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Review article

# Harnessing the plant microbiome for sustainable crop production

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## Abstract

Global research on the plant microbiome has enhanced our understanding of the complex interactions between plants and microorganisms. The structure and functions of plant-associated microorganisms, as well as the genetic, biochemical, physical and metabolic factors that influence the beneficial traits of plant microbiota have also been intensively studied. Harnessing the plant microbiome has led to the development of various microbial applications to improve crop productivity in the face of a range of challenges, for example, climate change, abiotic and biotic stresses, and declining soil properties. Microorganisms, particularly nitrogen-fixing rhizobia as well as mycorrhizae and biocontrol agents, have been applied for decades to improve plant nutrition and health. Still, there are limitations regarding efficacy and consistency under field conditions. Also, the wealth of expanding knowledge on microbiome diversity, functions and interactions represents a huge source of information to exploit for new types of application. In this Review, we explore plant microbiome functions, mechanisms, assembly and types of interaction, and discuss current applications and their pitfalls. Furthermore, we elaborate on how the latest findings in plant microbiome research may lead to the development of new or more advanced applications. Finally, we discuss research gaps to fully leverage microbiome functions for sustainable plant production.

## Sections

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## Introduction

The first descriptions of plant–microorganism associations date back more than 200 years. In the nineteenth century, scientists such as Heinrich Friedrich Link coined the term entophytae (meaning endophytes), and Anton de Bary introduced the concept of symbiosis. Many other researchers of that time, such as Victor Galippe, Willem Beijerinck and Hermann Hellriegel, reported on the beneficial effects of plant-associated microorganisms[1]. For decades, research focused primarily on the symbiosis between mycorrhizal fungi and plants, and between nitrogen gas ($N_2$)-fixing rhizobia and legumes. However, in the past two to three decades, a considerable amount of research has demonstrated that plants interact with highly diverse microbiota colonizing the rhizosphere, the plant episphere (that is, rhizoplane, phyllosphere) as well as the endosphere. Essentially all plant tissues are colonized, including roots, stems, leaves, flowers and seeds[2].

Advances in next-generation sequencing have enabled the high-throughput analysis of microbiome composition, which together with increasing awareness of the importance of microbiome functions, has resulted in an explosion of studies and publications on the plant microbiome. These studies have revealed the complex nature of plant–microbiome interactions and have increased our understanding of plant microbiome dynamics and assembly[3]. Furthermore, owing to promising reports on the effects of many plant-associated microorganisms on plant survival, growth, health and yield[4], there is increasing interest from industry as well as the farming sector to make use of plant-beneficial microorganisms as sustainable alternatives to chemical pesticides and fertilizers[5,6]. In addition to these classical applications, there is widespread interest in applying microorganisms to help plants cope with abiotic stresses such as drought, which is a burning issue as a result of climate change[7]. Farming, along with unsustainable practices, contributes to climate change and negatively impacts the environment; however, microbiome-based applications have the potential to provide mitigations that are sustainably based[8].

The integration of microbial products in farming practices is gaining importance, and there are microbial products with a long history of use, such as the application of rhizobia (including for example, *Bradyrhizobium japonicum*, *Rhizobium leguminosarum*) to achieve $N_2$ fixation in legumes or *Bacillus thuringiensis* as a powerful insecticide. In recent years, additional products have entered the market, which overall show positive and promising effects but also often inconsistent field efficacy[9]. Furthermore, most products are based on only a few microbial species, although there are many more taxa that show potential for application. However, there are approaches to overcome current limitations and to make use of the massive amount of data currently generated for precision and microbiome-based management practices[10–12].

Harnessing the microbiome to improve crop production will also lead to food products that are safe and have a high nutritional value. Considering the connectivity of microbiomes in specific environments[13] and the role of microbiomes in achieving Sustainable Development Goals (SDGs) and implementing the One Health concept[14,15] (Box 1), making use of plant microbiomes for sustainable crop production systems is of key importance.

## The plant microbiome

### Microbiota in the plant environment

Plants host taxonomically diverse microbial communities, which colonize different below- and above-ground plant parts, many of them representing unique microbial habitats (Fig. 1). Plant microbiota have important roles in plant growth and health[16], and they comprise primarily bacteria and to a lesser extent fungi, which are well studied[3], but also less-investigated groups, such as archaea, protists and viruses[17].

The most important reservoir of plant-associated microbiota is the soil and the rhizosphere environment. Owing to the presence of nutrients for microorganisms (that is, root exudates and decaying plant material), the rhizosphere is considered a hot spot of microbial activity and represents one of the most complex ecosystems[18]. Root exudation chemistry and bacterial substrate preferences determine microbiome assembly to a great extent in the rhizosphere[19], and volatile organic compounds emitted by plants along with phytohormones shape microbiomes[20]. In addition to the rhizosphere, microorganisms may colonize the rhizoplane and subsequently enter and colonize roots internally as root endophytes[1].

Above-ground plant tissues, including vegetative foliar tissues, leaves and floral parts, host endophytes as well as epiphytes. Most endophytes spread from the root environment via the xylem to distinct plant compartments; however, endophytes may also enter through aerial plant parts such as flowers and fruits using wounds or natural entry points such as stigma on flowers[21]. The phyllosphere represents an important habitat, hosting microorganisms passively transported via the atmosphere mostly from water, pollen and soil[13]. Furthermore, fruits, flowers and seeds host microbiota[21,22], which are often highly distinct from those found in other plant compartments such as roots[23] (Fig. 1). Seed microbiota may be transferred to the next plant generation[24], and some taxa such as the fungus *Epichloë* may be vertically transmitted to the next generation of seeds[25]. Overall, plants host microbiota that are distinct from that of bulk soil, and generally Actinomycetota, Pseudomonadota, Bacteroidota and Bacillota are enriched, whereas Acidobacteriota, Verrucomicrobiota and Gemmatimonadota are depleted[26]. Fungal communities have been less frequently investigated; however, available data indicate that these comprise Ascomycota and Basidiomycota, and show greater variations dependent on other factors than the plant compartment, such as biogeography, host species and stochastic effects[27,28].

### Factors shaping plant microbiota composition

Plant microbial communities show structural variation in composition and diversity between plant habitats and are shaped by a range of factors that are interconnected. The key influential drivers are the host (such as the plant compartment, plant species, genotype, age, development stage, health and fitness), abiotic and biotic environmental factors (including geography, soils, climatic conditions and agricultural management practices) and microbial interactions[3,29] (Fig. 2).

The host plant exerts considerable influence on the selection of microorganisms. Microorganisms then adapt to the specific niche of plant compartments, navigating the plant's immune system and utilizing plant-derived resources[30].

Plant compartments contain distinct microbiota, with substantial overlap observed across plant regions, with composition of each habitat shaped by differential forces. Host genomic diversity, encompassing genotype-dependent variation and differing plant species, is a major determinant[31,32]. The influence of the host genome is greater on the composition of the above-ground microbiota than on that of the root or rhizosphere microbiota, with environmental conditions contributing[33].

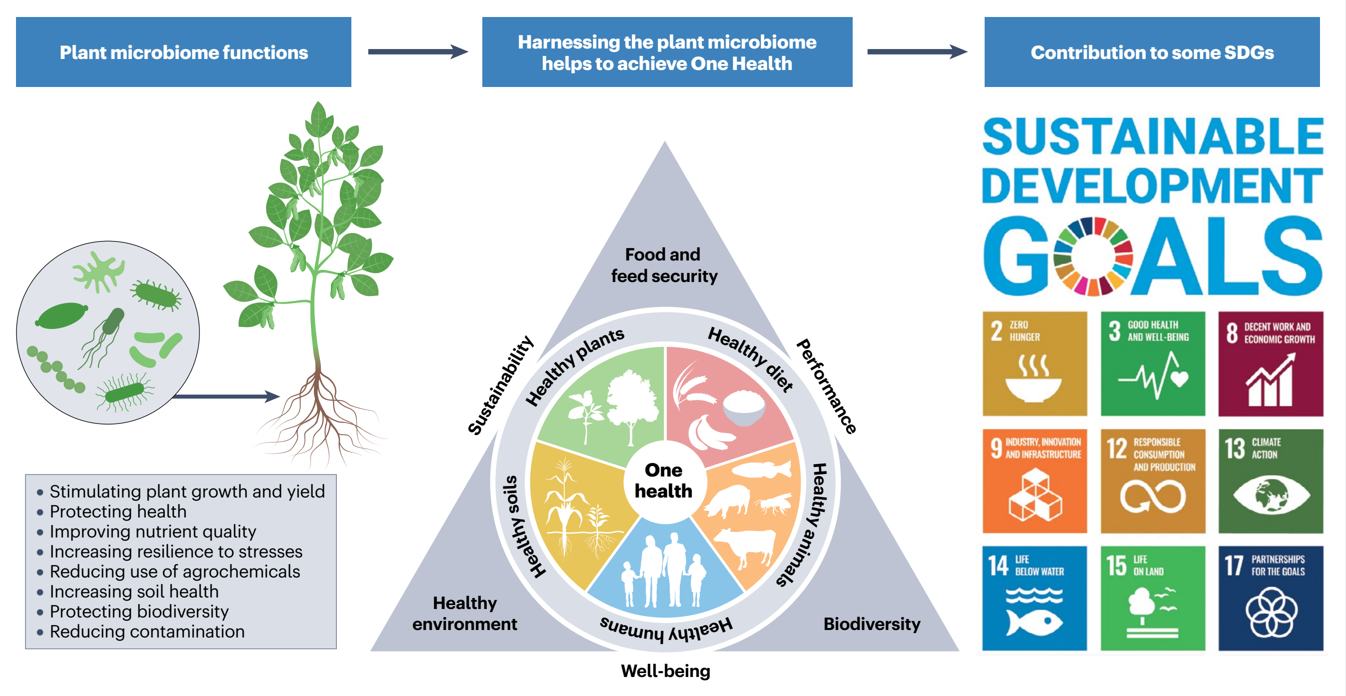
Phyllosphere microbial composition can be largely driven by environmental elements[33] with the host plant species or genotype as an additional determinant[34]. The harsh environmental exposure

## Box 1 | Using plant microbiomes for sustainable crop production supports Sustainable Development Goals and the One Health approach

In 2015, the United Nations directed the path towards an environmentally, socially and economically sustainable world. The United Nations Sustainable Development Goals (SDGs; https://sdgs.un.org/goals) enable an extensive framework to coordinate and shape government policies, and to engage the public with sustainability[153]. In 2016, 17 interlinked objectives and 169 associated targets were devised, and the SDGs officially came into force. However, it is predicted that no single country will meet all of the goals by 2030 (ref. 154).

Harnessing and using plant microbiomes for crop production can contribute to SDG2 (zero hunger) and SDG15 (life on land), as well as SDG3 (good health and well-being), SDG8 (decent work and economic growth), SDG9 (innovation and infrastructure), SDG12 (responsible consumption and production), SDG13 (climate action), SDG14 (life below water) and SDG17 (partnerships for the goals) (see the figure). Indeed, a multitude of studies has demonstrated that utilization of the plant microbiome includes several benefits. It can contribute to development of healthy food, avoid the use of (hazardous and harmful) agrochemical pesticides, protect biodiversity and increase plant productivity. Thereby, microbiome applications increase food security, water and environmental stability, contribute to economic growth and foster industrial innovation[29].

A One Health approach can accelerate progress towards the SDGs[155]. The One Health concept highlights that the health and well-being of humans are inseparably linked to the health of other ecosystem components such as soil, plants, water and animals[15]. Harnessing plant microbiome functions can contribute significantly to sustainable agricultural practices, thereby directly or indirectly protecting the various ecosystems[156]. One Health is directly connected to SDGs such as SDG3 (good health and well-being), SDG12 (responsible consumption and production), SDG13 (climate action), SDG14 (life below water) and SDG15 (life on land). Harnessing the plant microbiome can increase our potential to reach sustainable goals and make a more sustainable world for future generations.



on the leaf surface to acute fluctuations in temperature, humidity, ultraviolet light and limited nutrient availability combined with significant environmental heterogeneity, unevenly affects microbiota distribution and density[35]. A recent study evaluated leaf-scale microbiome diversity spanning global-scale gradients over continents and across a wide range of host species. This study revealed globally consistent responses of microbiome diversity to two environmental conditions (soil nutrients and herbivores), suggesting that general, predictive principles may govern diversity across spatial scales and host species[36].

### Core plant microbiota and keystone taxa

The core plant microbiota consists of a stable set of microorganisms that form core interaction networks. These members of the microbial community are persistent and ubiquitous in almost all communities associated with a particular plant host[37]. Core microbiota are expected to have pivotal roles in organizing the assembly of plant-associated microbial communities[37]. These microorganisms may function as mutualists, commensals or pathogens. One study proposed to focus on functional core microbiota based on functional traits that are present in a plant-associated community rather than address the

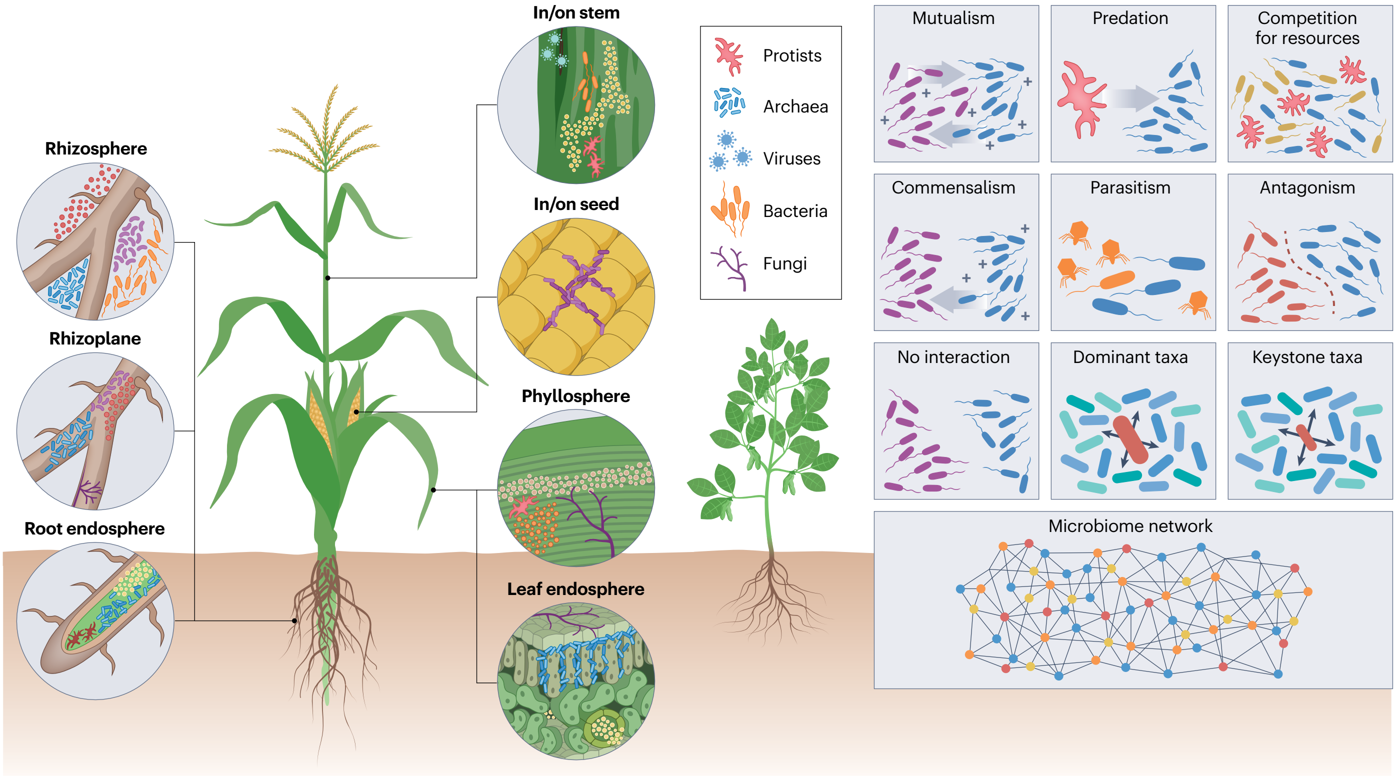


**Fig. 1 | The plant microbiome and microbial interactions.** The plant microbiome consists of bacteria, viruses, archaea, fungi and protists, each performing important community functions. Different microbial taxa can inhabit the rhizosphere, rhizoplane, phyllosphere, flowers, fruits, seeds and the endosphere (inside plant tissues). Microbial interactions in the microbiome network can be classed as mutualism (all species involved benefit from their interactions), antagonism (one organism benefits at the expense of another), predation (one organism, the predator, kills and eats another organism), commensalism (one species obtains food or other benefits from the other without either harming or benefiting the latter), parasitism (one organism lives on or in the other organism and benefits from it by causing some harm) and competition for resources. Dominant taxa, that is, taxa that are more abundant than others, have been proposed to have an important role for the functioning of the microbiome. Keystone taxa are highly connected taxa that are of key importance for ecosystem functioning even if they are not in high abundance.

taxonomic core microbiome[38]. Overall, the identification of core microbiota may help to identify sets of microorganisms that engage in facilitative and mutualistic interactions, which are crucial for establishing themselves in the plant environment. These interactions ideally exhibit synergistic effects to promote plant performance. For instance, a study[39] showed complementary roles of *B. japonicum* and *Azospirillum brasilense* in jointly producing distinct concentrations of the phytohormones auxin, gibberellic acid and zeatin, thereby fuelling early host growth.

In recent years, microbial network analysis has become an important tool to visualize co-occurrence patterns among microbial communities[40]. These networks have also been used to statistically identify keystone taxa or hubs representing taxa, which are highly associated in a microbiome[41] as their removal has been shown by computational means to cause significant shifts in the structure and functioning of microbiomes[42]. Keystone taxa do not necessarily represent taxa that occur in high abundance and may also include rare taxa that are of key importance for ecosystem functioning[43]. As keystone taxa steer microbial community assembly and functions, the consideration of keystone taxa is of increasing importance for selection of microorganisms to be applied as efficient inoculants in agriculture.

## Signalling and perception in plant–microbiome interactions

In the plant environment, communication between plants and microorganisms as well as between different microorganisms takes place and is mediated through specific compounds[44]. The two best-known plant signals acting on beneficial microorganisms are flavonoids and strigolactones. Legumes secrete flavonoids in the rhizosphere that regulate rhizobial *nod* gene expression, producing lipo-chito-oligosaccharides (LCOs), which are then recognized by plant lysine motif (LysM) receptor-like kinases (RLKs) that trigger a signal cascade that leads to root nodulation[45]. Plant strigolactones are hormones that are involved in the regulation of plant developmental processes and that facilitate interactions with microorganisms. They trigger production of Myc factors including LCOs by arbuscular mycorrhizal fungi (AMF), which are also recognized by LysM RLK receptors, leading to AMF colonization[46,47]. In addition, strigolactones have been reported to shape the rhizosphere microbiome and seem to be involved in multiple plant–microorganism interactions[48]. The interaction of the microbiome and the plants involves even more different types of plant molecule. Recent research showed that various metabolites, such as coumarins, benzoxazinoids, triterpenes and camalexin, shape microbiome activities[49–55].

Many microorganisms produce quorum-sensing signal molecules (for example, *N*-acyl homoserine lactones, diffusible signal factors) to coordinate their activities[44]. These molecules may also function as inter-kingdom signals that are recognized by the plant and induce plant development and immune responses (induced systemic resistance (ISR) and systemic acquired resistance (SAR))[44,56].

Plants recognize microorganisms, their surface components and their secreted molecules (microorganism-associated molecular patterns; MAMPs). They have developed a multi-layered microbial management system to control microbiota homeostasis[57], and microbiota have been shown to modulate plant immunity[12]. The plant uses several shields of defence[58] and the first shield involves surface-localized pattern recognition receptors that perceive MAMPs leading to MAMP-triggered immunity[55]. In pathogenic interactions, plants can also recognize specific virulence factors and induce an effector-triggered immunity, a robust defence response that involves local host cell death and systemic defence signalling. The timing and intensity of the plant response to MAMPs induced by beneficial microorganisms and pathogens typically differ, but these responses show a large overlap in gene expression[59]. The onset of all these plant recognition events often triggers plant systemic responses and involves either ISR (which depends on the jasmonic acid and ethylene signalling pathways) with non-pathogenic microorganisms, or SAR (with salicylic acid signalling), which is most commonly related to pathogens[55]. These signalling pathways modulate plant colonization by specific microbial taxa[60,61].

## Plant microbiome functions and mechanisms of beneficial plant–microorganism interactions

Plants are colonized by a multitude of beneficial microorganisms, which have essential roles in the niches they inhabit[3]. The plant-associated microbiome confers fitness advantages to the plant host (Fig. 2), including stress tolerance, nutrient uptake, growth promotion[62] and resistance to pathogens[63]. In addition, plant quality, nutrient composition and (secondary) metabolite concentration may be affected.

### Improving abiotic plant stress tolerance

At this time, abiotic stress is one of the most significant factors reducing agricultural productivity. Microbial mechanisms related to improvement of abiotic stress tolerance in plants[64] include the production of biopolymers such as exopolysaccharides, which provide a protective matrix around roots, or osmolytes, which can be soluble sugars, amino acids and organic solutes (for example, proline and glycine betaine) seen for instance with strains of *Pseudomonas putida*, *Pantoea brenneri* and *Acinetobacter calcoaceticus* isolated from halophytes or

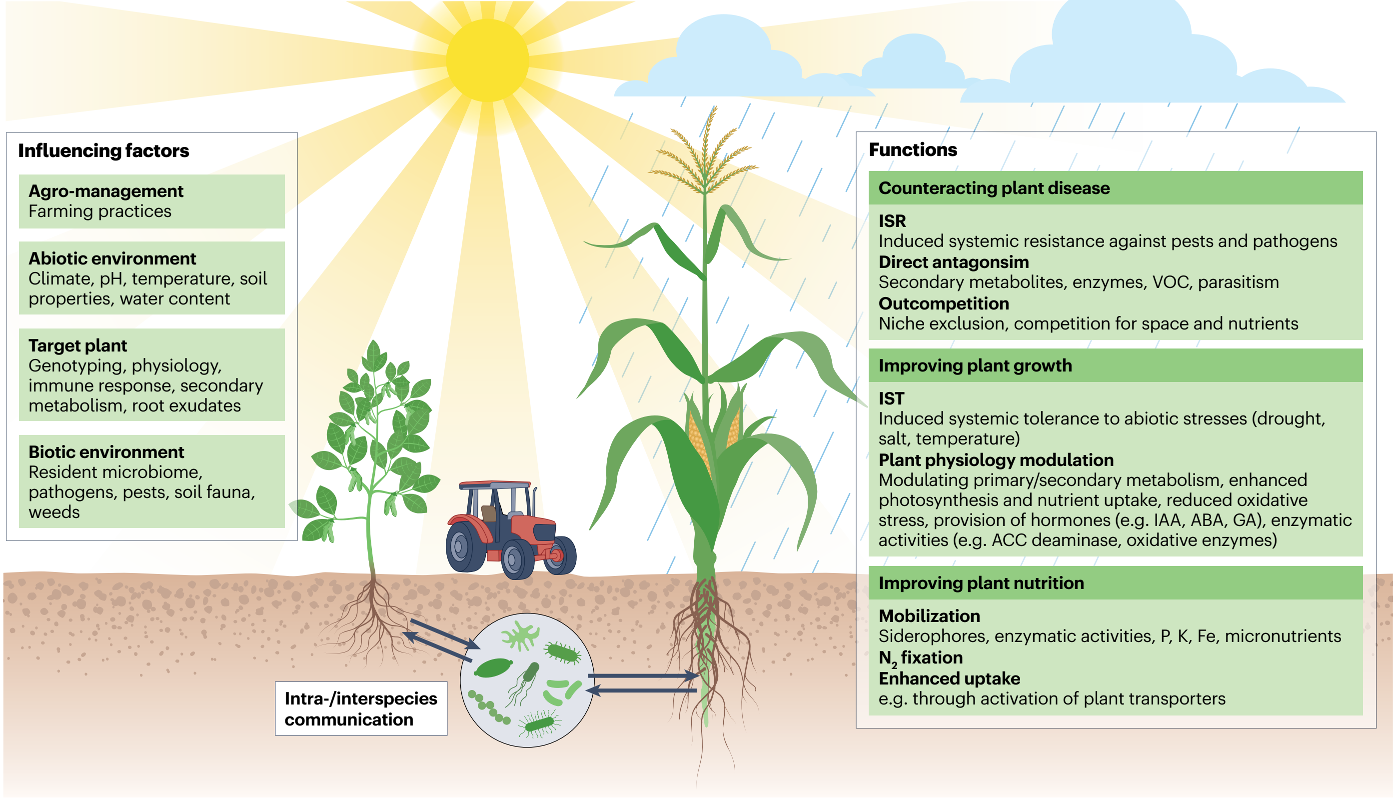


**Fig. 2 | The functions and influencing factors of the plant microbiome.** Several factors, such as the biotic and abiotic environment as well as agro-management practices and the plant itself, are known to have complex direct and indirect effects on plant microbiome components and their functions. The plant microbiome can counteract plant disease, pathogen establishment and spread through mechanisms that involve induced systemic resistance (ISR), out-competition of pathogens and direct antagonism. The plant microbiome is known to promote plant growth through induction of stress tolerance and plant physiology modulation. Furthermore, the plant microbiome may enhance plant nutrition through nitrogen fixation, nutrient mobilization or by enhancing nutrient uptake. ABA, abscisic acid; ACC deaminase, 1-aminocyclopropane-1-carboxylate deaminase; Fe, iron; GA, gibberellic acid; IAA, indole-3-acetic acid; IST, induced systemic tolerance; K, magnesium; P, phosphate; $N_2$, nitrogen gas; VOC, volatile organic compound.

drought-resistant plants[64]. Furthermore, phytohormones or volatiles typically elicit a plant response termed induced systemic tolerance (IST)[65], and the synthesis of 1-aminocyclopropane-1-carboxylate (ACC) deaminase lowers ethylene levels in plants. For instance, *Achromobacter piechaudii* ARV8, which produces ACC deaminase, confers IST to drought stress in pepper (*Capsicum annuum* L.) and tomato (*Solanum lycopersicum* L.) plants[65]. Oxidative stress may also be reduced by microbial antioxidant enzymes and antioxidant metabolites (for example, ascorbate, glutathione) as seen with *Pseudomonas* sp. and *P. brenneri* strains[64].

### Improving plant nutrition

The bioavailability of nutrients involves the release of nutrients from soil for plants[66]. Although the solubilization of P and K is better studied, there is ongoing research on the release of less-studied nutrients such as Ca, Mg, Fe, Mn and Zn into the rhizosphere through microbial activity[67]. The plant microbiome contributes to N bioavailability owing to the presence of both non-symbiotic bacteria[68] (for example, *Azospirillum* spp.) and symbiotic nitrogen-fixing bacteria[69] (for example, *Bradyrhizobium* spp., *Rhizobium* spp., *Mesorhizobium* spp., *Frankia* spp.), and recent studies have revealed that differences in plant nitrogen use efficiency are influenced by the recruitment of those bacteria, leading to more efficient mineral transformation processes in the root or rhizosphere environment[70]. Beneficial microorganisms are known to aid in the synthesis of phytohormones such as indole-3-acetic acid (IAA). The secretion of this molecule, in conjunction with plant recognition of bacterial proteins (for example, flagellin), changes root growth patterns by increasing the root surface, thereby improving the plant's access to water and nutrients as demonstrated with *Azospirillum* spp[71]. AMF also help plants to increase their water and nutrient uptake (for example, N, P, K, Ca and trace elements) owing to the extended hyphal network in the soil[72,73].

### Counteracting plant disease

Various microorganisms, such as members of *Pseudomonas*, *Bacillus* and *Trichoderma* genera, along with AMF, have been shown to induce ISR in plants, thereby protecting against a broad range of pathogens[74]. ISR leads to the expression of pathogenesis- or defence-related genes, enabling the production of, for example, phenylalanine ammonia-lyase, polyphenol oxidase, peroxidase, β-1,3-glucanase and chitinase, as well as the accumulation of reactive oxygen species[75]. Various volatiles and secondary metabolites such as bacterial quorum-sensing molecules, siderophores and cyclic lipopeptides are released by microorganisms to induce ISR[74]. Plant–microbiome interactions are modulated by interkingdom signalling and the induction of root exudation, which has been recently described as "Systemically Induced Root Exudation of Metabolites"[76]. This phenomenon should be taken into account to understand how ISR responses manifest under natural conditions.

In addition to ISR, microorganisms can have direct and indirect activities against plant pests and pathogens through various mechanisms. These activities involve antibiosis via secretion of diffusible and specific metabolites such as lipopeptides, bacteriocins, antibiotics, biosurfactants and cell-wall-degrading enzymes or volatile compounds that interfere with the metabolism of phytopathogens, thereby inhibiting pathogen development, as demonstrated for instance with many rhizospheric strains of *Bacillus* spp. and *Pseudomonas* spp.[29,77]. In bacteria, mechanisms for the control of plant pests depend largely on (insect order-specific) toxins[78] or insecticidal proteins[79]. Entomopathogenic fungi, instead, have a broader host range and rely on direct parasitism, with enzymatic activities such as chitinases and mycotoxins as essential virulence factors for successful insect infection[80]. Parasitic activities such as mycoparasitism, bacteriophagy and mycophagy are also known to have a role in direct activities against a range of plant pathogens. Moreover, a reduction in infection burden may be further mediated through competition for space and nutrients as well as niche exclusion[77] (Fig. 2).

### Effects on plant quality

Using microorganisms to improve plant nutrition and health will not only result in higher yields but also improve the nutritional quality of the plants. For example, nitrogen, manganese and zinc were shown to increase wheat grain protein content[81]. These elements can be provided through conventional fertilization, but also through microbial applications. Although the mechanisms are poorly understood, there are multiple indications that plant-associated microbiota can influence secondary metabolite production of their host[82,83], thereby influencing flavour and nutritional qualities of the plant. Microorganisms have also been used to improve food quality, for instance, the application of various combinations of AMF and pseudomonads yielded unique volatile component profiles and elemental composition of strawberry fruits[84]. Similarly, inoculation of AMF and pseudomonads onto tomato plants increased the concentration of organic acids (maleic and citric acid) and glucose, thus contributing to the sensory properties of tomatoes[85].

## Current microbial applications

Chemical products are used to increase yield and protect plants from diseases, and thus have an important role in fulfilling the continuously increasing food demand. However, there are increasing concerns about harmful impacts of many of these products on ecosystems[86,87]. One way to reduce the use of chemical and hazardous substances is the use of beneficial microorganisms[29], as certain microorganisms have the potential to improve plant growth and health as biofertilizers, biostimulants or biopesticides.

Although the market for microbial applications in agriculture is regarded as an emerging one, the first patent for a bioinoculant product was granted in 1896 (ref. 88). Currently, market development is driven by numerous factors, that is, stricter or changing regulations governing the use of chemical pesticides and fertilizers, policies promoting sustainable and climate-smart agricultural practices and consumer demand for healthy and sustainable food. Overall, there is continuous and strong market growth, for example, IDTechEx estimates that the worldwide market for agricultural biologics will reach US$19.5 billion by 2031 (ref. 5), whereas Markets and Markets estimate a market value of $27.9 billion by 2028 and project a market growth at a compound annual growth rate of 13.7%[6]. Nevertheless, some challenges remain, most notably the inconsistent efficacy compared with chemical products and the often unfavourable or uncertain regulatory landscape (Box 2).

Most common microbial products on the market are used for plant protection (biocontrol), plant nutrition (biofertilizers) and plant strengthening (biostimulants)[5,6,9] (Figs. 3 and 4 and Supplementary Information).

### Microbial plant protection

Current microbial plant protection products are registered for action largely against insect pests and soil-borne fungi[89]. Microbial products based on *Bacillus firmus* and *Purpureocillium lilacinum* acting against nematodes have also been registered in the European Union (EU) and in the USA[90,91], whereas the control of weeds with bioherbicides is still of limited use[92]. The most important biopesticides acting against insect pests are long-used products based on *B. thuringiensis*, *Beauveria bassiana* and *Metarhizium* spp. with *B. thuringiensis* products accounting for 90% of all biopesticides used[93]. Also, most biocontrol products that act against (soil-borne) fungi are based on *Bacillus* spp. (largely *Bacillus subtilis*, *Bacillus velezensis* and related species) or on various *Trichoderma* species (mainly *Trichoderma afroharzianum*, *Trichoderma asperellum*, *Trichoderma atroviride*, *Trichoderma gamsii* and *Trichoderma harzianum*), but several different bacterial, fungal and oomycete strains have also been developed to control fungal diseases[89]. Altogether, biocontrol products account for a single-digit percentage of total pesticide sales, but growth rates are estimated to be well over 10%[92].

### Microbial biofertilizers

The use of microorganisms in agriculture presents a promising technology for future sustainable farming systems, especially considering the rapid depletion of nutrient stocks in soils[94]. Biofertilizers are products that contain live microorganisms formulated to enhance soil fertility and nutrient uptake by plants (crops). The range of nutrients includes macronutrients (N, P, K), micronutrients (Fe, Zn, Co, Mo, Mn, Cu, among others) and/or other beneficial nutrients (Si). The spectrum of microbial mechanisms encompasses nitrogen fixation, phosphorus, potassium or zinc solubilization, and root uptake through phytostimulation[95]. Numerous microbial taxa have been proposed as biofertilizers over the past few decades; however, the symbiotic association between legumes and nitrogen-fixing rhizobia has been extensively harnessed worldwide. This concept has been successfully extended to cereal crops through the use of free-living rhizobacteria such as *Azospirillum* spp. These rhizobacteria possess the ability to enhance water and root uptake of $NO_3^-$, $NH_4^+$, $PO_4^-$, K, Rb, Mn, Cu, Zn and Fe (ref. 68). Additional examples include members of the genera *Pseudomonas*, *Bacillus*, *Paenibacillus*, *Serratia* and *Burkholderia*[96]. AMF have been available on the market for some time as products to increase P uptake in diverse crop types[97]. AMF are obligate symbionts of most land plants and deliver nutrients, in particular P, to their host by extending the root system through an extensive (extra-radical) network of hyphae in the soil[72]. P-solubilizing filamentous fungi widely investigated are *Aspergillus* and *Penicillium* species; however, only *Penicillium bilaiae* is commercially available on a large scale for P uptake, with varied crop yield benefits demonstrated, including in maize[98]. *P. bilaiae* secretes citric and oxalic acids and is reportedly more effective in low-P soils; however, stimulation of root hairs has also been linked to yield increases, particularly when P is not limited[98].

## Box 2 | Key features of global regulations for approving microbial applications in crop production

Depending on the intended use, microbial applications are considered as microbial biopesticides or biocontrol products or as microbial biostimulants and biofertilizers. These types of application are regulated differently in most countries, and biopesticides guidelines have been given as part of an international code of conduct on pesticide management by the WHO (WHO/HTM/NTD/WHOPES/2017.05), whereas regulations for biofertilizers and biostimulants are less clear and vary substantially. The USA considers any microbial product intended for use as a pesticide to fall under the Federal Insecticide, Fungicide, and Rodenticide Act (FIFRA) whereas fertilizer use is exempted from FIFRA regulation (https://www.epa.gov). The European Union (EU) handles biopesticides under regulation EC_1107/2009 and microbial biofertilizers and biostimulants under regulation EU_2019/1009. Analogous differentiation exits also in other countries such as China[157] and India[158]. The development of biopesticides must consider the safety for humans, animals, the environment and non-target organisms, and must also consider potential residues left on crops. For safety evaluation, the taxonomic position and origin of microorganisms are important criteria. In the EU, efficacy trials are part of the registration process. The cost and time required for registration vary substantially. A new biopesticide requires several years[159] for registration in the EU, whereas in the USA the average time frame is 19 months.

Recently, the OECD Expert Group on Biopesticides has worked on harmonized approaches for biopesticide registration (ENV/CBC/MONO(2023)10), and attempts to simplify biocontrol product registration have been made in the EU (2018/C 265/02). The USA and African states have less-stringent customized regulations for microbial biocontrol products to promote use and approval[160]. Biostimulant and biofertilizer registration is globally faster and requires less effort to obtain regulatory approval. Overall, although several efforts have been made to promote the use of microbial inoculants in agriculture, the incorporation of microbial products into frameworks designed for chemical substances is not always suitable for microorganisms and adaptation will require efforts of all stakeholders[159].

### Biostimulants

Also referred to as plant strengtheners, biostimulants are increasingly applied in agriculture[99] and are also described as positive plant growth regulators, biogenic stimulants, metabolic enhancers, elicitors, allelopathic preparation, plant conditioners or phyto-stimulators. They are produced from diverse starting materials or production processes and are composed of organic substances and inorganic materials including several substances and microorganisms[100]. Biostimulants differ from conventional fertilizers in that they do not directly supply nutrients to plants but may stimulate plant nutrient acquisition processes. They can be applied to the plant either as seed, foliar or rhizosphere applications. These methods stimulate plant physiology, enhance nutrient uptake capacity, increase abiotic stress tolerance capacity, crop productivity or yield. Microbial biostimulants can also alter the biological structure of the soil and stimulate the growth of beneficial microorganisms, enhancing soil fertility. Various products are on the market showing different activities and using different modes of action. For instance, *Bacillus simplex* S4 (found in a biostimulant product) produces IAA and ACC deaminase as well as siderophores, and has shown reproducible plant growth promotion of wheat and maize[101]. Another example is *Bacillus atrophaeus* strain ABi05, a cold-tolerant strain that promotes germination and growth of multiple crops[102].

### Applications for biofortification

Biofortification (that is, the enrichment of essential micronutrients and other health-promoting compounds) in crops to improve their nutritional value, is another promising microbial application[103] that offers an alternative to genetic biofortification (through breeding or

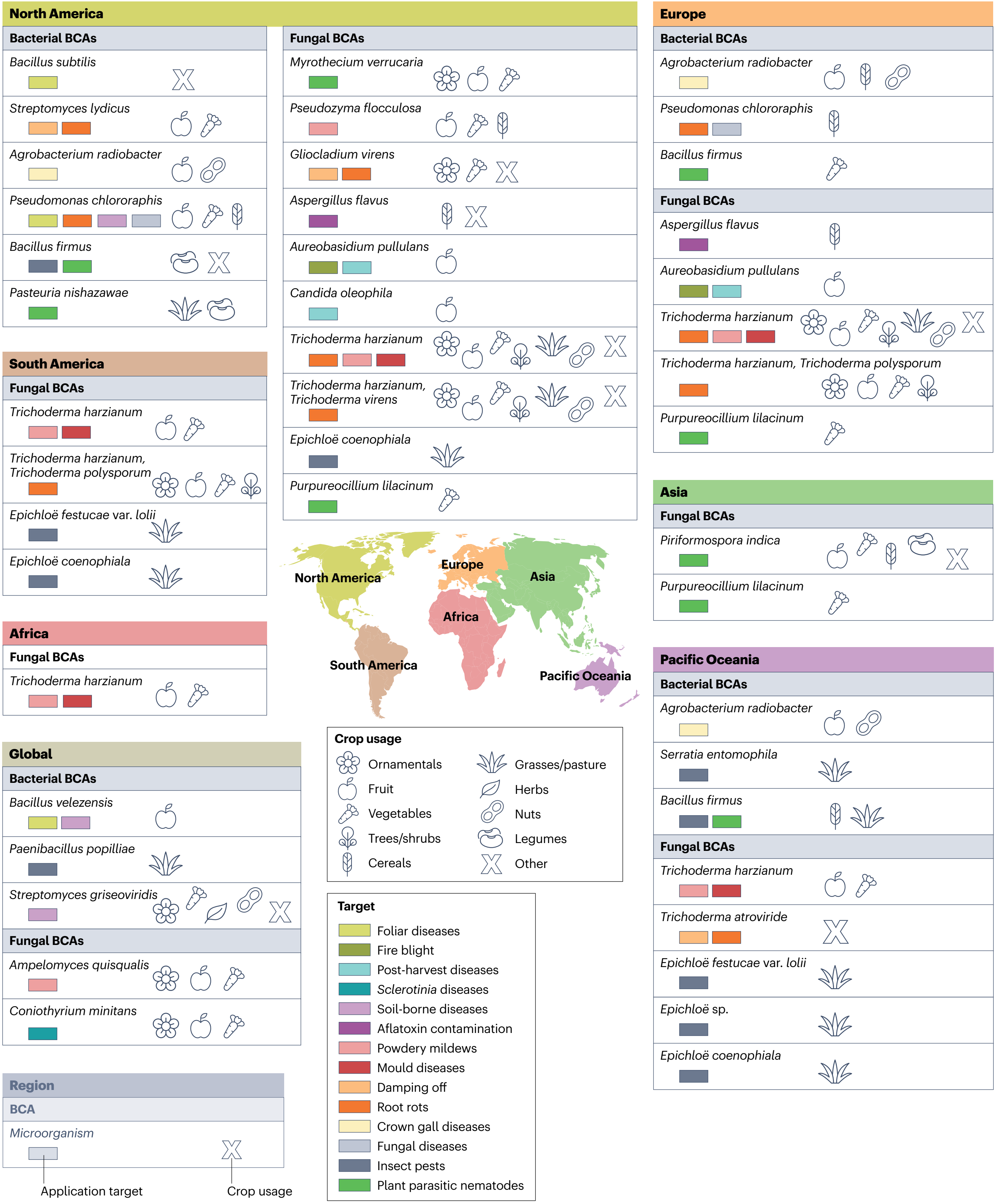

North America
Bacterial BCAs
Bacillus subtilis
Streptomyces lydicus
Agrobacterium radiobacter
Pseudomonas chlororaphis
Bacillus firmus
Pasteuria nishazawae
Fungal BCAs
Myrothecium verrucaria
Pseudozyma flocculosa
Gliocladium virens
Aspergillus flavus
Aureobasidium pullulans
Candida oleophila
Trichoderma harzianum
Trichoderma harzianum, Trichoderma virens
Epichloë coenophiala
Purpureocillium lilacinum
Europe
Bacterial BCAs
Agrobacterium radiobacter
Pseudomonas chlororaphis
Bacillus firmus
Fungal BCAs
Aspergillus flavus
Aureobasidium pullulans
Trichoderma harzianum
Trichoderma harzianum, Trichoderma polysporum
Purpureocillium lilacinum
South America
Fungal BCAs
Trichoderma harzianum
Trichoderma harzianum, Trichoderma polysporum
Epichloë festucae var. lolii
Epichloë coenophiala
Africa
Fungal BCAs
Trichoderma harzianum
North America
Europe
Asia
Africa
South America
Pacific Oceania
Asia
Fungal BCAs
Piriformospora indica
Purpureocillium lilacinum
Pacific Oceania
Bacterial BCAs
Agrobacterium radiobacter
Serratia entomophila
Bacillus firmus
Fungal BCAs
Trichoderma harzianum
Trichoderma atroviride
Epichloë festucae var. lolii
Epichloë sp.
Epichloë coenophiala
Global
Bacterial BCAs
Bacillus velezensis
Paenibacillus popilliae
Streptomyces griseoviridis
Fungal BCAs
Ampelomyces quisqualis
Coniothyrium minitans
Region
BCA
Microorganism
Application target
Crop usage
Crop usage
Ornamentals
Fruit
Vegetables
Trees/shrubs
Cereals
Grasses/pasture
Herbs
Nuts
Legumes
Other
Target
Foliar diseases
Fire blight
Post-harvest diseases
Sclerotinia diseases
Soil-borne diseases
Aflatoxin contamination
Powdery mildews
Mould diseases
Damping off
Root rots
Crown gall diseases
Fungal diseases
Insect pests
Plant parasitic nematodes

**Fig. 3 | Major microbial crop protection products.** World map showing several fungal and bacterial biocontrol agents (BCAs) that are currently used for various target diseases (diseases caused by insects, oomycetes, fungi, bacteria and nematodes) and crops (ornamentals, fruits, vegetables, trees and shrubs, cereals, grasses and pasture, herbs, nuts, legumes and others). More details on these agents are provided in the Supplementary Information. Representatives of selected major products are shown. Numerous other products are not shown owing to their smaller market size, and/or registration based on national approvals.

genome editing) and agronomic biofortification (through fertilizer application). Many biostimulants exhibit biofortification potential. For example, inoculation with AMF was shown to improve both yield and Fe and Zn concentration in chickpea grown under field conditions[73]. Likewise, in arsenic-contaminated soils, AMF was shown to decrease arsenic accumulation and increase Fe and Zn concentration in wheat grains[104]. Furthermore, numerous bacterial taxa have shown the potential to enrich plants with Fe, Zn and diverse vitamins such as C and $B_{12}$ (reviewed in ref. 105).

## Emerging plant microbiome applications

Currently, most microbial products for improving crop production are based on single microbial strains (Figs. 3 and 4). Recent meta-analyses have revealed that, at a global level, currently used microbial inoculants have shown the expected effects under field conditions[9,106]. However, the efficacy of first-generation microbial inoculants[10] (consisting mostly of single microbial strains in contrast to second-generation approaches that involve more advanced approaches such as the application of complex consortia, microbiome modulation or digital tools) is often highly variable depending on the conditions of the receiving environment, plant genotype and application method. Common bottlenecks represent the poor competitive ability of inoculants against the highly adapted soil microbiota, predation and low plant colonization rates. Most currently applied microbial strains are primarily selected on the basis of certain functional characteristics, for example, antagonism of a plant pathogen, instead of on competitive ability and persistence. A better understanding of the genetics that underlie microbial establishment in the plant environment, as well as of microbial and microbe–host interactions will lead to a more targeted and improved selection of inoculant strains.

### Strain improvement

Strain improvement is a well-established method of improving microbial strains used for enzyme and metabolite production in fermentation and includes the introduction of transgenes, directed evolution and adaptation to growth conditions or directed mutagenesis using CRISPR–Cas[107]. Although such approaches under contained conditions are widely used and accepted, the release of genetically improved strains and their risk management have long been discussed and are still under debate[108]. Nevertheless, CRISPR–Cas9 was recently used to target the modulation of a secondary metabolite pathway in the commercial AR37 strain of *Epichloë* to reduce or remove endophyte-induced mammalian toxicity while retaining activity against some important agricultural insect pests[109]. The method of gene inactivation deployed was classified as site-directed nuclease 1 type (SDN-1), which means that this strain improvement will not be regulated as a genetically modified organism in certain jurisdictions[110]. In many cases, traits that specifically improve fermentation processes (such as enzyme production or temperature optimization), may not necessarily translate directly into improved performance when applied in complex natural conditions. For some designer traits, the interaction with the whole microbiome could be affected and improved through synthetic biology approaches to microbiome engineering[49].

Furthermore, genetic engineering and the use of synthetic biology tools may drastically improve the efficacy of microbial inoculants. For example, the use of $N_2$-fixing microorganisms instead of inorganic fertilizers is of high interest, as the production of synthetic fertilizers is very energy demanding and half of the applied nitrogen is lost to the environment. However, $N_2$ fixation is a strongly regulated process and is usually repressed in the presence of nitrogen. To achieve $N_2$ fixation in nitrogen-rich soil conditions different approaches based on genetic engineering, synthetic biology and gene editing have been used to engineer $N_2$-fixing bacteria to eliminate the regulation of $N_2$ fixation by exogenous nitrogen[111,112].

### Synthetic communities

Triggered by recent outstanding research on synthetic communities (SynComs) to elucidate microbial functions and interactions, several second-generation microbiome application approaches have been developed using microbial consortia. There are examples of community and SynCom applications[113–118] for biofertilizers, biostimulants and biopesticide solutions. The applied consortia are designed to follow different rationales and may show different levels of complexity. One approach is to combine strains, from the same or different taxa, that show synergistic or complementary activities, for example, strains that show different mechanisms of promoting plant growth. Furthermore, strains that have similar functions related to plant growth but perform well under different environmental conditions (for example, showing different pH or temperature ranges) can be combined. The potential of using microbial consortia versus single strains was demonstrated in a recent meta-analysis[119]. Studies applying an ecology-based approach also provide improvements by combining diverse, genetically related strains, where the diversity effect is more important than strain identity. A study[120] showed that survival of introduced *Pseudomonas* spp. consortia and their biocontrol efficacy against the pathogen *Ralstonia solanacearum* increased with increasing diversity. Similarly, another study[121] successfully applied bacteriophage consortia to decrease the incidence of *R. solanacearum*.

Microbial consortia may have different levels of complexity. Consortia composed of three strains, which have been shown to shape the root microbiome, provide protection in the field from root-knot nematodes[122]. Plant growth promotion effects have also been shown with consortia applications with up to eight *Pseudomonas* spp. in tomato plants, which are also associated with microbiome reshaping[123]. More complex SynComs containing eight different bacterial strains have been shown to alter microbial communities in wheat, thereby promoting plant growth and suppression of the fungal pathogen *Fusarium pseudograminearum*[124]. Complex SynComs based on microbiome ecology have so far been used mostly to elucidate microbiome functions[125,126]; however, they have also been receiving increasing attention from an application point of view. A paper proposed to focus on core microbiomes, that is, sets of microorganisms that form cores of interactions that can be used to optimize microbial functions[37]. This concept was extended[127], and a three-step approach was proposed to identify taxa with the potential to promote plant production: first, dominant taxa; second, correlation networks; and third,

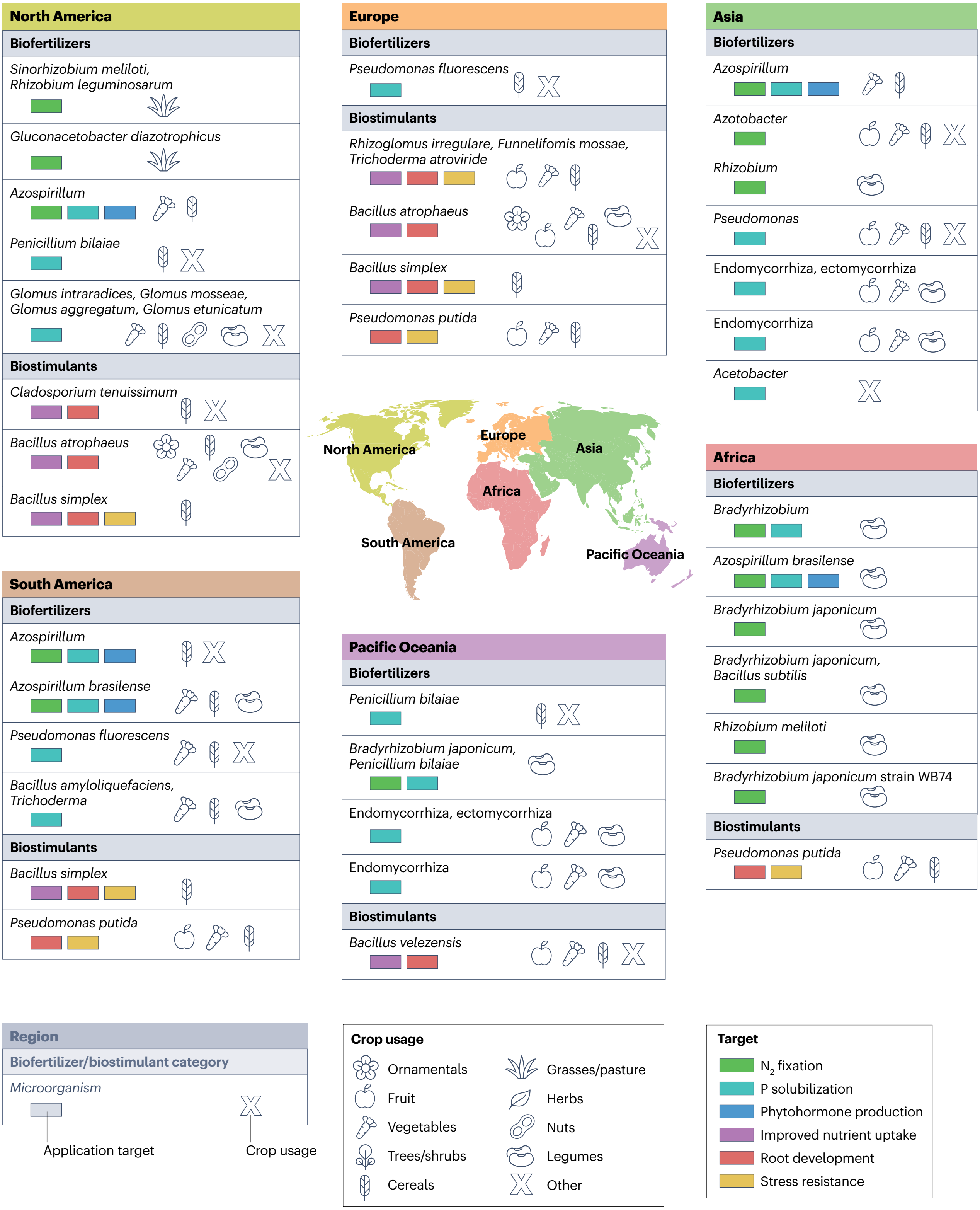


**Fig. 4 | Major microbial biofertilizers and biostimulants.** World map showing key microbial species that act as biofertilizers or biostimulants on crops (ornamentals, fruits, vegetables, trees and shrubs, cereals, grasses and pasture, herbs, nuts, legumes and others). More details on these species are provided in the Supplementary Information. Representatives of selected major products are shown. Numerous other products are not shown owing to a smaller market size, and/or registration based on national approvals.

microbial functions. Because of their dominance and connectedness, such complex microbial consortia based on microbiome information and ecological principles are likely to perform better and more consistently under field conditions than single strains or less complex consortia; however, production and application procedures still need to be developed.

### Soil transplantation and rewilding of plant microbiomes

Still in their infancy, but with high potential, are approaches based on shifting whole microbial communities, for example, by soil transplantation. A recent meta-analysis showed that translocation of soils supports the restoration of plant communities[128]. In line with these findings, a further study showed that soil microbial communities sourced from drier, warmer sites for the growth of tree seedlings mediated higher drought tolerance than soils from colder regions[129]. In addition, sourcing microorganisms from wild relatives of crops or transplanting ancestral microbiota has been proposed. Rewilding plant microbiomes is built on the assumption that wild ancestors harbour microorganisms with plant-beneficial traits that are lost or are strongly depleted in the microbiomes of modern day crops[130,131].

### Microbiome modulation

Numerous studies have shown that microbial inoculants may induce shifts in the microbial community of the receiving environment, often enriching taxa that are known for their plant-beneficial effects[132]. A paper proposed microbiome modulation as a novel mode of action, which may involve transient or more stable microbiome shifts associated with very specific enrichment of certain taxa or functions[133]. Furthermore, other organisms such as nematodes[134], viruses or phages[135] as well as specific compounds[136] may influence microbiome diversity. This suggests that targeted microbiome modulation may also be a future avenue to steer microbiome functions for the benefit of plant performance.

### Plant breeding for beneficial plant–microorganism interactions

During the domestication of cultivated plants, microorganisms were also unintentionally selected for specific associations with roots and the rhizosphere. Plant genes involved in the structure of roots and root exudation have been shown to indirectly shape the microbiome. For example, in barley a single mutation responsible for the size and density of root hairs decreased microbial alpha-diversity[137]. Thus, breeding for specific root phenotypes can have a significant impact on the recruitment of individual members of the microbiota. One study created a maize mapping population and identified several quantitative trait loci that support the feasibility of breeding crops to maximize gains from the symbiosis[138]. For many symbionts such as *Epichloë* endophytes or AMF, successful applications require compatible species and/or genotype–fungus combinations[139]. Plant breeding has overcome some of the incompatibility issues experienced with *Epichloë* endophytes in forage grasses, particularly those that arise when forming novel symbioses from across host species, such as when transferring an endophyte from tall fescue to perennial ryegrass. As a seed-borne technology, traits such as efficient colonization of grass tillers and transmission into seeds, as well as the ability to remain viable in seed, are hallmarks of compatible associations. Recurrent selection of repeated cycles of selection and breeding for such key traits in ryegrass, including expression of endophyte alkaloid profiles for better pest protection, has resulted in improved and stable trait expression[25,140].

### Digital tools

The increasing availability of microbiome data and correlated metadata combined with the advancements in digital technologies (in particular, artificial intelligence) and sensor systems have given rise to the idea of developing novel microbiome-based prediction and precision tools for agriculture[10,11,29,141]. The feasibility of this concept was demonstrated in several proof-of-concept studies. For example, a study showed correlation between the bulk soil microbiome and crop productivity[142]. The authors of this study identified taxa that correlate with higher and lower productivity areas and developed a machine learning model based on the microbiome composition that could predict productivity with an accuracy of 79%. Another study showed that changes in the rhizosphere microbiome composition could predict whether tomato plants remained healthy or became infected by the pathogen *R. solanacearum*[143]. Furthermore, the neural network approach was used to design novel synthetic communities that modified phosphate accumulation in the shoot and induced phosphate starvation-responsive genes in a predictable fashion[144]. Although these results are promising, further development is needed. The complexity of agronomic systems requires consideration of complex and diverse data (for example, microbiome data, genomic data, phenotypic data, environmental data) and the establishment of comprehensive, high-quality datasets along with appropriate models for a given task[141,145]. An overview of emerging solutions is shown in Fig. 5.

### New application areas

Plant microbiota are currently mostly used for plant protection and plant nutrition, whereas enhancing abiotic stress tolerance and improving nutritional plant quality represent emerging areas of application. An additional application area is improving the safety of plant produce, for example, by eliminating pesticide contamination. Many soil- and plant-associated microorganisms have the capacity to degrade a wide range of organic compounds, including pesticides[146], which may be used to treat plants and/or plant produce. Furthermore, endophytes have been shown to degrade herbicides, representing a reversible mechanism to achieve herbicide resistance in plants to enable weed control[147].

## Research gaps and perspectives

Owing to a constantly growing population, food production must increase substantially in the coming decades, while simultaneously there is an urgent need to reduce the environmental impact of agri-food production. Therefore, sustainable options represented by biofertilizers, biopesticides and biostimulants are of high interest and are increasingly gaining importance. Some products have been successfully applied for a long time, for example rhizobia as $N_2$-fixing inoculants. A Review effectively summarized the successful implementation of $N_2$-fixing *Bradyrhizobium*-containing inoculants for soybean production in Brazil[101]. For instance, in 2019–2020, approximately 20 million tons of N (equivalent to approximately 43 million tons of urea) were obtained through $N_2$ fixation, corresponding to approximately 430 million tons of $CO_2$-equivalent greenhouse gas emissions that would have been released with fertilizer use. Furthermore, co-inoculation of *Bradyrhizobium* spp. together with the biostimulant *Azospirillum* spp. has been adopted by farmers and was applied to 25% of the total soybean planted area in Brazil[148]. There are several more successful products on the market, including for example, biostimulants and biofertilizers using *P. bilaiae*, *B. atrophaeus* ABi05 or *B. simplex*. Furthermore, plant protection is achieved by several microbial products primarily based on strains belonging to *Trichoderma*, *Bacillus*, *Pseudomonas*, *Metarhizium*, *Beauveria* and

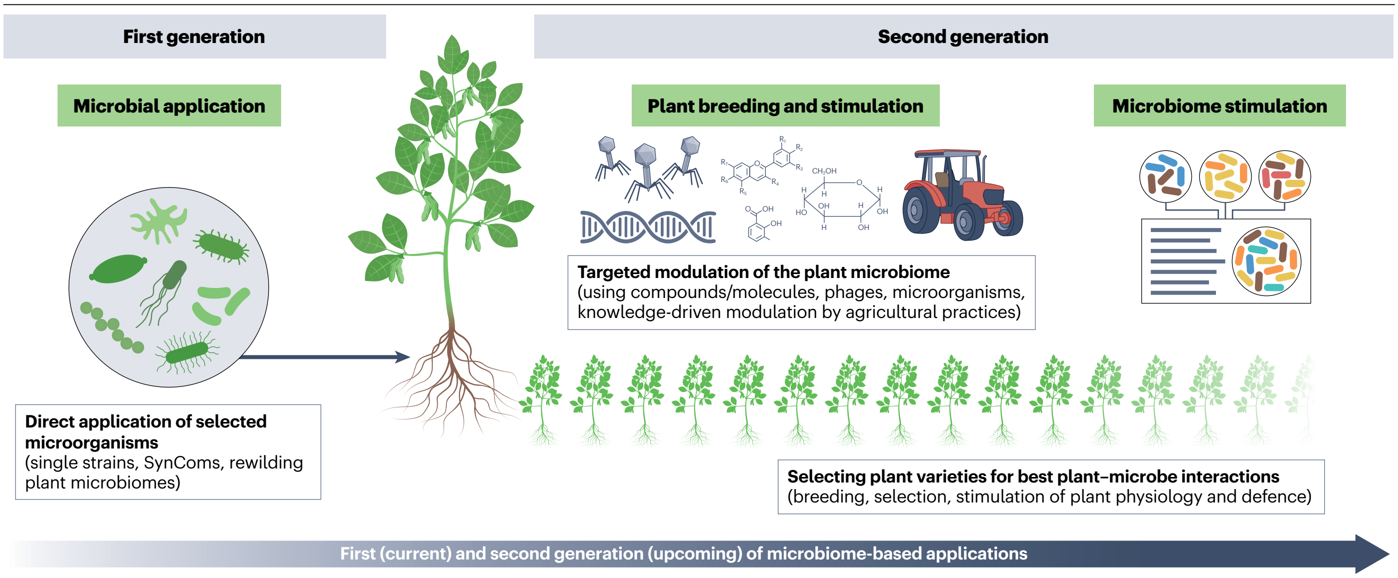


**Fig. 5 | Current and emerging microbiome-based applications for sustainable crop production.** The first (current) and second (emerging) generations of microbiome-based applications are depicted, with the first generation involving the direct application of selected microorganisms and the second generation focusing on selecting plant varieties for optimal plant–microorganism interactions and targeted modulation of the plant microbiome.

*Streptomyces* genera[149]. These success stories undoubtedly show the potential of microbial applications as alternatives to replace chemicals and will contribute to a more sustainable manner of plant production.

Despite these success stories and the huge potential, which raises high expectations, there are challenges to address. Most applications still yield inconsistent field success and there is a need to better link microbiome understanding with product development to achieve microbial products that perform well in natural environments. In the previous section we list various promising approaches to overcome limitations, all based on improved knowledge and understanding of microbiome interactions in relation to plant traits and to the establishment of inoculant strains. There is evidence that microbial consortia perform better than single strains[119], and several approaches to design multi-strain applications have been developed. Furthermore, microbiome modulation through substances, microorganisms or bacteriophages has started to be explored, and plant breeding for a more efficient interaction holds promise but is still at an early stage of development. Overall, one major bottleneck is the limited understanding of interactions within the microbiome, which are highly complex, influencing each other in activities and functions, ultimately affecting the plant host. Currently, only few microbial taxa are used in agriculture, and there is a need to further explore less-investigated taxa, evaluate their safety and develop formulations and up-scaling procedures. However, this effort is also limited by the difficulty in cultivating the full diversity of microorganisms. In addition, we must increase knowledge of the plant response to microorganisms and of how different varieties differ in their interactions with beneficial microbiota. Such an understanding of the compatibility between microorganism and host will advance plant breeding and enable the use of wild relatives or selected varieties to provide new sources of beneficial microorganisms. Many microbiome studies focus on model organisms such as *Arabidopsis thaliana* and rarely take into account variation in crops and their wild ancestors such as studies performed in barley[150]. The specificity of microbiomes in less-studied crops, particularly in their wild relatives, different cultivars and natural systems requires further attention[151] to develop informed and rational microbiome engineering[114].

A high potential lies in the better exploration of microbiome data, which could be integrated into precision farming applications, potentially through several machine learning approaches. However, gaps remain in microbiome data acquisition and management, and microbiome data comparability is generally low. There is an urgent need for a unified, coordinated approach that ensures compatibility of data to ensure linkage between bioinformatic databases[152]. Global cooperation is needed to comprehensively address the complexity and interconnectedness of plant microbiomes and to highlight the necessity for a unified approach to manage them effectively.

Product safety must be considered and is usually addressed in numerous regulations that typically address potential pathogenicity and environmental safety, and includes aspects such as horizontal gene transfer, effects on non-target organisms and antibiotic resistance. There is also concern that introduced microbial inoculants might have an invasive character, although invasiveness of microbial inoculants has so far not been observed. However, microbial inoculants, as well as farming practices or environmental conditions, might affect microbiome composition and function. There is a need to better understand such effects, also at the functional level, as well as to obtain more knowledge on the evolution of an inoculant strain in a natural environment. Microbiome-assisted crop production will support our efforts to achieve more sustainable crop production and One Health. Harnessing the plant microbiome will lead not only to higher yields but, considering microbiome connectivity[13], to healthier people and a healthier planet. Apart from product development, there is a need to follow a multi-stakeholder approach as well as to interact with farmers and citizens to ensure rapid implementation of a new approach to cope with challenges in agri-food production systems.

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## Author contributions

All authors researched data for the article. All authors contributed substantially to discussion of the content. All authors wrote the article. S.C. and A.S. reviewed and/or edited the manuscript before submission.

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The authors declare no competing interests.

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