negatively impacted modern maize biomass in the organic legacy soil in comparison to teosinte and landrace genotypes, and plant nutrition and biomass were significantly linked to rhizobiome structure. Nonetheless, our analyses do not provide conclusive evidence that the lower relative productivity of modern maize in the organic legacy soil is due to loss of beneficial taxa or N-cycling functions of its rhizobiome, and any extrapolation of these results to performance in agroecosystems should be tested with field studies.

The implications of a G x E interaction in maize-rhizobiome relationships without maladaptation to organic agroecosystems are encouraging. An improved understanding of the underlying mechanisms through host-microbiome GWAS could aid plant breeding programs emphasizing rhizosphere engineering (Dessaux et al., 2016; Ryan et al., 2009) in developing novel maize genotypes that maximize beneficial plant-rhizobiome interactions. Interest is already growing in using wild germplasm to enhance maize productivity (Hake and Richardson, 2019), and including genes related to beneficial rhizobiome interactions

would be a useful extension of these efforts. Such microbiome-based approaches have the potential to improve plant health and productivity, decrease reliance on chemical fertilizer and pesticide inputs, and create more sustainable agroecosystems to feed a growing population.

Funding

This work was supported by the University of California, Davis and the College of Agricultural and Environmental Sciences through a Graduate Scholars Fellowship to JS; the Foundation for Food and Agriculture Research; and the USDA National Institute of Food and Agriculture, Agricultural Experiment Station Project (grant number CA-D-PLS-2332-H to AG).

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

The authors would like to thank Garry Pearson and other members of the Department of Plant Sciences greenhouse administrative staff for technical assistance; Sada Egenriether at University of Illinois for assistance with qPCR; Katherine Dynarski and Caitlin Peterson for valuable reviews; and other members of the Gaudin lab for their contributions. Russell Ranch staff, researchers, and administrators deserve special acknowledgment for providing soil and support.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.soilbio.2020.107794.

Supplementary Table S1
Soil physicochemical properties.

	Conventional	Organic	Analysis Method
Texture	Clay loam	Clay loam	Sheldrick and Wang (1993)
pH	7.015	7.41	U.S. Salinity Laboratory Staff (1954)
% OM	2.57	3.5	Nelson and Sommers (1996)
CEC (meq/100g)	22.2	24.8	Thomas (1982)
% N	0.098	0.175	"AOAC Official Method 972.43, Microchemical Determination of Carbon, Hydrogen, and Nitrogen, Automated Method," 1997
% C	0.985	1.52	"AOAC Official Method 972.43, Microchemical Determination of Carbon, Hydrogen, and Nitrogen, Automated Method," 1997
NH_4^+ (ppm)	3.785	26.23	Hofer (2003)
NO_3^- (ppm)	30.755	38.78	Knepel (2003)
Olsen P (ppm)	20.2	49.7	Olsen and Sommers (1982); Prokopy (1995)
K^+ (ppm)	202.5	337	Thomas (1982)
K^+ (meq/100g)	0.52	0.86	Thomas (1982)
Na^+ (ppm)	41	132	Thomas (1982)
Na^+ (meq/100g)	0.18	0.57	Thomas (1982)
Ca^{2+} (meq/100g)	8.565	10.46	Thomas (1982)
Mg^{2+} (meq/100g)	12.95	12.9	Thomas (1982)

Supplementary Table S2
Genetic material

Group	ID	Source	Era
Teosinte	PI 566688	Mexico	Pre-domestication
	PI 566691	Mexico	Pre-domestication
Landrace	Ames 19897	Mexico	Early domestication
	PI 629258	Mexico	Early domestication
Inbred	B73 (PI 550473)	USA	Parents of modern germplasm
	Mo17 (PI 558532)	USA	Parents of modern germplasm
	OH43 (Ames 19288)	USA	Parents of modern germplasm
Hybrid	322HYB	USA (Pioneer ERA)	Released 1936; double cross hybrid
	354HYB	USA (Pioneer ERA)	Released 1953; double cross hybrid
	3382	USA (Pioneer ERA)	Released 1976; single cross hybrid
	3489	USA (Pioneer ERA)	Released 1994; single cross hybrid
	DKC64-69	USA (DeKalb)	Released 2013; transgenic

Supplementary Table S3
Sources of variation for rhizosphere microbial communities

Prokaryotes					
	Df	SS	*F*	R^2	*P*
Soil legacy	1	0.70	7.78	0.10	0.001***
Genetic group	3	0.40	1.50	0.061	0.001***
Group:genotype	8	0.71	0.98	0.11	0.520
Residuals	54	4.87		0.73	
Total	66	6.69		1	

(*continued on next page*)

Supplementary Table S3 (*continued*)

Prokaryotes					
	Df	SS	*F*	R^2	*P*
Fungi					
	Df	SS	*F*	R^2	*P*
Soil legacy	1	2.21	16.35	0.200	0.001***
Genetic group	3	0.59	1.45	0.053	0.001***
Group:genotype	8	1.09	1.01	0.099	0.388
Residuals	53	7.15		0.648	
Total	65	11.04		1	

Supplementary Table S4
Indicator ASVs

Environment[1]	Kingdom	Phylum	Class	Order	Family	Genus	Species
CL-CM	Bacteria	Actinobacteria	Actinobacteria	Micrococcales	Micrococcaceae	*Arthrobacter*	NA
CL-CM	Bacteria	Actinobacteria	Thermoleophilia	Gaiellales	Gaiellaceae	*Gaiella*	NA
CL-CI	Bacteria	Proteobacteria	Alphaproteobacteria	Rhizobiales	MNG7	NA	NA
CL-CI	Bacteria	Proteobacteria	Gammaproteobacteria	Xanthomonadales	Xanthomonadales_Incertae_Sedis	*Steroidobacter*	NA
CL-CI	Bacteria	Chloroflexi	Anaerolineae	Anaerolineales	Anaerolineaceae	NA	NA
CL-CI	Bacteria	Proteobacteria	Betaproteobacteria	Nitrosomonadales	Nitrosomonadaceae	NA	NA
CL-CI	Bacteria	Planctomycetes	Planctomycetacia	Planctomycetales	Planctomycetaceae	*Pirellula*	NA
CL-CI	Bacteria	Proteobacteria	Gammaproteobacteria	Xanthomonadales	Xanthomonadales_Incertae_Sedis	*Acidibacter*	NA
CL-CT	Bacteria	Proteobacteria	Alphaproteobacteria	Rhizobiales	Bradyrhizobiaceae	NA	NA
CM-CI	Bacteria	Proteobacteria	Betaproteobacteria	Burkholderiales	Oxalobacteraceae	*Massilia*	NA
CM-CI	Bacteria	Proteobacteria	Alphaproteobacteria	Sphingomonadales	Sphingomonadaceae	*Sphingobium*	NA
CM-CI	Bacteria	Proteobacteria	Betaproteobacteria	Burkholderiales	Comamonadaceae	*Caenimonas*	NA
CM-CI	Bacteria	Bacteroidetes	Sphingobacteriia	Sphingobacteriales	Sphingobacteriaceae	*Pedobacter*	NA
CM-CI	Bacteria	Proteobacteria	Alphaproteobacteria	Sphingomonadales	Sphingomonadaceae	*Sphingobium*	NA
CM-CI	Bacteria	Proteobacteria	Betaproteobacteria	Nitrosomonadales	Nitrosomonadaceae	NA	NA
CM-CI	Bacteria	Proteobacteria	Alphaproteobacteria	Rhodospirillales	Rhodospirillaceae	NA	NA
CM-CI	Bacteria	Bacteroidetes	Cytophagia	Cytophagales	Cytophagaceae	*Chryseolinea*	NA
CM-CI	Bacteria	Gemmatimonadetes	Gemmatimonadetes	Gemmatimonadales	Gemmatimonadaceae	NA	NA
CM-CI	Bacteria	Proteobacteria	Alphaproteobacteria	Rhizobiales	Rhizobiales_Incertae_Sedis	*Nordella*	NA
CM-CI	Bacteria	Proteobacteria	Alphaproteobacteria	Sphingomonadales	Sphingomonadaceae	*Sphingomonas*	NA
CM-CT	Bacteria	Proteobacteria	Betaproteobacteria	Burkholderiales	Oxalobacteraceae	*Janthinobacterium*	NA
CM-CT	Bacteria	Bacteroidetes	Cytophagia	Cytophagales	Cytophagaceae	*Rhodocytophaga*	NA
CT	Bacteria	Proteobacteria	Alphaproteobacteria	Caulobacterales	Caulobacteraceae	*Phenylobacterium*	NA
OL	Bacteria	Actinobacteria	Actinobacteria	Corynebacteriales	Mycobacteriaceae	*Mycobacterium*	NA
OM	Bacteria	Acidobacteria	Subgroup_6	NA	NA	NA	NA
OI	Bacteria	Bacteroidetes	Sphingobacteriia	Sphingobacteriales	Chitinophagaceae	*Flavisolibacter*	NA
CL-CM	Fungi	Ascomycota	Sordariomycetes	Glomerellales	Plectosphaerellaceae	*Gibellulopsis*	*piscis*
CL-CM	Fungi	Ascomycota	Sordariomycetes	Hypocreales	Bionectriaceae	NA	NA
CL-CM	Fungi	NA	NA	NA	NA	NA	NA
CL-CT	Fungi	Mucoromycota	Mucoromycetes	Mucorales	Cunninghamellaceae	*Absidia*	*koreana*
CM-CI	Fungi	Ascomycota	NA	NA	NA	NA	NA
CM-CI	Fungi	Ascomycota	Sordariomycetes	Hypocreales	Hypocreales_fam_Incertae_sedis	*Acremonium*	NA
CM-CI	Fungi	Ascomycota	Eurotiomycetes	Chaetothyriales	Herpotrichiellaceae	*Exophiala*	*pisciphila*
CM-CI	Fungi	Ascomycota	Sordariomycetes	Sordariales	Cephalothecaceae	*Phialemonium*	*globosum*
CM-CI	Fungi	Ascomycota	Leotiomycetes	Leotiomycetes_ ord_Incertae_sedis	Pseudeurotiaceae	*Pseudogymnoascus*	*appendiculatus*
CM-CI	Fungi	Ascomycota	Dothideomycetes	Venturiales	Sympoventuriaceae	*Ochroconis*	*tshawytschae*
CM-CI	Fungi	Ascomycota	Sordariomycetes	Hypocreales	Stachybotryaceae	*Sirastachys*	*phyllophila*
CM-CI	Fungi	Aphelidiomycota	Aphelidiomycetes	GS16	NA	NA	NA
CM-CT	Fungi	Mortierellomycota	Mortierellomycetes	Mortierellales	Mortierellaceae	*Mortierella*	*elongata*
CM-CT	Fungi	Ascomycota	Sordariomycetes	Coniochaetales	Coniochaetaceae	NA	NA
CT	Fungi	Ascomycota	Sordariomycetes	Melanosporales	Melanosporaceae	*Melanospora*	*damnosa*
OL	Fungi	Basidiomycota	Agaricomycetes	NA	NA	NA	NA
OL	Fungi	Ascomycota	Eurotiomycetes	Onygenales	NA	NA	NA
OL	Fungi	NA	NA	NA	NA	NA	NA

[1]An environment is defined here as a combination of soil management legacy and single genetic group or pair of genetic groups. NA indicates that the ASV could not be identified at that taxonomic level. C = conventional legacy soil, O = organic legacy soil, T = teosinte, L = landrace, I = inbred, M = modern.

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