New Phytologist

Research

Home-based microbial solution to boost crop growth in low-fertility soil

Meitong Jiang[1,2], Manuel Delgado-Baquerizo[3,4], Mengting Maggie Yuan[5], Jixian Ding[1,2], Etienne Yergeau[6], Jizhong Zhou[7], Thomas W. Crowther[8] and Yuting Liang[1,2]

[1]State Key Laboratory of Soil and Sustainable Agriculture, Institute of Soil Science, Chinese Academy of Sciences, Nanjing 210000, China; [2]University of Chinese Academy of Sciences, Beijing 100049, China; [3]Laboratorio de Biodiversidad y Funcionamiento Ecosistémico, Instituto de Recursos Naturales y Agrobiología de Sevilla (IRNAS), CSIC, Ave Reina Mercedes 10, E-41012 Sevilla, Spain; [4]Unidad Asociada CSIC-UPO (BioFun), Universidad Pablo de Olavide, 41013 Sevilla, Spain; [5]Department of Environmental Science, Policy and Management, University of California, Berkeley, CA 94720, USA; [6]Centre Armand-Frappier Santé Biotechnologie, Institut national de la recherche scientifique, Laval H7V 1B7, Québec, Canada; [7]Department of Microbiology and Plant Biology, Institute for Environmental Genomics, University of Oklahoma, Norman, OK 73019, USA; [8]Department of Environmental Systems Science, Institute of Integrative Biology, ETH Zurich, Zurich 8092, Switzerland

Author for correspondence:
Yuting Liang
Email: ytliang@issas.ac.cn

Received: *7 November 2022*
Accepted: *4 April 2023*

New Phytologist (2023)
doi: 10.1111/nph.18943

Key words: home-field advantage, metagenomic binning, niche structure, rhizosphere microbial community, soil fertility, synthetic microbial community.

Summary

- Soil microbial inoculants are expected to boost crop productivity under climate change and soil degradation. However, the efficiency of native vs commercialized microbial inoculants in soils with different fertility and impacts on resident microbial communities remain unclear.
- We investigated the differential plant growth responses to native synthetic microbial community (SynCom) and commercial plant growth-promoting rhizobacteria (PGPR). We quantified the microbial colonization and dynamic of niche structure to emphasize the home-field advantages for native microbial inoculants.
- A native SynCom of 21 bacterial strains, originating from three typical agricultural soils, conferred a special advantage in promoting maize growth under low-fertility conditions. The root : shoot ratio of fresh weight increased by 78–121% with SynCom but only 23–86% with PGPRs. This phenotype correlated with the potential robust colonization of SynCom and positive interactions with the resident community. Niche breadth analysis revealed that SynCom inoculation induced a neutral disturbance to the niche structure. However, even PGPRs failed to colonize the natural soil, they decreased niche breadth and increased niche overlap by 59.2–62.4%, exacerbating competition.
- These results suggest that the home-field advantage of native microbes may serve as a basis for engineering crop microbiomes to support food production in widely distributed poor soils.

Introduction

Microbial products are considered an environmentally friendly agricultural strategy, potentially promoting soil biodiversity and increasing crop productivity (Chaparro *et al.*, 2012; Jez *et al.*, 2016). Developing environmentally compatible and efficient soil microbial inoculants is critical to boost crop production in a world with a growing human population as well as stresses from climate change and soil degradation (McCarty & Ledesma-Amaro, 2019; Singh *et al.*, 2020). Microbial inoculants generally include potentially beneficial microorganisms with target functional traits in facilitating crop resistance to biotic and abiotic stress (Berg *et al.*, 2017). For example, plant growth-promoting rhizobacteria (PGPR) can promote plant tolerance to drought and salt stress (Sharma *et al.*, 2016; de Vries *et al.*, 2020). Beneficial plant–microbe interactions promote crop growth via associative nitrogen fixation, phosphorus solubilization, and phytohormone regulation (Richardson *et al.*, 2009; Lebeis *et al.*, 2015). However, the efficacy of commercial microbial inoculants remains unreliable due to a lack of assessment of environmental compatibility and in-field performance (Kaminsky *et al.*, 2019), since these commercial products are often applied in diverse environmental conditions to microbial taxa. Hence, one urgent concern is to evaluate the performance of these microbial consortia under varied environmental conditions, for example, soils with different fertility.

Microbial communities could optimize their performance and ecosystem functions at 'home' sites compared with those at 'foreign' sites, referred to as the 'home-field advantage' (Ayres *et al.*, 2009; Li *et al.*, 2017). Since the plant microbiome is particular to the host and soil type (Berg & Smalla, 2009), the success of exotic microbes in establishing in soil and delivering the desired functions is very context-dependent (Hartmann & Six, 2022). Therefore, external inoculants with unstable performance are poorly expected compared with native microbial inoculants. Commercialized microbial inoculants are mostly oversimplistic, comprising a few microbes from nonnative soils. The expectation that these microbial consortia can carry out

desired functions in field conditions often fails to consider metabolic plasticity, microbial interactions, and the fundamental importance of microbial diversity in promoting soil function (Delgado-Baquerizo *et al.*, 2017).

Alternatively, recent studies using synthetic microbial community (SynCom) approaches highlight the benefits of using indigenous microbes for increasing plant productivity and resilience against biotic and abiotic stress through various plant growth-promoting activities (Niu *et al.*, 2017; de Souza *et al.*, 2020). Having coevolved with the plant hosts in native soils under local environmental conditions, mutualistic microbial communities are expected to be highly efficient at supporting plant growth (Rua *et al.*, 2016). Native microbial communities can have long-lasting positive impacts (i.e. legacy effects) on soil functions and plant development (Crowther *et al.*, 2019), particularly in nutrient-limited conditions. However, this advantage may become counterbalanced – or even reversed – by host-specific pathogens in native microbial consortia (Fanin *et al.*, 2021). In particular, the introduction of exotic microbes may have a transient or persistent effect on resident microbes (Mallon *et al.*, 2018; Amor *et al.*, 2020), a phenomenon that remains unpredictable under varied soil types and environmental conditions. Microbial inoculants developed from indigenous beneficial microbes would have a relatively more predictable influence on their original soil environment, thus leading to an agriculturally safer choice. However, few studies have compared the effectiveness and performance of commercial, exotic PGPRs vs native microbial consortia on promoting crop productivity in soils with different fertility.

Here, we evaluated the contribution of native and exotic microbial consortia in promoting maize growth in soils ranging from high to low fertility. We compared the performance of two microbial inoculants, including a 21-species SynCom containing indigenous strains from maize rhizospheres across three typical upland agricultural soils and a microbial inoculant using commercial PGPRs. We hypothesized that native SynCom could rapidly colonize the rhizosphere through adaptation to growing conditions and alleviate plant nutrient stress by providing essential nutrients and phytohormones, especially in low-fertility soils. The impact of PGPRs, however, was context dependent, with exaggerated nutrient competition in low-fertility soils. Our results indicated that home-field advantage drives the positive impact of native SynCom on crop growth in low-fertility soils, guiding SynCom design for further field applications.

Materials and Methods

Research site and sample collection

The field experiment was set up at the Fengqiu National Agroecosystem Field Experiment Station of the Chinese Academy of Sciences (114°24′E, 35°00′N), which is at an altitude of 67.5 m, in Henan Province, China. The experimental site has a semihumid, semiarid warm, and monsoon climate with a mean annual temperature of 13.9°C and precipitation of 605 mm (June–September). Three typical agricultural soils that have been maintained under long-term dryland farming, including Mollisol (derived from Hailun, Heilongjiang Province), Inceptisol (Fengqiu, Henan Province), and Ultisol (Yingtan, Jiangxi Province), were used to set up microplots 1.4 m in length × 1.2 m in width × 1.0 m in depth, which were randomly placed. Mollisol is the world's most fertile, organic carbon-rich, and productive soil type (Wang *et al.*, 2021). Inceptisol has moderate productivity but a low nutritional environment with low organic matter content and available nitrogen and phosphorus (Ge *et al.*, 2008). Ultisol has the lowest fertility among the three soil types, with high acidity, low productivity, and poor organic carbon (Xu *et al.*, 2003). We conducted an NMR analysis to understand the carbon structures in the soil collected from the field trial (Supporting Information Methods S1). The relative contents of the various carbon chemical components were obtained by regional integration of spectral peak curves (Sun *et al.*, 2019). Each microplot was fenced by 20-cm cement mortar brick walls and underlaid by quartz sand (3 cm thick). Each soil had six biological replicates.

Zhengdan 958, a commercial maize hybrid, was bred by Institute of Food Crops, Henan Academy of Agricultural Sciences (http://www.hnagri.org.cn/liangshi/index.html). It is publicly available with a large planting area in China. The maize was planted in early June annually since 2006, and management measures were only taken for weeding by hand. Grain yield, aboveground biomass, and nutrient content, including total carbon, nitrogen, phosphorus, and potassium, in seed and straw were measured immediately after harvest. Rhizosphere soil samples were collected as follows: The loosely attached soil on the roots was removed with gentle shaking (shake-off method), and soils within *c.* 1–4 mm of the root were collected as rhizosphere soils, sealed in a polyethylene wrapper, stored on ice, and transported to the laboratory. Rhizosphere soils for geochemical analyses, including soil organic matter, total nitrogen, nitrate and ammonium nitrogen, available nitrogen, total phosphorus, available phosphorus, total potassium, and available potassium, were stored at 4°C (Methods S2), and those for DNA extraction were stored at −80°C. These soil samples were then used to investigate the diversity and composition of bacterial communities associated with the maize rhizosphere in three types of soils.

Bacterial identification and synthetic microbial community preparation

Maize rhizosphere samples from the three agricultural soils were used for the isolation of culturable bacteria using the standard serial dilution culture method (Methods S3). Different gradients of soil suspensions were smeared onto four different types of nutrient media for isolation and culture (Table S1). After incubation, single colonies were picked based on different morphologies and were restreaked at least twice to ensure purity. Pure cultures of the strains were cultured overnight in 50 ml Luria-Bertani (LB) medium. A total of 5 ml of each bacterial suspension were used for complete 16S rRNA sequencing performed by Personalbio (Shanghai, China). Therefore, 47 bacterial strains were obtained. Single colonies were picked and preserved on LB plates at 4°C. The bacterial 16S rRNA gene was amplified using primers 27F (5′-AGAGTTTGATCCTGGCTCAG-3′) and 1492R

(5′-CTACGGCTACCTTGTTACGA-3′). These strains were identified by blasting against the EzBioCloud 16S database (Methods S4; Yoon *et al.*, 2017). Finally, 21 unique indigenous species that commonly existed across three soil types were used to design a native microbial inoculant, referred to as SynCom (Table S2).

When preparing SynCom, the OD_{600} value of each bacterial suspension was controlled between 0.6 and 0.8 during the exponential growth phase. The cells of the culture were then collected by centrifugation at 2940 ***g*** for 10 min at 4°C and diluted to *c.* 10^8 cells ml^{-1}. The cell suspension of each strain was mixed in 50 ml of 1× phosphate-buffered saline (PBS) in an equal volume to prepare bacterial suspensions of the 21 different species.

Surface sterilization and germination of maize seeds

The surface sterilization and germination of maize seeds (Zhengdan 958) followed the standard protocols of Niu *et al.* (2017). Briefly, the seeds were immersed in 70% (v/v) ethanol for 3 min, then in 5% (v/v) sodium hypochlorite for 3 min, and finally rinsed with sterile distilled water three times. The surface sterilization surface-sterilized seeds were placed in a Petri dish (9 cm diameter) filled with 7 ml of sterile water and incubated at 30°C in the dark for 50–55 h until the seeds germinated. After incubation for 24 h, 100 µl of water was taken from the Petri dish and spread onto tryptone soya agar (TSA) plates, which were then incubated at 30°C to check for contamination.

Glasshouse experiment for maize plants with different microbial inoculants in soil

We conducted a glasshouse experiment under different fertility conditions to compare the effectiveness of native vs commercialized microbial inoculants in facilitating crop growth. The native microbial inoculant, SynCom, was derived from common species across Mollisol, Inceptisol, and Ultisol, while the commercial inoculant was composed of four model PGPRs from strain banks that have been reported to be applied in agricultural practice. They were selected with target traits, including *Rhizobium radiobacter* (J. M. Young), nitrogen fixation (Guo *et al.*, 2017); *Burkholderia cepacian* (Eiko Yabuuchi), phosphorus solubilization and antifungal activity (Zhao *et al.*, 2014); *Arthrobacter ilicis* (Collins M.D.), IAA production (Chou & Huang, 2005); and *Stenotrophomonas rhizophila* (Arite Wolf), antimicrobial compound production (Ryan *et al.*, 2009). The bacterial suspension of four PGPRs was prepared following the same steps as SynCom. SynCom + PGPRs were prepared with a 1 : 1 bacterial suspension of SynCom and PGPRs. Thus, four groups were included in the full-factor experimental design, including the SynCom, PGPRs, SynCom + PGPRs, and control treatments (without microbial inoculation). Note that this study calls any species that enters a habitat when it is not a resident taxon an 'exotic' species. This refers to the microbes selected based on available research, which have been well studied and shown to have a variety of essential functions that contribute to the maintenance of plant health.

Surface-sterilized and germinated maize seeds with primary roots of 1–2 cm were transplanted into the soil. Microbial inoculation was carried out in the V3 growth period. The microbial inoculum (50 ml) was poured into the soil near the growing roots of each seedling. The glasshouse experiment was set up with four replications for each treatment under three soil types. No nitrogen or phosphorus fertilizers were applied except for regular watering. The glasshouse experiment lasted for 59 d with a natural light cycle. From Day 29, the height and chlorophyll content of maize plants were measured every 7 d, and photographs were taken every 14 d. Plant tissues were removed from the soil at 59 d (V8 growth phase) after transplantation, and rhizosphere soil samples were harvested and stored at −80°C for microbiome analysis. Subsequently, physiological indicators such as plant height, chlorophyll content, and root weight were measured. The indole-3-acetic acid (IAA) concentration of rhizosphere microbial communities was determined by means of the Salkowski reagent method (Methods S5; Sarwar & Kremer, 1995).

Plant growth promotion test on axenic maize seedlings

To examine the plant growth-promoting effects of microbial inoculation in the absence of different soil matrixes, maize seedlings were grown in sterile ½-strength Murashige & Skoog agar in double-tube chambers (Niu *et al.*, 2017). Before the experiment, the rhizosphere soil suspension for inoculation was prepared by mixing 2 g of frozen rhizosphere soil in 20 ml of 1× PBS buffer, vortexing for 2 min, and then centrifuging for 6 min at 750 ***g*** at 30°C. All bacterial strains were propagated in 25 ml tryptic soy broth (TSB) medium for 2 d at 30°C. Each bacterial fermentation broth was centrifuged at 4000 ***g*** for 8 min and resuspended in rhizosphere soil suspension with the OD_{600} adjusted to 0.5 (*c.* 10^8 cells ml^{-1}). Six surface-sterilized and germinated maize seeds were soaked in soil suspension with or without microbial inoculations for 1 h. Sterile maize seedlings were used as bacteria-free controls. Thus, 13 groups were designed for this experiment, including three soil suspensions with or without microbial inoculations (SynCom, PGPRs, and SynCom + PGPRs) and axenic control treatments. The maize seedlings were placed in a plant growth chamber under the following conditions: 16 h : 8 h, light (day) : dark (night), 30°C, and relative humidity of 54%. Plants were photographed every 5 d and harvested from each treatment on day 15. Maize growth was evaluated by measuring the length and fresh weight of shoots and roots, as well as the plant height and chlorophyll content of plants.

Additionally, since the 21-species SynCom (S21) was taxonomically redundant, we downsized the synthetic community to 12 species (S12) at the genus level and 4 species (S4) at the order level (Table S2). The other 4-species SynCom (SF4) was designed to be similar to PGPRs at both taxonomic and functional levels. For each treatment, four surface-sterilized maize seedlings were used, and the experiments were performed under the same conditions for 10 d.

Measurements of the colonization of the microbial inoculants

To investigate the successful colonization of SynCom members in the rhizosphere under glasshouse conditions, we intended to track individual SynCom members through 16S rRNA qPCR and correlation analysis. The abundance of SynCom members was measured by qPCR using rhizosphere soil samples of the control group (without microbial inoculation) and SynCom treatment. Bacterial DNA was extracted using the TIANamp Bacteria DNA Kit (Tiangen, Beijing, China) according to the manufacturer's instructions. qPCR was performed on an ABI3730-XL (Applied Biosystems, Waltham, MA, USA) using TOROGreen® qPCR Master Mix (QST-100; Toroivd, Phoenix, AZ, USA) with the following cycle conditions: 40 cycles of 95°C for 15 s, 55°C for 15 s, and 72°C for 45 s. The specificity of the primers designed in this study and the quality of the PCR products were determined by gel analysis. All qPCRs were performed in triplicate. For the 16S rRNA correlation analysis, the representative ASVs of each species were identified from the microbiome sequencing data of the glasshouse by BLAST analysis. The matching ASVs displayed > 98.7%, 99%, and 100% sequence identity with the sequence of the full length of the 16S rRNA gene of each strain were kept as measurable, highly matched, and best-matched ASVs, respectively. The abundance of SynCom members and PGPRs at the genus level counted all measurable ASVs.

Rhizosphere microbiome analyses

For rhizosphere samples collected from the field, a high-throughput absolute quantification sequencing method was employed to obtain an accurate and reliable absolute abundance of soil bacteria. Genomic DNA from 0.5 g of rhizosphere soil was extracted with the HiSeq Reagent Kit (Illumina, San Diego, CA, USA) according to the manufacturer's instructions. The quality and quantity of the DNA were assessed by nanodrop and gel electrophoresis. The V4–V5 regions of the 16S rRNA gene were amplified using primers 515F (5′-GTGCCAGCMGCCGCGG-3′) and 907R (5′-CCGTCAATTCMTTTRAGTTT-3′). The spike-in sequences involved conserved regions identical to selected natural 16S rRNA genes and artificial variable regions, working as internal standards and allowing absolute quantification across samples (Mou *et al.*, 2020). The PCR procedure involved predenaturation at 94°C for 2 min, denaturation at 94°C for 30 s, annealing at 55°C for 30 s and 72°C for 60 s (a total of 25 cycles), and extension at 72°C for 10 min. Sequencing was performed using Illumina NovaSeq 2 × 250 bp (Genesky Biotechnologies Inc., Shanghai, China; Methods S6). TRIM GALORE (http://www.bioinformatics.babraham.ac.uk/projects/trim_galore/) and FLASH2 were used to process the final V4–V5 tag sequences. The spike-in sequences were filtered out, and reads were counted. The standard curve of spike-in sequences was generated for each sample, and the sequenced microbial DNA was quantified and estimated in reference to the representative standard curve. Sequences were assigned to each sample based on its unique barcode.

For rhizosphere samples from the glasshouse experiment, the relative quantification sequencing method was employed (Methods S7). The V4–V5 region of the bacterial 16S rRNA was chosen for amplification with 515F and 907R and sequenced on the Illumina NovaSeq platform. The relative quantification of 16S rRNA was carried out as described previously without spike-in sequences.

High-throughput sequencing and genome binning

Whole metagenomic shotgun sequencing was performed using the Illumina HiSeq platform and the 2 × 150 bp paired-end method (Methods S8). Clean reads were generated and assembled into scaffolds by SOAPDENOVO (v.1.05) based on De-Brujin graph construction. Open reading frames (ORFs) were predicted and further functionally annotated by BLAST 2.2.28+ against KEGG (Kyoto Encyclopedia of Genes and Genomes). Assembled scaffolds were then grouped into metagenomic bins using METAWRAP (Uritskiy *et al.*, 2018). Genome bins were assessed for estimated completeness and contamination markers by CHECKM (Parks *et al.*, 2015). The completeness and contamination can be estimated by the number of single-copy genes that the genome of the bin's taxonomy is expected to have. Genome bins were filtered to > 50% completeness and < 10% contamination. Binned genomes were submitted to RAST for classification and annotation of nutrient metabolism, plant hormone synthesis pathways, bacterial motility, and chemotaxis (Aziz *et al.*, 2008; Overbeek *et al.*, 2014; Brettin *et al.*, 2015). The phylogenetic tree of *rpoD* genes identified from each genome was constructed using MEGAX software.

Metabolic diversity of the microbial inoculants (Biolog EcoPlate™)

Since the glasshouse experiment was set up under different soil fertility conditions, the capability of SynCom and PGPRs to utilize carbon sources was tested by Biolog EcoPlate™, containing 31 kinds of carbon sources. The carbon sources were defined as carbohydrates ($n = 10$), carboxylic acids ($n = 7$), amino acids ($n = 6$), polymers ($n = 4$), phenolic compounds ($n = 2$), and amines ($n = 2$) (Choi & Dobbs, 1999). For each carbon source, $n = 3$ replicates in Biolog plates. For each treatment, $n = 4$ replicates of Biolog plates. The mixed bacterial suspensions were prepared as described previously and diluted to $OD_{600} = 0.05$. Then, 150 µl of the mixed bacterial suspensions was added to each microtiter well of the Biolog plates using an eight-channel pipette, and four replicates were set for each treatment. The plates were incubated at 30°C for 96 h, and the OD_{590} was measured every 12 h during incubation. Biolog plates use a tetrazolium violet redox dye to monitor cell respiration, and oxidation of the nutrients will lead to respiration, resulting in the formation of a purple color in the well. Water without any carbon source served as a control in triplicate (Bochner, 2009).

The collected data were then used to analyze the average well color development (AWCD) and the preference of the bacterial community for various carbon sources. $AWCD = \Sigma(Ci - R)/n$

where Ci is the difference between the absorbance values at 590 for each well, R is the absorbance value of the control well, and n is the total number of carbon sources (Garland, 1996). The AWCD value is an indicator of the ability of microorganisms to utilize carbon sources and the metabolic activity of microorganisms, as well as the growth rate of mixed bacterial cultures in wells. Principal component analysis (PCA) was used to characterize the functional structure of the bacterial community by community substrate utilization patterns. The microbial growth curve model based on the AWCD was constructed by ORIGIN 2019b.

Data processing and statistical analysis

The molecular ecological networks (MENs) were constructed using a random matrix theory (RMT)-based approach (http://ieg4.rccc.ou.edu/mena/), where the abundance data obtained from absolute quantitative sequencing were selected unless they occurred in > 80% of the samples. The network was constructed using Pearson's correlation analysis. Network parameters such as R^2, average path length, average connectivity, average clustering coefficient, and modularity were obtained by the MENA method; the network was visualized using GEPHI 0.9.2.

The analysis of soil physicochemical properties, microbiome statistical analyses, and the experimental data was performed using R 4.2.1, and plots were constructed using the GGPLOT2 package. All data were tested for normal distribution before conducting statistical analyses. A nonparametric Mann–Whitney or paired Wilcoxon rank-sum test was used for nonnormal data. Multiple comparisons were performed with nonparametric Nemenyi tests by the PMCMRPLUS packages (https://cran.r-project.org/web/packages/PMCMRplus/index.html). All samples were rarefied to 4000–6000 observations per sample. The alpha (Shannon and Chao1 indexes) and beta diversity of microbial community analyses were performed using the R package VEGAN (https://cran.r-project.org/web/packages/vegan/index.html). The beta-diversity analysis was conducted using Hellinger-transformed data. Analyses of niche breadth (Levins' niche breadth) and niche overlap (Levins' niche overlap) were performed by the SPAA package (https://cran.r-project.org/web/packages/spaa/index.html).

Results

Distinct microbiota in maize rhizospheres across soil types of different fertility

The diversity and composition of field maize rhizosphere bacterial communities in three types of soils were characterized by gradient spike-in absolute quantification sequencing of 16S rRNA (Table S3). The rarefaction curves show good coverage of the diversity (Fig. S1a). The Shannon diversity index of Mollisol and Inceptisol was much higher than that of Ultisol ($P < 0.05$; Fig. S1b), while the Chao1 index was the highest in the Inceptisol followed by Mollisol and Ultisol ($P < 0.05$; Fig. S1c). Redundancy analysis indicated that the soil type explained most of the variation in the soil microbial groups (Fig. S1d). The dominant genera were *Gp6*, *Gaiella*, and *Gp4* in Mollisol; *Nitrososphaera*, *Gp4*, and *Gp6* in Inceptisol; and *Nocardioides*, *Gaiella*, and *Arthrobacter* in Ultisol (Fig. S2). In addition, Mollisol soil showed high soil fertility, while Inceptisol and Ultisol soils were low-fertility soils according to the molecular composition of soil organic matter and nutrient contents, such as total nitrogen, total phosphorus, available nitrogen, and available phosphorus (Fig. S3; Table S4).

Design of native SynCom and its growth-promoting effects

There were 47 bacterial isolates obtained using four different nutrient media from the rhizosphere soil samples (Table S2). Twenty-one unique species commonly existed in the three soils belonging to the most abundant taxa at the order level (Figs 1a, S4). These species were reported to have plant beneficial capacities except for *Sphingomonas desiccabilis*, which has been reported to be isolated from biological soil crusts (Reddy & Garcia-Pichel, 2007). Thus, we used these 21 culturable strains to construct a native SynCom.

In the glasshouse experiment with SynCom, we found that the plant promotion effect of SynCom varied among fertility conditions (Fig. 1b,c). Consistently, during the maize development stages during V4–V8 at Days 35, 42, and 56, SynCom inoculation increased the chlorophyll content significantly by 24–35% ($P < 0.05$) in Ultisol, followed by Inceptisol (18–27%, $P < 0.05$) and Mollisol (1–3%, $P > 0.05$) compared with the uninoculated control. Plant height in Inceptisol showed an obvious increase with SynCom inoculation on Days 35 (67%, $P < 0.001$) and 56 (36%, $P < 0.001$). Meanwhile, plant height increased by 23–38% ($P < 0.05$) in the Ultisol and 9–21% ($P > 0.05$) in the Mollisol.

Potential functional traits of the native microbial community

The metagenomes of rhizosphere soil samples were sequenced to assess the composition and function of the original soil microbial community at 'home' sites (Table S5). The KEGG level 3 pathways were enriched in carbohydrate and amino acid metabolism in all soil samples (Fig. S5a). The metagenomes were then assembled to retrieve draft population genomes from the soil. The phylogeny of each scaffold was annotated at the family level, except for bin.6 at the order level (Table S6). A total of 27 bins were obtained with completeness > 50%. Six genomes showed < 5% contamination and were selected as high-quality genomes to annotate potential genomic functions (Fig. S5b). They belonged to Micrococcaceae, Conexibacteraceae, Rhizobiaceae, and Xanthomonadaceae, accounting for 9.5%, 4.2%, 6.8%, and 5.7% of the abundance at the family level, respectively. Burkholderiales accounted for 18.72% in abundance at the order level. The absolute abundances of Micrococcaceae and Rhizobiaceae were the highest in the Ultisol (Fig. 2a).

Subsequently, the high-quality assembled genomes were annotated by the RAST automated platform and were found to be related to nitrogen metabolism, the TCA cycle, cellular

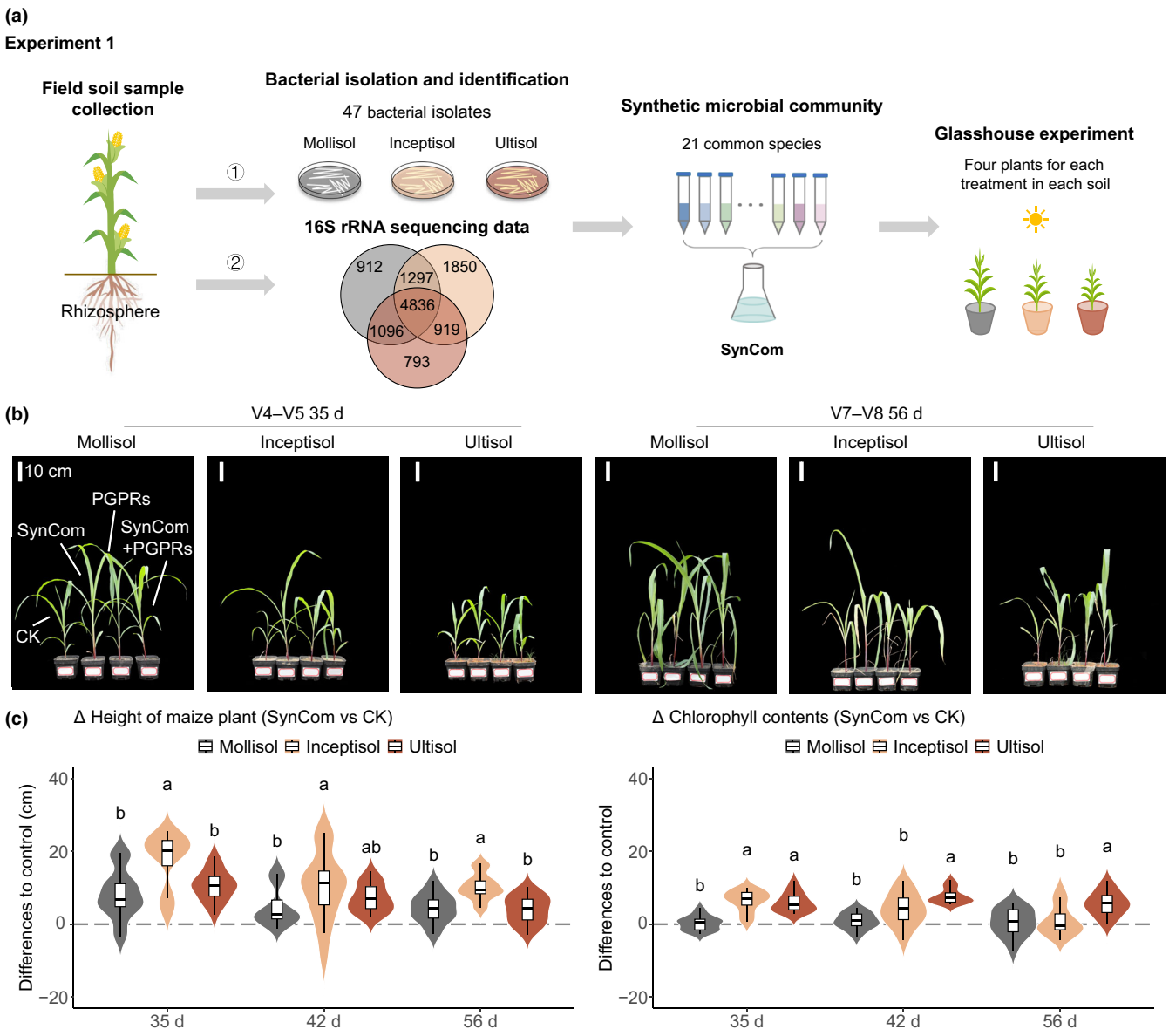

Fig. 1 Experimental glasshouse design and maize growth with synthetic microbial community (SynCom) inoculation. (a) Maize rhizosphere samples from the three agricultural soils were used for the isolation of culturable bacteria (①). Forty-seven bacterial isolates were obtained, and 21 unique species were identified as common species across the three soil types, Mollisol, Inceptisol, and Ultisol, as shown in the Venn diagram (②). Each strain was cultured independently and combined in equal proportions to create a native SynCom. Maize seedlings at the V3 growth stage were transplanted into soils with SynCom inoculation, and each treatment had four independent biological replications. The experiment ended at the V8 growth stage. (b) Maize (Zhengdan 958) phenotype with microbial inoculations at 35 d (V4–V5 stage) and 56 d (V7–V8 stage) in Mollisol, Inceptisol, and Ultisol. Bars, 10 cm. (c) Soil plant analysis development (SPAD) value of leaves and plant height between the SynCom treatment and control check (CK) at different developmental stages (35, 42, and 56 d). The symbol of Δ represents the differences between inoculated and inoculated treatments. The different letters in (c) indicate significant differences ($P < 0.05$) using multiple comparisons of nonparametric tests (Nemenyi test). Four biological replicates of maize plants were evaluated. For the SPAD value, each plant was measured three times. In violin plots, the horizontal bars represent medians. The tops and bottoms of the boxes show the 75th and 25th percentiles, respectively.

chemotaxis, oxidative stress, and biosynthesis of plant growth hormones, such as IAA production (Fig. 2b). Some of the genomes harbored pathways for assimilatory nitrogen reduction (*nirA*, *nirB*) and ammonification (*ure*). The inorganic phosphorus transporter gene (*pst*) with high affinity under low phosphorus conditions was found in all genomes. Tryptophan, the major precursor for IAA biosynthesis, is biosynthesized via the tryptophan operon (*trp*), identified in all assembled genomes. The indole-3-pyruvate (IPyA) pathway of bacterial auxin biosynthesis was found in the complete metabolic pathway of the bin.9 (Micrococcaceae), and bin.9 could produce IAA through the tryptamine (TAM) pathway.

Putative rhizosphere microbial networks were investigated using random matrix theory-based molecular ecological network

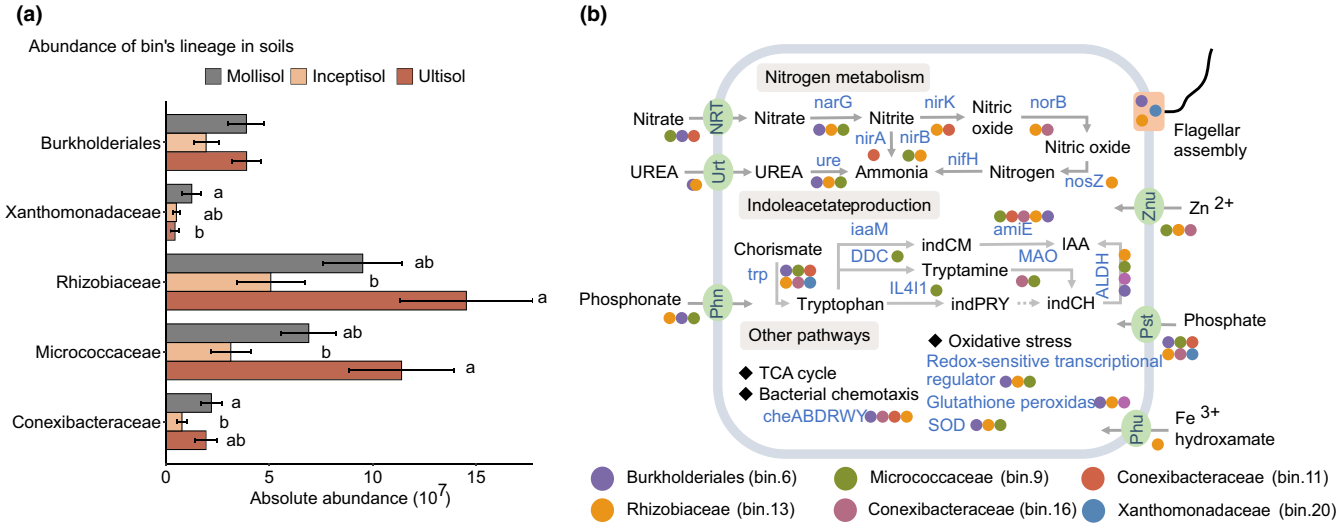

Fig. 2 High-quality genomes retrieved from soil metagenomes. (a) Absolute abundances of bin lineages across different soils. Data were obtained by absolute quantitative sequencing. The different letters in (a) indicate significant differences ($P < 0.05$) using multiple comparisons of nonparametric tests (Nemenyi test). Nonsignificant differences were not labeled. Data represent the means ± SE. (b) High-quality genome bins of the native microbial community (completeness > 50%, contamination < 5%) were indicative of metabolic flexibility and the potential for phytohormone production. Selected metabolic pathways, including nitrogen metabolism and indole acetic acid (IAA) production, were represented by the name of the gene known to encode the protein enzyme by searching predicted proteins against the KASS database. Other related cellular activities are listed. Pathways are displayed only if all or most genes of an operon involved in the same pathway/process are detected as present; if not, dotted lines are used. Colored circles alongside genes indicate that the bin assigned to that color (see key below) encoded the gene. IAA, indoleacetate; indCH, indole-3-acetaldehyde; indCM, indole-3-acetamide; indPRY, indolepyruvate; SOD, superoxide dismutase.

analysis (Fig. S6a). The main modules showed close relationships with maize straw and grain weight (Fig. S6b–d). The Inceptisol dominant module (Module #2) was positively and strongly correlated with seed and straw nitrogen content and seed phosphorus content. The Ultisol dominant module (Module #4) showed a similar correlation with seed carbon and phosphorus content, as well as biomass. Community assembly modules of resident taxa in low-fertility soils strongly correlated with crop yield, suggesting the natural advantage of resident microorganisms in promoting plant growth under stress conditions.

Fertility-dependent promotion efficiency of microbial inoculants

To further validate the relative effects of the native vs exotic microbial inoculants, we selected four commercial PGPRs that have similar plant growth-promoting properties as the native communities, including *R. radiobacter*, nitrogen fixation (Rasulov *et al.*, 2020); *B. cepacia*, phosphorus solubilization and antifungal activity (Zhao *et al.*, 2014); *A. ilicis*, IAA production (Chou & Huang, 2005); and *S. rhizophila*, antimicrobial compound production (Ryan *et al.*, 2009; Fig. 3a). We compared the effects of inoculating native SynCom, PGPRs, and SynCom + PGPRs to control check (CK) to quantify the performance of microbial inoculants under different fertility conditions. The glasshouse experiments showed that the impact of microbial inoculants was fertility dependent. The plants with SynCom inoculation were consistently and significantly higher than those with PGPRs and SynCom + PGPRs inoculants in the low-fertility soils Inceptisol and Ultisol (Fig. S7). Conversely, the plant grew better with PGPR inoculation under high-fertility conditions (Fig. 3b). Moreover, SynCom enhanced the secretion of IAA by rhizosphere microorganisms in low-fertility soils (Figs 3c, S8), a phytohormone that stimulated plant growth and development (Keswani *et al.*, 2020).

We questioned whether the low diversity in PGPRs resulted in the low metabolic activity of the PGPRs, making them less effective than SynComs in low-fertility soils. Unexpectedly, fast-growing PGPRs showed higher carbon metabolic capacity and metabolized wider carbon sources, including carbohydrates, amino acids, amines, and polymers (Fig. S9a,b; Table S7). However, SynCom showed different metabolic preferences for a few amino acids, carboxylic acids, and carbohydrates compared with PGPRs (Fig. S9c,d). Furthermore, genomic information obtained from the NCBI database indicated a diverse metabolic potential in exotic PGPRs for amino sugars, oligosaccharides, organic acids, sugar alcohols, monosaccharides, and polysaccharides (Fig. S9e). These results suggested that in addition to providing essential nutrients and IAA for plants, there could be other crucial factors influencing the efficacy of SynCom in stimulating plant growth and health in low-fertility soils.

SynCom colonization and dynamics of niche structure

With the fully sequenced 16S rRNA gene, the SynCom strains could be matched to ASVs from the glasshouse rhizosphere community survey, which indicated strain presence and relative abundance. The ASVs with > 98.7% sequence identity to any of the SynCom strains were considered targeted ASVs. The correlation analysis showed that there were 12 best-matched ASVs (100%

New Phytologist

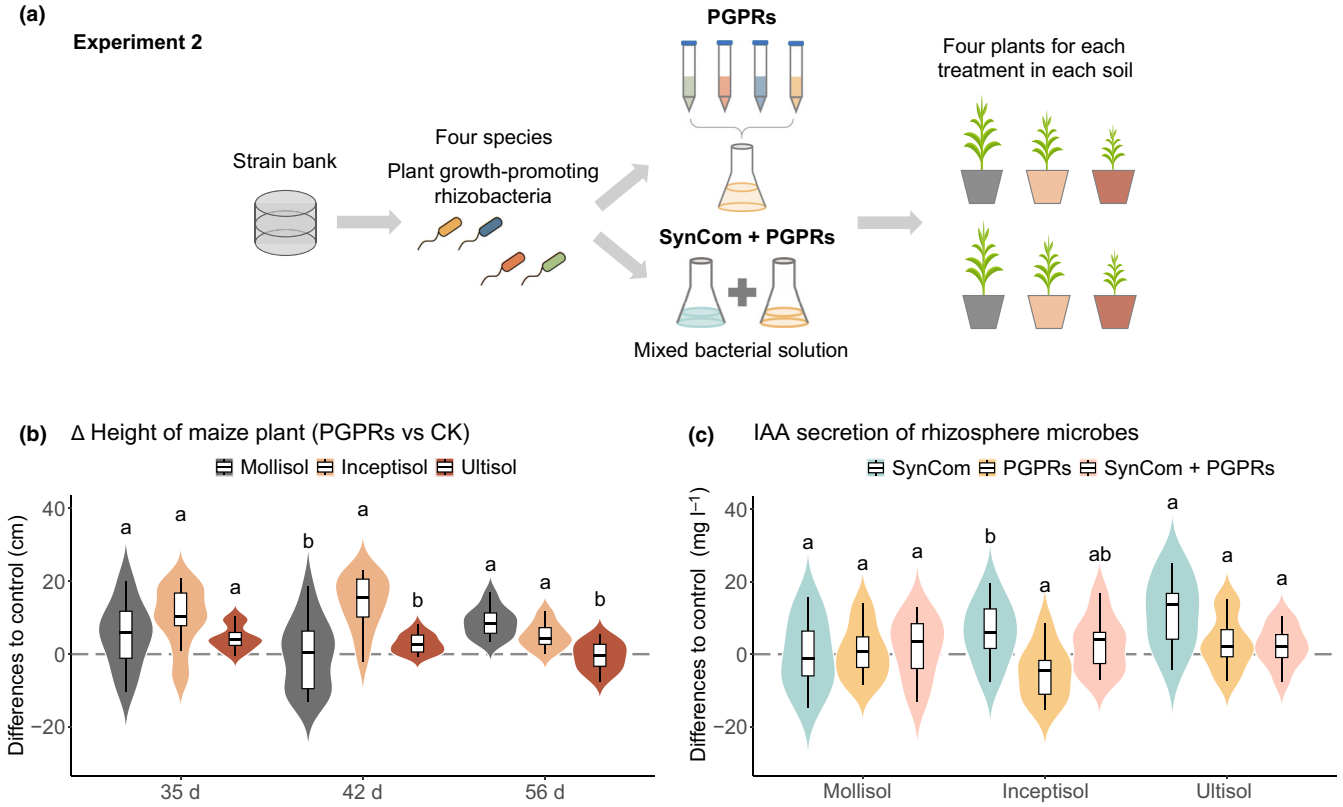

Fig. 3 (a) Experimental design and maize growth with plant growth-promoting rhizobacteria (PGPR) inoculation. Four model PGPR selected from strain banks were derived as commercial PGPRs. Green, *Rhizobium radiobacter*; red, *Stenotrophomonas rhizophila*; blue, *Burkholderia cepacia*; yellow, *Arthrobacter ilicis*. Each strain was cultured independently and combined in equal proportions. Maize seedlings at the V3 growth stage were transplanted into soils with different microbial inoculations, and each treatment had four independent biological replications. The experiment ended at the V8 growth stage. (b) Plant height of maize between the PGPR treatment and control check (CK) at different developmental stages (35, 42, and 56 d). Four biological replicates of maize plants were evaluated. The symbol of Δ represents the differences between inoculated and inoculated treatments. (c) Secretion of IAA by rhizosphere microorganisms with different microbial inoculations. Three rhizosphere soil samples were measured. The different letters in (b, c) indicate significant differences ($P < 0.05$) using multiple comparisons of nonparametric tests (Nemenyi test). In violin plots, the horizontal bars represent medians. The tops and bottoms of the boxes show the 75th and 25th percentiles, respectively.

sequence identity) and 3 highly matched ASVs (99% sequence identity; Table S2). At the species level, the relative abundances of ASV127 (*Pseudomonas* spp.), ASV1479 (*Pseudomonas aeruginosa*), ASV176 (*Klebsiella* spp.), ASV30 (*Serratia marcescens*), and ASV60 (*Pseudomonas geniculata*) significantly increased in low-fertility soils (Fig. S10). The relative abundances of ASV127, ASV1479, ASV176, and ASV60 were significantly higher in high-fertility soils. The Shannon index of rhizosphere microbial communities with SynCom inoculation expressively increased in the Ultisol (Fig. 4a; Table S8). At the genus level, out of 11 relevant genera of SynCom, including all targeted ASVs, the richness of six genera was considerably increased in Ultisol (Fig. 4b). However, neither the alpha diversity of the rhizosphere microbial community nor the richness of relevant genera corresponding to the four PGPRs varied after PGPRs inoculation (Fig. 4a,c).

Although it is difficult to definitively distinguish the inoculated species from the natural microbiome through 16S rRNA gene surveys in nonsterile substrates, such as soils, we managed to track 16 individual members of the SynCom through 12 primer pairs (Fig. S11a; Table S9). A7, A8, A9, and C8 shared the same primers, which are not described below. In particular, the relative abundances of *Acinetobacter pittii* (C15), *Bacillus cereus* (R5), *Enterobacter* spp. (R6 and C5), and *S. desiccabilis* (X2) were significantly increased in the Ultisol (Fig. S11b). *Pseudomonas koreensis* (R9), *Chryseobacterium cucumeris* (R11), and *S. desiccabilis* (X2) were notably enriched in Inceptisol, while *Enterobacter* spp. (R6 and C5), *Lysinibacillus macroides* (C6), and *B. cereus* (R5) were enriched in Mollisol. Taken together, these results supported that some bacterial strains in SynCom were able to colonize the rhizosphere in low-fertility soils.

We found that the microbial inoculations had no influence on the soil microbial community (Table S10). Hence, we further explored the changes in niche breadth at the community level induced by microbial inoculation. The niche breadths of the microbial community with SynCom inoculation were consistently greater than those with PGPRs ($P < 0.001$; Fig. S12a–c). In line with the community-level results, more ASVs (46.7–50.1%) increased their niches in low-fertility soils after SynCom inoculation than decreased their niches (40.1–43.7%; Fig. S12b, c). This indicated that species with wider niche breadth became more competitive, especially under low resource availability. By contrast, after PGPRs inoculation, more ASVs decreased their

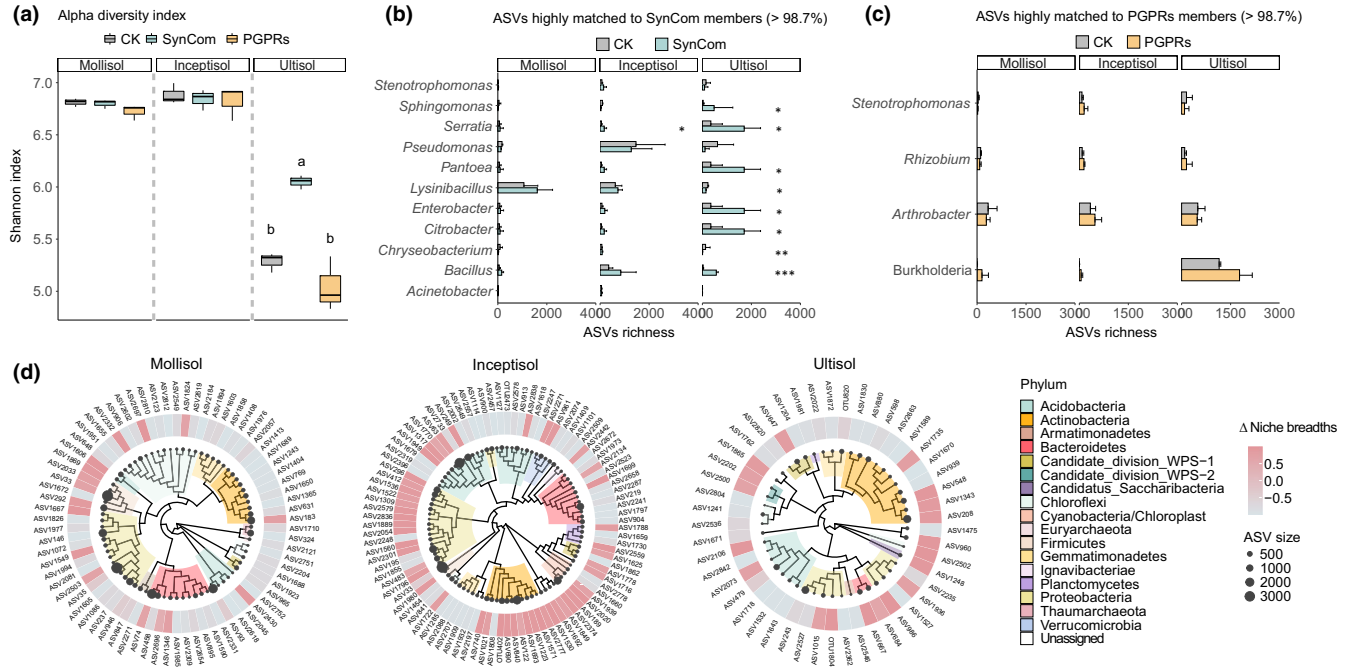

Fig. 4 Colonization of synthetic microbial community (SynCom) strains and dynamics of niche structure. (a) Shannon diversity of microbial communities in Mollisol, Inceptisol, and Ultisol after inoculation with SynCom and plant growth-promoting rhizobacterias (PGPRs). Three rhizosphere soil samples were measured. In box plots, the horizontal bars represent medians. The tops and bottoms of the boxes show the 75th and 25th percentiles, respectively. The different letters indicate significant differences ($P < 0.05$) using multiple comparisons of nonparametric tests (Nemenyi test). Nonsignificant differences were not labeled. (b, c) Relative abundance of ASVs highly matched to (b) SynCom and (c) PGPRs. The representative sequence of each ASV displays > 98.7% sequence identity with the sequence of the full length of the 16S rRNA gene of each strain. The error bar represents the SD. Statistical analyses were performed by a paired Wilcoxon rank-sum test: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. (d) Changes in niche breadths ($P < 0.05$) with PGPR inoculation compared with control check (CK). The phylogram was constructed using the neighbor joining (NJ) method and was colored at the phylum level. The relative abundance of bacterial taxa is shown in the 16S rRNA phylogenetic tree represented by the size of node.

niche breadth in all soils (Figs 4d, S12a). Moreover, the niche overlap of the ASVs with significantly increasing niches ($P < 0.05$) was calculated. The proportions of ASV pairs with increased and decreased niche overlaps tended to be balanced after SynCom inoculation, which was consistent across all soils (Fig. S12d). However, 62.4% and 59.2% pairs of ASVs presented significantly higher niche overlap levels ($P < 0.05$) in the low-fertility soils Inceptisol and Ultisol after PGPR inoculation, respectively (Fig. S12e), which reflected a sharp competition in the rhizosphere community (Pianka, 1974).

The dependence of SynCom efficiency on resident microbiota from low-fertility soil

To further assess the fertility-dependent plant growth-promoting effects of microbial inoculation, we carried out a plant growth promotion test for the 21-species SynCom and the 4-species PGPRs in the absence of soil matrixes on axenic maize seedlings (Fig. 5a,b). We maintained a simplified but representative natural microbial community using a rhizosphere soil suspension. We found that native SynCom significantly promoted maize seedling growth at 15 d in low-fertility soil, as indicated by the increased chlorophyll content, plant height, root weight, and root : shoot ratio of fresh weight (Fig. 5c). In particular, the root : shoot ratio increased by 78–121% ($P < 0.001$) with SynCom and 23–86% ($P < 0.01$) with PGPRs compared with the noninoculated control. A higher root : shoot ratio is an important morphological trait to support crop structure and enhance potential grain yield under nutrient-limited conditions, such as drought, low nitrogen, and phosphorous availability (Anderson, 1988; Liu *et al.*, 2004; Chen *et al.*, 2022). Meanwhile, the differential effect sizes showed that the interaction of SynCom with resident microbial communities from low-fertility soils resulted in better growth promotion than PGPRs (Fig. S13). However, PGPRs interacting with the microbial community from high-fertility soil promoted better plant growth, such as root weight.

To test whether native SynCom performed better than PGPRs merely because of its higher microbial diversity, we prepared inoculants containing subsets of SynCom with only 12 and 4 species (S12, S4, and SF4, see the Materials and Methods section). With decreased taxonomic diversity from SynCom to S12 and S4, there was a decreasing trend but no significant difference in their effect on promoting root development at 10 d in low-fertility soil (Fig. S14). Notably, SF4, designed to be similar to PGPRs at both taxonomic and functional levels, including *B. cereus* (phosphorus solubilization), *Lysinibacillus macrolides* (nitrogen fixation), *Stenotrophomonas maltophilia* (IAA production and antimicrobial activity), and *P. koreensis* (antifungal activity), did not outperform PGPRs in high-fertility soil or SynCom in low-fertility soil in promoting root length and root weight (Fig. S14). These findings demonstrated that the higher diversity of SynCom than PGPRs alone could not fully account for its

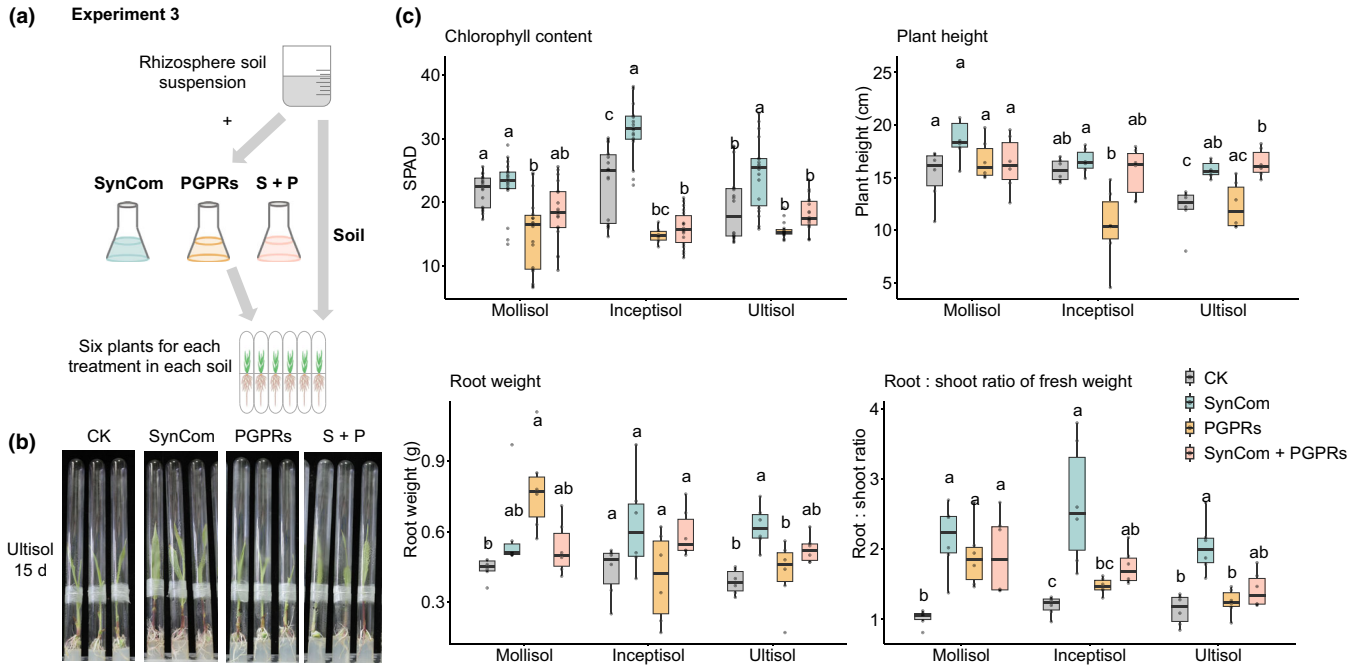

Fig. 5 Experimental design of the plant growth promotion test on axenic maize seedlings. (a, b) Sterile maize seedlings were grown in double-tube chambers for 15 d. S + P, synthetic microbial community (SynCom) + plant growth-promoting rhizobacterias (PGPRs). (c) Morphological traits of maize grown in double-tube chambers, including soil plant analysis development (SPAD) value, plant height, root weight, and root : shoot ratio of fresh weight. Six biological replicates of maize plants were sampled, except for $n = 2$ and $n = 5$ for plants grown in Inceptisol and Ultisol with PGPR treatments, respectively. For the SPAD value, each plant was measured three times. The different letters in (c) indicate significant differences ($P < 0.05$) using multiple comparisons of nonparametric tests (Nemenyi test). In box plots, the horizontal bars represent medians. The tops and bottoms of the boxes show the 75th and 25th percentiles, respectively.

success in promoting plant growth and health. The positive microbial interactions between SynCom and resident microbial communities in low-fertility soils could be critical to plant growth and health.

Discussion

Soil microbial inoculants for promoting crop productivity have been rapidly implemented since agricultural ecosystems are challenged by multiple environmental stresses associated with climate change and soil degradation (Singh, 2017). However, considerable challenges hinder the screening and development of microbial inoculants for the field (Kaminsky *et al.*, 2019). The efficacy of soil microbial inoculants remains unreliable and frequently depends on soil conditions (O'Callaghan, 2016; Hart *et al.*, 2018), with low performance in widespread low-fertility soils. Here, we constructed a native SynCom derived from common culturable species from maize rhizospheres in soils of varied fertility conditions. Native SynCom with agriculturally relevant traits, including nutrient facilitation, increased plant growth more effectively in low-fertility soil than in high-fertility soil. Specifically, compared with commercial PGPRs, its home-field advantage potentially contributed to its success in field colonization, which ultimately enhanced soil biodiversity, enabled positive microbial interactions, and maintained a stable niche structure in low-fertility soil (Fig. 6).

Previous research on home-field advantages, particularly in the case of obligate symbiosis, has emphasized the role of varying soil conditions in mediating plant responses to arbuscular mycorrhizal fungi (Pankova *et al.*, 2014; Rua *et al.*, 2016). In conjunction with our results, this general importance of home-field advantage may be exemplified in the bacterial adaptation to the local soil environment. For example, some SynCom members, including *Pseudomonas* spp., *Enterobacter* spp., and *Chryseobacterium* sp., which were described as the core microbial taxa in the maize rhizosphere by host-mediated selection (Niu *et al.*, 2017), successfully colonized under nonsterile conditions. Subsequently, their colonization induced an increasing alpha diversity in a less diverse Ultisol. We speculated that the home advantage confers intrinsic environmental adaptability to reenter the soil they were isolated from. Thus, plants could receive unexpected bonuses with lower risks from these host-associated inhabitants, for example, attracting beneficial microbes (Qiu *et al.*, 2019). Genetic features for successful plant colonization include functions related to carbon and nitrogen acquisition (de Souza *et al.*, 2019). Although the beneficial traits in native microbial communities were revealed by metagenomic analysis, more specific information targeting the SynCom species will be needed to confirm these beneficial traits. Further culture-independent single-cell techniques and metagenomics information will be conducive to rapidly deciphering the link between the microbial phenome and genome (Fierer *et al.*, 2014; Li *et al.*, 2022).

The primary obstacle for soil microbial inoculants is that resident soil communities compete with microbial inoculants for niches (Eisenhauer *et al.*, 2013), and nutrient resources (Yang *et al.*, 2017) and produce various antimicrobial metabolites (Chin-A-Woeng

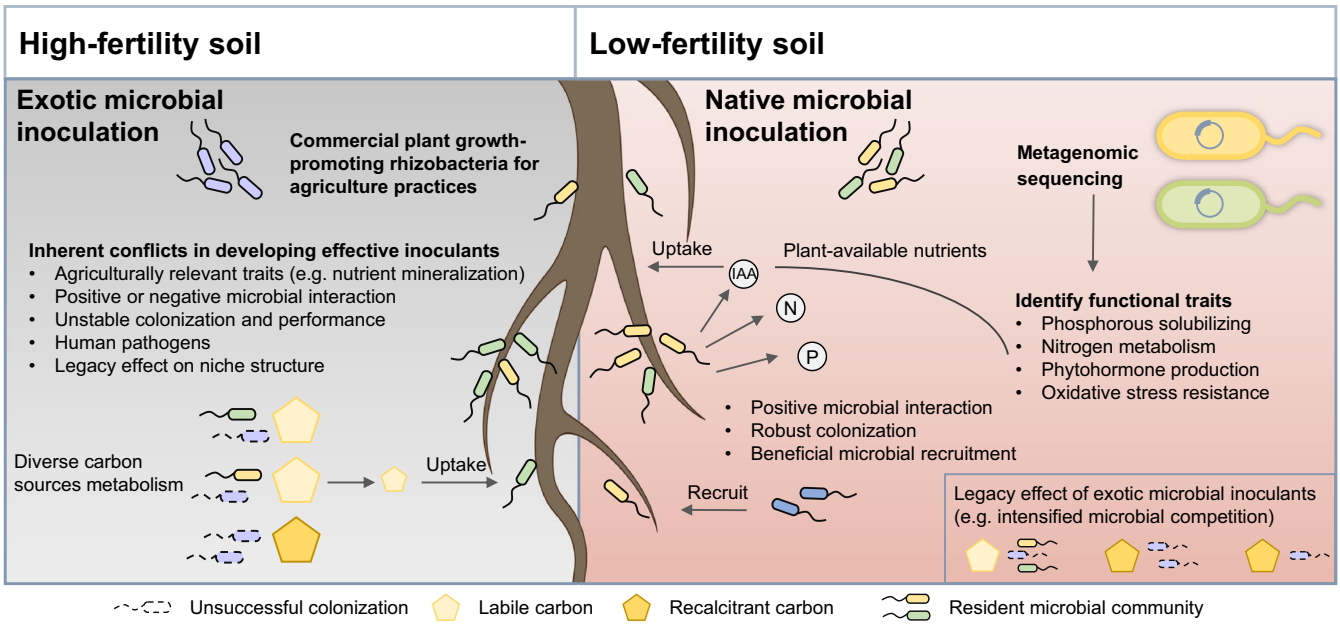

Fig. 6 Differential effects of microbial inoculants on crop growth and resident microbial community under different fertility conditions. Left: exotic microbial inoculants composed of commercial plant growth-promoting rhizobacterias (PGPRs) convey the inherent conflicts in their efficiency and safety concerns. Various biotic and abiotic factors will influence the soil colonization of exotic inoculants, leading to failed colonization and undesired performance. However, the legacy effect will persistently influence the community's niche structure. In high-fertility soil with abundant labile carbon sources, PGPRs with stronger metabolic capacity expand the potential exploitation of noncompetitive resources (recalcitrant carbon) to reduce potential competition. Right: native microbial inoculants composed of culturable species across varied fertility conditions possess a home-field advantage that specifically benefits plant growth in low-fertility soil. In the future, metagenomic sequencing combined with single-cell techniques will help to rapidly elucidate functional traits. Successful colonization contributes to positive microbial interactions, thus promoting plant growth through nutrient facilitation. On the contrary, PGPRs inoculated into low-fertility soil compete with the resident community for limited nutrients, thus increasing potential competition. The figure of root was downloaded from FIGDRAW (ID: TWTIYeedee).

et al., 2000). Niche breadth analysis provided more evidence for the home-field advantage of native SynCom. Specifically, SynCom inoculation increased the individual niche breadth and balanced the changes in niche overlap in low-fertility soil, implying a neutral disturbance to the resident community. Wider niches represent the metabolism of a broader range of resources, improving the efficiency of resource utilization in low-fertility soil (Xu *et al.*, 2022). Notably, applying multispecies consortia may result in more reliable survival than single strains across various environments (Gralka *et al.*, 2020). Our results showed that reducing taxonomic and functional diversity did not cause an obvious loss in the efficacy of these native-sourced microbial assemblies. However, statistical analysis based on sequencing data limited the investigation into true interactions. Future experimental work is required to address how metabolic cross-feeding interactions introduced by the native SynCom-resident group continuum drive coexistence in complex environments.

Conversely, the generalized-type and fast-growing PGPRs encroached on the niche space of other species but were eventually eliminated and failed to colonize all soils. The short-lived failed invasions showed legacy effects on the niche stricture (Mallon *et al.*, 2018; Amor *et al.*, 2020), including shrinking niche breadths and increasing niche overlaps. These observations may be explained by the diversity resistance hypothesis that diverse communities are highly resistant to exotic microbial invasions due to complex interactions and intensified competition for niche space (van Elsas *et al.*, 2012). Meanwhile, the presence of protozoan predators or viruses controls the fast-growing species (Simek *et al.*, 1997). While nitrogen and phosphorus are typically abundant in conventional agricultural soils, the easily accessed carbon may not, and competed by microorganisms and roots, represents a cost to crops (Kaminsky *et al.*, 2019). In high-fertility soil, the legacy effect after inoculating PGPRs expanded the potential exploitation of noncompetitive resources to reduce potential competition (Pianka, 1974). However, in low-fertility soils, the limited nutrients and substrates are poorly matched for PGPRs, negatively impacting microbial establishment and growth.

An inevitable issue in developing effective inoculants for crops is the concern of human health risks. The market demand for PGPR is increasing annually on a global basis to reduce harmful chemical fertilizers and pesticides (Waltz, 2023). Nevertheless, since various bacterial genera have been used as commercial PGPRs, it is necessary to evaluate their potential pathogenicity before applying microbial products in agricultural practices (Keswani *et al.*, 2019). In addition, given the taxonomic and functional redundancy of native SynCom, future work will focus on maximizing the community-level functional outcomes with the simplest species combination. These noteworthy efforts will provide a fundamental understanding of the *in vitro* assembly of complex synthetic communities and targeted manipulation of crop microbiomes to achieve sustainable crop production (Gralka *et al.*, 2020; Maynard *et al.*, 2020).

In conclusion, our study showed that microbial inoculants composed of diverse species isolated from various soil types specifically boosted plant growth more than commercial PGPRs under nutrient-limited conditions. In addition to the beneficial traits, the home-field advantage critically contributes to the potentially robust colonization of the SynCom and the positive interactions between SynCom and the resident community. Commercial PGPRs, however, may have little beneficial or even reverse effects on the rhizosphere environment through legacy effects on niche structure and increasing potential competition with the resident community. Furthermore, field trial data beyond the vegetative growth stages of maize are needed to fully assess the benefits of native SynCom. Nonetheless, our findings highlight the home-field advantage of native microbes in synthetic biology and suggest avenues to effectively promote the sustainability of agriculture in the context of a changing world with increasing desertification and soil degradation.

Acknowledgements

The authors are grateful to the editor and anonymous referees. YL is supported by National Key R&D Program of China (2021YFD1900400), Strategic Priority Research Program of the Chinese Academy of Sciences (XDA24020104), Innovation Program of Institute of Soil Science (ISSASIP2201), National Natural Science Foundation of China (41877060), and Youth Innovation Promotion Association of Chinese Academy of Sciences (2016284). D-BM is supported by the Spanish Ministry of Science and Innovation (PID2020-115813RA-I00) and a Project PAIDI 2020 from the Junta de Andalucía (P20_00879).

Competing interests

None declared.

Author contributions

All authors contributed intellectual input and assistance to this study and manuscript. YL, D-BM and TWC developed the original framework. MJ, JD and YL contributed to experiments and analysis. YL, MJ, D-BM and MMY wrote the manuscript with help from EY, JZ and TWC. All authors have reviewed and agreed with the manuscript.

ORCID

Thomas W. Crowther https://orcid.org/0000-0001-5674-8913
Manuel Delgado-Baquerizo https://orcid.org/0000-0002-6499-576X
Meitong Jiang https://orcid.org/0000-0003-4841-3122
Yuting Liang https://orcid.org/0000-0001-5443-4486
Etienne Yergeau https://orcid.org/0000-0002-7112-3425
Mengting Maggie Yuan https://orcid.org/0000-0003-0017-3908
Jizhong Zhou https://orcid.org/0000-0003-2014-0564

Data availability

The raw sequence data reported in this paper have been deposited in the Genome Sequence Archive in BIG Data Center, Beijing Institute of Genomics (BIG), Chinese Academy of Sciences, under accession nos. CRA004483, CRA004483, and CRA004428, which are publicly accessible at http://bigd.big.ac.cn/gsa.

References

Amor DR, Ratzke C, Gore J. 2020. Transient invaders can induce shifts between alternative stable states of microbial communities. *Science Advances* **6**: eaay8676.

Anderson ELUB. 1988. Tillage and N fertilization effects on maize root growth and root:shoot ratio. *Plant and Soil* **108**: 245–251.

Ayres E, Steltzer H, Simmons BL, Simpson RT, Steinweg JM, Wallenstein MD, Mellor N, Parton WJ, Moore JC, Wall DH. 2009. Home-field advantage accelerates leaf litter decomposition in forests. *Soil Biology and Biochemistry* **41**: 606–610.

Aziz RK, Bartels D, Best AA, DeJongh M, Disz T, Edwards RA, Formsma K, Gerdes S, Glass EM, Kubal M *et al.* 2008. The RAST Server: rapid annotations using subsystems technology. *BMC Genomics* **9**: 75.

Berg G, Koberl M, Rybakova D, Muller H, Grosch R, Smalla K. 2017. Plant microbial diversity is suggested as the key to future biocontrol and health trends. *FEMS Microbiology Ecology* **93**: fix050.

Berg G, Smalla K. 2009. Plant species and soil type cooperatively shape the structure and function of microbial communities in the rhizosphere. *FEMS Microbiology Ecology* **68**: 1–13.

Bochner BR. 2009. Global phenotypic characterization of bacteria. *FEMS Microbiology Reviews* **33**: 191–205.

Brettin T, Davis JJ, Disz T, Edwards RA, Gerdes S, Olsen GJ, Olson R, Overbeek R, Parrello B, Pusch GD *et al.* 2015. RASTtk: a modular and extensible implementation of the RAST algorithm for building custom annotation pipelines and annotating batches of genomes. *Scientific Reports* **5**: 8365.

Chaparro JM, Sheflin AM, Manter DK, Vivanco JM. 2012. Manipulating the soil microbiome to increase soil health and plant fertility. *Biology and Fertility of Soils* **48**: 489–499.

Chen Q, Hu T, Li X, Song CP, Zhu JK, Chen L, Zhao Y. 2022. Phosphorylation of SWEET sucrose transporters regulates plant root:shoot ratio under drought. *Nature Plants* **8**: 68–77.

Chin-A-Woeng TF, Bloemberg GV, Mulders IH, Dekkers LC, Lugtenberg BJ. 2000. Root colonization by phenazine-1-carboxamide-producing bacterium *Pseudomonas chlororaphis* PCL1391 is essential for biocontrol of tomato foot and root rot. *Molecular Plant–Microbe Interactions* **13**: 1340–1345.

Choi KH, Dobbs FC. 1999. Comparison of two kinds of Biolog microplates (GN and ECO) in their ability to distinguish among aquatic microbial communities. *Journal of Microbiological Methods* **36**: 203–213.

Chou JC, Huang YB. 2005. Induction and characterization of an indole-3-acetyl-l-alanine hydrolase from *Arthrobacter ilicis*. *Journal of Plant Growth Regulation* **24**: 11–18.

Crowther TW, van den Hoogen J, Wan J, Mayes MA, Keiser AD, Mo L, Averill C, Maynard DS. 2019. The global soil community and its influence on biogeochemistry. *Science* **365**: eaav0550.

Delgado-Baquerizo M, Trivedi P, Trivedi C, Eldridge DJ, Reich PB, Jeffries TC, Singh BK, Bennett A. 2017. Microbial richness and composition independently drive soil multifunctionality. *Functional Ecology* **31**: 2330–2343.

Eisenhauer N, Schulz W, Scheu S, Jousset A, Pfrender M. 2013. Niche dimensionality links biodiversity and invasibility of microbial communities. *Functional Ecology* **27**: 282–288.

van Elsas JD, Chiurazzi M, Mallon CA, Elhottova D, Kristufek V, Salles JF. 2012. Microbial diversity determines the invasion of soil by a bacterial pathogen. *Proceedings of the National Academy of Sciences, USA* **109**: 1159–1164.

Fanin N, Lin D, Freschet GT, Keiser AD, Augusto L, Wardle DA, Veen G. 2021. Home-field advantage of litter decomposition: from the phyllosphere to the soil. *New Phytologist* **231**: 1353–1358.

Fierer N, Barberan A, Laughlin DC. 2014. Seeing the forest for the genes: using metagenomics to infer the aggregated traits of microbial communities. *Frontiers in Microbiology* **5**: 614.

Garland JL. 1996. Analytical approaches to the characterization of samples of microbial communities using patterns of potential C source utilization. *Soil Biology and Biochemistry* **28**: 213–221.

Ge Y, Zhang J, Zhang L, Yang M, He J. 2008. Long-term fertilization regimes affect bacterial community structure and diversity of an agricultural soil in northern China. *Journal of Soils and Sediments* **8**: 43–50.

Gralka M, Szabo R, Stocker R, Cordero OX. 2020. Trophic interactions and the drivers of microbial community assembly. *Current Biology* **30**: R1176–R1188.

Guo H, Glaeser SP, Alabid I, Imani J, Haghighi H, Kampfer P, Kogel KH. 2017. The abundance of endofungal bacterium *Rhizobium radiobacter* (syn. *Agrobacterium tumefaciens*) increases in its fungal host *Piriformospora indica* during the tripartite sebacinalean symbiosis with higher plants. *Frontiers in Microbiology* **8**: 629.

Hart MM, Antunes PM, Chaudhary VB, Abbott LK, Field K, Field K. 2018. Fungal inoculants in the field: is the reward greater than the risk? *Functional Ecology* **32**: 126–135.

Hartmann M, Six J. 2022. Soil structure and microbiome functions in agroecosystems. *Nature Reviews Earth & Environment* **4**: 4–18.

Jez JM, Lee SG, Sherp AM. 2016. The next green movement: plant biology for the environment and sustainability. *Science* **353**: 1241–1244.

Kaminsky LM, Trexler RV, Malik RJ, Hockett KL, Bell TH. 2019. The inherent conflicts in developing soil microbial inoculants. *Trends in Biotechnology* **37**: 140–151.

Keswani C, Prakash O, Bharti N, Vilchez JI, Sansinenea E, Lally RD, Borriss R, Singh SP, Gupta VK, Fraceto LF *et al.* 2019. Re-addressing the biosafety issues of plant growth promoting rhizobacteria. *Science of the Total Environment* **690**: 841–852.

Keswani C, Singh SP, Cueto L, García-Estrada C, Mezaache-Aichour S, Glare TR, Borriss R, Singh SP, Blázquez MA, Sansinenea E. 2020. Auxins of microbial origin and their use in agriculture. *Applied Microbiology and Biotechnology* **104**: 8549–8565.

Lebeis SL, Paredes SH, Lundberg DS, Breakfield N, Gehring J, McDonald M, Malfatti S, Glavina DRT, Jones CD, Tringe SG *et al.* 2015. Salicylic acid modulates colonization of the root microbiome by specific bacterial taxa. *Science* **349**: 860–864.

Li H, Yang K, Liao H, Lassen SB, Su J, Zhang X, Cui L, Zhu Y. 2022. Active antibiotic resistome in soils unraveled by single-cell isotope probing and targeted metagenomics. *Proceedings of the National Academy of Sciences, USA* **119**: e2093494177.

Li Y, Li Q, Yang J, Lü X, Liang W, Han X, Bezemer TM, Sayer E. 2017. Home-field advantages of litter decomposition increase with increasing N deposition rates: a litter and soil perspective. *Functional Ecology* **31**: 1792–1801.

Liu Y, Mi G, Chen F, Zhang J, Zhang F. 2004. Rhizosphere effect and root growth of two maize (*Zea mays* L.) genotypes with contrasting P efficiency at low P availability. *Plant Science* **167**: 217–223.

Mallon CA, Le Roux X, van Doorn GS, Dini-Andreote F, Poly F, Salles JF. 2018. The impact of failure: unsuccessful bacterial invasions steer the soil microbial community away from the invader's niche. *ISME Journal* **12**: 728–741.

Maynard DS, Miller ZR, Allesina S. 2020. Predicting coexistence in experimental ecological communities. *Nature Ecology & Evolution* **4**: 91–100.

McCarty NS, Ledesma-Amaro R. 2019. Synthetic biology tools to engineer microbial communities for biotechnology. *Trends in Biotechnology* **37**: 181–197.

Mou J, Li Q, Shi W, Qi X, Song W, Yang J. 2020. Chain conformation, physicochemical properties of fucosylated chondroitin sulfate from sea cucumber *Stichopus chloronotus* and its *in vitro* fermentation by human gut microbiota. *Carbohydrate Polymers* **228**: 115359.

Niu B, Paulson JN, Zheng X, Kolter R. 2017. Simplified and representative bacterial community of maize roots. *Proceedings of the National Academy of Sciences, USA* **114**: E2450–E2459.

O'Callaghan M. 2016. Microbial inoculation of seed for improved crop performance: issues and opportunities. *Applied Microbiology and Biotechnology* **100**: 5729–5746.

Overbeek R, Olson R, Pusch GD, Olsen GJ, Davis JJ, Disz T, Edwards RA, Gerdes S, Parrello B, Shukla M *et al.* 2014. The SEED and the Rapid Annotation of microbial genomes using subsystems technology (RAST). *Nucleic Acids Research* **42**: D206–D214.

Pankova H, Raabova J, Munzbergova Z. 2014. Mycorrhizal symbiosis and local adaptation in *Aster amellus*: a field transplant experiment. *PLoS ONE* **9**: e93967.

Parks DH, Imelfort M, Skennerton CT, Hugenholtz P, Tyson GW. 2015. CheckM: assessing the quality of microbial genomes recovered from isolates, single cells, and metagenomes. *Genome Research* **25**: 1043–1055.

Pianka ER. 1974. Niche overlap and diffuse competition. *Proceedings of the National Academy of Sciences, USA* **71**: 2141–2145.

Qiu Z, Egidi E, Liu H, Kaur S, Singh BK. 2019. New frontiers in agriculture productivity: optimised microbial inoculants and *in situ* microbiome engineering. *Biotechnology Advances* **37**: 107371.

Rasulov BA, Dai J, Pattaeva MA, Yong-Hong L, Yili A, Aisa HA, Qiu D, Li WJ. 2020. Gene expression abundance dictated exopolysaccharide modification in *Rhizobium radiobacter* SZ4S7S14 as the cell's response to salt stress. *International Journal of Biological Macromolecules* **164**: 4339–4347.

Reddy G, Garcia-Pichel F. 2007. *Sphingomonas mucosissima* sp. nov. and *Sphingomonas desiccabilis* sp. nov., from biological soil crusts in the Colorado Plateau, USA. *International Journal of Systematic and Evolutionary Microbiology* **57** (Pt 5): 1028–1034.

Richardson AE, Barea J, McNeill AM, Prigent-Combaret C. 2009. Acquisition of phosphorus and nitrogen in the rhizosphere and plant growth promotion by microorganisms. *Plant and Soil* **321**: 305–339.

Rua MA, Antoninka A, Antunes PM, Chaudhary VB, Gehring C, Lamit LJ, Piculell BJ, Bever JD, Zabinski C, Meadow JF *et al.* 2016. Home-field advantage? evidence of local adaptation among plants, soil, and arbuscular mycorrhizal fungi through meta-analysis. *BMC Evolutionary Biology* **16**: 122.

Ryan RP, Monchy S, Cardinale M, Taghavi S, Crossman L, Avison MB, Berg G, van der Lelie D, Dow JM. 2009. The versatility and adaptation of bacteria from the genus *Stenotrophomonas*. *Nature Reviews Microbiology* **7**: 514–525.

Sarwar M, Kremer RJ. 1995. Determination of bacterially derived auxins using a microplate method. *Letters in Applied Microbiology* **20**: 282–285.

Sharma S, Kulkarni J, Jha B. 2016. Halotolerant rhizobacteria promote growth and enhance salinity tolerance in peanut. *Frontiers in Microbiology* **7**: 1600.

Simek K, Vrba J, Pernthaler J, Posch T, Hartman P, Nedoma J, Psenner R. 1997. Morphological and compositional shifts in an experimental bacterial community influenced by protists with contrasting feeding modes. *Applied and Environmental Microbiology* **63**: 587–595.

Singh BK. 2017. Creating new business, economic growth and regional prosperity through microbiome-based products in the agriculture industry. *Microbial Biotechnology* **10**: 224–227.

Singh BK, Trivedi P, Egidi E, Macdonald CA, Delgado-Baquerizo M. 2020. Crop microbiome and sustainable agriculture. *Nature Reviews Microbiology* **18**: 601–602.

de Souza R, Armanhi J, Arruda P. 2020. From microbiome to traits: designing synthetic microbial communities for improved crop resiliency. *Frontiers in Plant Science* **11**: 1179.

de Souza RSC, Armanhi JSL, Damasceno NDB, Imperial J, Arruda P. 2019. Genome sequences of a plant beneficial synthetic bacterial community reveal genetic features for successful plant colonization. *Frontiers in Microbiology* **10**: 1779.

Sun H, Jiang J, Cui L, Feng W, Wang Y, Zhang J. 2019. Soil organic carbon stabilization mechanisms in a subtropical mangrove and salt marsh ecosystems. *Science of the Total Environment* **673**: 502–510.

Uritskiy GV, DiRuggiero J, Taylor J. 2018. MetaWRAP – a flexible pipeline for genome-resolved metagenomic data analysis. *Microbiome* **6**: 158.

de Vries FT, Griffiths RI, Knight CG, Nicolitch O, Williams A. 2020. Harnessing rhizosphere microbiomes for drought-resilient crop production. *Science* **368**: 270–274.

Waltz E. 2023. Small innovators advance microbes as alternatives to chemical crop sprays. *Nature Biotechnology* **41**: 162–164.

Wang X, Bian Q, Jiang Y, Zhu L, Chen Y, Liang Y, Sun B. 2021. Organic amendments drive shifts in microbial community structure and keystone taxa

which increase C mineralization across aggregate size classes. *Soil Biology and Biochemistry* **153**: 108062.

Xu Q, Vandenkoornhuyse P, Li L, Guo J, Zhu C, Guo S, Ling N, Shen Q. 2022. Microbial generalists and specialists differently contribute to the community diversity in farmland soils. *Journal of Advanced Research* **40**: 17–27.

Xu R, Zhao A, Li Q, Kong X, Ji G. 2003. Acidity regime of the red Soils in a subtropical region of southern China under field conditions. *Geoderma* **115**: 75–84.

Yang T, Wei Z, Friman VP, Xu Y, Shen Q, Kowalchuk GA, Jousset A. 2017. Resource availability modulates biodiversity-invasion relationships by altering competitive interactions. *Environmental Microbiology* **19**: 2984–2991.

Yoon SH, Ha SM, Kwon S, Lim J, Kim Y, Seo H, Chun J. 2017. Introducing EzBioCloud: a taxonomically united database of 16S rRNA gene sequences and whole-genome assemblies. *International Journal of Systematic and Evolutionary Microbiology* **67**: 1613–1617.

Zhao K, Penttinen P, Zhang X, Ao X, Liu M, Yu X, Chen Q. 2014. Maize rhizosphere in Sichuan, China, hosts plant growth promoting *Burkholderia cepacia* with phosphate solubilizing and antifungal abilities. *Microbiological Research* **169**: 76–82.

Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Alpha and beta diversity of rhizosphere microbial communities in Mollisol, Inceptisol, and Ultisol.

Fig. S2 Absolute quantification of 16S rRNA to reveal rhizosphere microbial community composition.

Fig. S3 Physicochemical properties of environmental samples in the field.

Fig. S4 Twenty-one species of SynCom and four strains of PGPR belonged to the most abundant taxa at the order level.

Fig. S5 Metagenomic binning and functional clustering.

Fig. S6 Association of microbial network modules, metagenome bins and plant traits.

Fig. S7 Comparison of plant height of maize plants between the treatment and control groups at 35 d (V4–V5 stage), 42 d (V5–V6) and 56 d (V7–V8 stage).

Fig. S8 Standard curve of IAA content in suspension.

Fig. S9 Metabolic diversity of carbon sources.

Fig. S10 Relative abundances of the bacterial ASVs matched to SynCom members in the maize rhizosphere grown in the glasshouse.

Fig. S11 Detection of SynCom members by qPCR.

Fig. S12 Niche breadth and overlap across three types of soils with different microbial inoculants.

Fig. S13 Morphological traits of maize grown in the double-tube chambers at day 15 between microbial inoculations and CK.

Fig. S14 Root development of maize grown in the double-tube chambers at day 10 between microbial inoculations and CK.

Methods S1 Solid-state ^{13}C nuclear magnetic resonance analysis.

Methods S2 Soil physical and chemical properties.

Methods S3 Bacterial cultivation and isolation.

Methods S4 Identification of the isolated microbial strains.

Methods S5 IAA concentration of rhizosphere microbial communities.

Methods S6 Absolute quantification of 16S rRNA.

Methods S7 Relative quantification of 16S rRNA.

Methods S8 Whole metagenomic shotgun sequencing.

Table S1 Ingredients of four selective medium to culture the native rhizosphere bacteria.

Table S2 Plant growth-promoting traits of isolated microbial strains.

Table S3 Data quality of absolute quantification of the 16S rRNA gene.

Table S4 Physicochemical properties of rhizosphere samples.

Table S5 Metagenomic datasets and assembly results.

Table S6 Genome bins retrieved from soil metagenomes.

Table S7 Parameters of the logistic model of SynCom and PGPRs.

Table S8 Alpha diversity of rhizosphere soils after treatment with SynCom and PGPRs.

Table S9 Twelve primers used for qPCR analysis.

Table S10 PERMANOVA test statistics of the influence of soil types and microbial inoculations on the soil community composition.

Please note: Wiley is not responsible for the content or functionality of any Supporting Information supplied by the authors. Any queries (other than missing material) should be directed to the *New Phytologist* Central Office.