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Synergistic superiority of AMF and biochar in enhancing rhizosphere microbiomes to support plant growth under Cd stress

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Abstract

Arbuscular mycorrhizal fungi (AMF) and biochar (BC) exhibit considerable potential for remediation of Cd-contaminated soil. However, studies addressing the combined impact of AMF and BC on soil microbiomes under Cd stress across soils of varying fertility are lacking. In this study, bioinformatics methods were used to discern the distinctive microbiome in rhizosphere soil of Cd-contaminated plants after the application of AMF and BC, among which the representative cultivable bacterial strains were chosen for the construction of synthetic communities (SynComs). The co-application of AMF and BC effectively alleviated the detrimental impacts of Cd stress on plants, with significantly superior remediation efficacy observed in barren soils compared to fertile soil. Co-occurrence network analysis revealed that Cd-contaminated soils harbored more complex microbial interactions, and competitive interactions between bacteria were enhanced. Based on in vitro co-culture experiments (isolation of 34 strains from Cd-contaminated rhizosphere soil) and bioinformatics analysis (targeting differentially abundant taxa and co-occurrence network keystone species), 23 candidate strains for SynComs were screened. Based on the superior growth-promoting capabilities of single strains and their pairwise non-antagonistic interactions, we have constructed eight substitute SynComs. One of the SC3 (dominated by *Bacillaceae* and *Sphingomonadaceae*) based on the microbiome increased shoot biomass by 242.73% in barren soil and 350.24% in fertile soil, under Cd-contaminated conditions, showing the highest growth-promoting efficiency. This study provides a novel strategy for the ecological restoration and sustainable utilization of soil contaminated by heavy metals.

Highlights

- Co-application of AMF and biochar reshapes rhizosphere microbiomes in Cd-contaminated soil.
- AMF and biochar co-application demonstrated stronger soil remediation effects in barren soils.
- The synthetic microbial community promoted the plant growth in Cd-contaminated soil.

Keywords Heavy metals, Bioinformatics analysis, Soil remediation, Synthetic community, Microbial interaction

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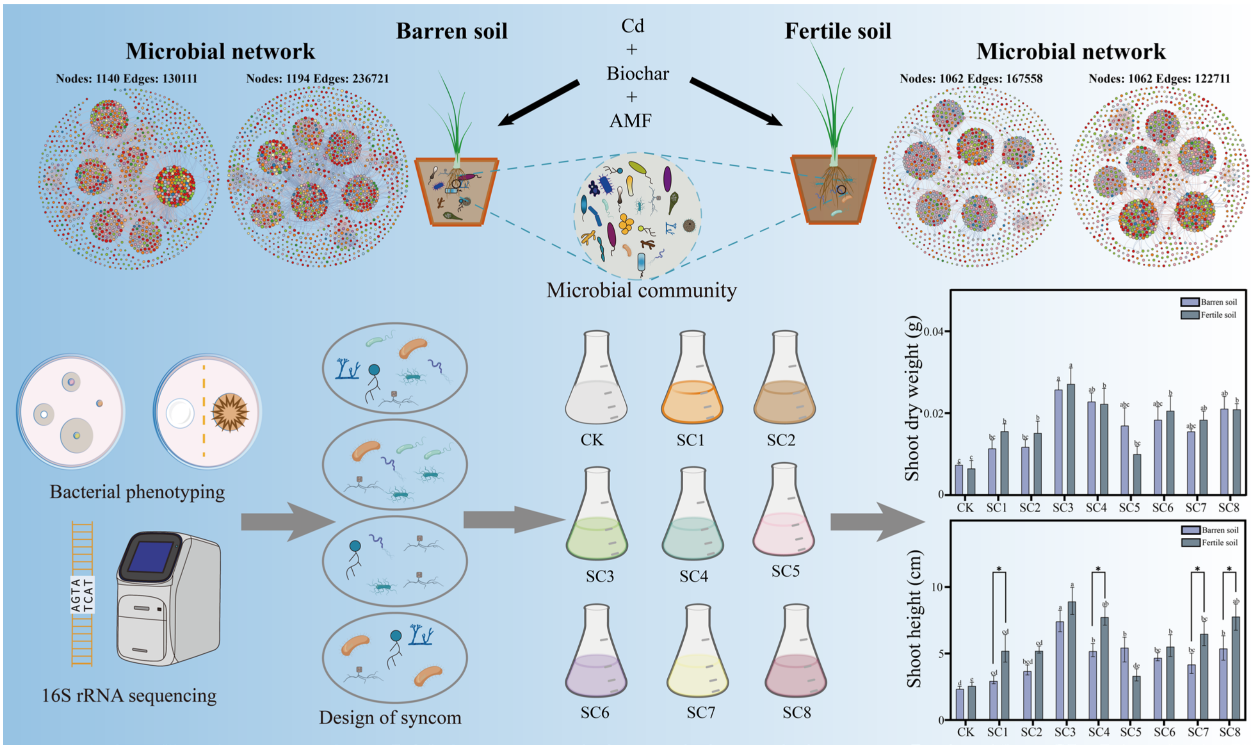
Graphical Abstract



1 Introduction

Soil heavy metal contamination has emerged as a significant environmental problem in global agriculture, primarily attributed to excessive agricultural activities, industrial emissions and human activities (Zhou et al. 2021; Liu et al. 2024). Among these heavy metal elements, cadmium (Cd) stands out as the primary contaminant exceeding standards in agricultural products due to its high bioavailability, which makes it more prone to accumulation in such products compared to other heavy metals (Zhao et al. 2023). Contamination by Cd has inflicted significant harm on ecosystems, resulting in economic losses and detrimental effects on the human food chain as well as health (Meers et al. 2010; Chen et al. 2013). Studies have indicated that excessive accumulation of Cd may induce severe diseases, such as cancer and osteomalacia (Sun et al. 2023). Cd pollution persists after being released into the environment, particularly into the soil, even at low concentrations (Sun et al. 2022). Interestingly, previous studies have reported that low doses of Cd can act as a hormone that may briefly stimulate plant growth under certain conditions, whereas high doses of Cd universally inhibit growth (Siddhu et al. 2008; Fan et al. 2021). Furthermore, contamination with Cd impacts soil fertility and disrupts microbial community structure. Therefore, the remediation of soil Cd contamination has become an urgent task.

In recent years, researchers have found that employing bioabsorption measures can also effectively inhibit the bioavailability of heavy metals. Biochar (BC) serves as a soil amendment characterized by its fine granularity, porosity, and high carbon content, effectively stabilizing heavy metals within soils while enhancing soil quality and the structure of microbial communities (Qian et al. 2016; Li et al. 2024). Arbuscular mycorrhizal fungi (AMF) establish an symbiotic relationship with the majority of cultivated vascular plants (Vilela and Barbosa 2019). AMF not only protect plants from a variety of stresses, but they also enhance the physicochemical properties of soil and serve as a physical barrier to prevent the infiltration of xenobiotics (Yang et al. 2015; Wu et al. 2019). AMF detoxify Cd through direct Cd adsorption onto their surfaces and immobilizes these metals within the soil matrix via glomalin production (Riaz et al. 2021).

The combined effect of BC and AMF has been confirmed in several studies which can be considered as an ecological composite fertilizer (ECF). For instance, in Cd-contaminated soils, the co-application of AMF and

BC enhanced phytoremediation efficiency compared to single treatments, primarily through improved root biomass and reduced metal translocation to shoots (Lu et al. 2023). It has also been shown that the co-application of AMF and BC effectively attenuates Cd-induced toxicity on *B. napus*, resulting in enhanced growth parameters (Yin et al. 2024). These findings highlight ECF's potential to reconcile plant growth and metal immobilization. However, the co-application of AMF and biochar requires careful consideration of material and energy to enhance the economic viability of ECF.

Synthetic microbial communities (SynComs)—consortia constructed to mimic native microbiome functions (Martins et al. 2023))—represent promising tools for soil pollution remediation and plant health enhancement through microbial approaches (Zhou et al. 2023). SynComs are microbial consortia that mimic natural communities, reducing complexity while preserving key interactions, enabling functionalities unachievable by single strains (Arnault et al. 2024). Niu et al. (2017) indicated that the simplified SynComs of maize roots resulted in a notable increase in maize plant biomass and reduced the levels of *Fusarium verticillioides*. Under low nutrient levels, the rhizosphere microorganism SynCom could promote soybean growth and improve nutrient uptake (Wang et al. 2021; Jiang et al. 2023). Recent studies demonstrate their potential in mitigating abiotic stresses, including heavy metal contamination. For instance, SynComs derived from metal-tolerant rhizosphere microbiomes enhanced plant biomass and Cd immobilization in *Sedum* under Cd stress (Huang et al. 2024). Notably, SynComs designed with keystone taxa from co-occurrence networks exhibit higher stability and adaptability in contaminated soils, as they mimic native microbiome dynamics (Gao et al. 2022; Jing et al. 2024). Therefore, the construction of synthetic communities from the perspective of simulated ecological functions can provide accurate microbiome management for sustainable agriculture under cadmium stress.

The construction of SynComs is a necessary approach in the study of microbiota-host plant interactions (Ma et al. 2021). We use chive (*Allium ascalonicum L.*), an important horticultural plant with high economic benefits, as our host plant (Li et al. 2024). This study evaluated the contribution of microbial communities to the promotion of plant growth through the co-application of AMF and BC in Cd-contaminated high-fertility and low-fertility soils. The objectives are: (1) to investigate the impact of the co-application of BC and AMF on plants and the soil microbiome in Cd-contaminated soils with different fertility levels; (2) to explore the potential of key microbiota, particularly SynComs constructed from these microorganisms, in enhancing the plant growth under Cd stress. This study presents new insights into improving remediation efficiency in Cd-contaminated agricultural ecosystems.

2 Materials and methods

2.1 Materials for experiments

The barren soil (long-term fallow field) and fertile soil (continuously cultivated field) were clay loam collected from an agricultural experimental site at Anhui Agricultural University (31.83°N, 117.24°E). The barren soil and fertile soil were classified as yellow cinnamon soil (Chromic-Leptic Luvisols in the WRB; Alfisols in the USDA Soil Taxonomy). The Supporting Materials describe the fundamental physicochemical properties of soil (Table S1). After removing the surface plant fragments, the soil was sieved through a 2-mm mesh and used for the greenhouse pot experiment. Chive (*Allium ascalonicum L.*) seeds were purchased from the Beijing Academy of Agricultural Sciences. The BC with a particle size < 2 mm was produced from rice husk at 800 °C for 4 h at the Functional Laboratory for Biomass Resource Transformation and Use, Anhui Agricultural University (Anhui, China). Biochar samples had a pH of 9.46 (1:10 w/v), and total C, total N, total P, total K, total ash, cation exchange capacity, and specific surface area levels of 42.21%, 8.34%, 2.31%, 16.12%, 7.23%, 19.4 cmol kg^{-1}, 246.18 m^2 g^{-1}, respectively. The AMF (*Rhizophagus irregular*, BGC DAOM, 197198) strains used were provided by the National and Local Joint Engineering Laboratory of Crop Stress Resistance Breeding and Disaster Reduction, Anhui Agricultural University (Anhui, China). The surface morphology of AMF and biochar at four Cd concentrations (0, 5, 20, 40 mg/kg) were investigated with scanning electron microscope (SEM) (GeminiSEM 500, Carl Zeiss Jena, Germany) at 1–2 kV (Fig. 1A–D).

Each pot (diameter 17.7 cm, depth 12 cm) was filled with 2 kg of soil. Ten chive seeds were sown in each pot, and subsequently six seedlings were retained per pot after ten days of growth. For each soil type, two dosage levels of Cd as $CdCl_2$ were set: 5 mg kg^{-1} Cd (low) and 20 mg kg^{-1} Cd (high). The pot experiment comprised four treatments and four replicates were designed for each treatment: Control group (CK): untreated soil; Ecological composite fertilizer (ECF): soil amended with 2% biochar (BC) and inoculated with 40 g AMF spores; BC, AMF, and 5 mg kg^{-1} Cd treatment (5%CdECF); BC, AMF, and 20 mg kg^{-1} Cd treatment (20%CdECF) (Fig. 1E).

2.2 Sample collection

After 55 days, plants and rhizosphere soil were harvested. The chive was removed from the pot and rinsed with deionized water. After absorbing the residual water with tissue paper, the height of aboveground

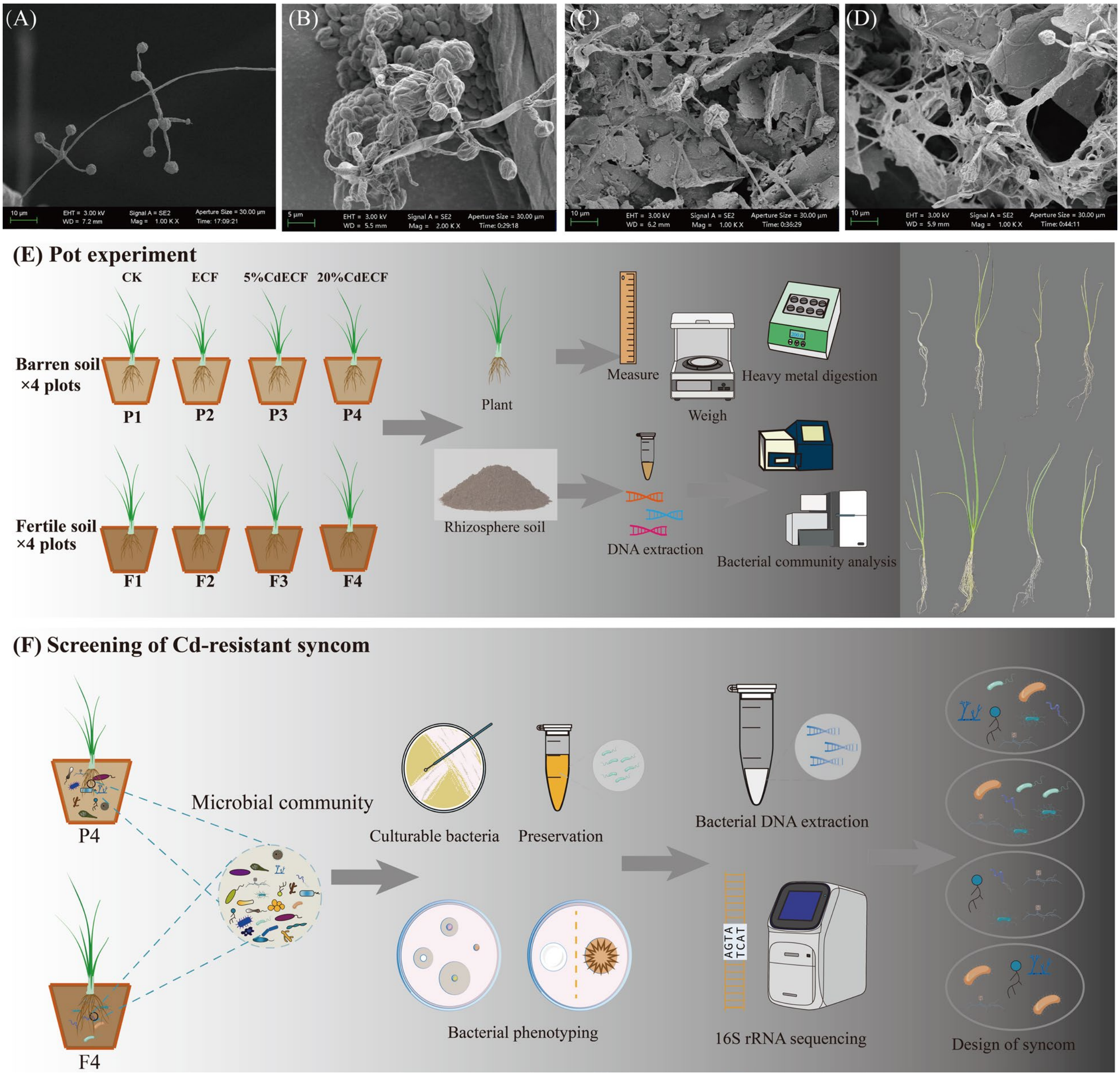


Fig. 1 Scanning electron microscope image (**A**–**D**) of AMF and biochar at four Cd concentrations (0, 5, 20, 40 mg kg^{-1}). **E** Soil samples were obtained from two distinct locations for use in pot experiments. The plant was collected for phenotypic measurement and heavy metal determination. The rhizosphere soil was collected for heavy metal determination, microbial community analysis, and functional analysis. **F** Soil from Cd contamination was used for microbial community analysis, identification, and screening of SynComs

biomass was measured, and the dry weights of shoots and roots were determined. The collected rhizosphere soil samples were sieved, thoroughly mixed, and divided into two parts. Rhizosphere soil samples from six plants per pot were mixed to form a composite soil sample as a replicate. The first part was air-dried for further chemical analysis, and the second part was placed at − 80 °C for DNA extraction.

2.3 Determination of Cd in plant and soil

The roots were meticulously rinsed with sterilized distilled water, following which the chive plants were separated into shoots and roots. These were subsequently dried at 80 ℃ until a stable weight. The dried plant material was then crushed and pulverized into a fine powder. For each sample, 0.2 g of this powder was accurately weighed, and 10 mL of nitric acid (65% HNO_3, v/v) and 2 mL of perchloric acid (70% $HClO_4$, v/v) were added. The mixture was then digested using a microwave digestor (MARS6; CEM, NC, USA). Post-digestion, the Cd concentration in the sample solutions was measured using ICP-MS. 0.5 g dry soil sample was digested with 6 mL HNO3, 2 mL HCl, and 1 mL HF, and then the sample was allowed to dissolve for 1 h at 200 ℃. The soil total Cd concentration was measured by inductively coupled plasma mass spectrometry (ICP-MS) (NexION 5000, PerkinElmer, MA, USA). The content of available Cd was determined by diethylenetriamine penta acetic acid (DTPA). The transport factor (TF) was calculated as the ratio of the Cd concentration in the shoot to the root. Similarly, the bioconcentration factor (BCF) was determined by calculating the ratio of the Cd concentration in the shoot to that in the Cd concentration present in the soil.

2.4 Total DNA extraction and amplicon sequencing

Fresh soil samples (0.5 g) were weighed for total DNA extraction using the Power Soil DNA Isolation Kit (Qiagen, San Diego, USA). To amplify the V3–V4 region of bacterial 16S rRNA gene, we used the bacterial-specific primer set 341 F (5'-CCTAYGGGRBGCASCAG-3')/806 R (5'- GGACTACNNGGGTATCTAAT-3') (Liu et al. 2020). Each 25 μL volume mixture consisted of 12.5 μL Phusion® High-Fidelity PCR Master Mix (New England Biolabs), 10 ng DNA, 1 mg mL − 1, and 1 μL of forward and reverse primers (5 μmol L^{-1}). We used 2% agar gel electrophoresis to detect the amplified PCR products and purified amplification products using the Qiagen Gel Extraction Kit (Qiagen, Germany). Raw sequence analysis was performed using the QIIME2 software package (Caporaso et al. 2010). Amplicon sequence variants (ASVs) were generated following the DADA2 pipeline (version 1.24.0; Callahan et al. 2016) as described in the official tutorial (https://benjjneb.github.io/dada2/tutorial.html). The pre-trained Greengenes database (13.8) and UNITE database (7.2) were then used to classify bacterial and fungal sequences, employing the feature-classifier plugin at 99% sequence similarity threshold (Nilsson et al. 2019). The resulting ASV table documented the number of observations for each precise ASV in each sample. The National Center for Biotechnology Information (NCBI) Sequence Read Archive (SRA) database was utilized to store all obtained sequence data (Bacterial Accession Number: PRJNA1183442).

2.5 Isolation and identification of culturable bacteria

Rhizosphere soil of chive was collected from two different soils under the 20%Cd condition. These samples were subsequently mixed thoroughly and evenly divided into four portions. To each portion, 200 mL of sterile phosphate-buffered saline (PBS) was added, followed by shaking for 30 min to obtain a suspension of soil bacteria. The resultant homogenized solutions were then diluted to various concentrations, ranging from 10^{-1} to 10^{-6}. Lastly, 50 μL aliquots of the diluted bacterial suspension were inoculated onto five different types of bacterial isolation culture media (Table S2). Following a culture period of 3 to 5 days, bacterial colonies were purified based on their morphological characteristics. Amplification of DNA sequences from the 16S rRNA region was carried out with the aid of primers 27 F (5'-AGAGTTTGATCCTGGCTC-3') and 1492 R (5'-CGGCTACCTTGTTACGACTT-3'). The integrity of the amplified sequences was assessed through agarose gel electrophoresis, followed by sequencing at Tongyong Biosystems (Anhui) Co., Ltd. in China.

2.6 Selection of member strains of the SynCom

Subsequently, 23 strains were inoculated separately to promote the growth of plants. The seeds of chives were sterilized with 75% ethanol. After germination, the seeds were placed in 1/2 MS medium and three seedlings were cultured with each solution. The plants were exposed to light at 25 °C for 16 h and dark for 8 h for 10 days. The capacity of nitrogen fixation, IAA production, phosphate, siderophore, and Cd mobilization of the isolates were further evaluated (Zhou et al. 2024).

Bacterial interactions were conducted to ascertain whether the depleted strains exhibited mutual reinforcement or antagonism. A total of 23 strains (Table S3) were inoculated into 5 mL of TSA and incubated at 30 °C with shaking at 180 rpm overnight. The optical density of these bacterial cultures was then standardized to 0.5 at a wavelength of 600 nm. The specific operation methods adhered to the standard protocols outlined by 32.

2.7 Plant growth in axenic chive seedlings

The potential for plant growth within the chosen synthetic community was assessed under axenic conditions. A solution of cadmium salt (CdCl2·H2O) was prepared by dissolving the necessary quantity in deionized water to achieve a Cd concentration of 40 mg kg^{-1}, while the control group underwent the same procedure but was irrigated with sterilized deionized water instead of the Cd-contaminated solution. Before plant cultivation, all tubes were sterilized at 121 °C for 20 min. Germinated seeds were immersed in the prepared suspension of the synthetic community and subsequently grown in 1/2 MS agar. Hence, this experiment comprised 18 groups, which incorporated two soil suspensions: one with microbial inoculations (SynCom1-8) and another serving as an axenic control. The chive seedlings were positioned in a plant growth chamber maintained under a 16-h light (day) and 8-h dark (night) cycle, a temperature of 28 °C, and a relative humidity of 30%. On day 10, plants were harvested from each treatment, and chive growth was assessed by measuring the plant's length and fresh weight.

2.8 Bioinformatic and statistical analysis of 16S rRNA gene sequencing data

Statistical analysis was performed using SPSS 25.0 software (SPSS Inc., Armonk, NY, USA). One-way analysis of variance (ANOVA) with the least significant difference (LSD) was used to analyze the different treatment groups ($P<0.05$). Before ANOVA analysis, all data were subjected to homogeneity test in order to check the assumptions for the ANOVA performance. Bacterial alpha diversity (Richness, Shannon and Sobs index) was by using the R package "vegan". The non-metric multidimensional analysis (NMDS) based on Bray–Curtis distances was performed to assess variations in bacterial community structure among the treatments. The iTol.py command was used to generate an interactive Tree of Life (iTol) tree and table. Phylogenetic trees were visualized and annotated using iTol (iTol.ember.de). The abundance differences of bacterial ASVs were analyzed utilizing DESeq2. The molecular ecological network was constructed by using the phylogenetic molecular ecological network to show the relationship between microbial networks of different components and the co-occurrence mode between core microbial groups (pMENs; http://ieg4.rccc.ou.edu/mena/). ASVs with relative abundance < 0.01% in all samples were removed. Only correlations with $|\rho|>0.6$ and $P<0.01$ were retained. The networks were visualized using Gephi. In this study, we utilized a Z-P diagram to classify nodes according to their Zi (intra-module connectivity) and Pi (inter-module connectivity) coefficients and define the topology species of specific nodes in the network. In order to evaluate the relative importance of the 71 shared bacterial genera, the random forest model was constructed using the "randomForest" packages.

3 Result

3.1 BC and AMF promoted plant growth in Cd-contaminated soil

Our findings revealed that in both soil types, the ECF group exhibited increases in shoots dry weight of 320.1% and 157.4%, and in plant height of 54.9% and 45.8%, respectively, compared to the control group ($P<0.05$) (Fig. 2A–C). In barren soil, plants exhibited superior growth performance under high Cd conditions compared to low Cd environments, with plant height and dry weight increased by 29.35% (Fig. 2A) and 96.43% (Fig. 2B), respectively. However, the situation was completely reversed in fertile soil, possibly because its inherent nutrient richness reduced the dependency on the biochar amendment. Cd uptake by the shoots and roots was reduced ($P<0.05$) in fertile soil compared to barren soil in considering AMF and BC (Fig. 2D, E). The addition of Cd led to a substantial rise in both the total concentration of Cd in the soil and the DTPA-Cd levels (Fig. 2F, G). The concentration of DTPA-Cd in fertile soil was significantly higher than that in barren soil (Fig. 2G). Under the two distinct soil conditions, the TF exhibited a gradual decline as Cd stress increased. Nonetheless, under the two Cd concentrations stress, the TF in fertile soil was 112.9% and 51.1% higher than that in barren soil, respectively (Fig. 2H). At the identical level of Cd stress, no notable discrepancy was detected in the shoot Cd BCF between the two soil types (Fig. 2I). The combined use of BC and AMF had different effects on plants and soil under different levels of Cd pollution. These findings highlight that the synergistic effect of AMF and BC is particularly pronounced in low-fertility soils with high Cd contamination.

3.2 Variation in rhizosphere bacterial community characteristics under different treatments

The different treatments exhibited a consistent trend in their impact on the alpha-diversity index of microbial communities in both barren and fertile soils (Fig. 3A–C). We noted a significantly higher microbial diversity in the 5%CdECF and 20%CdECF groups than in the other treatment groups, with the 20%CdECF group exhibiting the highest diversity. There were lower values in the richness, Shannon index, and Sobs indices of the CK and ECF groups in the fertile soil compared to the barren soil. On the other hand, the alpha-diversity indices of the 5%CdECF and 20%CdECF groups showed higher values. To ascertain the disparities among treatments regarding the composition of bacterial communities in rhizosphere soils, Nonmetric multidimensional scaling (NMDS) analyses were conducted. The findings revealed that all samples exhibited primary differentiation along the first NMDS axis, indicating significant differences in the bacterial community among the different treatments (ANOSIM, $P<0.001$, Fig. 3D). The analyses of β diversity decomposition revealed that differences in bacterial community across all treatments were primarily driven by species replacement processes (Fig.S1).

Taxonomic assignments of representative reads of the ASVs revealed a total of 47 phylum, of which Proteobacteria (48.07–19.6%), Actinobacteriota (11.14 −29.35%), Acidobacteriota (3.06–23.43%), Firmicutes (3.09–27.39%), Chloroflexi (0.84–13.05%), Gemmatimonadota (1.02–15.38%), and Bacteroidota (1.57–10.05%) were the dominant phyla corresponding to more than 80% of

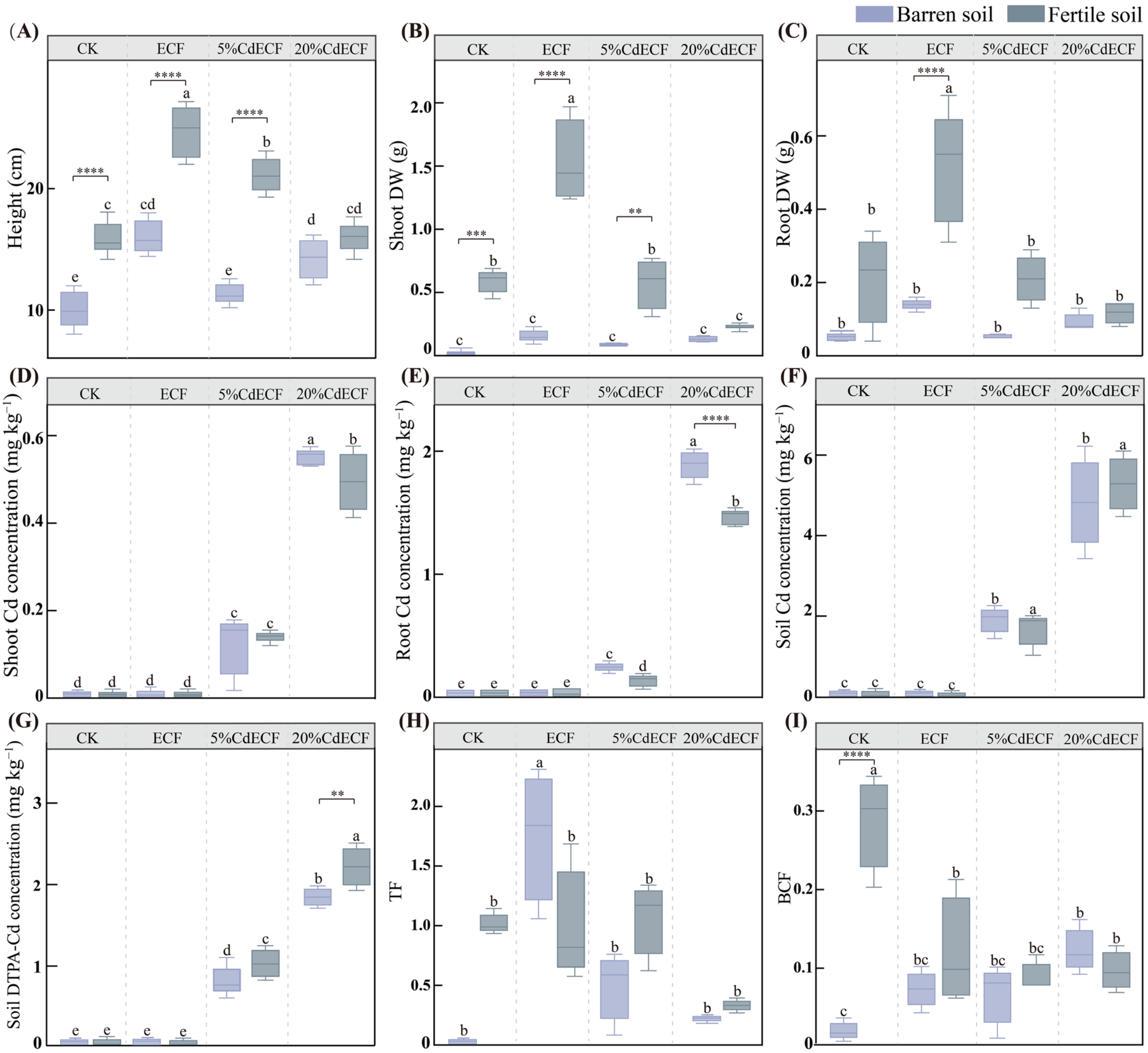


Fig. 2 The height and weight of shallot under different treatments. **A** Height; **B** Shoot dry weight, Shoot DW; **C** Root dry weight, Root DW; **D** Shoot Cd concentration; **E** Root Cd concentration; **F** Soil Cd concentration; **G** Soil DTPA-Cd concentration; **H** Translocation factor, TF; **I** Bioconcentration factor, BCF. All data in the figure are mean (n = 4) ± standard deviation, and different lowercase letters indicate significant differences at the $P < 0.05$ level

all reads among the samples (Fig. 3E). The addition of AMF, BC and Cd had a more complex effect at the phylum level, with large changes in the relative abundance of dominant microorganisms in the soil. The Cd-contaminated soil was enriched with a higher abundance of Acidobacteriota and Chloroflexi, while Proteobacteria and Bacteroidota were less prevalent. In comparison to barren soil, the 5%CdECF and 20%CdECF groups of fertile exhibited increased proportions of Acidobacteriota and Chloroflexi, and decreased proportions of Proteobacteria and Bacteroidota. UpsetView diagram showed 30 mutual ASVs among eight groups (Fig. S2). The analysis of differences revealed that the introduction of AMF and BC resulted in minimal changes to species abundance relative to the CK (Fig. S3). The difference analysis revealed that in the barren soil as compared to the CK, the 5% CdECF and 20% CdECF treatment exhibited significant alterations in 70 (18 down and 52 up) and 71 (20 down and 51 up) ASVs, respectively, amounting to 2.98% and 3.01% of the total ASVs, respectively (Fig. 3F, G). In the fertile soil as compared to the CK, the 5% CdECF and 20% CdECF treatment exhibited significant alterations

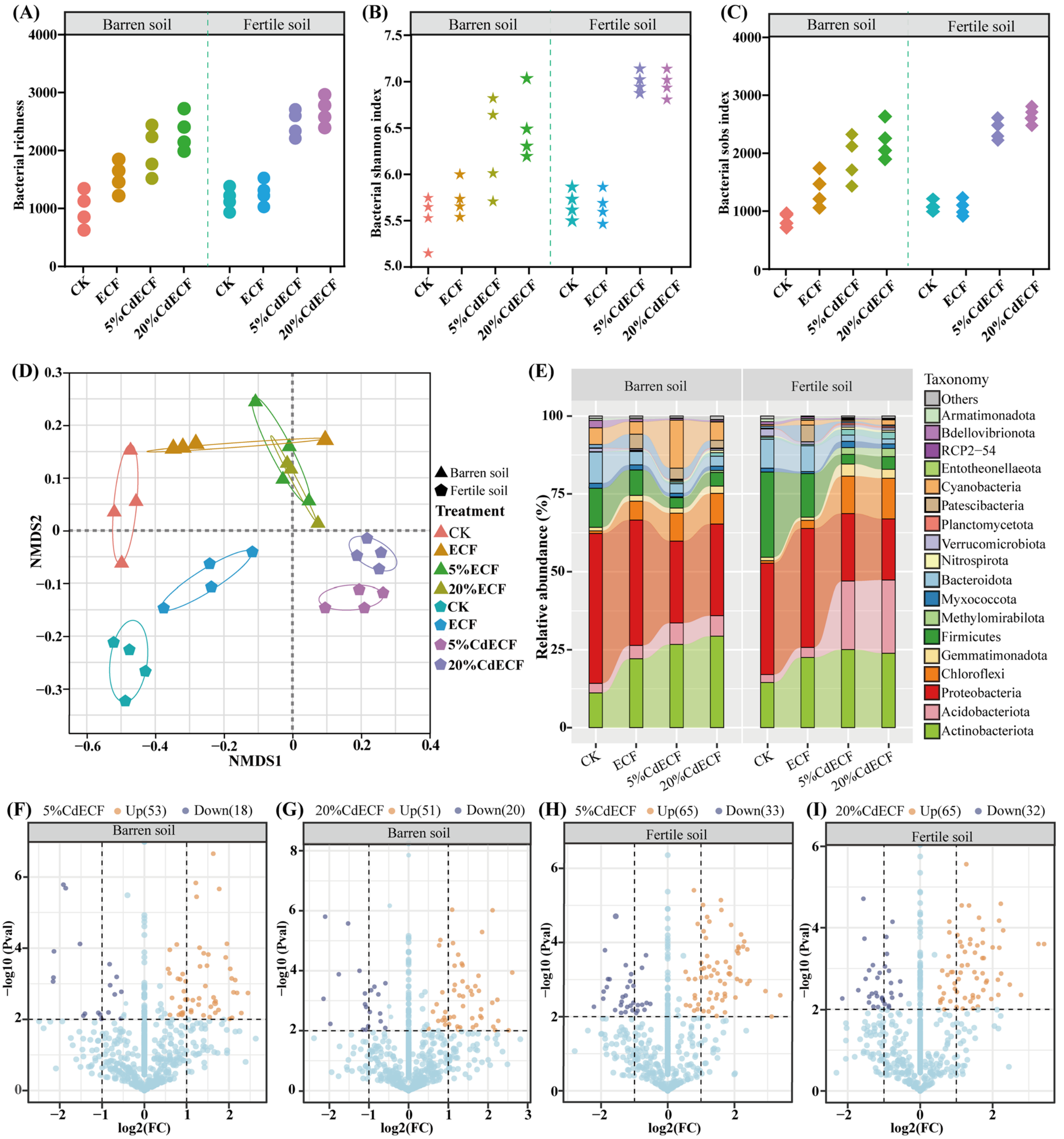


Fig. 3 Rhizosphere soil bacterial diversity and composition under different treatments. **A** Bacterial richness; **B** Bacterial Shannon index; **C** Bacterial sobs index; **D** NMDS of bacterial communities in rhizosphere soil. **E** Distribution of the soil bacteria in different treatments at the phyla level. **F**-**G** Compared with CK, enriched or depleted genus in Cd contaminated barren soil (F: 5%CdECF group; G: 20%CdECF group). **H**-**I** Compared with CK, enriched or depleted genus in Cd contaminated fertile soil (H: 5%CdECF group; I: 20%CdECF group) (DESeq2, $P < 0.05$, FDR adjustment)

in 98 (33 down and 65 up) and 97 (32 down and 65 up) ASVs, respectively, amounting to 3.71% and 3.49% of the total ASVs, respectively (Fig. 3H-I). Differential microorganisms were mainly concentrated in Actinobacteriota and Proteobacteria.

3.3 Acquisition of bacterial taxa for SynComs

Apart from the variations observed in microbial diversity and community structure, the co-occurrence networks in the different treatment groups were also different (Fig. 4A, B). The microbiome networks of the 5%CdECF and 20%CdECF groups were much more complex, with a higher number of nodes and edges compared to those of the CK and ECF groups. In barren soil, the microbiome network of the 20%CdECF group exhibited a greater number of nodes and edges compared to that of the 5%CdECF group (Fig. 4A); however, the opposite consequence was observed under fertile soil conditions (Fig. 4B). In barren soil, compared to other treatments, the bacterial co-occurrence networks in the 20%CdECF group showed higher community correlation with higher average degree(avgk), network density and average clustering coefficient (avgCC) (Fig. 4C, D; Fig. S4). In fertile soil, the 5%CdECF group had the highest avgk and keystones, the ECF group had the highest avgCC, and the 20%CdECF group had the lowest avgk and avgCC. Moreover, the ratio of positive to negative cohesions decreased within both the 5%CdECF and 20%CdECF groups, suggesting heightened competitive interactions among bacterial assemblages in the rhizosphere soil under the Cd contamination (Fig. 4E).

By integrating the findings of network and difference analysis, 71 shared bacteria genera enriched in chive rhizosphere soil (Fig. 4F, Fig.S5). We applied the random forest model to assess the impact of these 71 shared bacterial genera on community structure (Fig. 4G). Among the bacterial genera, *Peribacillus* and *Paenibacillus* exhibited the highest importance scores in community structure. We isolated and purified 34 bacterial strains from two types of rhizosphere soils with 17 bacterial genera belonging to these 71 shared bacterial genera (Fig. 1F). In summary, 23 strains were selected, belonging to 23 species and 17 genera (Table S3).

3.4 Growth characteristics of the candidate strain and SynCom development

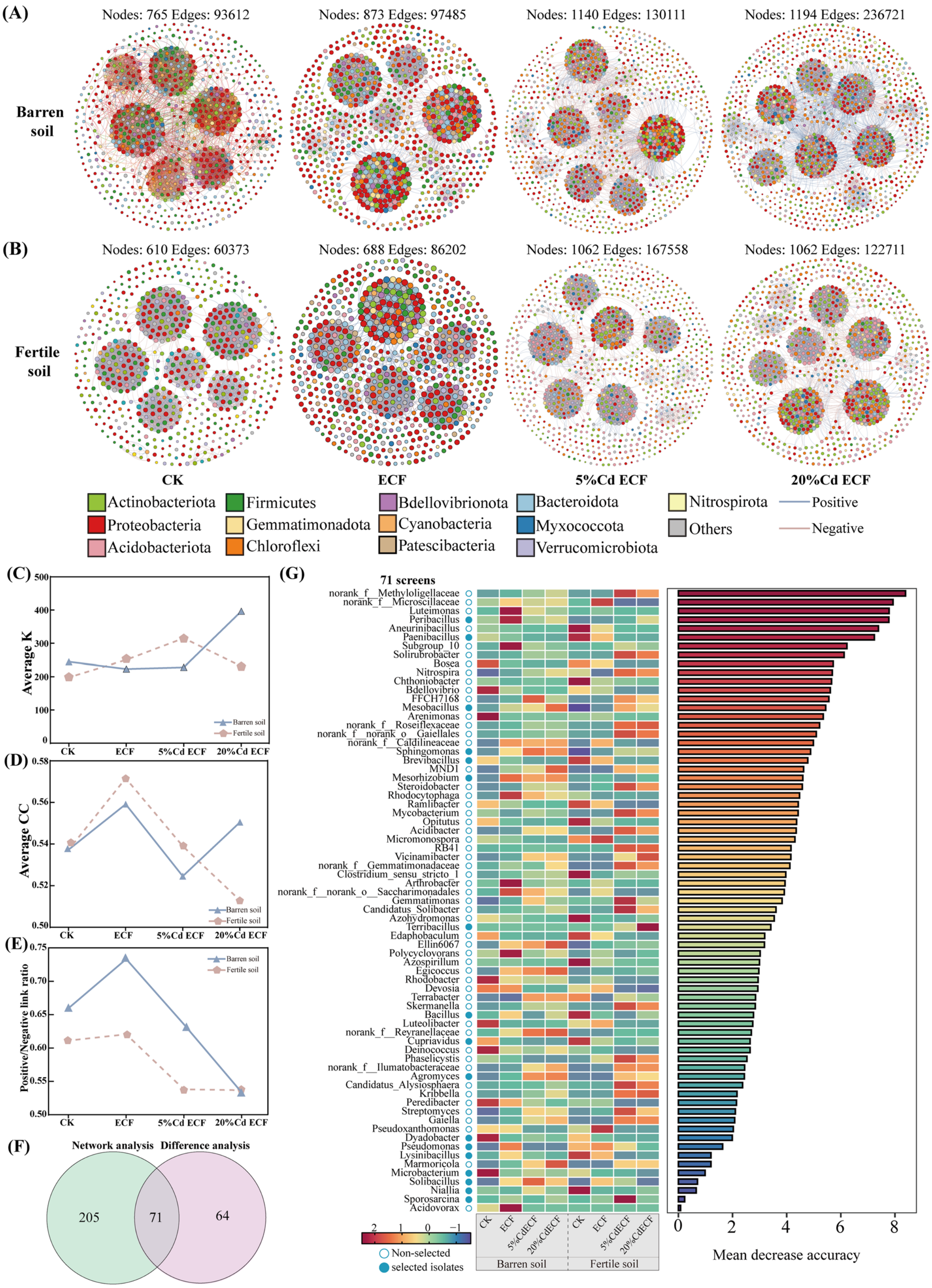
We assessed the growth-promoting ability of 23 strains inoculated alone on plants (Fig. 5A, B) and the abilities of each strain to fix nitrogen, produce IAA, solubilize phosphorus, and generate siderophores (Fig. 5C). Compared with uninoculated plants, all strains showed growth promoting effects on chive. Six strains have the ability to fix nitrogen, among which the top three with the most prominent nitrogen fixation capabilities are *Brevibacillus limnophilus*, *Mesobacillus harenae*, and *Niallia circulans*. All strains have the ability to produce IAA, among which the top three with the most prominent IAA production capabilities were *Peribacillus frigoritolerans*, *Paenibacillus woosongensis*, and *Agromyces ramosus*. The top three with the most solubilized phosphorus capabilities are *Sphingomonas kyeonggiensis*, *Microbacterium oxydans*, and T*erribacillus saccharophilus*. Twelve strains have the ability to generate siderophores, among which the top three with the most siderophore production capabilities are *Sphingomonas leidyi*, *Lysinibacillus mangiferihumi*, and *Paenibacillus lautus*. All 23 strains demonstrated cadmium resistance, with 13 of them exhibiting better growth on a medium with a Cd concentration of 40 mg L^{-1} compared to their performance on a medium with 20 mg L^{-1} (Fig. 5D).

To identify the interaction effect within the 23 strains, we constructed an interaction matrix based on OD600 values between pairwise interactions (Fig. 5E). The experiments on pairwise interactions revealed that a majority of the strains were capable of coexisting and demonstrated positive interactions with each other. From the strains capable of fixing nitrogen, producing IAA, solubilizing phosphorus, generating siderophores, and exhibiting Cd resistance, we selected the top three performers and constructed eight SynComs based on their demonstrated non-antagonistic interactions between pairwise interactions (Fig. 5E).

To evaluate whether microbial inoculation stimulates plant growth enhancement, we quantified the impact of 8 SynComs inoculation on chive growth in the absence of soil substrates (Fig. 6A). In comparison to the CK, the inoculation of 8 SynComs notably stimulated the growth of chive seedlings after 10 days in two soils, as evidenced by the enhanced shoot height and shoot fresh weight (Fig. 6B, C). Meanwhile, the shoot height and plant weight in SC3 treatment significantly increased compared with other treatments. In barren soil, the growth-promoting effects of SynComs were as follows: SC3 > SC4 > SC5 > SC8 > SC6 > SC7 > SC2 > SC1 (with above-ground fresh weight increases of 242.73%, 204.41%, 126.43%, 181.06%, 145.37%, 107.93%, 57.71%, and 52.86%, respectively). In fertile soil, the growth-promoting effects of SynComs were as follows: SC3 > SC4 > SC8 > SC6 > SC7 > SC1 > SC2 > SC5 (with above-ground fresh

(See figure on next page.)

Fig. 4 Visualization of bacterial (**A, B**) networks under different treatment conditions. Nodes represent ASVs (node size proportional to relative abundance; color indicates phylum). Lines between the nodes represent significant correlations, with blue and pink indicating positive and negative correlations, respectively. The bacterial community node-level co-occurrence networks topological properties (**C–E**) of the different treatments, avgK average degree, avgCC average degree, and Positive and negative link ratio, respectively. **F** Venn of rhizosphere soil ASVs in difference and network analysis. **G** The random forest is constructed by isolated strains. Heat maps showing the relative abundance of core ASVs and isolated strains in rhizosphere soil.



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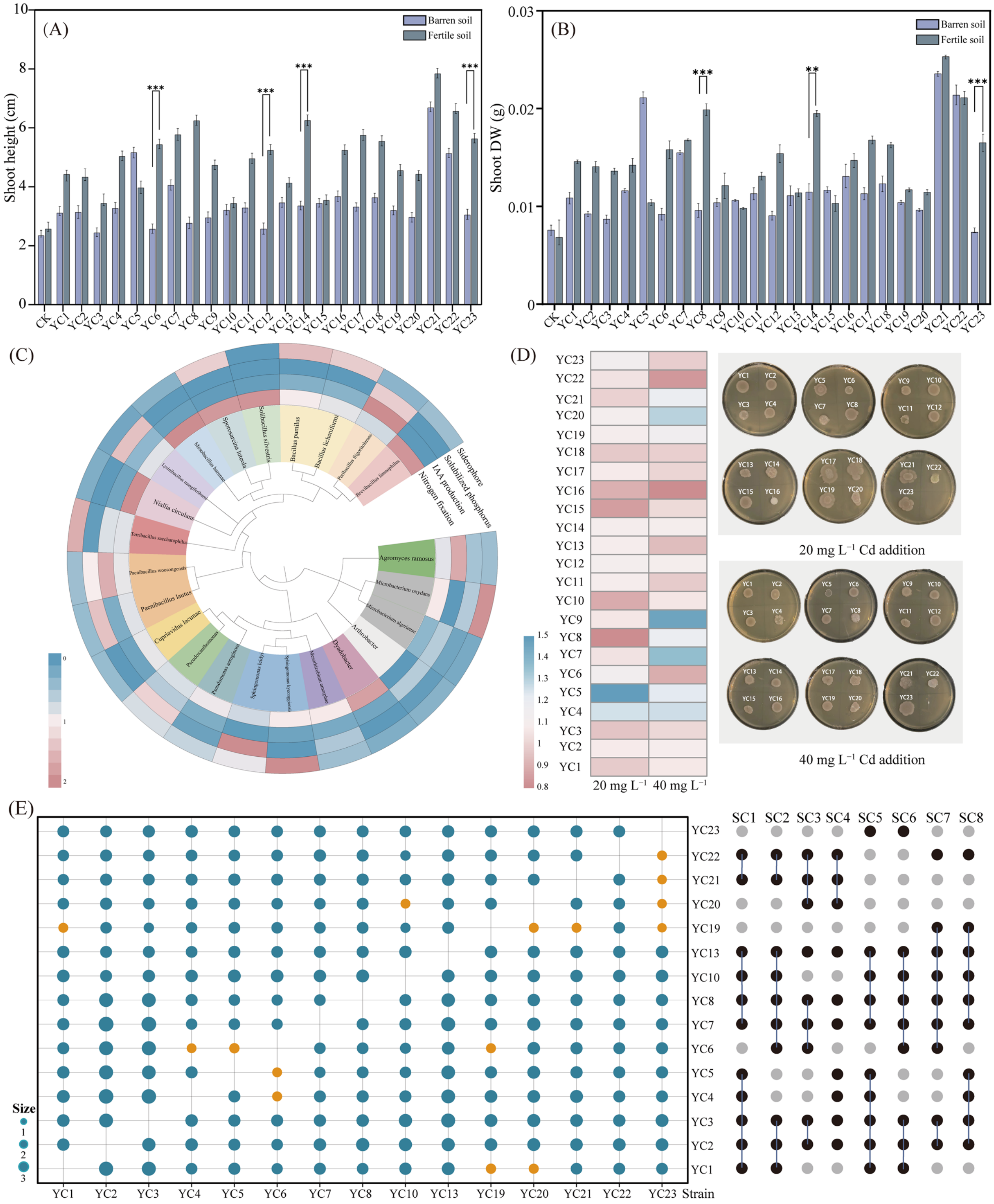

Fig. 5 A Soil from Cd contamination was used for microbial community analysis, identification, and screening of SynComs. Evaluation of the growth-promoting effect of 23 strains on chive. **A** Shoot height; **B** Shoot dry weight; **C** The phylogenetic tree of 23 strains on chive, with blue, yellow, red, and green indicating nitrogen fixation, IAA production, solubilized phosphorus, and siderophore. **D** The heatmap shows the growth state of 23 strains under the addition of 20 mg L^{-1} and 40 mg L^{-1} Cd. **E** The construction of SynComs and the pairwise interaction of growth-stimulating bacteria were conducted. The circle's size signifies OD (YC + supernatant)/OD(YC)

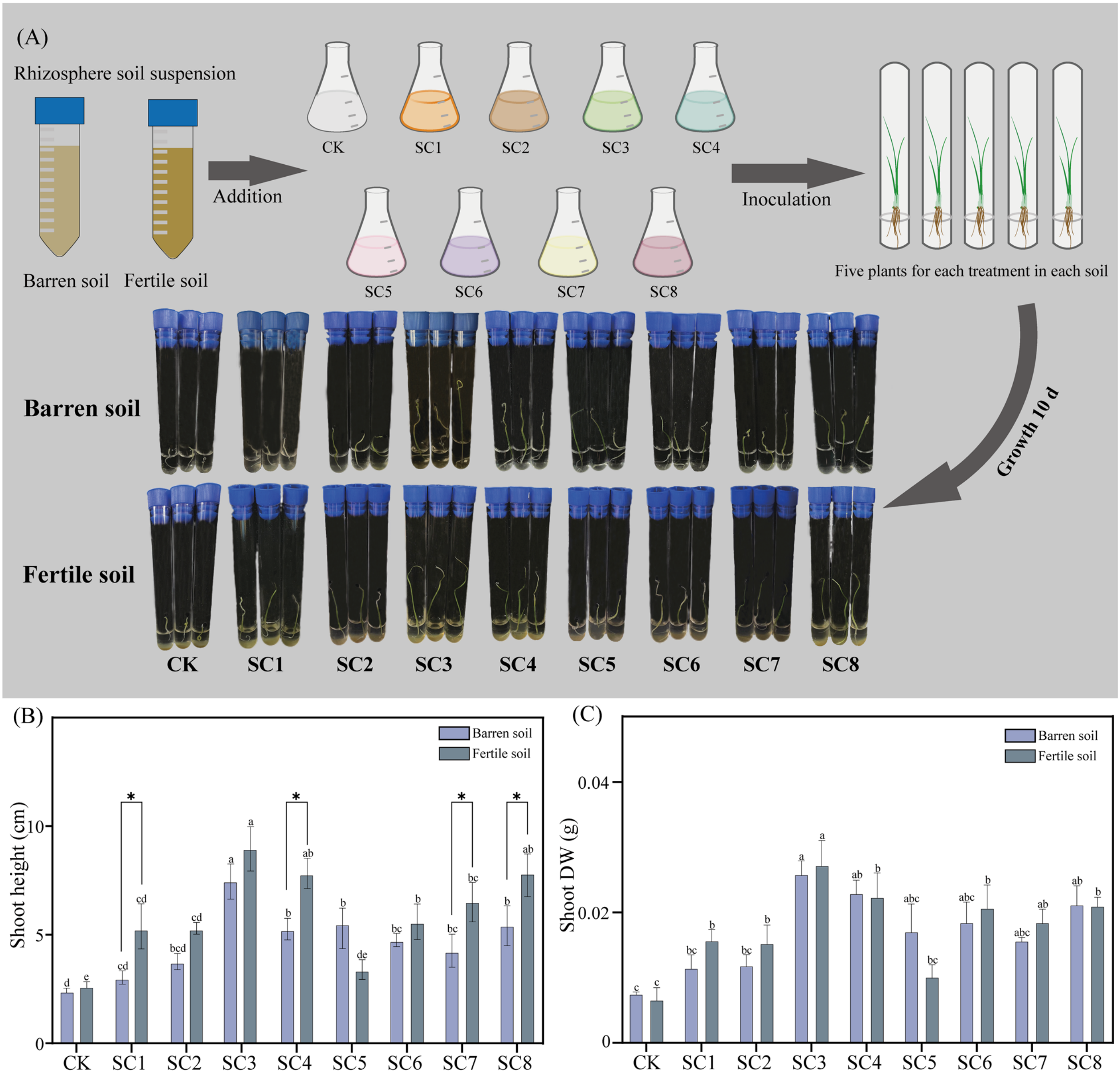

Fig. 6 SynCom construction and plant growth promotion experimental design. **A** Axenic chive seedlings were cultivated within tubular chambers for a duration of 10 days. Growth traits of chive in tube chambers. **B**, **C** Shoot height and weight

weight increases of 350.24%, 230.24%, 210.73%, 205.85%, 173.66%, 132.68%, 126.83%, and 51.22%, respectively).

4 Discussion

Enhancing soil health through green and environmentally friendly methods is considered a pivotal strategy, crucial for the improvement of soil nutrients and the surrounding environment, thereby ensuring global food security (Efthimiou 2025). In our study, the combined application of AMF and BC has shown positive impacts on plant growth and soil remediation. AMF inoculation enhances plant growth through antioxidative defense, photosynthesis, and nutrient uptake. BC supplies nutrients and habitat to facilitate AMF colonization, thereby synergistically promoting plant growth (Li et al. 2024; Nirukshan et al. 2022). Recent studies have shown that the combined application of AMF and BC in Cd-contaminated soil promoted wheat growth in an unexpected manner and significantly reduced Cd concentration in plants (Khan et al. 2020; Zhuo et al. 2020). Consistent with previous research, our findings revealed that the synergistic application of AMF and BC in Cd-contaminated soil augmented plant resilience and ameliorated soil quality to a certain degree in comparison to CK (Fig. 2). BC has been widely reported to possess high specific surface area and porous structure, which enhances soil porosity and permeability (Zhao et al. 2025; Jin et al. 2023). Additionally, it exhibits strong adsorption capacity for Cd, effectively immobilizing Cd in soils and reducing its availability (Cui et al. 2019; Chen et al. 2023a). The synergistic application of BC and AMF further amplified these effects, significantly alleviating Cd toxicity in Cd-contaminated soils and enhancing plant growth performance. Interestingly, the combined application of AMF and BC exhibited greater effectiveness in remediating barren soils contaminated with high concentrations of Cd (Fig. 2). Previous research showed that the synergistic effect of AMF and BC might vary depending on soil conditions and the type and concentration of heavy metals (Riaz et al. 2021; Fayuan et al. 2022). The synergistic effects of AMF and BC are reciprocal in alleviating nutrient limitations inherent in barren soils. In barren soil, the addition of BC improved soil characteristics, created a favorable microenvironment for AMF colonization, and promoted mycelial extension and nutrient absorption (Lehmann et al. 2011; Zhao et al. 2024). In addition, we found that the presence of high concentration of Cd in barren soil the microbial network more complex (Fig. 4A). We presume that in high Cd concentrations, microorganisms become more closely related to each other in order to survive and adapt, which may promote Cd adsorption. In barren soils, the length of the root system under high Cd stress was higher than that under low Cd stress (Fig. 2D). The root system is the primary organ for plants to absorb nutrients (Cochavi et al. 2020). This further promotes plant growth and increases biomass to mitigate the adverse effects of heavy metals. The higher TF values observed in fertile soils may be due to differences in soil properties (Fig. 2H). This could be attributed to the elevated pH and SOC content in fertile soils (Table S1), which facilitates the chelation of Cd with dissolved organic acids, thereby increasing the mobility of cadmium from the roots to the shoots (Chen et al. 2020). Consistent with previous research, inadequate nutrient upkeep in barren soils may restrict the transport of Cd (Li et al. 2022). Moreover, compared to fertile soils, barren soils exhibit lower pH and SOC content (Tab.S1). Previous studies have reported that Cd adsorption and desorption are closely associated with soil properties (Suda and Makino 2016; Yu et al. 2016). Soil pH influences metal solubility and speciation in soils, thereby determining their mobility and bioavailability, and negatively correlates with plant metal uptake (Zhao et al. 2010; Naz et al. 2022). SOC in soil both retains heavy metals through exchangeable forms and increases their bioavailability to plants by providing organic chelators (Zeng et al. 2011; Williams et al. 2012).

Utilizing the beneficial properties of microbial inoculants is considered an approach to sustainable development (Liu et al. 2023a). Although single strain inoculants have been well-documented for their growth-promoting responses in plants under both abiotic and biotic stress, they often struggle to perform in field conditions due to competition from the native microbiome (Zhou et al. 2023; Vorholt et al. 2017; Liu et al. 2023b). Therefore, the "one-microbe-at-a-time" approach has developed into creating SynComs that are more competitive and can maintain beneficial traits for plant growth (Wang et al. 2025; Shayanthan et al. 2022). We subsequently manipulated the microbiome after the co-application of AMF and BC with the aim of enhancing plant rhizosphere capacity against Cd contamination in soil. The diversity of rhizosphere microbial communities increased with increasing Cd concentration, suggesting that the rhizosphere may enrich more diverse species under Cd stress (Fig. 3). The relative importance of a strain is is typically inferred from the correlation between its abundance and the triggered effect (Naylor et al. 2017). To further exploration of these microorganisms enriched under Cd stress, we identified 64 Cd tolerant microbial strains through differential microbial analysis. Constructing SynComs by directly filtering bacteria possessing particular abilities from a single perspective frequently leads to inadequate application outcomes, as the interactions among candidate strains within their local community are not explicitly taken into account (Martins et al. 2023; Lin et al. 2022). Thus, co-occurrence network analyses offered proof of synergistic relationships among the inoculated microorganisms, with networks associated with Cd pollution exhibiting more complex connections (Fig. 4). Interestingly, 205 key microbes were identified in the Cd-contaminated network. Previous research has demonstrated that keystone taxa may exert a substantial influence on ecosystems, contribute to the keeping network structure, and interact with other microbes (Kwak et al. 2018; Chen et al. 2023). Based on species divergence and co-occurrence network analysis, our research aims to identify microorganisms capable of overcoming environmental dependencies and exhibiting broad adaptability (Figs. 3, 4). Hence, there is potential in recognizing the microorganisms that participate in the constitution of the plant microbiome and harnessing them for practical benefits. Interestingly, the significance of the screened microorganisms was evaluated by random forests, with culturable bacteria being ranked comparatively lower (Fig. 4G). Previous studies have indicated that bacterial species with low abundance contribute to specific functional characteristics (Rivett and Bell 2018) and exhibit a heightened response to external environment compared to more general species (Bickel et al. 2019; Bickel and Or 2021). Among these bacteria, numerous strains present difficulties in isolation and cultivation (Bergmann et al. 2011). Nonetheless, multiple cultivable bacteria have consistently demonstrated significant potential in assisting phytoremediation efforts. For instance, *Pseudomonas* serves as a biocontrol agent, exerting its influence on plants through the induction of systemic resistance via diverse mechanisms of action (Fakhar et al. 2022). *Microbacterium* are significant in enhancing plant growth and reducing heavy metal toxicity (Yadav et al. 2022).

The practical application of SynComs is significantly hindered by the neglect of natural interactions among microorganisms (Zhou et al. 2024; Ratzke et al. 2020). The paired antagonism experiments were employed to select bacteria that reciprocally utilize metabolic resources for mutual growth promotion (Qiao et al. 2024; Ruan et al. 2024). Furthermore, SynComs as an entirety encounter nutrient competition and resource exploitation (Liu et al. 2020; Culp and Goodman 2023). The strains used to construct SynComs all possess the abilities of nitrogen fixation, phosphorus solubilization, IAA production, siderophore production, and Cd resistance. The results showed that SynComs constructed from these strains significantly improve host plant growth under Cd pollution conditions (Fig. 5A). These SynComs included key strains possessing essential functions for host performance. The potentially beneficial genera *Paenibacillus*, *Pseudomonas*, and *Bacillus* have been widely reported to improve the resilience of host plants (Olishevska et al. 2019; Yan et al. 2024). In comparison to other SynComs, SC3 exhibited a notable superiority in promoting plant growth, with a higher proportion of *Bacillaceae*, followed by *Microbacteriaceae* and *Sphingomonadaceae* (Figs. 4, 5). Previous studies showed that Bacillaceae exhibit enhanced resistance to pollution stresses and severe environmental conditions, potentially resulting in their preponderance in Cd contaminated soils (Wang et al. 2024). Other studies have indicated that Microbacteriaceae act as resource acquisition strategists and can survive in environments with scarce nutrients (Liao et al. 2024; Algora et al. 2022). Therefore, the aim of this study is to effectively promote plant growth and alleviate heavy metal stress from the perspective of overall microorganisms, meaning that SymComs should transition from performing essential functions to activating community-wide functionalities. AMF and biochar hold promise for the remediation of Cd contaminated agricultural soils. However, this study was conducted in controlled greenhouse conditions, and field trials across diverse soils are warranted to validate findings. Challenges persist in optimizing the cost-effectiveness of AMF inoculum production and ensuring the long-term persistence and ecological stability of biochar in soil matrices. The next step is developing the trinity technology of "functional flora + biochar + inoculated microorganism" to improve the colonization efficiency of microorganisms through surface modification of biochar, obtain highly adaptable microbe-plant symbionts through continuous culture, and improve the basic ecology.

In summary, our results suggest that the combined application of AMF and BC plays a role in the remediation of Cd contaminated soil. The application of AMF and BC demonstrated greater efficacy in the remediation of soils with high Cd contamination under conditions of nutrient limitation. Based on these findings, we constructed different SynComs and identified SynCom3 as the most effective in enhancing plant growth, which reduces heavy metal stress for plants and supports sustainable agricultural production. Our results provide valuable information for the development of synthetic microbial fertilizers, which can be followed up to explore their effects on the yield further.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1007/s42773-025-00498-4.

Additional file 1

Author contributions

Zishan Li: Writing—original draft, Visualization, Methodology, Formal analysis, Conceptualization. Yu Wang, Keqing Lin, and Yuxin Zhai: Software, Data curation. Boyan Wang, Meiling Ping, Yizhen Meng, Wumei Luo: Methodology, Resources, Conceptualization. Xiaoyu Li and Chen Jin: Writing—review & editing, Funding acquisition.

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Data availability

The datasets utilized or analyzed during this study are available from the corresponding author upon reasonable request.

Declarations

Competing interests

The authors declare that they have no competing financial interests or personal relationships that may affect the coverage of this article.

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