Review

How plants recruit their microbiome? New insights into beneficial interactions

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**Highlights**

- Plant-microbiome interaction occurs at the rhizosphere, endosphere, and phyllosphere.
- Root exudates can favor the recruitment of a beneficial microbiome in the rhizosphere.
- Plant topology and phytochemistry influence the recruitment of the phyllosphere microbiome.
- Diverse plant strategies selectively recruit beneficial microbiomes.
- Multiple plant mechanisms displace potential pathogens from the rhizosphere.
- The beneficial microbiome helps plants to recruit other beneficial microbiota.

**Abstract**

**Background:** Research on beneficial mechanisms by plant-associated microbiomes, such as plant growth stimulation and protection from plant pathogens, has gained considerable attention over the past decades; however, the mechanisms used by plants to recruit their microbiome is largely unknown.

**Aim of Review:** Here, we review the latest studies that have begun to reveal plant strategies in selectively recruiting beneficial microorganisms, and how they manage to exclude potential pathogens.

**Key Scientific concepts of Review:** We examine how plants attract beneficial microbiota from the main areas of interaction, such as the rhizosphere, endosphere, and phyllosphere, and demonstrate that such process occurs by producing root exudates, and recognizing molecules produced by the beneficial microbiota or distinguishing pathogens using specific receptors, or by triggering signals that support plant-microbiome homeostasis. Second, we analyzed the main environmental or biotic factors that modulate the structure and successional dynamics of microbial communities. Finally, we review how the associated microbiome is capable of engaging with other synergistic microbes, hence providing an additional element of selection. Collectively, this study reveals the importance of understanding the complex network of plant interactions, which will improve the understanding of bioinoculant application in agriculture, based on a microbiome that interacts efficiently with plant organs under different environmental conditions.

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Introduction

The association between plants and microorganisms is over 400 million years old; there exists fossil record that supports the establishment of interactions between plants and certain fungi, such as arbuscular mycorrhiza. It is possible that there are no fossil records of plant-bacteria associations due to their fragile unicellular nature [1,2]. Thus, this association is expected, since microorganisms occurred before plants and colonized a major portion of the planet's ecosystems. Therefore, plants perhaps encountered microorganisms, and since then, formed symbiotic and commensal associations [3]. In this regard, both groups of organisms began establishing chemical and physical communications, where multicellular and larger plants enabled selected microbes to establish and colonize their internal compartments, such as roots, stems, and leaves [4]. Certain groups even generated organelles such as chloroplasts and mitochondria, according to the symbiotic theory of Margulis [5].

However, initially, not all associations are beneficial, since certain microorganisms, such as bacteria, fungi, or viruses, exploited their genetic resources to evolve, attack, and infect systems to survive, at the expense of harming their host (i.e., pathogenesis) [6]. In contrast, when non-pathogenic microorganisms thrive in association with plants, both benefit, since the plant secretes compounds that are produced during photosynthesis, while heterotrophic microbes provide protection against pathogens, in addition to stimulating their growth and fitness through the synthesis and excretion of compounds of diverse origin and function [7–10]. For example, multiple species of avirulent fungi of the genus Trichoderma or bacteria of the genus Bacillus or Pseudomonas, are capable of synthesizing hundreds of compounds that have a fundamental role during interaction with plants, either by stimulating their growth or antagonizing fungal pathogens or nematodes [11,12]. Similarly, other groups of mycorrhizal fungi, which inhabit and are associated with biogeochemical cycles, are capable of improving soil fertility conditions, thereby improving the nutritional status of the plant [13]. This plant-associated microbiota with beneficial metabolic capacities have been used as bioinoculants (i.e., biofungicides/biofertilizers or both) to improve the growth and production of grains, vegetables, and fruits in various agricultural systems [14–16]. Thus, they are an excellent replacement to using agrochemicals that pollute the environment and are toxic to human health [17,18].

These diverse ecological interactions between plants and microorganisms raise a question: how do plants recruit their associated microbiota? This has been examined in the last few decades via field and laboratory approaches. However, this question remains central to the field of molecular plant–microbe interaction [19]. Recently, various omics techniques have unveiled a global panorama of stimulus–response in both directions of plant-microorganism or vice versa [20–22]. In this study, we review the most recent and important literature to determine how plants recruit beneficial microbiota, mainly from zones such as the rhizosphere, endosphere, and phyllosphere. The strong interaction of beneficial microbiome in these zones provides several beneficial services, such as plant protection and growth stimulation under different environmental conditions (see Fig. 1). Several recent reviews have illustrated these beneficial microbial activities [23,24]. In addition, we will discuss the selection system that enables plant to preferentially associate with the microbiota, which provides certain adaptive advantage (versus opportunistic pathogens), and the possible factors aiding this adaptation. Finally, we propose that the same plant-associated microbiome favors the recruitment of other beneficial organisms through diverse mechanisms.

Plant-microbiome interactions

The vast majority of microorganisms existing in the environment does not interact with when encountering plants, which indicates a neutral interaction between them [25]. In contrast, certain microorganisms form parasitic interactions (pathogens), which affects the host plant's health and development [26–28]. In commensalism relationship, which is a relationship between individuals of two species, one species benefits and the other is neither positively nor negatively affected [29]. Finally, in symbiotic or mutualistic relationships, both plants and microorganisms obtain certain advantage and/or receive some benefit. In certain cases, the symbiosis can be extremely narrow and obligate, where neither organism can survive without the other. To the best of our knowledge, obligate symbiosis are rare between plants of agronomic interest and associated organisms, but are beneficial to both, if discovered [30–32]. One such bacteria identified as rhizobia (free-living saprophytes), inhabit the rhizosphere, which communicates specifically with certain species of legumes by forming nodules in the roots and fixing atmospheric nitrogen. The obtained ammonia after nitrogen fixing can be used by the plant, while the symbiont receives a “home to live” and nutrients to survive [33,34]. Such reciprocal interactions between the rhizobiome (and non-rhizobial bacteria associated with root nodules) and the plant defines what few authors call the “MicrobiHome” [35,36].

Factors affecting plant-microbiome short- and long-term associations

In general, the type of interactions can be defined depending on their duration, that is, the plant can casually (short-term) associate with certain microbes, and stops interacting in due course [37,38]. In contrast, certain associations are long-term, perhaps during the life cycle of plants and beyond [39]. The microorganisms with long-term association are called the core microbiome [1,40], which can be defined as the total microbiota associated with the plant (and its genomic reservoirs) that presents long-term interactions, which can survive, thrive, and interact with different tissues such as roots, shoots, leaves, flowers, and locations [7,41–43]. Defining the core microbiome of each plant is essential to better understand the species-specific relationships and recognize the advantage of applied aspects, such as in agrobiotechnology, which increases the efficiency of bioinoculants applied for various environmental situations.

Various abiotic and biotic factors affect the short- and long-term association between plants and their microbiome [44]. Abiotic factors include soil pH, supposedly for the microbiome–plant interactions in the rhizosphere, in addition to the availability of resources, such as nutrients, oxygen, temperature, water, presence of contaminating metals or metalloids, salinity, and soil type [45–47]. In a study using rhizoboxes, Blossfeld et al. [48] performed non-invasive analyses of the presence of oxygen and pH standards in the rhizosphere of plants (Juncus spp.). Interestingly, the study concluded that the dynamic interaction of O2 concentration gradients and pH, and the organic acids exuded, were key parameters in the physicochemical environment of the rhizosphere. It is important to evaluate the population dynamics of the rhizospheric microbiome through different gradients of O2, pH, and the presence of root exudates, and observe how these factors, in the presence of certain microbial species, can modulate (or be modulated) and influence the growth and suitability of the plant.
A review by Philippot et al. [49] also showed that, in general, the bacterial phylum Proteobacteria was dominant in the rhizosphere, while the fungal phyla Ascomycota and Glomeromycota were also the most abundant and regularly observed in the plant rhizosphere. Their study concluded that the microbiome in natural environments can be distinctly influenced by the agricultural ecosystems. For example, the main drivers of microbiota diversity in an agricultural ecosystem are agricultural practices, followed by environmental conditions, soil type, and plant species, whereas in natural ecosystems, mainly biotic interactions, plant species, and plant diversity play a relevant role in modulating microbial communities.

However, biotic factors can also affect plant-microbiome dynamics. For example, the plant can interact specifically depending on its developmental stage. The type of tissue or part that interacts include the root (rhizosphere), the stem or the leaves, and an internal zone (endosphere) or external/superficial (phylosphere) region of the plant. Furthermore, Chaparro et al. [50] reported that the rhizospheric microbiome of Arabidopsis plants varies depending on their stage of development (seedling, vegetative, bolting, and flowering), and that certain phyla such as Acidobacteria, Actinobacteria, Bacteroidetes, Cyanobacteria, and specific genera were strongly correlated with the types of root exudates. Their work showed that plants exude different compounds depending on their developmental stage, and in return, these exudates aid in assembling a specific microbiome for the plant. Studies by Bai and colleagues [51] showed that the microbiome of Arabidopsis leaves differs from that of the rhizosphere, but there exists a huge functional overlap of more than 400 analyzed genomes. This suggests that the microorganisms in both niches may perform similar functions when interacting with the plant, although not at the level of species diversity. Multiple species (gram-positive or gram-negative) such as various plant growth-promoting strains of the genera Pseudomonas spp. and Bacillus spp., can perform similar beneficial functions.

From beneficial to pathogenic interactions

Importantly, the interactions between the plant and its microbiome can notably change, that is, they can proceed from a neutral or commensal state to a pathogenic state. Newton et al. [29] reviewed certain factors that ignite a state of pathogenesis in few plant–associated organisms, such as bacteria or fungi. For example, the authors highlight the importance of its trophic requirements and environmental conditions, or a simple exposure of the host can transform a mutualist organism to a parasite/pathogen. In particular, the fungus Pectobacterium atrosepticum, can transform from a symbiont to a pathogen, depending on its interaction with the plant host, or resembling the opportunistic bacterium Pseudomonas syringae, whose ability to infect depends on quorum sensing. Similarly, certain plant species are more susceptible to attack by certain opportunistic pathogens than the others, depending on their chemical defenses and immune response, and the associated microbiome itself that stimulates their defense and helps in their protection [52].

Plant call to recruit the microbiome

Plants, being sessile organisms, are restricted to associating with surrounding organisms, as compared to migrating animals, which can look for new interactions [53]. However, the offspring of some plants achieve this by managing to colonize new areas through seed dispersal mechanisms or reproductive structures. Some seeds can travel a long distance before finding suitable conditions for germination [54]. However, once the seeds germinate, they interact with the resident soil microbiota through the roots (rhizosphere) [55]. The aerial zones of the plant (phyllosphere) are also prone to colonization by microbes that reach their tissues, such as leaves, stems, flowers, and fruits, via air [56]. Furthermore, plants have an internal compartment known as the endosphere, which are also predisposed to colonization by rhizospheric and phyllospheric microorganisms [57,58]. Thus, the interaction (or recruitment) of microbiome with plants occurs at three main zones: the rhizosphere, phyllosphere, and endosphere.

Recruitment in the rhizosphere

Root activities modify microbial activity, along with the physiochemical properties of the surrounding soil or rhizosphere [59,60]. The rhizosphere is defined as a narrow part of the soil that is influ-
enced by root exudates, which is the habitat of thousands of micro-
bacterial species, including bacteria, fungi, oomycetes, viruses, and
archaea, and few other macro-organisms such as nematodes or
insects [61]. These microbiota can interact with the plant through
the roots, which not only functions as a soil anchoring system, but
also perceives and communicates with abiotic elements. Some of
these abiotic factors have been previously described. A plant initi-
ates recruitment or “call” to generate its own microbiome from
seeds (endophyte reservoirs), or through the planting of cuttings,
bulbs, rhizomes, or stolons [62,63]. These structures are known
to contain diverse endophytic microorganisms that are inherited
vertically from mother plants, including seeds [39,64].

The number of endophytic cells may be low compared to
mature plants; the roots emerge and interact with the microbiota
of the bulk soil, and forms the rhizosphere, where the exudates
first attract the future associated microbiome. Exudates can
contain amino acids (i.e. α-Alanine, β-alanine, γ-aminobutyric, α-
aminoadipic, arginine, asparagine, aspartic, citrulline, cystathion-
ine, cysteine, cystine, deoxymugineic, 3-epihydroxyxymugineic,
glutamine, glutamic, glycine, histidine, and homoserine), sugars
(arabinose, fructose, galactose, glucose, maltose, mannose, mucil-
gales of various compositions, oligosaccharides, raffnose, rhamnose,
ribose, sucrose, xylose, deoxyribose), growth factors and vitamins
(p-amino benzoic acid, biotin, choline, inositol, N-methyl nicotinic
acid, niacin, pathothenic, pantothenate, pyridoxine ribofavin,
strigolactones, thiamine), fatty acids (linoleic, linolenic, oleic, pal-
mallic, stearic), organic acids (acetic, acetic, ascorbic, aldonic, ben-
zoic, butyric, caffeic, citric, p-coumaric, erythronic, ferulic, formic,
fumaric, glutaric, glycolic, lactic, glyoxilic, malic, malonic, oxalace-
tic, oxalic), and other chemoattractants [65]. Additionally, some
exudates such as flavonoids, citrate, malate, oxalate coumarins,
malic acid, camalexin, benzoxazinoids, or even ethylene, can be
specific taxon recruiters [7].

Under certain conditions of environmental stress, such as phos-
phate or iron limitation, some plants tend to enhance the secretion
of citrate, malate, or oxalate to enrich
the rhizosphere with organic carbon, which attracts beneficial
microorganisms [65]. This hypothesis was confirmed in an in-
teresting study published by Kost et al. [66], who reported a strict
association between beneficial Burkholderia species and their abi-
ity to use oxalate as a carbon source. Interestingly, the authors
when analyzing other species of the genus Burkholderia, such as
B. glumae and B. plantarii, which are characterized as plant patho-
gen, or even human opportunistic pathogens, such as Burkholderia
cepacia, they were unable to degrade oxalate. Therefore, the
oxalotrophy or ability to use oxalate as a carbon source was
strongly associated with the ability of the beneficial strain B.
phytofirmans PsJN to colonize lupine (Lupinus albus L.) and maize
(Zea mays). Finally, a mutant with deleted oxc gene was impaired
during the early colonization of lupine and maize seedlings, con-
firming the role of oxalotrophy in colonizing the plant, and in turn,
confirming that certain root exudates selectively favor a bene-
ificial microbiome.

Multiple factors such as identically associated-microbiota and
their volatile organic compounds (VOCs), influence the diversity
of root exudates excreted by the plant. For example, a recent study
showed that inoculation with PGPR Bacillus amyloliquefaciens GB-
03 stimulates the production of volatiles in tomato plants (i.e., β-
caryophyllene), which are perceived in the neighboring plants. By
detecting these VOCs, the “receiver” plants modify the production
of their root exudates (i.e., salicylic acid), in turn modifying the
rhizospheric microbiota. Interestingly, the receiver plants and emit-
ting plants display a broad similarity in their rhizosphere-
associated microbial communities. This was the first study to
demonstrate the involvement of microbe-induced plant volatiles
(MIPVs) in generating signals that modify (and synchronize) the
rhizosphere-associated microbial communities of the neighboring
plants [67].

In contrast, depending on the bulk soil type surrounding the
plant and the resident microbiota, a specific rhizospheric micro-
biome can be formed (along with the seed microbiome) [39,47,62,68]. In particular, the ability of a plant to recruit an asso-
ciated microbiome can be restricted by the native soil microbiota.
This was demonstrated by Bakker et al. [69], who observed that the
microbiome formation is dynamic and largely depends on the soil
type, and the input of resources (cocktail of exudates and carbon
content) in corn plants. Similarly, in the microbiota that inhabited
each of the four analyzed soil types (sandy loam, clay 1, silt loam,
and clay 2), certain microbial communities were more sensitive to
variations in nutrient availability, which decreased their diversity,
while others handled the change better. Certain amendments, such
as ferulic acid, reportedly stimulated the abundance of a few phyla,
and decreased the diversity of the rhizospheric microbiome (bacte-
ria and fungi) of Cucumis sativus L. (cucumber) plants [70].

Furthermore, plant species can specifically interact with certain
groups of microorganisms. For example, legume plants excrete
phenolic compounds, such as flavonoids and isoflavonoids, which
induces the expression of nodulation (nod) genes in nitrogen-
fixing symbiotic bacteria, prominently known as rhizobia. In
response, rhizobia produces nod factors, which are lipo-
quitosylsaccharides, whose function is to induce a series of phys-
iological changes in the plant root to subsequently form nitrogen-
fixing nodules. This type of rather specific communication between
certain species of rhizobia and legume species (with exceptions),
occurred approximately 75–80 million years ago [71]. A few exam-
examples of this type of symbiotic and extremely specific interactions
are Rhizobium spp. that are symbionts of Phaseolus spp. (e.g., com-
mon bean), Sinorhizobium spp. of Medicago species (e.g., alfalfa),
Mesorhizobium spp. of Lotus spp. (e.g., lotus, chickpea), and
Bradyrhizobium spp. of Glycine spp. (e.g., soybean, cowpea) [72–
75]. Endosymbiosis of rhizobia within plant roots suggest a shared
signaling pathway in plants for fungi (e.g., arbuscular mycorrhizal
fungi) and symbiotic proteobacteria, which has been termed as the
common symbiotic pathway (CSP) [76,77]. Recently Genre and
Russo [76] reviewed works suggesting the role of at least ten pro-
teins, such as HMGRI (3-Hydroxy-3-Methylglutaryl CoA Reductase
1), a key enzyme in the mevalonate biosynthetic pathway, and
kinases like SYMRK (receptor-like kinase) and CaMK (nuclear
calcium- and calmodulin-dependent kinase), which participate in
common signaling pathways in mutualistic symbioses of plants
with species of rhizobia and glomeromycetes, the so-called CSP
[76].

However, recent work with rice plants suggests that the plant
responds to the endophytic colonization of Azorarcus sp., inducing
metabolic changes and Ca2+-dependent signaling, without CSP
[78]. This further highlights the exclusivity of plant-endophyte
bacterial interactions and recognition. Similarly, Liu et al. [79]
recently observed that the genotype of soybean plants (Glycine
max) is important in structuring the rhizospheric microbiome.
Regardless of the soil type, specific bacterial genera such as Rhizo-
bium, Novosphingobium, Phenyllobacterium, Streptomyces, and
Nocardioides were found in abundance. Finally, their results pre-
dicted a convergent metabolic capacity between soil types and
genotypes in the rhizosphere of Glycine max, and pathways related
to xenobiotic degradation, plant–microbe interactions, and nutri-
ent transport. Studies by Micallef et al. [80] suggested that the
plant age and genotype impact the successional progression of the
rhizospheric bacterial community in model plants such as Ara-
bidopsis thaliana. In conclusion, their results imply that variations
in exudation during plant development are highly specific and
depend on the genotype, suggesting the local and unique co-
evolution of certain communication processes, which developed
because of the accessions between Arabidopsis and its endemic microbiota.

A recent work by Son et al. [81] involved the screening of Arabidopsis thaliana mutants, where the identified FERONIA (RES) receptor kinase mutant (fer-8) “allowed” the enrichment of bacterial species Pseudomonas fluorescens in the rhizosphere. Interestingly, the fer-8 mutant showed basal levels of reactive oxygen species (ROS) in roots, suggesting that under these conditions, pseudomonads took advantage by increasing their abundance, concluding that FER-MEDIATED ROS production regulates the levels of beneficial pseudomonads in the rhizospheric microbiome. P. fluorescens is widely known for its direct and indirect plant growth promoting capabilities [82]; therefore, this work provides a novel approach in communicating and recruiting beneficial bacteria in the rhizosphere, and possibly facilitating endophytic colonization.

Successional conformation of the rhizosphere microbiome

The rhizosphere, being a dynamic ecosystem, poses a challenge due to its microbial diversity and the complex interactions that occur within, such as competing for nutrients and spaces, survival in the presence of antibiotics, and other activities that shape the community structure [83,84]. Certain succession studies have shown interest in establishing the role of certain plant species in reshaping the microbial communities that inhabit the soil. Recently, the work done by Sun et al. [85] demonstrated the important role of pioneer plants and their impact on the diversity and structure of bacterial communities in the rhizosphere and bulk soil of copper mine tailings in China. A taxonomic analysis using Illumina MiSeq sequencing showed that Alphaproteobacteria, Deltaproteobacteria, Chloroflexi, Acidobacteria, and Gemmatimonadetes significantly increased their relative abundance in the rhizosphere and bulk soil. In contrast, Gammaproteobacteria and Firmicutes were abundant in bare tailings, in which Bacillus, Pseudomonas, and Lactococcus constituted 63.04% of the total bacterial community.

Similarly, Shi et al. [59] analyzed the succession response of soil bacterial communities during the onset of roots of the common annual grass Avena fatua via 16 s rRNA gene sequencing over two growth periods. The results were as follows: the roots of Avena fatua caused a successional change in the conformation of the rhizospheric bacterial community, which was characterized by the overall reduction in its diversity by decreasing the relative abundance of Acidobacteria, Actinobacteria, and Firmicutes, which was evaluated using taxonomic and phylogenetic analysis; in other cases, plant roots selectively stimulated the relative abundance of bacterial groups such as Alphaproteobacteria, Betaproteobacteria, and Bacteroidetes.

Another interesting work performed recently [38], involved the authors growing modern and wild tomato genotypes, Solanum lycopersicum var. During four successive cycles of Moneymaker (modern) and the wild relative S. pimpinellifolium LA1578, the assembly of the microbiome differed between the two genotypes, and these differences significantly amplified over time. The authors analyzed certain core genera of the rhizospheric microbiome of tomato, and highlighted that the wild tomato increased the abundance of the genera Acidovorax, Massilia, and Rhizobium, whereas the modern tomato plants were enriched by bacterial species of the genus Pseudomonas.

Together, these results suggest and corroborate the dynamic aspect of the plant microbiome assembly, in addition to the fact that certain bacterial taxa may be selected (i.e., selection of a beneficial microbiome from bulk soil), and plant genotype plays the role of another selection factor. Fig. 2 illustrates the dynamic aspects of plant microbiome recruitment during different periods of plant growth (i.e., an agricultural ecosystem).

Colonizing the endosphere

Plants can recruit microbiome from above-ground or below-ground areas. As previously mentioned, rhizodeposits fundamentally influence the gradual recruitment of rhizospheric microbiome [86]. A significant progress in understanding the approach by which plant roots recruit the endophytic microbiome from the rhizosphere is in the work of Edwards et al. [87]. Through a detailed analysis, conducted under different experimental conditions, either in greenhouse or in field, and in various plant models, the authors detected gradual changes in the microbial composition at three interacting root zones: rhizosphere (soil close to and influenced by the root surface), rhizoplane (root surface), and the endosphere (root interior). The results observed gradual changes in the microbiota composition that inhabited the three microecosystems associated with the roots, rhizosphere, rhizoplane, and endosphere. This work is consistent with the two-step model, although with certain variations, proposed by [88,89], where soil abiotic properties (first step) and plant rhizodeposits (second step) are selective factors that filter (and recruit) certain microbial diversity from the rhizosphere. This model has recently been tested in wild tomato plants and domesticated varieties, indicating that the associated microbiome can be influenced by plant domestication trade-offs [90].

Once the rhizosphere microbiota manage to pass the rhizoplane and penetrate the root tissues, these endophytes will have the opportunity to colonize other plant compartments. The trip includes a walk through the vascular system of the plant toward aerial tissues, such as stem or leaves, along with the flowers and fruits (once the plant enters these developmental stages) [91]. The rhizosphere, which is below-ground and in close contact with the soil microbiota, may also contain unexpected entry zones into the internal tissues of the roots, including root wounds or cracks, which may not require an active system to penetrate tissues. In contrast, rhizospheric bacteria desiring an entry must exhibit more active colonization determinants in the rhizosphere, with characteristics such as the ability to hydrolyze the cells of the plant host, produce biofilms for better attachment, have motility, quorum sensing, and synthesize antibiotics to displace other competitors, in addition to producing antioxidant enzymes [57,92,93]. Although no evident genetic differences exist between rhizospheric and endophytic bacteria, a list of genes coding for the aforementioned functions has been suggested.

A pioneering work [94], proposed certain differences between rhizobacteria and endophytes by comparing the genomes of nine endophytic species, including Burkholderia phytofirmans PsJN, Burkholderia spp. strain JK006, Azospirillum lipoferum 4B, Enterobacter cloacae ENHKU01, Klebsiella pneumoniae 342, Pseudomonas putida W619, Enterobacter spp. 638, Azorarcus spp. BH72, and Serratia proteamaculans 568. The authors found a match for approximately 40 genes that could be involved in endophyte behavior, such as transporters, secretion and delivery systems, detoxification and redox maintenance potential, and plant polymer degradation, among other transcriptional regulators. Unfortunately, for decades, only few genes have been identified as important factors in endophytic colonization and existence. However, some important studies have been previously reviewed [57]. For example, Meneses et al. [95] generated mutants in the gumD gene of the N2-fixing bacterium, Gluconacetobacter diazotrophicus, for the production of exopolysaccharides, which are required to generate biofilms and for the endophytic colonization of rice plants. Similarly, in the same bacterial species, Alquéres et al. [96] characterized relevant activities of glutathione reductase (gr::Tn5) and superoxide dismutase (sod::Tn5) in endophytic colonization. In the case of Azorarcus sp. strain BH72, mutations in pilA and egIA, affecting twitching
motility and endoglucanase activities, respectively, were described as essential for endophytic colonization of rice plant roots [97]. Furthermore, Buschart et al. [98] generated mutants containing three copies of $fliC$ genes, which encode the major structural protein flagellin. However, only the $fliC$ copy was functional and necessary for motility, and was associated with rice roots. Endophytic colonization of rice roots was significantly reduced in the $fliC$ mutant. Interestingly, other activities in the rhizosphere, such as the establishment of microcolonies on the root surface remained unaffected, which further confirmed its important role in the endophyte lifecycle.

In contrast, mutant strains affecting swimming motility ($fliC$) or siderophore pyoverdine production ($pvdI$) in the rhizobacterium *Pseudomonas fluorescens* PICF7, and the facultative endophytes in the olive tree roots (*Olea europaea* L.) did not significantly differ from the wild strain PICF7 in its endophytic colonization capacity. Therefore, these characteristics were rejected as being relevant to the endophytic lifestyle of this strain. However, as a facultative endophyte, it reveals that certain functions, such as motility, may be relevant in other non-facultative endophytic strains. Accordingly, in the case of *Azoarcus olearius* BH72, where mechanisms such as motility are relevant for endophytic colonization of rice, plant defenses are not induced (i.e. bacterial molecular components or MAMPs) [99,100].

More recently, the importance of motility activities and the production of cyclic di-GMP (c-di-GMP) have been reported in the bacterium *Azoarcus* sp. CIB strains to endophytically colonize rice plants [101]. Previously, the significant role of c-di-GMP for endophytic lifestyle in *Azoarcus* sp. species has also been suggested through transcriptional analysis [100]. Interestingly, c-di-GMP in bacteria is involved in modulating the synthesis of exopolysaccharides, adhesins, and the formation of biofilms. As previously mentioned, these functions regulate various mechanisms, including colony morphology, quorum sensing processes, cell motility, nodulation, and virulence [101].

Pathogen-associated molecular patterns (PAMPs) by pattern recognition receptors (PRRs) are one of the main mechanisms recognizing the invasive pathogens [99,102]. Plants can also detect other "non-pathogenic" microorganisms, including bacteria, from microbe-associated molecular patterns (MAMPs), which regulate the plant defense responses through its innate immune system. These PRRs are the first recognition filter, the second being the intracellular immune receptors, also known as the NOD-like receptor (NLR) type. These receptors directly or indirectly recognize virulence effectors secreted by pathogens within host cells, thereby inducing effector-triggered immunity (ETI) [99,103]. Although considerable progress has been made in studying these microbial recognition mechanisms by plants, only a few examples of PRRs have been studied in Arabidopsis and rice [104], and other plant models need to be investigated and compared.

Systems, such as MAMPs, individually recognize and detect colonizing microorganisms, which attempt to form beneficial associations with their plant hosts. Other active players include phytohormones, such as salicylic acid (SA), jasmonate acid (JA), abscisic acid (ABA), and ethylene (ET) which may be related to defense functions [105–108]. In general, SA responds to the interaction between abiotic stimuli, and biotrophic and hemibiotrophic organisms, inducing the defense response in plants, called systemic acquired resistance or SAR [109]. In contrast, JA/ET is an alternative plant pathway that respond to the interaction of beneficial organisms, such as PGPBs [110]. However, some studies [111], reported observed concentration changes in the SA and JA content in *Metarhizium* (an entomopathogenic fungi)-treated maize (*Zea mays*) plants, which corresponds to plant responses related to the known SA and JA/JA pathways.

Another work performed by Sheoran et al. [112] mentions that the endophytic bacterium *Pseudomonas putida* BP25, capably alters...
the root architecture and triggers signaling using SA as a feedback loop in regulating endophytic colonization in Arabidopsis. The same working group has previously reported the beneficial characteristics of BP25 strain, such as the production of a broad spectrum of volatile compounds that suppress a broad range of plant pathogens [113]. Moreover, Lebeis et al. (2015) used mutants in the immune system of Arabidopsis thaliana Col-0 plants, and observed that SA plays an important role in the selection of certain bacterial taxa and structuring their root microbiome, including those that colonize the rhizosphere and endosphere. The authors also reported that endophytic communities were less abundant than rhizosphere inhabitants. Interestingly, the cell densities of some isolates of genera such as Terracoccus sp., Streptomyces sp., and Mitsuaria sp., were modulated in culture media supplemented with or without SA.

More recently, Chen et al. [104] found contradictory results, where they observed that JA, and not SA, is the pathway that restricts endophytic colonization of the beneficial endophyte Azofarcus olearius BH72 in rice plants, while the pathogen Xanthomonas oryzae pv. oryzae PX099 induces a response to the SA pathway only in roots. As expected, the PX099 strain induced a considerably higher defense response than BH72, which is non-pathogenic. Interestingly, both endophytes induced the expression of genes encoding several enzymes involved in phytoalexin biosynthesis, ROS production, and pathogenesis-related (PR) proteins. To elucidate the detailed response pathways in both endophytes, rice mutant lines cpm2 deficient in jasmonate synthesis, and NPR1 (by RNAi), which mediates responses by SA were used. The authors found that only BH72 increased its endophytic colonization in cpm2, while PX099 was unaffected. The authors concluded that the JA pathway regulates the selective interaction with beneficial endophytic species, modulating their beneficial microbiome.

ET, conversely, is a gaseous plant hormone that is involved in other plant responses such as senescence or fruit ripening. At low concentrations, it can participate as a signal for seed germination, elongation of plant roots, the formation of leaf and root primordia, and flowering initiation [115]. In addition, ET responds or increases its levels when the plant experiences different abiotic or biotic stress, such as attack by pathogens. Therefore, lowering their levels under stress is important for maintaining growth and fitness [116]. To achieve this, the plant can also associate with 1-amino cyclopropane-1-carboxylic acid (ACC) deaminase-producing bacteria. ACC deaminase is widely studied for its ability to reduce ethylene levels in plants through the hydrolysis of ACC, a precursor of ET synthesis, generating α-ketobutyrate and ammonia [117,118]. Multiple bacterial species have been reported to inhabit the rhizosphere, endosphere, and phyllosphere that contain this function, which helps the plant reduce its ethylene levels under stress conditions, stimulating its growth. In the case of plants of agricultural interest, it has been observed that the application of biofertilizers based on ACC-producing bacteria increases the production and protection of crops [119].

Reaching the phyllosphere

The phyllosphere is an ecosystem that is particularly different from the rhizosphere and endosphere. It is perhaps the most challenging habitat for microorganisms that “desire” to establish long associations with their hosts. This is due to abiotic factors such as insolation, UV rays, drastic temperature variations, rain, and wind [36]. Additionally, the microbiota that is relatively new to the epiphytic life must compete for space and nutrients with the resident and well-established biota. Therefore, adventitious microbes that reach the rhizosphere must be resilient during extremely stressful situations [120,121]. However, in certain predominately studied bacteria, certain determinants such as exopolysaccharides, biofilm and/or adhesion compounds, the flagellum, antibiotics, biosurfactant compounds, free radical detoxifying proteins (catalases and superoxide dismutases), versatile metabolism, and quorum sensing signal molecules that reportedly aid in colonizing habitats such as the rhizosphere or the endosphere, can also be of significance in colonizing the phyllosphere [122,123]. In contrast, the production of pigments by epiphytic bacteria displays a protective mechanism against ultraviolet radiation, which is essential for survival in an epiphytic lifestyle. Jacobs et al. [124] demonstrated the use of mutants in the synthesis of pigments (orange, cream, and pink) in Clavibacter michiganensis, which was highly sensitive when exposed to solar UV radiation (UVR), with lower leaf survival rate, compared to wild strains.

Microscopy analyses have revealed that the vast majority of bacterial cells may be located in the grooves formed by the junctions of the epidermal or epilamella of plant cells, where water and certain nutrients can flow and serve as a reservoir for the microbiota. Other structures, such as the presence of veins, stomata, trichomes, and hydathodes, can also alter nutrient availability (i.e., sugars such as fructose and sucrose) [125].

The phyllosphere of plants can be considered as one of the most abundant areas or ecosystems on earth. Some data suggest that such an environment, measured as global leaf area, can reach figures of more than 500 million square kilometers [40,123]. These habitats are considered highly abundant, since a square centimeter of leaf surface can host between 10⁶ and 10⁷ bacterial cells [126]. In an excellent review documented by Vorholt [123], the phyllosphere can be widely diverse, where groups such as Proteobacteria (α, β, γ, and δ), Actinobacteria, and Bacteroidetes are among the most abundant in rice, clover, soybean, and Arabidopsis plants. However, differences are observed between these four plant models, since genera such as Agrobacterium, Methylobacterium (Alphaproteobacteria), and Mycobacterium (Actinobacteria), are the commonly reported epiphytes of rice plants, whereas Pseudomonas is a common inhabitant of soybean, clover, and Arabidopsis. These data are based on the frequency reads of predicted protein coding and rRNA genes within the metagenomes of microbial communities obtained from MG-RAST.

Driving plant factors allowing/restricting microbiome phyllosphere establishment

To date, notably the plant’s immune system and signaling pathways that consider the action of phytohormones, among other determinants, can be factors that encourage the intimate interaction and selection of a specific microbiome in ecosystems such as the rhizosphere and the endosphere [19,127,128]. However, defense systems in plant aerial zones can act in a systematic and localized manner. Therefore, some authors, such as Schlechter et al. [56], suggest that “to better understand this impact (immune responses of plants), it is necessary to study bacterial communities at a micrometric resolution, which is a scale that is relevant for members of the community.” The microenvironments present on the plant leaf surface can be defined at the micrometer level. Thus, it has been suggested that plant topology and phytochemistry may influence the recruitment of a particular microbiome [129,130].

Microscopic analysis has revealed the presence of vast majority of bacterial cells in the grooves formed by the junctions of the plant cell epidermis or epilamella. This is where water and some nutrients flow and serve as a reservoir for the microbiota. Other structures, such as the presence of veins, stomata, trichomes, and hydathodes, can also alter the availability of nutrients (e.g., sugars such as fructose and sucrose) [125].

Therefore, there may be local and systemic responses in leaves. According to [131], plants use internal immune receptors that rec-
ognize specific bacterial effectors, which leads to effector-activated immunity (ETI), which can detect and distinguish the presence of potential pathogens. These immune responses are located at the site of interaction (or infection), which causes the early entry of calcium ions (Ca^{2+}) and MAP kinase, and activation of calcium-dependent protein kinase. This cascade of signals subsequently comprises callose deposition and stomatal closure as defense against pathogens, in addition to cell death (for more information, see [56,131]).

As aforementioned, certain factors can successfully colonize environments such as the phyllosphere [56]. However, stochastic events also influence the composition of a plant-associated microbiome. As demonstrated by Maignien et al. [132], when analyzing more than 260,000 sequences from hypervariable regions of the 16S rRNA gene, they managed to characterize the phyllosphere bacterial community structure on 32 plant and 21 air samples over 73 days. Their results confirmed that in addition to ecological successions, a stochastic variation influences the assembly of bacterial communities associated with the microenvironments of the A. thaliana phyllosphere. Alternatively, the phyllospheric microbiome of plants can be colonized by those microbes that reside not only in the air but also that originate from the rhizosphere [133], as previously mentioned.

In an extensive study of the fungal and bacterial communities of the Arabidopsis thaliana phyllosphere, the host genotype was also a contributing factor that determined the presence or absence of certain microbial groups. This result was achieved through genome-wide association studies (GWAS), which revealed that certain genes responsible for defense, kinase-related activities, and cell wall integrity (comprising the polysaccharides cellulose, callose, and pectin) impact the community variations [134].

In an interesting study, the availability of O$_2$ in the marine plant phyllosphere was considered an important factor in the conformation of the associated microbiome, which modulates the microbial metabolic processes that occur within epiphytic biofilms [135]. Although O$_2$ is available in terrestrial environments, other gases such as CO$_2$ can affect the diversity of the phyllosphere (and endosphere) of rice plants [136]. However, it would be interesting to observe their influence in the colonization and microbial activity in the resident plant phyllosphere in regions with high levels of environmental pollution (with gases such as CO$_2$ or other elements).

Can the plant microbiome help to recruit other beneficial microbes?

The plant associated-microbiome provides different services to the plant, such as protection against pathogens, stimulation of its growth, and increased levels of resistance against different abiotic stresses. The examples are diverse, and the literature is filled with these reports (see [137, 138, 139]). However, few reports illustrate the beneficial action by the associated microbiome in recruiting new members to provide beneficial services to the plant. One way to evaluate this hypothesis is by analyzing the inoculation of a “microbial agent” in the rhizosphere, endosphere or phyllosphere, and observe a rearrangement in the associated-microbial composition; hence, improvement in health, plant growth or fitness will be indirectly observed compared to those plants that were not previously inoculated with the “microbial agent.”

This type of work was conducted by Zhang et al. [140], who observed that the pre-inoculation of pepper seedlings with the PGPR Bacillus velezensis NJAU-Z9 induced changes in the composition of the rhizospheric microbiome in a field experiment over two seasons. This pre-inoculation significantly increased the abundance of bacterial genera, such as Sphingomonas, Sphingopyxis, Bradyrhizobium, Chitinophaga, Dyadobacter, Streptomyces, Lysobacter, Pseudomonas, and Rhizomicrobium, and the fungal genera such as Aspergillus, Cladorrhinum, and Cladorrhinum. Similarly, the transplanted seedlings pre-colonized with NJAU-Z9 significantly increased pepper yield by 11% and 24%, respectively, compared to non-inoculated plants.

Another study by [141] also showed that the nodule-endophyte Agrobacterium sp. 10C2 affects the richness and structure of rhizosphere bacterial communities of common bean plants (Phaseolus vulgaris). The inoculation also induced plant nodulation and growth. Some of the bacterial taxa that increased their relative abundance were mainly members of the genus Bacillus, such as Bacillus licheniformis, Bacillus pumilus, Bacillus senegalensis, Bacillus subtilis, Bacillus firmus, and Paenibacillus korreens. These Bacillus species have been widely reported as PGPB.

In addition, to the beneficial agents modulating the beneficial microbiome of plants, their presence or infection by fungal pathogens can induce changes in the microbiota. In some cases, the plant detects the presence of the pathogen (through unknown mechanisms) and increases the population of beneficial endophytic microorganisms that help protect the host. This was demonstrated by the excellent work of Carrión et al. [142], who inoculated an endophytic consortium of Flavobacterium and Chitinophaga in sugar beet seedling plants, previously identified by their population increase and stimulation, in the presence of the fungal pathogen Rhizoctonia solani, which also increased plant protection. Another work conducted by Solís-García et al. [143] also suggest that pathogens such as Phytophthora oomycete can cause disease in avocado plants and modify the rhizosphere microbiota. Interestingly, root rot increased the proportion of Pseudomonadales and Burkholderiales, which are PGPR agents, while the abundance of other opportunistic fungal pathogens, such as Mortierella sp., Fusarium spp., Lasiodiplodia sp., and Sycalidium sp. was also increased. The previous inoculation of one, two, or an entire microbiome can also prohibit the establishment or colonization of pathogens in plant rhizosphere, including those that cause disease in humans, such as E.coli [144].

Previous studies have shown that the inoculation of unique species can modify an entire plant-associated microbiome, that is, they stimulate the abundance of certain genera that may also exert direct and indirect mechanisms that influences plant growth and protection. However, there remains a question about how they stimulate the presence of other beneficial taxa. Certain new evidence may arise from the synergistic interaction between species, as shown in the study by Baas et al. [145] where, through the inoculation of a phosphate-solubilizing consortium, which includes the species Comamonas testosteroni, Pseudomonas putida, Enterobacter cloacae, and Citrobacter freundii, the growth and productivity increased twice as that of the uninoculated cultures. The cultures that benefited from the consortium were red winter wheat (Triticum aestivum), fescue turf grass (Festuca arundinacea; Kentucky 31 variety), jalapeño (Capsicum annuum; early jalapeño variety), cherry tomato (Solanum lycopersicum; Sweetie variety), and basil (Ocimum basilicum; Italian Genovese variety).

Another study on the beneficial interaction between PGPB is that of [146], who observed that Bacillus thuringiensis and Pseudomonas fluorescens strains can interact physically, which additively and/or synergistically stimulate the growth of husk plants tomato (Physalis ixocarpa Bro. ex Horn.). Notably, even certain PGPR mechanisms in a single PGPB can exhibit synergistic action to stimulate the growth of tomato plants under salinity conditions, such as the production of ACC deaminase and trehalose in PGPB
Pseudomonas sp. UW4. However, there are other studies, where inoculation through microbial strains or consortia have improved the growth or production of different cultures [147], but the effect on the associated microbiota was not evaluated in the plant, and its effect is unknown. Therefore, it is advisable to incorporate this analysis with new bioinoculant agents, to understand if the beneficial interactions with another associated microbiota can also indirectly benefit the plant.

Microbial communication plays a significant role in promoting the abundance of certain plant-associated microbial taxa. Therefore, quorum sensing (QS) molecules, such as N-acyl homoserine lactones (AHL), play an important role in this communication to regulate and sense bacterial populations in environments, such as the rhizosphere. Similarly, plants can sense AHL and produce different signals or defense pathways. Although Rodriguez et al. [148] mentioned that AHLs are also produced by pathogens, these molecules do not provide sufficient information for plants to provide a defense response signal, but they do suggest that “Possibly the combinations and concentrations of QS molecules may indicate an imbalanced microbial composition.”

Other signal molecules, with functions similar to AHL, have been reported in studies such as those by Orozco-Mosqueda et al., Velázquez-Becerra et al., and Martínez-Cámara et al. [149–151]. These studies have identified and characterized volatile molecules such as dimethylhexadecylamine, produced by the curl-and endobacterium Arthrobacter agilis UMCV2, which may play an important role in communicating with other beneficial taxa in the rhizosphere or the endosphere of plants, since this molecule has an antifungal action and modulates the growth and swarming motility of other bacterial species, among other stimulating activities of plant growth and nutrition. However, the modulating role of microbial communities in the rhizosphere or endosphere of plants is still unknown.

Other molecules that are involved in microbial communication are lipopolysaccharides, which have been widely studied in beneficial bacteria, and whose functions are diverse, including stimulating plant growth, biofilms function, communication with the environment, recognition between microorganisms, and antagonism towards pathogens [152]. It would be important to know whether the mutant strains in the synthesis of polysaccharides, such as Bacillus velezensis NJAU-Z9 [140] or Agrobacterium sp. 10C2 [141], increase the abundance and diversity of beneficial taxa in environments such as the rhizosphere.

Restricting the recruitment of harmful microbes

The microbiota not only helps the plant recruit other beneficial microorganisms, but it can also restrict access to others, including potential pathogens [153]. The mechanisms by which certain microbes restrict growth are mainly antibiotics [154]. For example, PGPB of the genus Pseudomonas is widely known for producing compounds such as phenazine-1-carboxylic acid, phenazine-1-carboxyamide, 2,4-diacetyl phloroglucinol, pyoluteorin, pyrrolnitrin, volatile hydrogen cyanide, and dimethyl disulfide (DMDS) [155, 156]. In addition, PGPB can synthesize lytic enzymes, such as glucanases or cellulases, which are capable of degrading the membranes of plant pathogenic fungi. In addition, Bacillus species can restrict the growth of pathogens through the production of lipopeptides such as fengycin, surfactin, and iturin [157, 158]. Other beneficial mechanisms that interact with plant hosts, such as Trichoderma, can restrict growth in the rhizosphere of plants through physical mechanisms, by occupying spaces, in addition to producing antibiotics [159, 160]. In general, there are multiple plant pro-
tection services provided by the plant-associated microbiota from different microecosystems, such as the rhizosphere, endosphere, and phyllosphere, thus avoiding harmful interactions with the host.

Evidently, there are still sufficient gaps in microbe-microbe interaction, and the plant social network [161], and in understanding how certain stimulating strains of the beneficial plant microbiome can achieve this function. Therefore, it is necessary to further investigate the aspects that regulate these functions, including the important abiotic factors [162], such as pH and soil type, salinity, or even the type of root exudate. Fig. 3 shows several abiotic and biotic factors affecting the recruitment of the plant microbiome into the three different interaction zones reviewed here: the rhizosphere, endosphere, and phyllosphere.

Conclusions and perspectives

Plant-host interactions, whether beneficial or pathogenic, are complex and involve a wide variety of stimuli and connections that affect the type of final association [76,161]. In particular, the question of how plants recruit their beneficial microbiota/microbiome, and how they differentiate them from pathogens desiring to infect them, is only just being answered [19], which undoubtedly requires different approaches (biochemical, microbiological, microscopic, omics techniques, etc.) to identify the molecules, metabolites, interaction networks, signaling pathways, genes, and the physical interactions involved in recruiting the associated microbiome.

In addition, the vast majority of plant-host interaction analyses use model plants such as Arabidopsis [89,114,132] (with undeniable genetic advantages); however, other plant species of agricultural importance still lack data. In addition, more than 300,000 plant species have been proposed to exist worldwide [163], which is expected to have broad and diverse modes of interaction and recruitment of their associated microbiome. Therefore, future research is needed to provide new insights into the molecular interactions and recruitment of beneficial organisms, whose function is still particularly unknown in natural ecosystems.

Finally, different agricultural systems should consider the use of beneficial microorganisms as a requirement for sustainable agricultural practices. For example, the inoculation of microbial agents or consortia in seeds prior to sowing should be considered a routine activity. In some regions, synthetic fertilizers or fungicides (i.e., captan or benomyl) are applied to avoid subsequent fungal infection by pathogens. However, the collateral damage exerted by these agrochemicals on the environment, human, and animal health is widely documented. Therefore, the application of microbial biocontrols or biostimulants, previously evaluated as active ingredients, will allow agricultural products that provide a sustainable future.

Compliance with ethics requirements

This article does not contain any studies with human or animal subjects.

CRediT authorship contribution statement

Gustavo Santoyo: Conceptualization, Visualization, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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