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# *Bacillus amyloliquefaciens* FH-1 significantly affects cucumber seedlings and the rhizosphere bacterial community but not soil

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Plant growth-promoting bacteria (PGPB) inoculants have been applied worldwide. However, the ecological roles of PGPB under different soil conditions are still not well understood. The present study aimed to explore the ecological roles of *Bacillus amyloliquefaciens* FH-1 (FH) on cucumber seedlings, rhizosphere soil properties, and the bacterial community in pot experiments. The results showed that FH had significant effects on cucumber seedlings and the rhizosphere bacterial community but not on soil properties. The FH promoted cucumber seedlings growth, reduced the rhizosphere bacterial diversity, increased Proteobacteria, and decreased Acidobacteria. Linear discriminant analysis (LDA) effect size (LEfSe) revealed that FH enriched two taxa (GKS2_174 and Nannocystaceae) and inhibited 18 taxa (mainly Acidobacteria, Actinobacteria, BRC1, Chloroflexi, Plantctomycetes, and Verrucomicrobia). Co-occurrence network analysis demonstrated that FH increased bacteria-bacteria interactions and that *Bacillus* (genus of FH) had few interactions with the enriched and inhibited taxa. This might indicate that FH does not directly affect the enriched and inhibited taxa. Correlation analysis results displayed that cucumber seedlings' weight and height/length (except root length) were significantly correlated with the 18 inhibited taxa and the enriched taxa Nannocystaceae. It was speculated that FH might promote cucumber seedling growth by indirectly enriching Nannocystaceae and inhibiting some taxa from Acidobacteria, Actinobacteria, BRC1, Chloroflexi, Plantctomycetes, and Verrucomicrobia.

Cucumber is an important vegetable in many countries, including China. Due to the higher requirements, higher productivity of cucumbers relies heavily on chemical fertilizers and pesticides[1]. With increasing pollution and costs of chemical fertilizers and pesticides, plant growth-promoting bacteria (PGPB) inoculants are advantageous for the development of sustainable agriculture[2,3]. A substantial number of PGPB inoculants have been applied and commercialized for various crops worldwide[4–6]. PGPB mainly promote the growth of plants by providing nutrients, secreting hormones, antagonizing pathogens, and resisting stress[7,8]. However, poor productivity and stability impede the large-scale application of microbial inoculants in mainstream agriculture[9,10]. Understanding the ecological roles of the PGPB in the complex soil system may guide the development and application of PGPB inoculants in future.

*Bacillus amyloliquefaciens* is known for its ability to suppress plant pathogens and promote plant growth[11,12]. It has been widely applied on rice, tomato, cucumber, and lettuce, among others[13–15]. Many studies have demonstrated that *B. amyloliquefaciens* can reduce the incidence or severity of various diseases on a diversity of hosts[13,16,17]. This might be related to the secretion of antimicrobial lipopeptides, antibiotics, and hydrolases and might also be related to the regulation of the rhizosphere microbiome[12,13]. Many reports have shown that *B. amyloliquefaciens* can promote the growth of crops and improve the yield and quality of crops. This might be related to the secretion of indoleacetic acid (IAA), the improvement of available nutrients in soil through nitrogen fixation, phosphorus removal, and potassium dissolving, and the regulation of the rhizosphere microbiome[18–20].

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| Cucumber seedlings | CK | FH |
|---|---|---|
| **Fresh weight (g)** | | |
| *Plant* | 1.90 ± 0.20b | 3.25 ± 1.04a |
| *Shoot* | 1.71 ± 0.19b | 2.82 ± 0.90a |
| *Root* | 0.19 ± 0.04b | 0.43 ± 0.17a |
| **Dry weight (g)** | | |
| Plant | 0.15 ± 0.06b | 0.37 ± 0.17a |
| Shoot | 0.12 ± 0.06a | 0.25 ± 0.11a |
| Root | 0.03 ± 0.01a | 0.12 ± 0.09a |
| **Height/length (cm)** | | |
| Plant | 14.22 ± 1.09a | 16.23 ± 2.00a |
| *Shoot* | 9.73 ± 0.33b | 11.65 ± 1.55a |
| Root | 4.49 ± 1.00a | 4.58 ± 0.65a |

**Table 1.** Effects of *Bacillus amyloliquefaciens* FH-1 inoculation on cucumber seedlings. Values (means ± SD, n = 5) within the same row followed by different letters are significantly different at $P < 0.05$ according to Independent-Samples t Test. *CK* non-inoculated, *FH* inoculated with *Bacillus amyloliquefaciens* FH-1.

| | CK | FH |
|---|---|---|
| pH | 8.48 ± 0.07a | 8.46 ± 0.09a |
| TOC (g/kg) | 6.44 ± 3.40a | 4.08 ± 0.61a |
| TN (mg/kg) | 733.20 ± 199.73a | 765.60 ± 151.03a |
| TP (mg/kg) | 311.86 ± 20.96a | 342.35 ± 66.18a |
| NO$_3$-N (mg/kg) | 107.07 ± 16.23a | 117.51 ± 20.82a |
| AP (mg/kg) | 88.11 ± 0.95a | 89.65 ± 1.62a |

**Table 2.** Effects of *Bacillus amyloliquefaciens* FH-1 inoculation on rhizosphere soil properties. Values (means ± SD, n = 5) within the same row followed by different letters are significantly different at $P < 0.05$ according to Independent-Samples t Test. *TOC* total organic carbon, *TN* total nitrogen, *TP* total phosphate, *NO$_3$-N* nitrate nitrogen, *AP* available phosphate, *CK* non-inoculated, *FH* inoculated with *Bacillus amyloliquefaciens* FH-1.

In recent years, with the recognition of the importance of the rhizosphere microbiome, research on the effect of *B. amyloliquefaciens* on the rhizosphere microbiome has increased. Rhizosphere microbiomes play key roles in the disease, health, growth, and development of their host[21–24]. Many reports have indicated that the application of microbial inoculants could influence resident microbial communities[8,25–27]. The effects of *B. amyloliquefaciens* on the rhizosphere microbial communities of tomato, rice, lettuce, banana, tobacco, and cucumber were investigated (Table S3). However, most studies focus on community composition and diversity, while only a few focus on co-occurrence network analysis. Co-occurrence network analysis of taxon co-occurrence patterns might help identify potential biotic interactions between inoculants and soil indigenous microorganisms and increase the understanding of how inoculants affect microbial communities[13,28,29]. In addition, many studies on cucumbers are based on peat and vermiculite[13,19]. This may be different from the results based on soil. Moreover, the ecological roles of *B. amyloliquefaciens* under soil conditions are not well understood. The comprehensive effects of *B. amyloliquefaciens* on crops, soil, and microorganisms still lack systematic and in-depth study.

To better understand the ecological roles of *B. amyloliquefaciens* under soil conditions, we investigated the effects of *B. amyloliquefaciens* FH-1 (FH), which could significantly promote rice growth in field experiments[18], on cucumber seedlings, rhizosphere soil properties, and the bacterial community in soil by using high-throughput sequencing technology, network analysis, and multivariate statistical methods. This will provide theoretical guidance for the development and application of PGPB inoculants in future.

## Results
**FH had significant effects on cucumber seedlings.** The cucumber seedlings' weight and height were significantly affected by FH (Table 1). FH significantly increased the fresh weight of plants, shoots, and roots and increased the plant dry weight and shoot height of cucumber seedlings compared to those drenched with sterile deionized water (CK).

**FH had no significant effect on rhizosphere soil properties.** FH had no significant effect on soil pH, total organic carbon, total nitrogen, total phosphorus, nitrate nitrogen, or available phosphorus (Table 2). However, the soil total nitrogen, total phosphorus, nitrate nitrogen, and available phosphorus in FH were generally higher than that in CK.
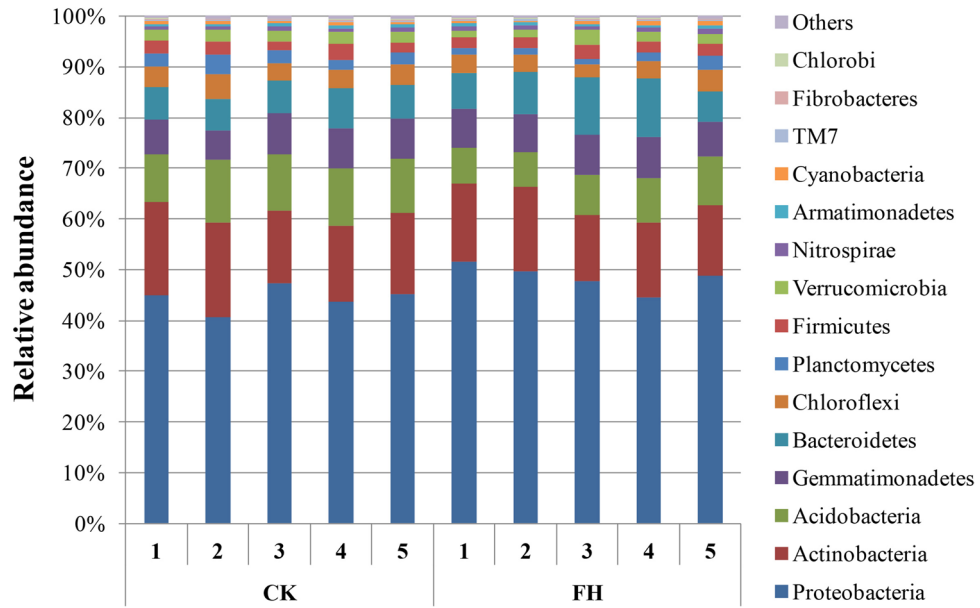
**Figure 1.** Relative abundance of the dominant rhizosphere bacterial phyla (proteobacterial classes) under different treatments. *CK* non-inoculated, *FH* inoculated with *Bacillus amyloliquefaciens* FH-1.
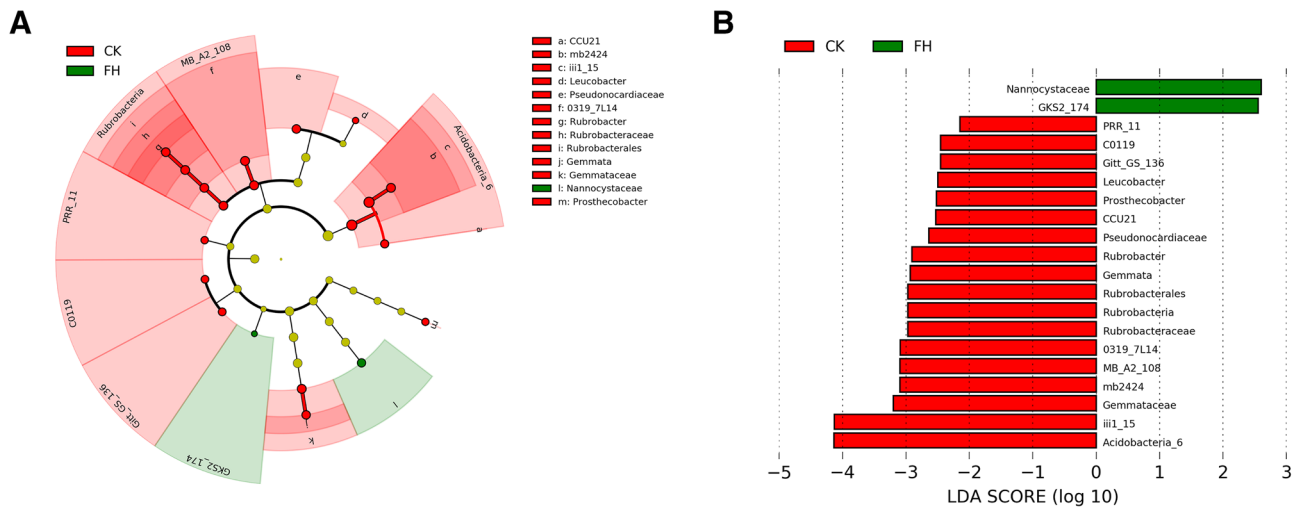


**Figure 2.** Cladogram (**A**) and linear discriminant analysis (LDA) score (**B**) of LEfSe analysis of the rhizosphere bacterial community between CK (red) and FH (green) treatments. *CK* non-inoculated, *FH* inoculated with *Bacillus amyloliquefaciens* FH-1.

**FH significantly affects rhizosphere bacterial community composition.** Across all samples, a total of 634,513 high-quality sequences and 57,039–68,492 sequences per sample (mean = 63,451) were obtained. After being rarefied to 57,000 sequences per sample, Alphaproteobacteria, Actinobacteria, Acidobacteria, Betaproteobacteria, Gammaproteobacteria, Deltaproteobacteria, Gemmatimonadetes, Bacteroidetes, Chloroflexi, Planctomycetes, Firmicutes, Verrucomicrobia, Nitrospirae, Armatimonadetes, Cyanobacteria, TM7, Fibrobacteres, and Chlorobi were found to be the dominant phyla (> 1%) across all treatments (Fig. 1). These dominant phyla accounted for more than 94% of the bacterial sequences from each soil sample. Deltaproteobacteria ($P = 0.01$) was significantly increased, while Acidobacteria ($P = 0.00$) was significantly decreased by FH (Table S1).

LEfSe analysis showed that a total of 20 bacterial groups were distinct between FH and CK treatments using the logarithmic (LDA) value of 2 (Fig. 2). The bacterial taxa enriched in FH were GKS2-174 and Nannocystaceae. Acidobacteria-6 (the class and its order CCU21 and iii1-15, the order and its family mb2424), MB-A2-108 (the class and its order 0319-7L14), Rubrobacteria (the class and its order Rubrobacterales, the order and its family Rubrobacteraceae), PRR-11, C0119, Gitt-GS-136, Gemmataceae (the family and its genus *Gemmata*), Pseudonocardiaceae, *Leucobacter,* and Prosthecobacter were enriched in CK, which also could be regarded as inhibited taxa in FH.

|  | CK | FH |
|---|---|---|
| Chao1 | 7176.53 ± 117.44a | 6971.29 ± 159.56a |
| Observed_otus | 4789.86 ± 98.59a | 4599.68 ± 64.80b |
| PD_whole_tree | 253.21 ± 3.46a | 246.76 ± 2.38b |
| Shannon index | 9.74 ± 0.11a | 9.63 ± 0.07a |

**Table 3.** Effects of *Bacillus amyloliquefaciens* FH-1 inoculation on rhizosphere bacterial alpha diversity. Values (means ± SD, n = 5) within the same row followed by different letters are significantly different at *P* < 0.05 according to Independent-Samples t Test. *Chao1* richness of the Chao1 estimator, *Observed_otus* observed operational taxonomic units, *Shannon index* nonparametric Shannon diversity index, *CK* non-inoculated, *FH* inoculated with *Bacillus amyloliquefaciens* FH-1.
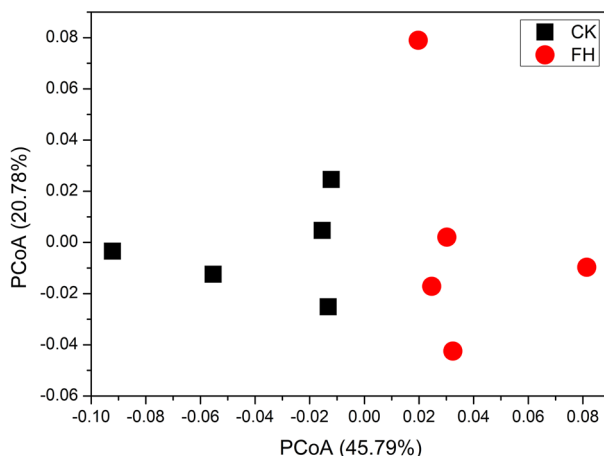


**Figure 3.** Principal coordinate analysis (PCoA) of weighted UniFrac distances of the rhizosphere bacterial community under different treatments. *CK* non-inoculated, *FH* inoculated with *Bacillus amyloliquefaciens* FH-1.

The relative abundances of both *B. amyloliquefaciens* and *Bacillus* spp. were slightly higher in FH than in CK (Fig. S1). This suggested that *B. amyloliquefaciens* FH-1 might slightly colonize cucumber rhizosphere soil.

**FH had negative effects on rhizosphere bacterial diversity.** The rhizosphere bacterial α-diversity was negatively affected by FH (Table 3). FH significantly decreased Observed_otus (*P* = 0.01) and PD_whole_tree (*P* = 0.02). Chao1 (*P* = 0.07) and the Shannon index (*P* = 0.10) were lower in FH than in CK.

Principal coordinate analysis (PCoA) revealed that the rhizosphere bacterial communities of FH were distinct from those of CK (Fig. 3). ANOSIM analysis (global R = 0.488, *P* = 0.008) and PERMANOVA analysis (R$^2$ = 0.326, *P* = 0.009) demonstrated that the structure of bacterial communities was significantly changed by FH.

**FH modified rhizosphere bacterial networks.** Whether FH affected the interaction of bacterial communities and whether FH interacted with enriched or inhibited taxa at the genus level were determined using co-occurrence network analysis based on a strong (Spearman's r > 0.6) and significant (*P* < 0.05) correlation. The calculated modularity index was larger than 0.4, and the random modularity index (Table 4) indicated a typical module structure[30]. Overall, the FH showed a remarkable influence on the co-occurrence networks in bacterial communities (Fig. 4). The number of positive correlations was higher than that of the negative correlations in both networks. FH had higher edges, negative correlations, and an average degree and modularity but lower positive correlations than CK (Table 4). There were more species interacting with *Bacillus* in FH than that in CK. There were 19 genera that interacted with *Bacillus*, and seven of them had positive interactions in FH. In CK, only seven genera interacted with *Bacillus*, and six of them had positive interactions (Fig. 4 and Table S2). *Bacillus* only had positive interactions with the inhibited taxa *Leucobacter* in CK and the inhibited taxa MB-A2-108 in FH.

**Cucumber seedling characteristics were significantly correlated with the bacteria inhibited and enriched by FH.** Correlation analysis showed that cucumber seedlings' weight and height/length (except root length) had a significant correlation with the bacteria taxa inhibited and enriched by FH (Fig. 5). All 18 inhibited taxa (mainly Acidobacteria, Actinobacteria, BRC1, Chloroflexi, Plantctomycetes, and Verrucomicrobia) were significantly and negatively correlated with some cucumber seedlings' characteristics. These inhibited taxa had a closer relationship with cucumber shoots than roots. Enriched taxa Nannocystaceae had a significant positive correlation with cucumber shoot height.

|  | CK | FH |
|---|---|---|
| **Empirical networks** | | |
| Number of nodes | 817 | 817 |
| Number of edges | 3963 | 4107 |
| Number of positive correlations | 2743 (69.22%) | 2635 (64.16%) |
| Number of negative correlations | 1220 (30.78%) | 1472 (35.84%) |
| Average degree | 4.851 | 10.054 |
| Average clustering coefficient | 1 | 1 |
| Average path length | 1 | 1 |
| Network diameter | 1 | 1 |
| Graph density | 0.012 | 0.012 |
| Modularity | 0.967 | 0.970 |
| **Random networks** | | |
| Average clustering coefficient | $0.012 \pm 0.001$ | $0.012 \pm 0.001$ |
| Average path length | $3.202 \pm 0.003$ | $3.157 \pm 0.002$ |
| Modularity | $0.284 \pm 0.004$ | $0.278 \pm 0.004$ |

**Table 4.** Topological properties of rhizosphere bacterial networks obtained from different treatments. *CK* non-inoculated, *FH* inoculated with *Bacillus amyloliquefaciens* FH-1.
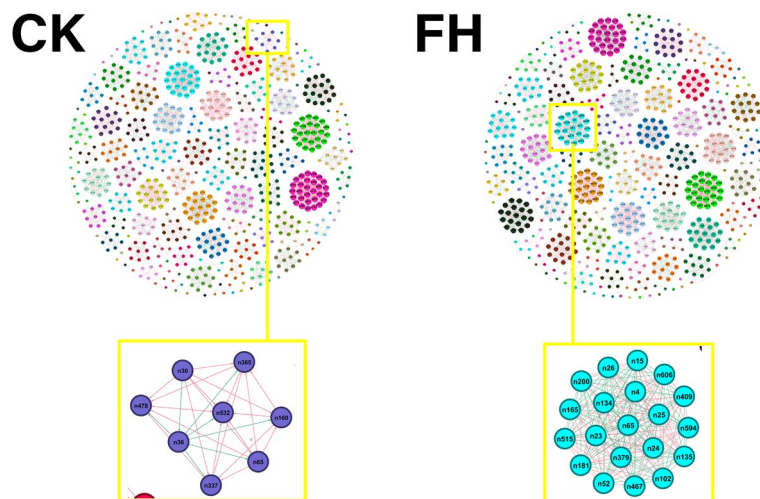


**Figure 4.** Networks of co-occurring rhizosphere bacterial genera in non-inoculated (CK) and *Bacillus amyloliquefaciens* FH-1 inoculated (FH) soil based on correlation analysis. A connection stands for a strong (Spearman's r > 0.6) and significant (*P* < 0.05) correlation. A blue edge indicates a negative interaction between two individual nodes, while a red edge indicates a positive interaction. The thickness of each connection between two nodes (i.e., edge) is proportional to the value of Spearman's correlation coefficient. The co-occurring networks are colored by modularity class. The size of each node is proportional to the number of connections (i.e., degree). *Bacillus* is labeled n65.

## Discussion

In this study, the ecological roles of inoculant *B. amyloliquefaciens* FH-1 on cucumber seedlings, rhizosphere soil, and the bacterial community were investigated. The results illustrated that FH had a significant effect on cucumber seedlings and the rhizosphere bacterial community but not on soil.

Rhizosphere bacterial communities play a key role in the disease, health, growth, and development of plants[31–33]. The effect of PGPB on the bacterial community is still unclear. As a well-known PGPB, the effect of *B. amyloliquefaciens* on the bacterial community has been widely studied (Table S3). Some studies have shown that *B. amyloliquefaciens* has no influence on rhizosphere bacteria, while some have a significant influence. Some increased diversity, while some decreased diversity, and some improved Proteobacteria, while some improved Firmicutes[13–19,34–38]. In this study, we found that FH inoculation significantly reduced bacterial diversity, increased Proteobacteria that may belong to r-strategies, and decreased Acidobacteria that may belong to k-strategies[14]. The influence of *B. amyloliquefaciens* on the bacterial community may be attributed to different strains, plant species, soil types, and environmental factors. Therefore, it is necessary to investigate the influence of *B. amyloliquefaciens*
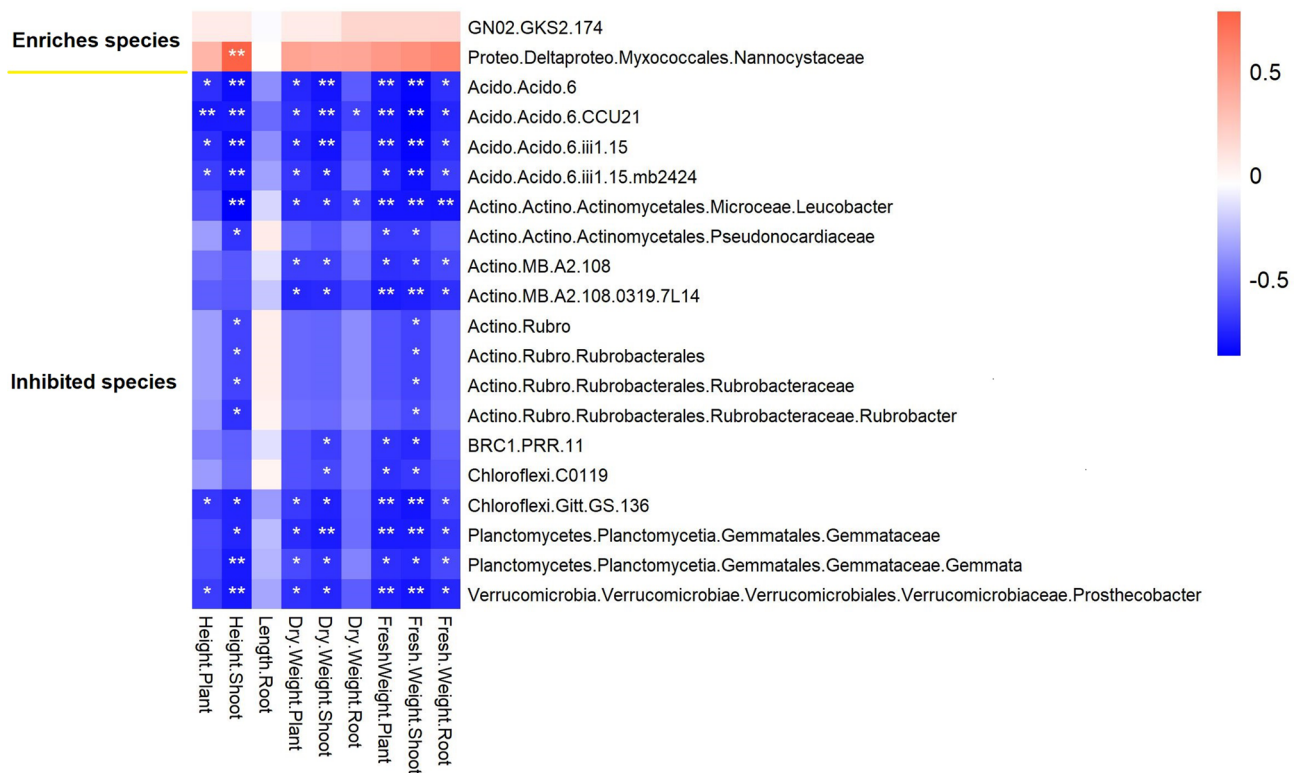
**Figure 5.** Heatmap of Spearman's correlation coefficients between cucumber seedlings and bacteria inhibited and enriched by FH. The colors represent the correlation, with red being more positive and blue being more negative. Significance is given as *($P < 0.05$) and **($P < 0.01$).

on the bacterial community of the same crop in different soils or different crops in the same soil to reveal the regulation of *B. amyloliquefaciens* on the bacterial community.

LEfSe was used to identify taxa that were inhibited and enriched by FH. The inhibited taxa were mainly Acidobacteria, Actinobacteria, Chloroflexi, BRC1, Planctomycetes, and Verrucomicrobia. The inhibited Acidobacteria_6 was universal in soil, yet our knowledge of the role of these diverse organisms remained rudimentary[39,40]. Some Actinobacteria are pathogenic to plants. The vast majority of Actinobacteria are important saprophytes capable of decomposing plant and animal debris[41]. Species of Pseudonocardiaceae are recognized as emerging opportunistic pathogens of plants and animals[42]. *Rubrobacter* spp. are extremophiles with radioresistant characteristics[43,44]. *Leucobacter* spp. are generally identified as chromium reducers[45,46]. Certain subspecies of *Leucobacter* have the potential for pathogenic interactions with nematodes[47]. Chloroflexi usually exist in some extreme environments[48,49]. Planctomycetes, Verrucomicrobia, and BRC1 belong to the PVC superphylum. This group appeared to be ubiquitous and contained pathogenic species[50]. *Prosthecobacter* has been found in freshwater, activated sludges, and *Panax notoginseng*[51,52]. Gemmataceae and its genus *Gemmata* have been found in wastewater plants, acid bogs, swamps, and the soil[53,54]. The inhibited taxa were not common disease bacteria. They may be potentially harmful bacteria or useless bacteria on cucumbers. The enriched taxa contained GN02_GKS2_174 and Nannocystaceae. At present, little is known about the ecological function of GN02. Nannocystaceae was reported to promote *Brassica napus* growth[55].

In addition, network analysis was used to understand how *B. amyloliquefaciens* FH-1 affected the interactions of bacterial communities and to explore whether *B. amyloliquefaciens* FH-1 interacted with the enriched and inhibited taxa. The relative abundance of *B. amyloliquefaciens* was too low; so, a co-occurrence network at the genus level was constructed. The results showed that FH increased the complexity of the whole network, especially the negative interactions. The higher complexity of networks was more resilient to environmental stressors, as different species can complement each other[56]. A negative correlation may mean competition[57]. It is possible that FH increased the competition among bacterial communities and led to the decrease of some taxa and the α-diversity. FH also increased the interactions of *Bacillus* with other genera, especially negative interactions. Except for MB-A2-108 and *Leucobacter* in Actinobacteria, *Bacillus* had no interaction with other inhibited or enriched taxa. This might indicate that *B. amyloliquefaciens* FH-1 does not directly affect the enriched and inhibited taxa. In CK and FH, *Bacillus* and the taxa it interacted with belonged to a module (Fig. 4). Modules reflect the heterogeneity of habitats, aggregation of closely related species in phylogeny, niche overlap, and co-evolution of species[58]. The genera interacting with *Bacillus* in FH (nine phyla) were completely different from those in CK (four phyla) (Table S2). It was speculated that the function of the module with *Bacillus* as the core changed after being inoculated with *B. amyloliquefaciens* FH-1.

Correlation analysis showed that except for GN02_GKS2_174, all inhibited and enriched taxa had significant correlations with cucumber seedlings' weight and height/length, except root length. This indicated that

*B. amyloliquefaciens* FH-1 might promote cucumber seedling growth by regulating the bacterial community and indirectly enriching Nannocystaceae and inhibiting some taxa from Acidobacteria, Actinobacteria, BRC1, Chloroflexi, Plantctomycetes, and Verrucomicrobia. This result was roughly supported by many previously published studies[18,59]. Regulating the rhizosphere microbiome is an important mechanism for PGPB to promote plant growth. Whole genome data showed that *B. amyloliquefaciens* FH-1 had no complete pathway for nitrogen fixation or secretion of IAA, gibberellin (GA), abscisic acid (ABA), or ethylene but had a complete pathway to secrete organic acids (malic acid, acetic acid, succinic acid, and gluconic acid), phytase, zeatin, and siderophore (data not shown). This study showed that FH had no significant effect on soil properties, suggesting that the ability of *B. amyloliquefaciens* FH-1 to dissolve phosphorus and potassium did not play a role in soil characteristics. In our next work, we will verify whether FH promotes cucumber seedling growth by secreting zeatin and siderophore.

## Materials and methods

**Bacterial inoculum preparation.**   *B. amyloliquefaciens* FH-1 was grown at 30 °C for 48 h in Luria–Bertani (LB) broth on a rotary shaker (180 rpm). The cells were harvested by centrifugation ($5000 \times g$ for 10 min), and the bacterial pellet was washed three times with 0.9% NaCl and finally resuspended in sterile deionized water at $1 \times 10^8$ CFU/ml.

**Pot experiment for the cultivation of cucumber seedlings.**   For future applications in coastal saline-alkali land, soil (pH 8.14, 4.1 g/kg organic matter, 655 mg/kg total N, 18 mg/kg available N, 250 mg/kg total P, 155 mg/kg available P, 4893 mg/kg total K, and 124 mg/kg available K) was collected from the upper 30 cm of a weed field in an airport economic area in Tianjin, China. The sampled soil was air dried and mixed thoroughly, followed by a sieving step (0.5-cm mesh) to remove plant debris. Cucumber seeds (Jin you NO.1, Tianjin Kerun Agricultural Science Technologies Inc., Tianjin, China) were procured from the local market (Fig. S2). Two cucumber seeds were sown in each plastic pot (diameter 8 cm; height 10 cm) containing 300 g of soil. Pot soils were drenched with 300 ml of the prepared inoculums or equivalent sterile deionized water. In total, there were two treatments: (1) soil drenched with *B. amyloliquefaciens* FH-1 (FH), and (2) soil drenched with sterile deionized water (CK). Five replications of each treatment were set up during the entire experimental period. Pots were placed randomly in a growth chamber at 28 °C day/17 °C night, 75% relative humidity, and 9 h light, and watered weekly. All methods were carried out in accordance with relevant guidelines and regulations.

**Plant characteristics and soil chemical properties.**   At 35 days after sowing, plants of each pot were harvested and carefully separated into roots and shoots to determine the growth parameters, including length, fresh weight, and dry weight, using rulers and balances. Meanwhile, rhizosphere soil was shaken off of the roots of each treatment to be collected and stored at 4 °C and − 80 °C, respectively.

The rhizosphere soil pH, total organic carbon, total nitrogen, total phosphorus, nitrate nitrogen, and available phosphorus were determined using commercial chemical assay kits (Suzhou Comin Biotechnology Co. Ltd., Suzhou, China) following the manufacturer's instructions.

**DNA extraction, PCR amplification, and Hiseq sequencing.**   Soil metagenomic DNA was isolated from 10 soil samples by the PowerSoil DNA isolation kit (MO BIO Laboratories Inc., Carlsbad, CA, USA) according to the manufacturer's instructions. DNA purity and concentration were monitored by 1% agarose gels and NanoDrop ND-2000 spectrophotometry (NanoDrop Technologies, Wilmington, DE, USA), respectively. The bacterial hypervariable regions (V4) of the 16S rRNA genes were amplified using primer 515F-806R with a barcode[60]. PCR products were purified and sequenced using the Miseq platform at Novogene Co. Ltd (Tianjin, China). The raw sequence data were deposited in the NCBI Sequence Read Archive as accession PRJNA544608 for bacteria. Raw data were processed and analyzed as previously described using the QIIME[60]. The relative abundance of *B. amyloliquefaciens* was determined by local BLAST.

**Data analyses.**   All statistical analyses were performed using R (version 3.1.1)[61]. The cucumber seedlings' characteristics, soil properties, bacterial α-diversity indices, and relative abundance of taxa in different treatments were compared using Independent Sample t tests. Principal coordinate analysis (PCoA), analysis of similarity (ANOSIM), and permutational multivariate analysis of variance (PERMANOVA) with the ADONIS function based on weighted UniFrac distance were performed to evaluate the overall differences in the bacterial community[62]. Linear discriminant analysis (LDA) effect size (LEfSe) analysis was used to identify taxa that were enriched and inhibited by FH[63]. Network analysis was used to explore whether FH affected bacteria-bacteria interactions and whether FH directly interacted with the enriched or inhibited taxa at the genus level. The co-occurrence network was inferred based on the Spearman correlation matrix constructed with the 'Hmisc' and 'igraph' package in R. We generated network images and calculated network properties with Gephi[64,65]. Spearman's rank correlation coefficient was used to evaluate the relationships between cucumber seedlings and the taxa enriched and inhibited by FH. Heatmaps that illustrate correlation data were generated using the 'pheatmap' package in R.

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## Author contributions

J.W. participated in the design of the experiment, performed pot experiment, data analysis, and manuscript writing. S.X. and W.Z. performed data analysis. R.Y., D.Z., and X.Z performed pot experiments and data analysis. Z.H. participated in the conception of the project. All authors reviewed the manuscript.

## Competing interests

The authors declare no competing interests.

## Additional information

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