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REVIEW

# Interactions of PGPR from the phylum bacillota with native rhizosphere microbiota: current insights and future perspectives

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**Abstract**
The intensive use of synthetic fertilizers and pesticides has increased crop productivity but also contributed to soil degradation and biodiversity loss, highlighting the need for more sustainable agricultural strategies. Among emerging solutions, plant growth-promoting rhizobacteria (PGPR), particularly members of the Bacillota phylum, are gaining attention as effective bioinoculants that enhance plant growth and tolerance to biotic and abiotic stresses. However, introduced strains do not function in isolation. They enter complex microbial communities, shaped by plant type and developmental stage, influenced by soil properties and environmental conditions. While the positive effects of PGPR on plant performance are well documented, their impact on indigenous rhizosphere microbiota remains less studied. This review synthesizes current knowledge on how Bacillota-based inoculants influence native microbial communities in cereals, vegetables, orchard crops, and fiber plants. Most studies report shifts toward plant-beneficial taxa and reduced abundance of potential pathogens following Bacillota application. Frequently enriched genera include *Bacillus*, *Pseudomonas*, *Lysobacter*, *Sphingomonas*, *Streptomyces*, *Azotobacter*, *Arthrobacter*, *Pseudarthrobacter*, *Bradyrhizobium*, *Devosia*, *Flavobacterium*, *Klebsiella*, *Herbaspirillum*, and *Rhodanobacter*. These changes are often associated with improved plant growth and yield, and stress resilience. However, responses strongly depend on strain, plant and methodological approach. We summarize commonly applied approaches used to assess these interactions. Despite technological advances, limitations remain, such as single time-point sampling, simplified experimental systems, and insufficient integration of inoculant persistence with community analyses. Standardized, multi-site experimental frameworks, with multiple sampling terms are needed to improve predictability and ensure the safe implementation of PGPR-based solutions in sustainable agriculture.

**Keywords** Plant growth-promoting rhizobacteria · Bacillota · Rhizosphere microbiome · Microbiome modulation

## Introduction

The global population is increasing at an unusual rate, driving a continuously rising demand for food production. Enhancement of agricultural productivity often relied on the intensive use of synthetic fertilizers, pesticides and large-scale monocultures. However, these practices contribute to soil degradation, biodiversity loss, and increase of climate changes (Tripathi et al. 2020; Pereira et al. 2025). Additionally, soil erosion and climate-related pressures intensify abiotic stress, in consequence reducing both the quantity and quality of crop yields (2021; Poria et al. 2022; Ocwa et al. 2023; Hussen et al. 2026). In response to these challenges, there is a growing pressure on development of sustainable and environmentally friendly strategies that can reduce overusing inorganic fertilizers and enhance plant resilience to biotic and abiotic stress. Among the promising approaches, gaining increasing attention, is the application of plant growth-promoting rhizobacteria (PGPR), which offer a potential pathway toward more sustainable agricultural systems (Lopes et al. 2021; Dobrzyński et al. 2026c).

Rhizobacteria, bacteria inhabiting the rhizosphere, often establish mutualistic interactions with their host plants, contributing to plant growth promotion and suppression of phytopathogens. Increasing evidence suggests that PGPR can enhance the growth and performance of a wide range of host plants across different taxonomic groups (Khoso et al.

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2024; Naziębło et al. 2025). Among the most promising and most studied rhizobacteria genera are *Pseudomonas*, *Bacillus*, *Paenibacillus*, *Enterobacter*, *Serratia*, *Burkholderia*, *Azotobacter*, *Acinetobacter*, *Mesorhizobium*, *Rhizobium*, *Arthrobacter*, and *Klebsiella* (including *Raoultella*) (Li et al. 2022; Dobrzyński and Jakubowska 2025; Dobrzyński et al. 2026b). *Bacillus* and *Paenibacillus* are considered particularly promising as eco-friendly alternatives, due to their biocontrol properties and ability to form resilient endospores that increase survival chances under diverse environmental conditions (Radhakrishnan et al. 2017; Tariq et al. 2025).

The number of studies investigating beneficial effects of PGPR on various plant species increased each year. However, the majority of this research has primarily focused on direct plant-bacteria interactions, while the impact of inoculants on the native rhizosphere microbiota has often been overlooked (De Andrade et al. 2023; Yang et al. 2024b). In cases where such interactions have been examined, studies frequently lack consistency and are limited to one sampling term, single conditions type, and single soil type (Oulkhir et al. 2025; Patyka et al. 2025). This limitation reduces the likelihood of obtaining reproducible and generalizable results.

Despite inconsistencies across studies, most evidence indicates that PGPR inoculation indeed affects the native microbiota (Mawarda et al. 2020). Understanding the interactions between native microbial communities and introduced inoculants is essential for optimizing the effectiveness and ensuring safety of PGPR applications in agriculture (Berg et al. 2021). PGPR inoculants often have problems with surviving in soil, which can reduce their overall effectiveness. Consequently, there is a growing interest in using PGPR not only as direct plant growth enhancers but also as modulators of the native rhizosphere microbiota, which plays crucial role in maintaining soil homeostasis and plant health (Orozco-Mosqueda et al. 2018; Vuolo et al. 2022; Dobrzyński et al. 2026d).

The aim of this review is to summarize the current state of knowledge, identify existing gaps and methodological limitations in assessing the impact of PGPR from Bacillota on native microbial communities, and highlight emerging approaches that may provide more comprehensive insights into these complex interactions.

## Plant growth-promoting rhizobacteria interaction

Soil directly surrounding plant roots, called rhizosphere, is characterized by greater microbial abundance and decreased taxonomic diversity compared to bulk soil. This enrichment is primarily driven by root exudates released by plants, which increase the availability of the organic carbon in the soil (Bakker et al. 2013; Sasse et al. 2018; Pathan et al. 2020). Easily available organic compounds make the rhizosphere an attractive niche for a wide range of micro- and macroorganisms, including viruses, bacteria, archaea, fungi, and even other plants and animals. These organisms interact in diverse ways, which can be broadly categorized as antagonistic (e.g., predation, parasitism, or competition) or non-antagonistic (e.g., mutualism or symbiosis) (Leach et al. 2017; Yang et al. 2024a). Rhizobacteria interact both with their host plants and with other members of the microbial community (Fig. 1). The outcomes of these interactions play a crucial role in shaping microbiome structure and directly influence plant health (Chepsergon and Moleleki 2023).

### PGPR interaction with host plants

Rhizosphere bacteria frequently establish mutualistic interactions with plants (Khoso et al. 2024). They protect the host from pathogens, for instance by competing with other microorganisms, including bacteria and fungi, and simultaneously promote plant growth through the production of metabolites and enzymes. Among them, plant growth-promoting rhizobacteria enhance plant development via both direct and indirect mechanisms (Chen et al. 2024). Direct effects include secretion of phytohormones (Goud et al. 2025), nitrogen fixation (Kazerooni et al. 2021), and solubilization of essential minerals such as phosphorus and potassium (Wani et al. 2007; Xiang et al. 2023). Indirect mechanisms involve responding to biotic and abiotic stresses, for instance through induction of systemic resistance (ISR) (Fatouros et al. 2018; Dobrzyński et al. 2023), production of fungistatic and antibiotic compounds, such as lipopeptides (Selim et al. 2010; Bouchard-Rochette et al. 2022) and volatile organic compounds (VOCs) (Liu et al. 2008; Raza et al. 2015; Poulaki and Tjamos 2023), and secretion of hydrolytic enzymes that degrade the cell walls of pathogens (Drewnowska et al. 2020). Rhizobacteria can employ multiple growth-promoting mechanisms simultaneously, with their activity depending on environmental conditions and developmental stage of the host plant (Li et al. 2022).

## PGPR interaction with native microbiota

In contrast to the extensively studied interactions between PGPR and host plants, interactions between PGPR and other bacteria in the rhizosphere remain relatively understudied. Most available studies focused primarily on antagonistic relationships between PGPR and plant pathogens. However, to fully use the potential of PGPR inoculants and improve

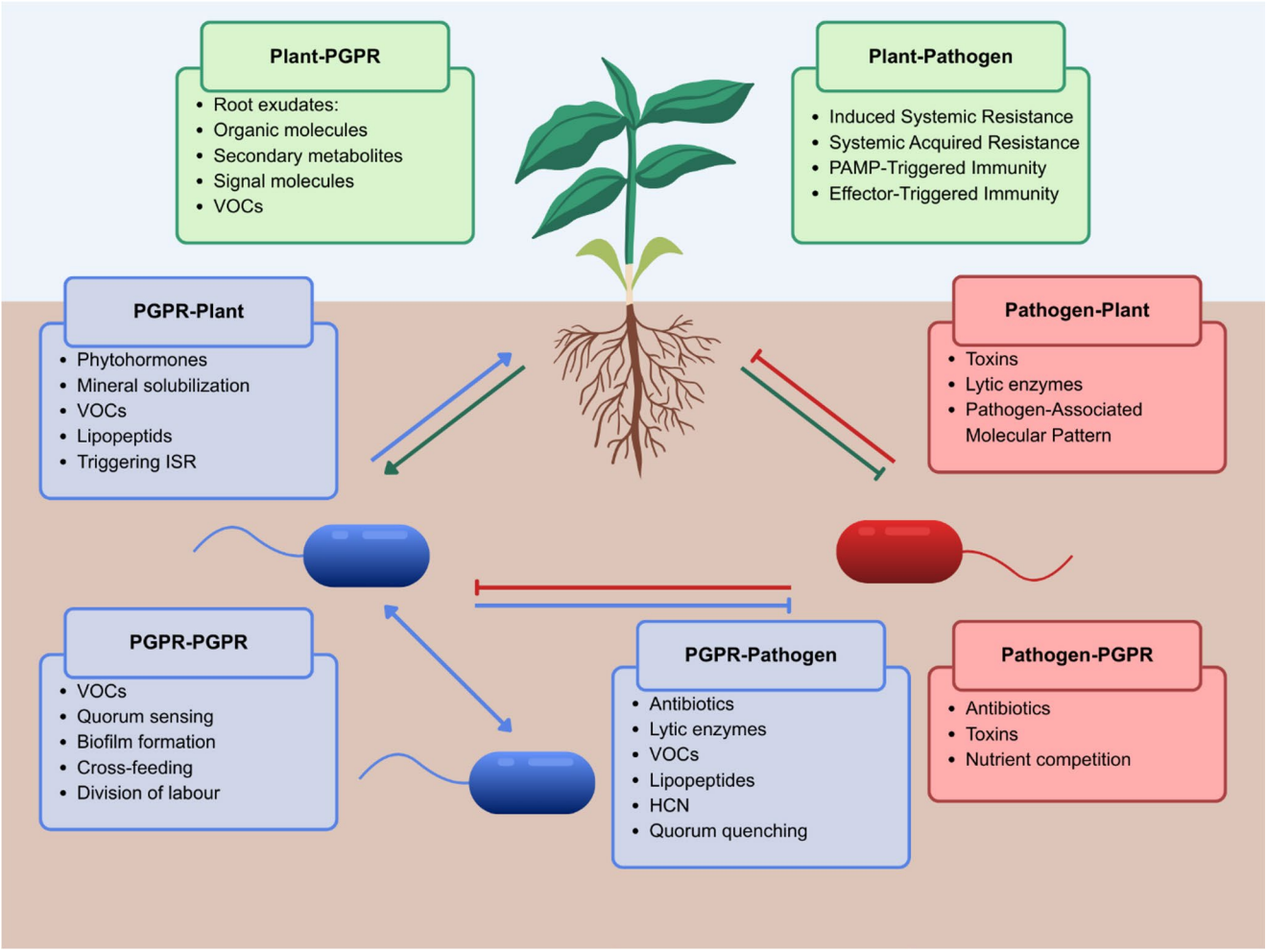


**Fig. 1** Overview of interaction in the rhizosphere amongst PGPR, host plant, and pathogens (Laishram et al. 2025; Simas et al. 2025; Sibanyoni et al. 2026)

their effectiveness and persistence in soil, it is essential to understand both antagonistic and non-antagonistic interactions between introduced strains and the native microbiota (Berg et al. 2021; Cotta et al. 2025).

Bacteria typically inhabit environments densely populated by numerous species, where intense competition for limited nutrients drives strong selective pressures. Consequently, many bacterial taxa evolved diverse and highly specialized systems for nutrient acquisition, including siderophore production and efficient uptake transporters. In parallel, bacteria frequently synthesize a wide array of antimicrobial compounds that enable them to eliminate competing microorganisms (Chepsergon and Moleleki 2023).

*Bacillus*, *Paenibacillus*, *Priestia* and *Brevibacillus* are among the most extensively studied PGPR genera within the Bacillota phylum. These bacteria are known for producing a broad spectrum of antimicrobial metabolites, including lipopeptides, VOCs, and hydrolytic enzymes. Lipopeptides are cyclic amphiphilic oligopeptides with strong antimicrobial activity, synthesized by numerous *Bacillus* and *Paenibacillus* species. The most prominent classes of these compounds include surfactins, iturins, fengycins and polymyxins (Jiang et al. 2016; Fujita and Yokota 2019; Zhou et al. 2020; Hossain et al. 2023). VOCs are low-molecular-weight chemicals that easily evaporate and disperse under standard temperature and pressure conditions. They are produced by both plants and microorganisms, serving as key mediators of interspecies communication. Microbial VOCs (MVOCs) affect gene expression, membrane permeability, and enzymatic activity in target organisms. Acting as signaling molecules, VOCs may have either positive or negative effects on targeted organisms, by modulating their physiological and behavioral responses (Veselova et al. 2019; Poveda 2021). Some MVOCs exhibit inhibitory or antimicrobial activity against other microorganisms or induce ISR in plants, enhancing their defense against pathogens (Raza et al. 2015; Poulaki and Tjamos 2023). Interestingly, certain bacterial

VOCs may stimulate the growth of specific microbial taxa while suppressing others (Garbeva et al. 2014; Kong et al. 2021). Siderophores represent another key class of secondary metabolites produced by rhizosphere bacteria. These iron-chelating compounds are taken up through highly specific receptor-mediated transport systems, allowing bacteria equipped with compatible receptors to access chelated iron. As a result, siderophore production serves as competitive advantage by limiting iron availability to organisms lacking the appropriate uptake mechanisms, while simultaneously facilitating cooperative interactions within closely related species that share similar siderophore receptors (Singh et al. 2022; Chepsergon and Moleleki 2023).

Except for antagonistic interactions, PGPR can also engage in neutral or beneficial interplays with members of native microbiota, contributing to increased microbial diversity and enrichment of beneficial microbials (Mmotla et al. 2025). PGPR inoculation can modify soil physicochemical properties, such as nutrient availability and pH, thereby constructing ecological niches that enhance their own fitness and persistence (Moore et al. 2022). In addition, PGPR can influence rhizosphere functioning by modulating root exudation patterns (Zuluaga et al. 2021). Root exudates serve not only as sources of carbon and nitrogen but also as chemoattractants or chemorepellents, playing a crucial role in microbial colonization and biofilm formation (Mahapatra et al. 2022). Members of dominant PGPR groups, including *Bacillus* spp., are well-known biofilm-forming bacteria. Cooperative biofilm formation represents an important survival strategy that favor PGPR persistence in soil under stress conditions and promotes bacterial communication and cooperation (Ahmad Ansari et al. 2023; Rafique et al. 2024). Yannarell et al. (2019) demonstrated cooperative biofilm formation between *Bacillus subtilis* and *Pantoea agglomerans*, which required *P. agglomerans* exopolysaccharide and the *B. subtilis* amyloid-like protein TasA. Synergistic biofilm formation depending on TasA was later confirmed by Sun et al. (2022) between *Bacillus velezensis* SQR9 and *Pseudomonas stutzeri* XL272. Such interspecies cooperation is hypothesized to be facilitated by exchanging nutrients through cross-feeding. Cross-feeding between *B. velezensis* SQR9 and *Pseudomonas* spp. was further reported by Gu et al. (2025). Another cooperation strategy that is essential for microbiome functioning is the division of labor. Division of labor refers to the specialization of distinct microbial populations in specific steps of a complex metabolic pathway, with the overall process being completed collectively (Zhang et al. 2016). Nitrification is one of fundamental examples of division of labor in the rhizosphere. Nitrification, the oxidation of ammonia ($NH_3$) via nitrite ($NO^{-2}$) to nitrate ($NO^{-3}$), is usually performed in two steps by ammonia-oxidizing bacteria or archea (AOB, AOA) and then nitrite-oxidizing bacteria (NOB) (Besset-Manzoni et al. 2018).

## Reported impact of Bacillota inoculation on native rhizosphere microbiota

In recent years, an increasing number of studies on PGPR have investigated their effects on the native rhizosphere microbiota. According to Berg et al. (2021), six major types of microbiome modulation can be distinguished: transient microbiome shifts, stabilization or increases in microbial diversity or evenness, restoration of dysbiosis, targeted shifts toward potentially beneficial taxa, and depletion of potential pathogens. This chapter will review the documented impacts of PGPR inoculation from Bacillota phylum on native rhizosphere microbiota of plants relevant to agriculture, horticulture, and fiber production.

## Cereal crops

Several studies have demonstrated that inoculation with bacteria from the Bacillota phylum reshapes structure of the native rhizosphere microbiota, modulates microbial diversity and evenness, and decreases relative abundance of plant pathogens in the rhizosphere of cereal crops. These changes were typically correlated with improvements in biometric parameters and crop yield and quality. A detailed overview of the effect of inoculation with bacteria from the Bacillota phylum on the native microbiome of cereal crops is presented in Table 1.

The most frequently observed effect following inoculation is a shift in the microbiome toward beneficial bacterial groups, including plant growth-promoting taxa. For example, Zhao et al. (2023) reported that inoculation of maize with *B. subtilis* NCD-2 led to an increased relative abundance of genera associated with plant growth promotion, including *Azotobacter*, *Kribbella*, *Rhodococcus*, and *Actinoplanes*. Likewise, Li et al. (2021b) reported enrichment of several genera linked to plant health, such as *Bacillus*, *Pseudomonas*, *Salinimicrobium*, *Lysobacter*, *Devosia*, *Klebsiella*, and *Azotobacter*, after inoculation maize with nitrogen-fixing *Paenibacillus triticisoli* BJ-18. Additionally, treatment with *P. triticisoli* BJ-18 decreased relative abundance of potential fungal pathogens (*Fusarium* and *Gibberella*). Similar trends were observed following the application of *B. velezensis* BS89 and *B. megatrium* OQ560352, where PGPR treatments also promoted a shift toward plant-beneficial bacterial groups (Chebotar et al. 2023; Zhu et al. 2023).

Corresponding pattern was demonstrated by Patyka et al. (2025) in winter wheat following treatment with *B. subtilis*

**Table 1** Reported impact of Bacillota inoculation on the rhizosphere microbiota of cereal crops. Types of microbiome modulation described by Berg et al. (2021): (A) transient microbiome shifts, (B) stabilization or increase of microbial diversity, (C) stabilization or increase of microbiome evenness, (D) restoration of a dysbiosis/compensation or reduction of a pathogen-induced shift, (E) targeted shifts toward potential beneficial phyla, and (F) depletion of potential pathogens

| Inoculant strain(s) | PGP traits | Plant | Type of experiments | Sampling | Impact detection method | Microbiome response | Microbiome modulation type | Reference |
|---|---|---|---|---|---|---|---|---|
| *Paenibacillus triticisoli* BJ-18 | **Nutrient availability**: $N_2$-fixing, siderophores production; **Plant hormone modulation**: IAA and IPA production | Maize | Greenhouse experiment | 35 days after transplanting | qPCR − 16 S rRNA, ITS, total diazotrophic *nifH* and *P. triticisoli* BJ-18 *nifH* gene; NGS (Illumina MiSeq) − 16 S rRNA & ITS | **Increase** of potential beneficial bacterial genera (*Bacillus*, *Pseudomonas*, *Salinimicrobium*, *Lysobacter*, *Devosia*, *Klebsiella*, and *Azotobacter*); **Decrease** of potential pathogens (*Fusarium* and *Gibberella*) | E, F | (Li et al. 2021b) |
| *Bacillus velezensis* BS89 | **Antagonistic functions**: hydrolytic enzymes; **Plant hormone modulation**: IAA production | Maize | Field experiment | Before harvest | Pyrosequencing (Roche GSJunior) − 16 S rRNA | **Increase** of potential beneficial bacterial phyla (Verrucomicrobiota, Chloroflexota, Planctomycetota, Pseudomonadota, Bacillota, and Chlamydiota) | E | (Chebotar et al. 2023) |
| *Bacillus subtilis* NCD-2 | **Antagonistic functions**: fengycin and surfactin production; **Activating ISR** | Maize | Pot experiment | 35 days after inoculation | NGS (Illumina MiSeq) − 16 S rRNA & ITS; qPCR - strain persistence | **Increase** of Bacteroidota and Gemmatimonadota; **Increase** of potential beneficial bacterial genera (*Kribbella*, *Rhodococcus*, *Actinoplanes*, *Azotobacter*, and *Conexibacter*) **Decrease** of Patescibacteriota, Cyanobacteriota; **Increase** of *Byssochlamys*, *Aspergillus*, *Trichoderma*, *Cephalotrichum*, and *Neurospora*; **Decrease** of *Arthrobotrys*, *Peziza*, and *Simplicillium* | E | (Zhao et al. 2023) |
| *Bacillus megaterium* OQ560352 | Enhancing organic phosphorus utilization | Maize | Greenhouse experiment | after 50 days, at seven-leaf and eleven-leaf stages | NGS (Illumina MiSeq) − 16 S rRNA; WGS (HiSeq 4000) | **Increase** of potential beneficial bacterial phyla (Actinomycetota, Verrucomicrobiota, Bacteroidota, Bacillota, and Mucoromycotina) | E | (Zhu et al. 2023) |
| *Bacillus subtilis* ED24 | **Antagonistic functions**: cellulase production; **Nutrient availability**: siderophores production; **Plant hormone modulation**: ACC deaminase production | Durum wheat | Pot experiment | 115 days after sowing | NGS (Illumina MiSeq) − 16 S rRNA & ITS | **Increase** of potential beneficial bacterial genera (*Paramesorhizobium*, *Ensifer*, and *Hoeflea*); **Increase** of potential beneficial fungal genera (*Eurotiomycetes* and *Dothideomycetes*); **Decrease** of potential pathogens (*Sordariomycetes* and *Mycoplasma*) | E, F | (Oulkhir et al. 2025) |

**Table 1** (continued)

| Inoculant strain(s) | PGP traits | Plant | Type of experiments | Sampling | Impact detection method | Microbiome response | Microbiome modulation type | Reference |
|---|---|---|---|---|---|---|---|---|
| *Paenibacillus triticisoli* BJ-18 | **Nutrient availability**: $N_2$-fixing, siderophores production; **Plant hormone modulation**: IAA and IPA production | Winter wheat | Field experiment | April, May, June | NGS (Illumina MiSeq) − 16 S rRNA & ITS; WGS (HiSeq 2000) | **Increase** bacterial diversity; **Increase** of Bacillota and Planctomycetota; **Increase** of potential beneficial bacterial genera (*Pseudarthrobacter*, *Bacillus*, *Pseudomonas*, *Azospirillum*, *Klebsiella*, and *Paenibacillus*); **Decrease** of potential pathogens (*Alternaria* and *Gibberella*) | B, E, F | (Li et al. 2021c) |
| *Bacillus subtilis* H38 | NA | Winter wheat | Field experiment | Flowering stage | NGS (Illumina MiSeq) − 16 S rRNA; WGS (Illumina NovaSeq 6000); LC-MS/MS | **Increase** bacterial diversity and evenness; **Increase** of potential beneficial bacterial genera (*Bacillus*, *Pseudomonas*, *Azotobacter*, *Streptomyces*, and *Arthrobacter*); **Decrease** of *Sphingomonas* and *Variovorax* | B, C, E | (Patyka et al. 2025) |
| *Bacillus pumilus* TUAT-1 | **Nutrient availability**: siderophores production; **Plant hormone modulation**: IAA production | Rice | Greenhouse experiment | 2 and 5 weeks after transplantation | NGS (Illumina MiSeq) − 16 S rRNA; qPCR - strain persistence | **Increase** bacterial diversity; **Increase** of *Desulfuromonadales*; **Decrease** of *Xanthomonadales* | B | (Win et al. 2020) |
| *Bacillus altitudinis* LZP02 | Enhancing carbohydrate metabolism and phenylpropanoid biosynthesis | Rice | Pot experiment | 2 weeks after germination | NGS (Illumina MiSeq) − 16 S rRNA & ITS; WGS (HiSeq 2500 PE150) | **Increase** of potential beneficial bacterial genera (*Novosphingobium*, *Acidovorax*, *Sphingomonas*, *Lacibacter*, *Flavobacterium*, *Devosia*, *Rhizobacter*, *Derxia*, *Pelomonas*, *Herbaspirillum*, and *Azospirillum*) | E | (Chang et al. 2024) |
| *Priestia megaterium* YB-3 | Nematicidal properties; **Activating ISR** | Rice | Field experiment | 10, 40 and 60 days after treatment | NGS (Illumina MiSeq) − 16 S rRNA & ITS; qPCR - strain persistence; Fluorescent microscope - *gfp* marked strain colonisation assay | **Increase** abundance of Acidobacteriota, Bacteroidota, and Ascomycota | E | (Ye et al. 2024) |

**Table 1** (continued)

| Inoculant strain(s) | PGP traits | Plant | Type of experiments | Sampling | Impact detection method | Microbiome response | Microbiome modulation type | Reference |
|---|---|---|---|---|---|---|---|---|
| *Bacillus velezensis* FZB42 | **Antagonistic functions**: fengycin, surfactin, bacillomycin D, macrolactin, bacilysin, difficidin and VOCs production; **Plant hormone modulation**: IAA production **Activating ISR** | Rice | Pot experiment | At the end of the experiment | NGS (Illumina MiSeq) − 16 S rRNA & ITS | **Decrease** of pathogenic fungi | D, F | (Ali et al. 2025) |

H38. Inoculation increased bacterial diversity and evenness, while enriching plant-growth promoting genera, such as *Bacillus*, *Pseudomonas*, *Azotobacter*, *Streptomyces*, and *Arthrobacter*. Similarly, Li et al. (2021c) reported increased abundance of *Bacillus* and *Pseudomonas* and other beneficial genera (*Pseudarthrobacter*, *Azospirillum*, *Klebsiella*, and *Paenibacillus*) after application with *P. triticisoli* BJ-18. Likewise, Oulkhir et al. (2025) observed increased relative abundance of genera known for their roles in nitrogen fixation and phytohormone production, such as *Paramesorhizobium*, *Ensifer*, and *Hoeflea* in durum wheat inoculated with *B. subtilis* ED24.

In rice Win et al. (2020) noted an increase of bacterial diversity after treatment with *B. pumilus* TUAT-1. Enrichment of beneficial bacterial taxa was reported by Ye et al. (2024) after inoculation of *Priestia megaterium* YB-3. Correspondingly, Chang et al. (2024) observed enrichment of several plant-growth promoting genera, for example *Sphingomonas*, *Flavobacterium*, *Devosia*, *Rhizobacter*, *Herbaspirillum*, and *Azospirillum*, after application with *Bacillus altitudinis* LZP02. Ali et al. (2025) demonstrated depletion of pathogenic fungi and restoration of dysbiosis caused by pathogens, after treatment with *B. velezensis* FZB42.

## Vegetables

Most research on vegetables has shown, similar to findings in cereal crops, a shift toward beneficial microbial groups following inoculation with Bacillota (Table 2). However, some studies have reported only transient changes in the microbial community.

Qiao et al. (2017) demonstrated that application of *B. subtilis* PTS-394 to tomato induced a short-term increase in the relative abundance of several beneficial genera, including *Thermomonas*, *Pseudomonas*, *Lactococcus* and *Rhodanobacter*, while also increasing the overall abundance of the Bacillota phylum. Corresponding pattern was reported by Zhao et al. (2023) following tomato inoculation with *B. subtilis* NCD-2. Treatment enriched well-known beneficial bacterial genera, such as *Bacillus*, *Sphingobium*, and *Ramlibacter*. This type of modulation was also observed after treatment with nitrogen-fixing *B. cereus* DW019 (Dong et al. 2023). Interestingly, Lee Diaz et al. (2024) compared the effects of individual inoculants - *B. amyloliquefaciens*, *Pseudomonas azotoformans*, *Trichoderma harzianum*, and *Rhizophagus irregularis* - with a synthetic community (SynCom) composed of all four strains on the tomato rhizosphere microbiome. Both single bacterial and fungal inoculants, as well as the SynCom, influenced the composition of the rhizosphere microbiome, yet their effects were distinct from each other. Notably, plants inoculated with *B. amyloliquefaciens* CECT8238 or *T. harzianum* T22 exhibited the lowest microbial diversity and the highest number of differentially abundant ASVs compared to other treatments. Despite these differences, all treatments consistently increased the relative abundance of *Ramlibacter*, *Blastococcus* and *Ohtaekwangia*.

Moreover, Kong et al. (2021) demonstrated that tomato inoculation with *B. amyloliquefaciens* GB03 influenced not only the rhizosphere microbiome of the treated plants but also that of neighboring, non-inoculated individuals, effect was mediated by plant-produced VOCs and root exudates.

Qin et al. (2017) reported increment of the relative abundance of *Paenibacillus*, *Rhodanobacter*, and *Pseudomonas*

**Table 2** Reported impact of Bacillota inoculation on the rhizosphere microbiota of vegetables crops. Types of microbiome modulation described by Berg et al. (2021): (A) transient microbiome shifts, (B) stabilization or increase of microbial diversity, (C) stabilization or increase of microbiome evenness, (D) restoration of a dysbiosis/compensation or reduction of a pathogen-induced shift, (E) targeted shifts toward potential beneficial phyla, and (F) depletion of potential pathogens

| Inoculant strain(s) | PGP traits | Plant | Type of experiments | Samplig | Impact detection method | Microbiome response | Microbiome modulation type | Reference |
|---|---|---|---|---|---|---|---|---|
| *Bacillus subtilis* PTS-394 | **Antagonistic functions**: fengycin, iturin and surfactin production | Tomato | Pot experiment | 1, 3, 7, 9 and 14 days after treatment | Pyrosequencing (Roche 454 GS FLX) − 16 S rRNA & ITS | Transient microbiome shift: **Increase** of Bacillota; **Increase** of potential beneficial bacterial genera (*Thermomonas*, *Pseudomonas*, *Lactococcus*, and *Rhodanobacter*) | A, E | (Qiao et al. 2017) |
| *Bacillus amyloliquefaciens* GB03 | **Antagonistic functions**: VOCs production; **Activating ISR** | Tomato | Pot experiment | 14 days after treatment | NGS (Illumina MiSeq) − 16 S rRNA | **Increase** bacterial diversity; Microbiome shift (VOCs) | B, E | (Kong et al. 2021) |
| *Bacillus cereus* DW019 | **Nutrient availability**: $N_2$-fixing, siderophores production; **Plant hormone modulation**: IAA production | Cherry tomato | Pot experiment | 70 days after inoculation | NGS − 16 S rRNA | **Increase** of Pseudomonadota and Actinomycetota; **Decrease** of Gemmatimonadota, Acidobacteriota, and Myxococcota | E | (Dong et al. 2023) |
| *Bacillus subtilis* NCD-2 | **Antagonistic functions**: fengycin and surfactin production; **Activating ISR** | Tomato | Pot experiment | 35 days after inoculation | NGS (Illumina MiSeq) − 16 S rRNA & ITS; qPCR - strain persistence | **Increase** of Pseudomonadota and Bacillota; **Increase** of potential beneficial bacterial genera (*Bacillus*, *Sphingobium*, and *Ramlibacter*); **Increase** of *Fusarium*, *Clonostachys*, and *Neurospora*; **Decrease** of *Byssochlamys*, *Aspergillus*, and *Fibulochlamys* | E | (Zhao et al. 2023) |
| *Bacillus amyloliquefaciens* CECT8238; SynCom consortium | NA | Tomato | Greenhouse experiment | At 8 week | NGS (Illumina MiSeq or NovaSeq6000) − 16 S rRNA & ITS | Different effects with single strains and SynCom; **Increase** of potential beneficial bacterial genera (*Blastococcus*, *Ramilibacter*, and *Ohtaekwangia*) | E | (Lee Díaz et al. 2024) |

**Table 2** (continued)

| Inoculant strain(s) | PGP traits | Plant | Type of experiments | Samplig | Impact detection method | Microbiome response | Microbiome modulation type | Reference |
|---|---|---|---|---|---|---|---|---|
| *Bacillus amyloliquefaciens* L-S60 | Fungicidal properties | Cucumber | Greenhouse experiment | 5, 10, 15, 20 and 25 days after sprout | NGS (Illumina HiSeq2500) − 16 S rRNA | **Increase** of potential beneficial bacterial genera (*Paenibacillus*, *Rhodanobacter*, and *Pseudomonas*) **Decrease** of Acidobacteriota and Gemmatimonadota | E | (Qin et al. 2017) |
| *Paenibacillus polymyxa* NSY50 | Fungicidal properties | Cucumber | Pot experiment | 30 days after inoculation with FOC | NGS (Illumina MiSeq) − 16 S rRNA & ITS | **Increase** of potential beneficial bacterial genera (*Bacillus*, *Actinobacteria*, *Streptomyces*, *Actinospica*, *Catenulispora*, and *Pseudomonas*); **Decrease** of potential pathogens (*Fusarium*) | D, E, F | (Shi et al. 2017) |
| *Bacillus amyloliquefaciens* FH-1 | **Antagonistic functions**; **Nutrient availability**: $N_2$-fixing, phosphate and potassium solubilization, siderophores production; **Plant hormone modulation**: ACC deaminase production | Cucumber | Pot experiment | 35 days after sowing | NGS (Illumina MiSeq) − 16 S rRNA | **Increase** of Myxococcota, *Nannocystaceae*; **Decrease** of Acidobacteriota | E | (Wang et al. 2021) |
| *Bacillus subtilis* S1 | Fungicidal properties | Cucumber | Pot experiment | 15, 30 and 45 days after last treatment | NGS (Illumina MiSeq 300) − 16 S rRNA | Transient microbiome shift (on day 15 and 30): **Increase** of potential beneficial bacterial families (*Xanthomonadaceae*, *Comamonadaceae*, Cyclobactericae, *Rhodobacteraceae*, and *Acetobacteraceae*) | A | (Zhang et al. 2024) |

**Table 2** (continued)

| Inoculant strain(s) | PGP traits | Plant | Type of experiments | Samplig | Impact detection method | Microbiome response | Microbiome modulation type | Reference |
|---|---|---|---|---|---|---|---|---|
| *Bacillus velezensis* NJAU-Z9 | **Nutrient availability**: ammonia production; **Plant hormone modulation**: IAA production | Pepper | Field experiment | At seedling, flowering and mature state | NGS (Illumina MiSeq) −16 S rRNA & ITS; qPCR - strain persistence | **Increase** bacterial diversity, **decrease** fungal diversity; **Increase** of potential beneficial bacterial genera (*Sphingomonas*, *Sphingopyxis*, *Bradyrhizobium*, *Chitinophaga*, *Dyadobacter*, *Streptomyces*, *Lysobacter*, *Pseudomonas*, and *Rhizomicrobium*); **Increase** of potential beneficial fungal genera (*Cladorrhinum*, *Cladosporium*, and *Aspergillus*) | B, E | (Zhang et al. 2019) |
| *Bacillus subtilis* Ydj3 | **Plant hormone modulation**: IAA production | Pepper | Field experiment | At the beginning of planting and at harvest | NGS (Illumina MiSeq 300) −16 S rRNA Scanning electron microscope - root colonization assay | **Increase** of potential beneficial bacterial genera (*Nocardioides*, *Bacillus*, and *Gemmatimonas*) | E | (Liang et al. 2022) |
| *Bacillus subtilis* NCD-2 | **Antagonistic functions**: fengycin and surfactin production; **Activating ISR** | Pepper | Pot experiment | 35 days after inoculation | NGS (Illumina MiSeq) −16 S rRNA & ITS; qPCR - strain persistence | **Increase** of Pseudomonadota and Bacillota; **Increase** of potential beneficial bacterial genera (*Bacillus*, *Sphingobium*, and *Lysobacter*); **Decrease** of Actinomycetota, Acidobacteriota, and Cyanobacteriota; **Increase** of *Byssochlamys*, *Acremonium*, and *Peziza*; **Decrease** of *Verticillium*, *Nectria*, and *Guehomyces* | E | (Zhao et al. 2023) |

**Table 2** (continued)

| Inoculant strain(s) | PGP traits | Plant | Type of experiments | Samplig | Impact detection method | Microbiome response | Microbiome modulation type | Reference |
|---|---|---|---|---|---|---|---|---|
| *Bacillus velezensis* FZB42 | **Antagonistic functions**: fengycin, surfactin, bacillomycin D, macrolactin, bacilysin, difficidin and VOCs production **Plant hormone modulation**: IAA production **Activating ISR** | Lettuce | Pot and field experiment | At planting, 2 and 4 weeks after planting (pot); at planting, 2 and 5 weeks after planting (field) | T-RFLP | Transient microbiome shift | A | (Chowdhury et al. 2013) |
| *Bacillus velezensis* FZB42 | **Antagonistic functions**: fengycin, surfactin, bacillomycin D, macrolactin, bacilysin, difficidin and VOCs production **Plant hormone modulation**: IAA production **Activating ISR** | Lettuce | Field experiment | At planting, 2 weeks and 5 weeks after planting | WGS | Transient microbiome shift | A | (Kröber et al. 2014) |
| *Bacillus velezensis* SAAS-63 | NA | Lettuce | Pot experiment | 30 days after the first treatment | NGS (Illumina MiSeq) −16 S rRNA & ITS; UHPLC-MS/MS | **Increase** of Verrucomicrobiota and Chloroflexota under nutrient deficiency; **Increase** of beneficia bacterial taxa (*Streptomyces* and *Actinoallomurus)* under nutrient deficiency | E | (Bai et al. 2024) |

**Table 2** (continued)

| Inoculant strain(s) | PGP traits | Plant | Type of experiments | Samplig | Impact detection method | Microbiome response | Microbiome modulation type | Reference |
|---|---|---|---|---|---|---|---|---|
| *Bacillus amyloliquefaciens* G02 | **Nutrient availability**: phosphate and selenium solubilization, siderophores production; **Plant hormone modulation**: IAA and ACC deaminase production | Lettuce | Pot experiment | Month after transplanting | NGS − 16 S rRNA | **Increase** of Bacillota, Acidobacteriota, and Cyanobacteriota; **Increase** of potential beneficial bacterial genera (*Bacillus*, *Vicinamibacterales*, *Sphingomonas*, *Intrasporangium*, *Roseiflexaceae*, and *Nocardioides*); **Decrease** of Chloroflexota, Myxococcota, and *Flavisolibacter* | E | (Huang et al. 2025) |
| *Brevibacillus laterosporus* AMCC100017 | **Plant hormone modulation**: IAA and production | Potato | Pot experiment | Seedling, flowering, tuber bulking and harvesting stage | T-RFLP | **Increase** microbial diversity (in the flowering and the harvesting stage); Transient microbiome shift: **Increase** of potential beneficial bacterial taxa (*Bacillus*, *Pseudomonas*, and Actimomycetes) | A, B, E | (Chen et al. 2017) |
| *Brevibacillus laterosporus* BL12 | Fungicidal properties | Potato | Pot experiment | Early tuber bulking, tuber bulking and harvesting stage | NGS (Illumina MiSeq PE300) − 16 S rRNA | **Increase** of Verrucomicrobiota; **Increase** of potential beneficial bacterial taxa (*Pseudomonas*, *Pseudarthrobacter*, *Brevibacillus*, *Massilia*, *Bosea*, *Devosia*, and *Peanibacillaceae*); **Decrease** of *Streptomyces*, *Parasegetibacter*, *Pedobacter*, and *Terrimonas* | D, E | (Li et al. 2021a) |
| *Bacillus subtilis* Bv17 | NA | Potato | Field experiment | At two-month intervals, three times | NGS (Illumina HiSeq2500) − 16 S rRNA & ITS | **Increase** microbial diversity; **Increase** of Acidobacteriota; **Decrease** of Actinomycetota, *Alternaria* and *Humicola* | B, F | (Song et al. 2021) |

**Table 2** (continued)

| Inoculant strain(s) | PGP traits | Plant | Type of experiments | Samplig | Impact detection method | Microbiome response | Microbiome modulation type | Reference |
|---|---|---|---|---|---|---|---|---|
| *Bacillus amyloliquefaciens* QST713 | Fungicidal properties | Potato | Field experiment | 30 days after emergence | NGS (Illumina MiSeq) − 16 S rRNA & ITS | **Increase** of potential beneficial microbial genera (*Nitrosocosmicus* and *Sphingomonas*); **Decrease** of potential pathogens (*Fusarium*) | E, F | (Adamo et al. 2024) |
| *Bacillus subtilis* NCD-2 | **Antagonistic functions**: fengycin and surfactin production; **Activating ISR** | Eggplant | Pot experiment | 35 days after inoculation | NGS (Illumina MiSeq) − 16 S rRNA & ITS; qPCR - strain persistence | **Increase** of Pseudomonadota and Bacillota; **Increase** of potential beneficial bacterial genera (*Bacillus*, *Sphingobium*, *Lysobacter*, and *Ramlibacter*) **Increase** of *Byssochlamys*, *Penicillium*, *Mortierella*, and *Cladorrhinum*; **Decrease** of Actinomycetota, Acidobacteriota, and Cyanobacteriota; **Decrease** of *Fibulochlamys* | E | (Zhao et al. 2023) |
| *Bacillus subtilis* A-5 | Fungicidal properties; γ-PGA production | Chinese cabbage | Pot experiment | 60 days after planting | NGS (Illumina MiSeq PE300) − 16 S rRNA | **Increase** of Bacillota and *Micrococcaceae*; **Decrease** of Gemmatimonadota, Myxococcota, and Chloroflexota | E | (Bai et al. 2022) |

in the cucumber rhizosphere following application with *B. amyloliquefaciens* L-S60. Corresponding results were presented by Shi et al. (2017) after *P. polymyxa* NSY50 treatment. *P. polymyxa* NSY50 application enriched beneficial genera, such as *Bacillus*, *Streptomyces*, and *Pseudomonas*, while decreasing relative abundance of potential fungal pathogens (*Fusarium*). Enrichment of beneficial taxa in cucumber rhizosphere was also observed after inoculation with nitrogen-fixing *B. amyloliquefaciens* FH-1 and *B. subtilis* S1 (Wang et al. 2021; Zhang et al. 2024).

Zhang et al. (2019) reported that treatment with *B. velezensis* NJAU-Z9 increased bacterial diversity and relative abundance of several PGPR-associated genera, including *Sphingomonas*, *Bradyrhizobium*, *Streptomyces*, *Lysobacter*, and *Pseudomonas* in the pepper rhizosphere. Zhao et al. (2023) observed a similar pattern, where *B. subtilis* NCD-2 inoculation also enriched *Bacillus* and *Lysobacter*. Likewise, Liang et al. (2022) reported increased relative abundance of beneficial genera, including *Bacillus*.

As for the lettuce rhizosphere Bai et al. (2024) reported that inoculation with *B. velezensis* SAAS-63 increased relative abundance of *Streptomyces* and *Actinoallomurus* under nutrient deficiency. Correspondingly, Huang et al. (2025) observed enrichment in several beneficial taxa, including *Bacillus* and *Sphingomonas*, following application with phosphate solubilizing *B. amyloliquefaciens* G02.

Application with *Brevibacillus laterosporus* AMCC100017 to potato increased microbial diversity and relative abundance of *Bacillus* and *Pseudomonas* (Chen et al. 2017). Likewise, Li et al. (2021a) reported that treatment with *B. laterosporus* BL12 also enriched *Pseudomonas* and other beneficial genera, such as *Pseudarthrobacter*, *Brevibacillus*, *Massilia*, *Bosea*, and *Devosia*. However, treatment also decreased the relative abundance of *Streptomyces*,

*Pedobacter*, and *Terrimonas*, which are considered as plant-beneficial. *B. amyloliquefaciens* QST713 inoculation enriched *Sphingomonas*, while decreasing fungal pathogens (*Fusarium*) (Adamo et al. 2024).

Depletion of fungal pathogens was also reported by Song et al. (2021) after inoculation with *B. subtilis* Bv17. Treatment with *B. subtilis* NCD-2 to eggplant increased relative abundance of *Bacillus*, *Sphingobium*, *Lysobacter*, and *Ramlibacter* (Zhao et al. 2023).

Furthermore, application of *B. subtilis* A-5 and its metabolite γ-PGA to the Chinese cabbage rhizosphere increased the relative abundance of taxa commonly considered beneficial (Bai et al. 2022).

### Orchard plants

The most commonly reported effects of Bacillota inoculation on the native microbiomes of orchard plants include shifts toward beneficial microbial groups and depletion of potential pathogens (Table 3).

Mahmoud et al. (2025) reported that *P. megaterium* B1L5 application to apple reduced early-stage root damage caused by apple replant disease and short-term decreased relative abundance of potential fungal pathogens: *Melanconiella* and *Fusarium*. Moreover, treatment increased the relative abundance of several genera known for their antifungal properties, such as *Luteimonas*, *Lysobacter*, *Pseudomonas*, *Sphingomonas*, *Paenibacillus*, *Flavobacterium*, *Rhodanobacter*, and *Pedobacter*. Corresponding pattern was reported in melon by Dong et al. (2025), where *P. polymyxa* NBmelon-1 also depleted *Melanconiella* and *Fusarium*, while increasing relative abundance of potentially beneficial taxa. A decrease in the relative abundance of potentially pathogenic taxa was also observed by Shen et al. (2015) in the banana rhizosphere after inoculation with *B. amyloliquefaciens* NJN-6. Furthermore, Tao et al. (2020) reported an increase in the indigenous *Pseudomonas* population after application of *B. amyloliquefaciens* W19. A similar pattern was noted by Shi et al. (2022a) in the rhizosphere of Chinese wild peach following inoculation with a *B. velezensis* consortium, which enriched several beneficial genera, including *Pseudomonas*, *Flavobacterium*, and *Arenimonas*. Consistently, Wang et al. (2022) demonstrated that application of *B. velezensis* SQR9 to pear rhizosphere increased the relative abundance of *Bacillus*, *Mycolicibacterium*, *Novosphingobium*, and *Sphingobium*, taxa associated with soil nutrient transformation. Shi et al. (2022b) examined the impact of three Bacillota inoculants, separately, on the American pecan rhizosphere microbiome. All of them decreased relative abundance of some potentially pathogenic fungal genera and increased relative abundance of several plant-growth promoting genera. However, all treatments also depleted some of the beneficial bacterial genera. Interestingly, all inoculants decreased relative abundance of *Pseudomonas*, *Pseudarthrobacter*, and *Ramlibacter*. Moreover, *Rhodovastum* was enriched by *Brevibacillus reuszeri* MPT17 application, but was depleted by *B. velezensis* YH20. Similarly, *Rhodanobacter* was enriched by *B. reuszeri* MPT17, while depleting by *B. pumilus* HR10 and *B. velezensis* YH20. Likewise, Xu et al. (2025) observed decrease in some potentially beneficial genera in peanut rhizosphere following inoculation with *B. laterosporus*. Treatment decreased relative abundance of *Sphingomonas* and *Bacillus*, increased bacterial diversity, and depleted *Fusarium*.

## Fiber plants

Research on the impact of Bacillota inoculation on the rhizosphere of fiber crops has focused predominantly on cotton, while other economically important species such as hemp or flax remain largely overlooked. In cotton, the most frequently reported type of microbial modulation is a shift in the rhizosphere microbiome toward beneficial microbial groups (Table 4). This pattern is consistent with findings observed in other crops.

Qin et al. (2021) observed that inoculation with *B. circulans* GN03 increased relative abundance of *Lysobacter* and *Herbaspirillum*. Likewise, Zhao et al. (2023) reported that *B. subtilis* NCD-2 also increased relative abundance of *Lysobacter* and other beneficial genera, including *Bdellovibrio*, *Pseudomonas*, *Peredibacter*, *Limnobacter*, and *Pedobacter*. Correspondingly, Yu et al. (2025) noted enrichment of *Lysobacter* and *Arthrobacter*, *Pseudarthrobacter*, and *Flavobacterium*, following treatment with *B. amyloliquefaciens*. Xu et al. (2023) similarly reported that *Bacillus paralicheniformis* RP01 increased relative abundance of beneficial bacterial genera, such as *Streptomyces*, *Bradyrhizobium*, and *Acinetobacter*.

Studies on PGPR from the Bacillota phylum consistently demonstrate that their inoculation most commonly induces targeted shifts in the rhizosphere microbiome. Across cereals, vegetables, orchard crops, and fiber plants, the dominant pattern is a shift toward beneficial taxa and depletion of potential pathogens, particularly *Fusarium* (Fig. 2). The most frequently enriched bacterial genera include *Bacillus*, *Pseudomonas*, *Lysobacter*, *Sphingomonas*, *Streptomyces*, *Azotobacter*, *Arthrobacter*, *Pseudarthrobacter*, *Bradyrhizobium*, *Devosia*, *Flavobacterium*, *Klebsiella*, *Herbaspirillum*, and *Rhodanobacter*. These taxa are recognized as plant-beneficial and are linked to key functions, such as nitrogen fixation, nutrient transformation, phytohormone production, and biocontrol.

**Table 3** Reported impact of Bacillota inoculation on the rhizosphere microbiota of orchard plants. Types of microbiome modulation described by Berg et al. (2021): (A) transient microbiome shifts, (B) stabilization or increase of microbial diversity, (C) stabilization or increase of microbiome evenness, (D) restoration of a dysbiosis/compensation or reduction of a pathogen-induced shift, (E) targeted shifts toward potential beneficial phyla, and (F) depletion of potential pathogens

| Inoculant strain(s) | PGP traits | Plant | Type of experiments | Sampling | Impact detection method | Microbiome response | Microbiome modulation type | Reference |
|---|---|---|---|---|---|---|---|---|
| *Priestia megaterium* B1L5 (vegetative cells and spores) | Fungicidal properties | Apple | Pot experiment | 6 and 33 days after inoculation | NGS − 16 S rRNA & ITS; qPCR - strain persistence (gfp gene); Confocal laser scanning microscope - gfp marked strain colonisation assay | **Increase** of potential beneficial bacterial genera (*Luteimonas*, *Lysobacter*, *Pseudomonas*, *Sphingomonas*, *Paenibacillus*, *Flavobacterium*, *Sphingobacterium*, *Rhodanobacter*, and *Pedobacter*); **Decrease** of potential pathogens (*Melanconiella* and *Fusarium*) | D, E, F | (Mahmoud et al. 2025) |
| *Paenibacillus polymyxa* NBmelon-1 | Fungicidal properties | Melon | Greenhouse experiment | Autumn and spring (during fruit maturation) | NGS (Illumina MiSeq PE 250) − 16 S rRNA & ITS | **Increase** of Acidobacteriota and Bacillota; **Decrease** of potential pathogens (*Melanconiella* and *Fusarium*) | E, F | (Dong et al. 2025) |
| *Bacillus amyloliquefaciens* NJN-6 | **Antagonistic functions**: iturin, bacillomycin D and macrolactin and VOCs production; **Plant hormone modulation**: IAA and GA3 production | Banana | Field experiment | At harvest (2 years after start of the experiment) | PCR-DGGE − 16 S rRNA & ITS | **Increase** microbial diversity; **Increase** of Acidobacteriota, Bacillota, Chloroflexota, Armatimonadota, Gemmatimonadota, and Nitrospirota; **Decrease** of Pseudomonadota and Ascomycota | B, E, F | (Shen et al. 2015) |
| *Bacillus amyloliquefaciens* W19 | Fungicidal properties | Banana | Greenhouse experiment | After 4 months | NGS (Illumina NovaSeq 6000) − 16 S rRNA & ITS; qPCR (total bacteria, fungi, *Fusarium oxysporum*, *Bacillus* and *Pseudomonas*) | **Increase** of potential beneficial bacterial genera (*Bacillus* and *Pseudomonas*) | E | (Tao et al. 2020) |

**Table 3** (continued)

| Inoculant strain(s) | PGP traits | Plant | Type of experiments | Sampling | Impact detection method | Microbiome response | Microbiome modulation type | Reference |
|---|---|---|---|---|---|---|---|---|
| *Bacillus velezensis* YH-18 *and B. velezensis* YH-20 | *Bacillus velezensis* YH-18: **Antagonistic functions**: antibacterial proteins, lipopeptides and VOCs production; **Nutrient availability**: $N_2$-fixing *B. velezensis* YH-20: **Antagonistic functions**: antibacterial proteins, lipopeptides and VOCs production; **Nutrient availability**: increase available nitrogen and available potassium; **Plant hormone modulation**: IAA production | Chinese wild peach | Pot experiment | 15 and 30 days after inoculation | NGS (Illumina MiSeq) − 16 S rRNA | **Increase** of potential beneficial bacterial genera (*Sphingomonas*, *Pseudomonas*, *Flavobacterium*, *Arenimonas*, *Aquicella*, *Devosia*, *Novosphingobium*, and *Ferruginibacter*); **Decrease** of *Bryobacter*, *Chryseolinea*, *Nitrospira*, and *Haliangium* | E | (Shi et al. 2022a) |
| *Bacillus velezensis* SQR9 | **Antagonistic functions**: bacillibactin, bacillomycin D, fengycin, surfactin, bacillaene, difficidin, macrolactin, bacilysin and bacillunoic acid production; **Nutrient availability**: siderophores production; **Plant hormone modulation**: IAA production; **Activating ISR** | Pear | Field experiment | 2 years after start of the experiment | WGS (Illumina NovaSeq 6000 S4) | **Increase** of potential beneficial bacterial genera (*Bacillus*, *Mycolicibacterium*, *Novosphingobium*, and *Sphingobium*) | E | (Wang et al. 2022) |

**Table 3** (continued)

| Inoculant strain(s) | PGP traits | Plant | Type of experiments | Sampling | Impact detection method | Microbiome response | Microbiome modulation type | Reference |
|---|---|---|---|---|---|---|---|---|
| *Bacillus pumilus* HR10 | Fungicidal properties; **Activating ISR** | American pecan | Pot experiment | 15 days after inoculation | NGS (Illumina NovaSeq 6000) − 16 S rRNA & ITS | **Increase** of Bacillota; **Increase** of potential beneficial bacterial genera (*Sphingomonas*, *Chujaibacter*, *Bacillus*, *Acidipila*, *Bryobacter*, and *Mizugakiibacter);* **Decrease** of *Rhodanobacter*, *Pseudomonas*, *Massilia*, *Lysobacter*, *Nitrospira*, *Pseudarthrobacter*, and *Ramlibacter;* **Increase** of mycorrhizal fungi; **Decrease** of potential pathogens (*Didimella*) | E, F | (Shi et al. 2022b) |
| *Bacillus velezensis* YH20 | **Antagonistic functions**: antibacterial proteins, lipopeptides and VOCs production; **Nutrient availability**: increase available nitrogen and available potassium; **Plant hormone modulation**: IAA production | American pecan | Pot experiment | 15 days after inoculation | NGS (Illumina NovaSeq 6000) − 16 S rRNA & ITS | **Increase** of Actinomycetota; **Increase** of potential beneficial bacterial genera (*Sphingomonas*, *Chujaibacter*, *Acidibacter*, *Pseudolabrys*, *Acidipila*, *Brukholderia*, *Acidothermus*, *Granulicella*, *Bradyrhizobium*, *Streptomyces*, *Bryobacter*, *Devosia*, and *Actinospica*); **Decrease** of *Rhodanobacter*, *Pseudomonas*, *Lysobacter*, *Nitrospira*, *Pseudarthrobacter*, *Rhodovastum*, and *Ramlibacter;* **Increase** of mycorrhizal fungi; **Decrease** of potential pathogens (*Didimella*) | E, F | (Shi et al. 2022b) |
| *Brevibacillus reuszeri* MPT17 | **Nutrient availability**: increase available phosphorus and available potassium | American pecan | Pot experiment | 15 days after inoculation | NGS (Illumina NovaSeq 6000) − 16 S rRNA & ITS | **Increase** of potential beneficial bacterial genera (*Rhodanobacter*, *Chujaibacter Gemmatimonas*, *Acidipila*, *Brukholderia*, *Reyranella*, *Rhodovastum*, and *Aquicella*); **Decrease** of *Pseudomonas*, *Massilia*, *Pseudarthrobacter*, and *Ramlibacter;* **Increase** of mycorrhizal fungi; **Decrease** of potential pathogens (*Fusarium* and *Didimella*) | E, F | (Shi et al. 2022b) |

**Table 3** (continued)

| Inoculant strain(s) | PGP traits | Plant | Type of experiments | Sampling | Impact detection method | Microbiome response | Microbiome modulation type | Reference |
|---|---|---|---|---|---|---|---|---|
| *Brevibacillus laterosporus* | Fungicidal properties; **Nutrient availability**: ligninolytic enzymes | Peanut | Pot experiment | 120 days after planting | NGS (Illumina MiSeq) − 16 S rRNA & ITS | **Increase** bacterial diversity; **Increase** of *Anaerolinea* and *Anaeromyxobacter*; **Decrease** of *Gemmatimonas*, *Sphingomonas*, and *Bacillus*; **Decrease** of potential pathogens (*Fusarium*) | B, F | (Xu et al. 2025) |

However, effects are not universally positive for all these groups. Several studies have reported depletion of genera typically considered beneficial, including *Bacillus* (Xu et al. 2025), *Pseudomonas* (Shi et al. 2022b), *Lysobacter* (Shi et al. 2022b), *Sphingomonas* (Xu et al. 2025; Patyka et al. 2025), *Streptomyces* (Li et al. 2021a), *Pseudarthrobacter* (Shi et al. 2022b), and *Rhodanobacter* (Shi et al. 2022b). Notably, Shi et al. (2022b) demonstrated that different Bacillota strains applied to the same plant species produced contrasting effects on some genera, for example *Rhodanobacter* was enriched by *B. reuszeri* MPT17, and depleted by *B. pumilus* HR10 and *B. velezensis* YH20. At the same time, certain strains showed reproducible effects across multiple crops. Zhao et al. (2023) examined the effect of inoculation with *B. subtilis* NCD-2 to five different plants and reported consistent results. Likewise, treatment with *P. triticisoli* BJ-18 induced comparable shifts in both maize and winter wheat rhizosphere (Li et al. 2021b, c). Overall, Bacillota inoculation most commonly enriches PGPR-associated taxa, increases bacterial diversity, and suppresses fungal pathogens. However, microbiome responses remain strongly strain- and plant-dependent, and comparative studies evaluating multiple inoculants within the same plant species or the same inoculant across multiple plants are still limited.

## Detection methods

The detected impact of PGPR inoculation strongly depends on the sampling time, experimental design, and, more broadly, on the methodological approaches employed (Renoud et al. 2022; Kool et al. 2023; Lin et al. 2024). The investigation of how PGPR inoculation modulates the native rhizosphere microbiota has evolved substantially over the past decades, following advances in molecular biology and high-throughput technologies. Early studies relied primarily on culture-based techniques and low-resolution molecular fingerprinting, whereas recent studies are mainly based on next-generation sequencing (NGS) and multi-omics approaches to capture comprehensive community changes (Lagos et al. 2015; Garg et al. 2024; Rajguru et al. 2024).

### PCR-based methods

Initially, analyses were dominated by molecular fingerprinting techniques such as PCR-DGGE (denaturing gradient gel electrophoresis), T-RFLP (terminal restriction fragment length polymorphism), SSCP (single-stranded conformational polymorphism), and ARISA (automated ribosomal intergenic spacer analysis) (Chowdhury et al. 2013; Schmidt et al. 2014; Shen et al. 2015). These approaches rely on the separation of PCR-amplified molecular marker genes fragments, mainly the 16 S rRNA gene for bacteria and internal transcribed spacer (ITS) region for fungi, to generate community profiles. Fingerprinting methods provide early insights into microbial community shifts following PGPR inoculation, however their interpretative power is limited by low taxonomic resolution, reduced sensitivity to rare taxa, and lack of functional information (Mawarda et al. 2020). Currently, PCR-based approaches, primarily quantitative PCR (qPCR), are more commonly applied to assess functional modulation of resident microbial communities rather than microbiome taxonomic shifts. Frequently targeted genes include functional genes, such as *nifH* (nitrogen fixation), *acdS* (ACC deaminase activity), *phoD* (phosphorus solubilization), *amoA* (nitrification), and *nosZ* (denitrification) or marker genes (Li et al. 2021c; Wang et al. 2023). By comparing gene copy numbers between inoculated and non-inoculated treatments, qPCR enables detection of functional shifts within the native microbiome, even when overall community composition remains relatively stable. This approach is particularly effective in capturing enrichment or suppression of specific native microbial populations and serves as a valuable complement to sequencing-based methods (Jian et al. 2020). In addition to detecting changes

**Table 4** Reported impact of Bacillota inoculation on the rhizosphere microbiota of fiber plants. Types of microbiome modulation described by Berg et al. (2021): (A) transient microbiome shifts, (B) stabilization or increase of microbial diversity, (C) stabilization or increase of microbiome evenness, (D) restoration of a dysbiosis/compensation or reduction of a pathogen-induced shift, (E) targeted shifts toward potential beneficial phyla, and (F) depletion of potential pathogens

| Inoculant strain(s) | PGP traits | Plant | Type of experiments | Sampling | Impact detection method | Microbiome response | Microbiome modulation type | Reference |
|---|---|---|---|---|---|---|---|---|
| *Bacillus circulans* GN03 | **Plant hormone modulation**: IAA, GA, BR, SA and JA production; **Activating ISR** | Cotton | Pot experiment | 30 days after inoculation | NGS (Illumina MiSeq) −16 S rRNA | **Increase** of potential beneficial bacterial genera (*Lysobacter* and *Herbaspirillum*); **Decrease** of *Geobacter*, *Curvibacter*, and *Methylocysti* | A, E | (Qin et al. 2021) |
| *Bacillus paralicheniformis* RP01 | **Plant hormone modulation**: IAA, BR, SA and JA production; | Cotton | Pot experiment | 30 days after inoculation | NGS (Illumina MiSeq) −16 S rRNA | **Increase** of potential beneficial bacterial genera (*Streptomyces*, *Bradyrhizobium*, *Gemmatirosa*, *Candidatus_Solibacter*, and *Acinetobacter*) | E | (Xu et al. 2023) |
| *Bacillus subtilis* NCD-2 | **Antagonistic functions**: fengycin and surfactin production; **Activating ISR** | Cotton | Pot experiment | 35 days after inoculation | NGS (Illumina MiSeq) −16 S rRNA & ITS; qPCR - strain persistence | **Increase** of Bacteroidota and Gemmatimonadota; **Increase** of potential beneficial bacterial genera (*Lysobacter*, *Bdellovibrio*, *Pseudomonas*, *Peredibacter*, *Limnobacter*, and *Pedobacter*); **Decrease** of Patescibacteriota, Cyanobacteriota; **Increase** of *Acremonium* and *Guehomyces*; **Decrease** of *Byssochlamys*, *Neurospora*, and *Arthrobotrys* | E | (Zhao et al. 2023) |
| *Bacillus amyloliquefaciens* | NA | Cotton | Field experiment | At harvest (2 years after start of the experiment) | WGS (Illumina NovaSeq X Plus) | **Increase** of potential beneficial bacterial genera (*Arthrobacter*, *Pseudarthrobacter*, *Flavobacterium*, and *Lysobacter*); **Decrease** of Acidobacteriota and Chloroflexota; **Increase** of potential beneficial fungal genera (*Glomus*); **Decrease** of potential pathogens (*Fusarium*) | E, F | (Yu et al. 2025) |

in microbiome function, qPCR is mainly used to track the persistence of an inoculated PGPR strain in the rhizosphere using strain-specific primers (Couillerot et al. 2010; Zhao et al. 2023).

## Sequencing-based methods

With the development of next generation sequencing (NGS), sequencing-based approaches have become state-of-the-art techniques for characterizing rhizosphere microbial communities. NGS technologies are often classified by read length as second generation (100 to 800 bp) and third generation (over 10,000 bp) (Satam et al. 2023; Garg et al. 2024). The most popular platforms for the second generation are Illumina MiSeq and HiSeq, and Ion Torrent Personal Genome Machine (PGM) (Hu et al. 2021). Second generation sequencing (SGS) workflow consists of creating single-stranded DNA libraries by DNA

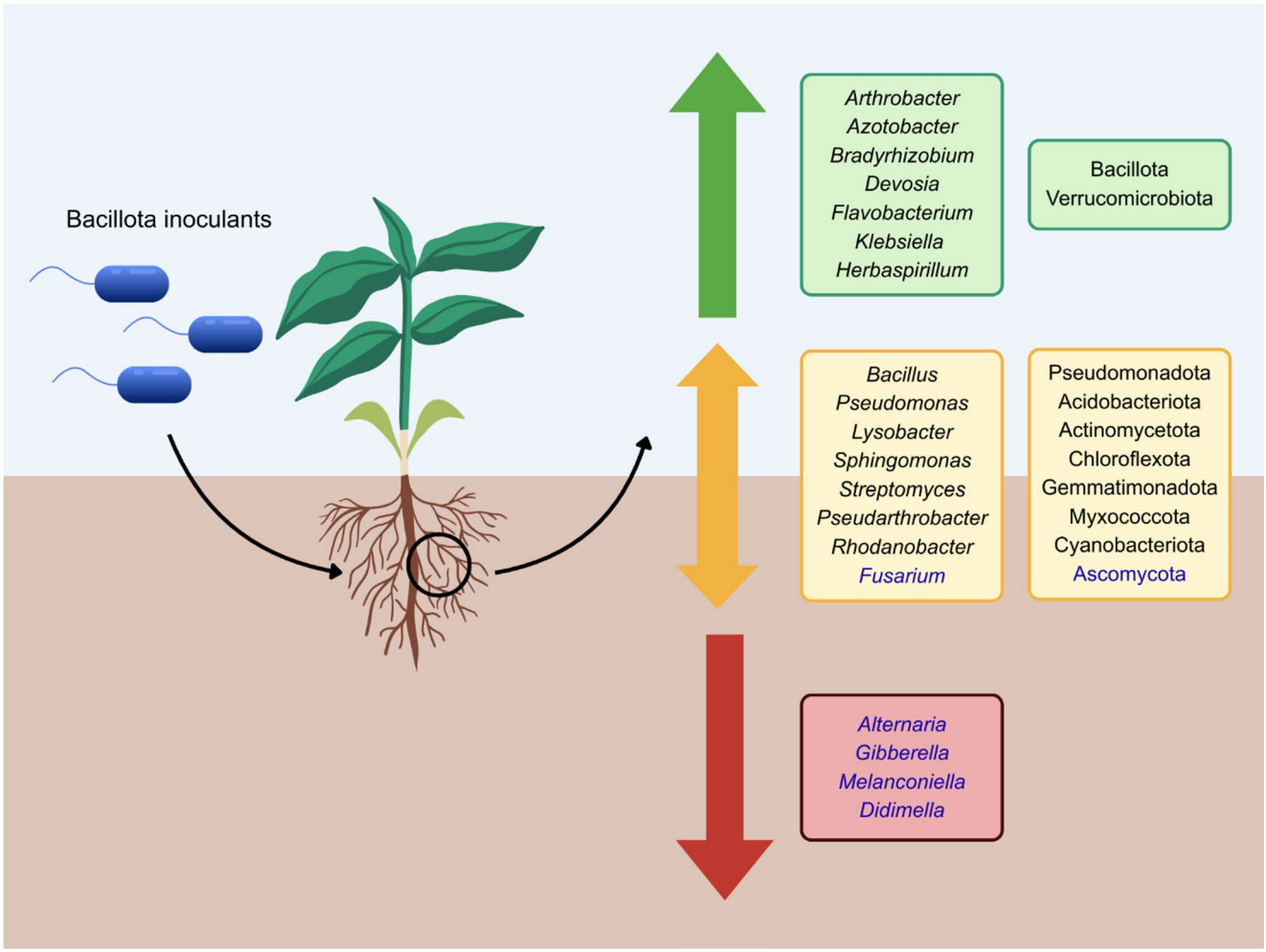


**Fig. 2** Schematic representation of the microbial taxa most frequently affected by Bacillota-based inoculants. Fungal taxa are marked in blue, and bacterial taxa in black. Taxa highlighted in green boxes have been reported exclusively as enriched, those in yellow boxes as either enriched or depleted, and those in red boxes exclusively as depleted

fragmentation, adapters ligation and amplification using PCR, sequencing by synthesis, and data analysis (Mandlik et al. 2024). Unlike first generation sequencing, millions of DNA fragments are sequenced simultaneously (mass parallel sequencing), thus increasing efficiency of sequencing and reducing costs. However, SGS still has some difficulties such as errors during PCR or hardships with assembling complex genome fragments (Hu et al. 2021). The third-generation sequencing (TGS) overcame most of these limitations. These technologies enable generating long sequences (> 10 kb) directly from native DNA, without creating libraries. Currently, two main platforms are used in TGS, Pacific Biosciences Single Molecule, Real-Time (PacBio SMRT) and Oxford Nanopore Technologies (ONT) (Scarano et al. 2024).

Metagenomics analysis, based on sequencing methods, can be divided into two main approaches. The first one, metabarcoding or targeted metagenomics is primarily used for the identification of the microorganism community composition and its diversity. In this approach, extracted DNA is amplified during PCR with specific primers targeting genes of interest, most commonly marker or functional genes (Zhao et al. 2023; Oulkhir et al. 2025). Amplicon sequencing of the 16 S rRNA gene or ITS region provides significantly higher taxonomic resolution than fingerprinting techniques, thus enabling detailed analyses of diversity and community composition at genus level. Targeted metagenomics enables detecting changes in rare taxa that were previously undetectable using PCR-based profiling (Morgan et al. 2017; Changey et al. 2022). This method is fast and cost-effective, however, its ability to predict functional potential is limited, as it relies mainly on taxonomic and relative abundance data. To overcome these limitations, whole-genome sequencing (WGS, global metagenomics, shotgun metagenomics) is increasingly applied. Unlike amplicon-based methods, shotgun metagenomics captures

the entire genetic content of microbial communities, allowing assessment of both, taxonomic composition and functional potential (Li et al. 2021b; Zhu et al. 2023; Chang et al. 2024; Yu et al. 2025). WGS enables identification of crucial metabolic pathways related to nutrient cycling, antimicrobial compounds synthesis or phytohormones production, thereby providing border insight in microbiome functioning.

Importantly, advances in bioinformatic reconstruction now allow the recovery of metagenome-assembled genomes (MAGs) from shotgun datasets. MAGs enable the reconstruction of near-complete or partial genomes of individual microbial populations directly from environmental samples (Setubal 2021; Mirete et al. 2025). This enables the association of observed taxonomic variation with the functional potential encoded within reconstructed genomes, facilitating the attribution of metabolic capacities and biosynthetic pathways to specific microbial lineages. Consequently, MAG-based analyses provide a more integrative understanding of how changes in community composition translate into functional alterations within the microbiome, offering a powerful tool to connect structure and function in complex soil ecosystems (Wang et al. 2025; Naziębło et al. 2025; Dobrzyński et al. 2026a).

## Multi-omics

Metagenomics is a key method to understand composition of microbial communities. However, application of post-genomic approaches, such as metatranscriptomics and metaproteomics can promote a deeper understanding of gene functions and protein expression, thus unraveling complex interaction between PGPR inoculants and the native rhizosphere microbiota (Mmotla et al. 2025). Multi-omics is a gaining-attention strategy that combines different omics methods (metagenomics, metatranscriptomics, metaproteomics, and metabolomics), thus linking overall genetic potential with the actual gene expression and protein synthesis (Sahoo et al. 2025). While metagenomics provides information about the whole genetic potential of microbiota, metatranscriptomics focus only on functional genes expressed by viable bacteria microbes. It is a particularly effective method to assess the impacts of PGPR inoculation on microbial community function, such as enhancing or inhibiting important metabolic pathways (Liu et al. 2025; Ai et al. 2025). Metaproteomics and metabolomics analyze the content of proteins or metabolites produced by the microbial community. These approaches provide even deeper insight into microbiome interactions and function and are an efficient way to study interactions between inoculants, microbiome and host plant (Bai et al. 2024; Francioli et al. 2025; Patyka et al. 2025).

## Limitations

Although the number of studies investigating the impact of PGPR on native rhizosphere microbiota has increased substantially in recent years, significant methodological and conceptual limitations still constrain our understanding of these complex interactions. While numerous reports describe shifts in microbial community composition following inoculation often indicating enrichment of beneficial taxa or depletion of pathogens – comprehensive or long-term studies remain scarce.

First, most studies investigating the effects of PGPR on rhizosphere microbial communities evaluate community structure at a single sampling point, most commonly at the end of the experimental period. Only a limited number of reports incorporate sampling at different stages of plant development, and even fewer monitor microbial dynamics over extended time frames (Chen et al. 2017; Zhu et al. 2023). Consequently, it remains uncertain whether the reported shifts in microbiome composition reflect transient disturbances, short-term enrichment of specific taxa, or more stable and sustained restructuring of the indigenous microbial community. Considering that rhizosphere interactions are inherently dynamic and are shaped by plant developmental stage, seasonal fluctuations, and environmental variability, single end-point assessments provide only a partial and potentially misleading representation of PGPR–microbiome interactions (Ajilogba et al. 2022). Therefore, long-term studies encompassing multiple plant growth stages and successive growing seasons are essential to accurately evaluate the stability and ecological significance of PGPR-induced changes in native microbial communities.

Second, most of the available studies have been conducted under controlled greenhouse or pot conditions, typically using a single soil type (Tables 1, 2, 3 and 4). Even field experiments are often restricted to one location. However, soil physicochemical properties, such as pH, texture, organic matter content, and nutrient availability – are key determinants of microbial community structure and function. The limited number of multi-site and multi-soil investigations therefore constrains the assessment of reproducibility and broader applicability of the reported findings. As a consequence, it remains unclear whether the observed microbiome shifts are strongly context-dependent or reflect more generalizable patterns. Comparative studies conducted across contrasting soil types and environmental conditions are thus essential to determine the robustness, consistency, and ecological relevance of PGPR-induced modulation of native microbial communities.

Third, only a limited number of studies quantitatively relate the abundance or persistence of introduced strains

to changes observed in native rhizobacterial communities. Although next-generation sequencing approaches (e.g., 16 S rRNA amplicon sequencing or metagenomics) are widely used to characterize community composition, they are less frequently complemented by quantitative methods such as strain-specific qPCR, persistence assays, or direct assessment of rhizosphere colonization (Zhang et al. 2019; Win et al. 2020; Zhao et al. 2023; Ye et al. 2024; Mahmoud et al. 2025). Consequently, the relationship between inoculant population dynamics and shifts in indigenous microbial taxa remains insufficiently resolved.

## Concluding remarks

Accumulating evidence demonstrates that inoculation with PGPR from the Bacillota phylum can significantly modulate native rhizosphere microbiota across a wide range of agriculturally relevant crops. The most frequently observed outcomes include enrichment of plant-beneficial taxa, suppression of pathogens, and increases in microbial diversity or evenness. These microbiome shifts were often correlated with improved plant growth, stress tolerance, and yield performance. However, responses are not universally consistent, in some cases, taxa commonly regarded as beneficial are depleted. Microbiome modulation is strongly strain- and plant-dependent, and influenced by environmental conditions, sampling terms and methodological approaches.

Despite major advances in sequencing technologies and multi-omics approaches, important knowledge gaps remain. Most studies rely on short-term experiments and single sampling points, limiting our ability to distinguish transient shifts from stable, ecologically meaningful restructuring of microbial communities. Furthermore, the persistence and colonization dynamics of introduced strains are rarely quantitatively linked to observed shifts in indigenous microbiota.

Future research should prioritize long-term, replicated experiments across multiple soil types and environmental conditions, combined with integrated structural and functional analyses. Linking multi-omics data with quantitative tracking of inoculant populations will be essential to establish causal relationships between PGPR application, microbiome modulation, and plant performance. Comparative studies evaluating multiple inoculants within the same crop, as well as single strains across diverse hosts, are also needed to disentangle strain-specific from host-driven effects.

Deeper understanding of PGPR-microbiome interactions is crucial for optimizing bioinoculant formulations, improving their persistence and consistency under field conditions, and ensuring ecological safety. Such knowledge will ultimately support the development of microbial-based strategies for sustainable and climate-resilient agriculture.

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## Declarations

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