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# Bacterial endophytome sources, profile and dynamics—a conceptual framework

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Currently, it seems inconceivable to dispute the major role of microorganisms in human health or insects with endosymbionts. Although microbial endophytes were discovered long ago, little is known about the roles of plant-associated microorganisms. Some endophytes are horizontally transmitted, whereas others are seed-borne; together, they influence plant health. Beneficial endophytes can promote plant growth and yield by increasing plant resistance to biotic and abiotic stresses. Recently, the tools available to study the phytobiome have much improved, opening doors for a better understanding of the fascinating interactions taking place at the plant level. This review redefines the conceptual framework for “endophyte” and “endophytome,” focusing on the intricate dynamics of bacterial endophytomes. Systematically examining the formation pathways and profiling endophytes allows for a comprehensive exploration of the intricate dynamics governing plant-microbe interactions. Additionally, the assessment of how endophytomes are influenced by both biotic and abiotic factors provides essential insights into the adaptability and resilience of plant-associated microorganisms. Our comprehensive analysis integrates genomic insights with environmental considerations, offering a nuanced perspective on the functional roles of bacterial endophytomes. Therefore, a new, inclusive definition is essential to accurately represent the complexity of interactions within the plant microbiome as well as having the whole picture of associated concepts.

## KEYWORDS

endophytome, community structure, bacteria, plant-endophyte interactions, plant-microbe interactions, microbiome, phytobiome, dysbiosis

## Introduction

Plants naturally host distinct microbial communities outside and inside their tissues in the phyllosphere (i.e., air-plant interface), rhizosphere (i.e., root-soil interface), and endosphere (i.e., internal tissues of the plant). Microorganisms associated with the endosphere, known as endophytes, directly influence plant metabolism and plant cells. Several studies have highlighted the benefits of endophytes in improving plant health (Harman et al., 2021) by revealing their ability to enhance nutrient uptake, disease resistance, stress tolerance, conserve water, and promote soil health, which contributes to reducing environmental impacts, increasing productivity, and long-term sustainability in agriculture (Hardoim et al., 2008; Compant et al., 2010; Hardoim et al., 2015). Therefore, harnessing these natural benefits as

biocontrol agents can reduce environmental impacts of pest management, offer targeted pests and disease control, and enhance agricultural system resilience.

In endophyte studies, conventional methods often entail isolating bacteria from culture media after surface disinfection, followed by reinoculation into plants. A critical issue with this approach is its heavy reliance on cultivating endophytes in artificial culture media, despite the majority of the microbial diversity in natural environments remaining unculturable. Additionally, the surface disinfection step used to isolate endophytes introduces biases limiting the recovered isolates' diversity. Therefore, the isolated strains might not accurately represent the full diversity of plant-associated endophytes. Furthermore, reinoculation of endophytes from one plant into another of the same species, as practiced in the conventional approach, disrupts natural host-specific interactions between endophytes and their host plants. These knowledge gaps hamper our ability to understand the ecological significance and functional potential of endophytes fully (Hardoim et al., 2015; Compant et al., 2019; Papik et al., 2020).

Given these limitations, there is an urgent need for a timely review and re-evaluation of the conventional methods employed in endophyte research. Emerging techniques such as metagenomics, metatranscriptomics, and single-cell sequencing can provide valuable insights into the diversity, functionality, and dynamics of endophytes without the constraints of cultivation-based methods. A more effective approach would be directly examining the endophytic communities to evaluate how abiotic and biotic stressors influence their dynamics and evolution. Rapid progress in sequencing techniques has enabled the *in situ* study of these endophytic communities, thereby advancing the understanding of their functional roles in plants. Although progress has been made on plant endophytes, there is still a long way to go to achieve what has been done so far on human microbiota (Gilbert et al., 2018).

Here, we discuss the multifaceted nature of plant-endophyte interactions, redefine the concept of endophytes, explore the formation of the bacterial endophytome, examine the existence of a bacterial endophytome profile, analyze the factors driving variation in endophyte communities. This will provide a conclusion and future perspectives on the topic and highlight how understanding the interactions between plants and endophytes can contribute to sustainable agriculture.

## Plant-endophyte multifaceted relations

### Back to the roots—defining endophyte

The term 'endophyte' is derived from the Greek words 'endon' meaning 'within' and 'phyton' meaning 'plant'. The term was coined by De Bary et al. (1866) referring to the presence of 'bacteria' living inside a fern called *Ophioglossum*. At that time, the term 'bacteria' was used to encompass all living organisms, including those living inside a plant.

Endophytes have been defined thereafter in different ways, not always including the full range of living organisms able to reside within their host plants. Petrini (1961) proposed restricting the definition to 'all organisms inhabiting plant organs that, at some time

in their life, can colonize internal plant tissues without causing apparent harm to the host'. Several other definitions have been proposed, often restricting endophytes to a group of organisms (e.g., fungi or bacteria), symbiotic and/or commensal microorganisms, or facultative and/or mandatory microorganisms (Cabral et al., 1993; Quadt-Hallmann et al., 1997; Rosenblueth and Martínez-Romero, 2006; Hardoim et al., 2015; de Medeiros Azevedo et al., 2021).

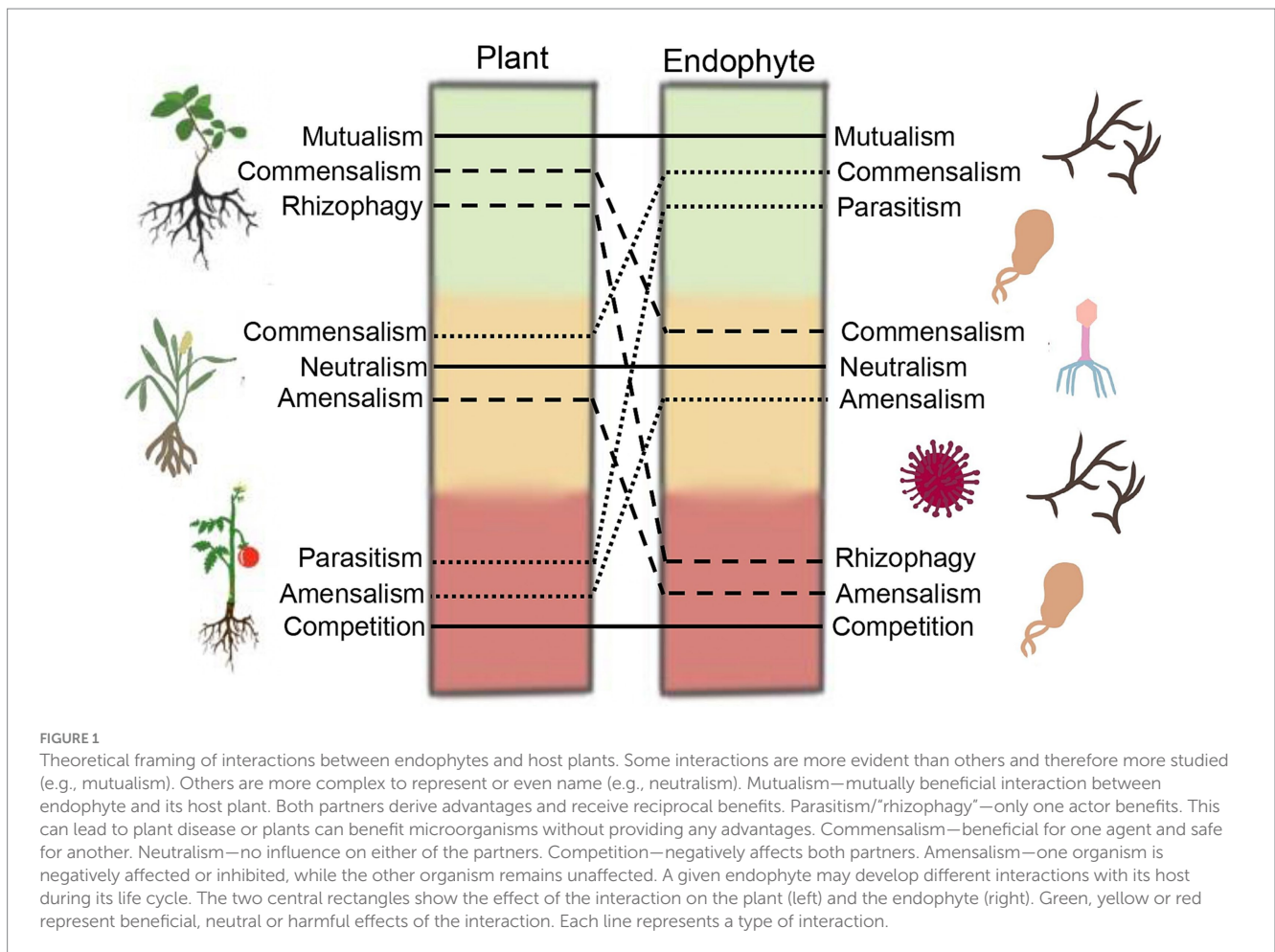
Recent technological advances, facilitated by metagenomic studies and drastic reduction in sequencing costs, have provided a much better view of the diversity and the type of microorganisms associated with plants, with emerging terms like 'phytobiome' referring to the collective community of microorganisms, including bacteria, fungi, archaea, viruses, and other microbes, that interact with plants within a specific environment. It encompasses a plant-associated microbiome that includes both endophytic and rhizospheric microorganisms. The term 'holobiome' is defined as the collective assemblage of all organisms, including plants, animals, and microorganisms, as well as their genetic material, that coexist within a specific ecological niche or habitat. Redefining the term 'endophytome' with regard to these newly defined terms is also necessary for the precision, clarity, and elucidation of the complex interactions and synergistic relationships between organisms, as well as their combined contributions to ecosystem functioning, health, and resilience.

Several plant-associated microbes may sometimes cause disease but stay associated with their host plants simply as commensals. For example, *Xylella fastidiosa* has been associated with more than 600 asymptomatic host plants (Delbianco et al., 2021). Similarly, *Clavibacter* and *Curtobacterium* are often associated with asymptomatic plants, although some species are dangerous plant pathogens (Eichenlaub and Gartemann, 2011; Bulgari et al., 2014). Using a metagenomic approach to search for plant viruses has revealed the presence of numerous viral sequences and viruses that do not cause diseases (Roossinck, 2010). Some plant pathogens, individuals of the same species, or even strains, are also found in alternate hosts, where they do not cause diseases (Salvaudon et al., 2005). What drives the shift of such organisms along the 'parasite-mutualist continuum' has yet to be explained (Drew et al., 2021). Dependent on the host-microorganism association, excluding the 'pathogen' from the endophyte definition is impossible considering these examples.

To fully capture the complexity and diversity of endophytic organisms and their relationships with plants and elucidate the complex network of interactions and dependencies in endophytic microbial populations in plants, there is an urgent need to return to the original definition proposed by De Bary et al. (1866). As our understanding of endophytes continues to evolve, it is essential to develop a comprehensive and inclusive definition encompassing all aspects of their ecology and biology.

Based on the definition of the human microbiome, we propose to define the "endophytome" as a collective community of endophytes, including bacteria, fungi, archaea, viruses, and other microbes, that inhabit plants as obligatory or facultative organisms that are vertically or horizontally transmitted. The endophytome is composed of endophytes that may interact dynamically with plants through (Kogel et al., 2006; Buée et al., 2009; Agler et al., 2016; Berendsen et al., 2018; Papik et al., 2020; Swanson et al., 2022; Figure 1):

Mutualism—mutually beneficial relationships or interactions between endophytes and their host plants, in which both partners derive advantages and receive reciprocal benefits. Example: Arbuscular



mycorrhizae fungi (from Glomeromycota phylum) form structures called arbuscules inside the plant root cells, facilitating carbohydrates exchange and plant ability to absorb water and nutrients enhancement (Stürmer and Kemmelmeier, 2021). Recognized as a prominent endophyte model, the strain *Gluconacetobacter diazotrophicus* PAL5 employs a multifaceted strategy to bolster plant growth. Its repertoire includes biological nitrogen fixation, the synthesis of siderophores and antimicrobial substances, and the facilitation of mineral nutrient solubilization (Saravanan et al., 2008; De Oliveira et al., 2016). PAL5 demonstrates remarkable resilience, exhibiting improved plant growth even under challenging conditions such as salt, drought, and low nitrogen stress (De Oliveira et al., 2016; Filgueiras et al., 2020; Tufail et al., 2021). Studies have elucidated the bacterium's adaptive responses to salt stress, involving morphological adjustments, cellular viability modifications, and significant proteomic alterations. The pivotal role of the DegP protease in stress tolerance has been underscored, shedding light on molecular mechanisms crucial for bacterial adaptation to environmental pressures (Leandro et al., 2021). Furthermore, PAL5's contribution to plant colonization, particularly in rice roots, has highlighted the indispensable roles of superoxide dismutase and glutathione reductase. These enzymes play critical roles in defending the bacterium against oxidative stress, thereby fostering successful symbiosis with host plants and enhancing overall stress tolerance and health (Alquères et al., 2013). Availability of nitrogen often limiting plant growth, intensive research on bacteria fixing

nitrogen was conducted (Lima et al., 1987; Boddey, 1995). Among those bacteria, *Azoarcus* sp. strain BH72 was often used as a model (Hurek and Reinhold-Hurek, 2003). *Azoarcus* is a diazotrophic endophyte usually colonizing rice or grass roots mainly studied for its ability to fix nitrogen, its roots colonization process (Hurek and Reinhold-Hurek, 2003; Reinhold-Hurek and Hurek, 2007; Krause et al., 2017; Chen et al., 2020; Plucani do Amaral et al., 2023).

Parasitism/“rhizophagy”—where only one actor benefits. This interaction can either lead to plant disease or the plant can benefit from the microorganisms without providing any advantages. Example: (1) Rhizophagy is a mechanism where plant can internalize and digest nutrients from symbiotic microbes (bacteria and fungi; White et al., 2018). (2) The genus *Xanthomonas* often are plant associated bacteria, collectively causing diseases on hundreds of host plants, including crops and ornamental plants (Mansfield et al., 2012; Peduzzi et al., 2022).

Commensalism—where it is beneficial for one agent and safe for the other. Example: (1) Fungal endophyte *Epichloë* residing within the tissues of grass can produce secondary metabolites, such as alkaloids beneficial for plant host (Bastias et al., 2017). (2) The protist *Polymyxa betae*, is a potential vector of sugar beet viruses. When free of virus, it alleviates plant defense response, playing hide-and-seek with sugar beet and allowing for their mutual development (Desoignies and Legreve, 2011; Decroës et al., 2022).

Competition—where both partners are negatively affected by the interaction. Example: *Xylella fastidiosa* is a bacterium that colonizes

the xylem vessels, the water-carrying channels in the plant. It depends on the plant for its nutrition and survival. When it rapidly kills the host plant, the source of nutrients on which the bacterium depends is rapidly exhausted. This can lead to a significant halt or slowdown in bacterial growth (Landa et al., 2022).

Neutralism—where the interaction does not influence either partners.

Amensalism—where one organism is negatively affected or inhibited, whereas the other remains unaffected.

These last two interactions are difficult to illustrate concerning the endophytome due to lack of knowledge and should only be considered as theoretical. As endophytes are present within the plant for at least part of their cycle, it would be difficult to imagine that no benefits would result from these interactions.

A given endophyte may develop different interactions with its host during its life cycle and a “healthy” endophytome refers to microbiome presence in absence of any disease and shows a large degree of diversity that may be shaped by the host plant (genera, species), the stage of development, and the environment. The endophytome can also be characterized as a functional core or a complement of metabolic and other molecular functions that are performed by the microbiome with a plant part but are not necessary provided by the same organisms in different species/ individual as seen in human microbiome (Lloyd-Price et al., 2016).

The following sections focus on bacterial endophytomes. Our focus will now shift toward unraveling the entry pathways of bacterial endophytes and exploring whether transmission occurs through vertical or horizontal pathways. We will explore the drivers of the diversity and composition of bacterial endophytes. By unraveling the mystery of the bacterial endophytome, we aimed to gain deeper insights into its functional roles and potential applications in agriculture and ecosystem management.

## Where does bacterial endophytome come from?

The endophytome comprises seed-transmitted microorganisms and microorganisms from the environment. Endophytes colonize the host vertically from parent to offspring, mainly via seed or vegetative propagation, horizontally through the environment, or in mixed modes (Bright and Bulgheresi, 2010; Figure 2).

Vertical pathway: This pathway involves the transmission of bacteria through seeds or vegetative propagation (Cankar et al., 2005; Mastretta et al., 2009; dos Santos et al., 2018). Endophytes present in the seeds can be acquired from pollen, flowers, fruits, or the plant’s soil. Bacteria reach the reproductive organs from the seed via xylem vessels or the shoot apical meristem and differentiate into reproductive organs (Frank et al., 2017). Most vertically transferred bacteria must spend their entire lives inside the host, on which they depend to survive. Vertical transmission has been identified as a factor that helps align the interests of mutualists, suggesting that symbiotic endophytes transferred vertically are mutualists and likely provide an indispensable function (Herre et al., 1999). Indeed, seed endophytes have been shown to benefit their hosts by releasing seeds from dormancy, facilitating germination, protecting against pathogens, and promoting the growth of seedlings (Puente et al., 2009). Typical

members include the genera *Acinetobacter*, *Bacillus*, *Micrococcus*, *Paenibacillus*, *Pantoea*, and *Pseudomonas* (Truyens et al., 2015).

Horizontal pathway: Horizontal transfer is mainly realized by the soil-to-root route because roots are considered the main entry point for microorganisms. Indeed, bacteria can penetrate the endodermis, the innermost layer of the root cortex, through root hair channels, cracks in the epidermis, cell-to-cell junctions, or through root cap cells that detach as the roots grow (Hardoim et al., 2008). Once bacteria reach the endodermis, they must pass through the Casparian strip, a cell wall thickening that prevents the free diffusion of molecules and ions between the root cortex and vascular tissues. Studies suggest that some bacteria can pass through the Casparian strip by inducing the expression of endodermal transporters, such as aquaporins, which allow bacteria to cross the endodermal barrier (Bulgarelli et al., 2013). Additionally, some bacteria secrete cell wall-degrading enzymes or manipulate host cell signaling pathways to facilitate their entry into the endodermis. Once in the endodermis, endophytes mainly move into the xylem vascular system, allowing systemic colonization of internal plant compartments (James et al., 2002). They can colonize xylem vessels and perforation plates between these vessels (James et al., 2002; Compant et al., 2005). In addition to this main transport route, other endophytes also colonize intercellular spaces (Hardoim et al., 2015). This pathway can be considered passive or active (Hardoim et al., 2008) depending on the penetration mode within the plant. An active penetration pathway can be mediated by the attachment of bacterial endophytes to plant cells using their flagellum and the secretion of metabolites that facilitate the penetration process (mostly exopolysaccharides [EPS] and cell wall degrading enzyme; Kandel et al., 2017; Pinski et al., 2019; Ullah et al., 2019). To some extent, root exudates and rhizodeposits can attract certain types of microorganisms *in planta* (Hallmann et al., 1997; Germida et al., 1998; Sessitsch et al., 2002; Cocking, 2003; Compant et al., 2010; Hardoim et al., 2011; dos Santos et al., 2018). Bacterial endophytes can also be horizontally transmitted to the phyllosphere level (Redford et al., 2010; Kembel et al., 2014; dos Santos et al., 2018) from dust, rainwater, or surrounding pollinators. Hydathodes, lenticels, and stomata are the primary gateways for endophytes in these environments (Compant et al., 2010; Hardoim et al., 2011; Frank et al., 2017). Plants can close or open their stomata upon contact with different microbial antigens (Gimenez-Ibanez et al., 2017; Melotto et al., 2017), which suggests that the plant immune system plays a role in the selection of microbes entering the endosphere (Fesel and Zuccaro, 2016). However, some foliar endophytes also control stomatal opening (Rho et al., 2018). Plant- and sap-feeding insects can be endophyte vectors. These insects have piercing-sucking mouthparts and can directly puncture the phloem and/or xylem cells that transmit the endophytes (Frank et al., 2017). Finally, only compatible endophyte-plant interactions can successfully colonize the endosphere, which explains the reduced number of endophytes compared with rhizospheric bacteria (Hardoim et al., 2011; Khare et al., 2018). An analysis of all sequenced 16S rRNA gene available in the International Nucleotide Sequence Database Collaboration identified four phyla containing more than 96% sequenced endophytic prokaryotes: Proteobacteria (54%), Actinobacteria (20%), Firmicutes (16%), and Bacteroidetes (6%). Most endophytic bacteria belong to the class *Gammaproteobacteria*, including *Acinetobacter*, *Enterobacter*, *Pantoea*, *Pseudomonas*, *Stenotrophomonas*, and *Serratia* (Hardoim et al., 2011).

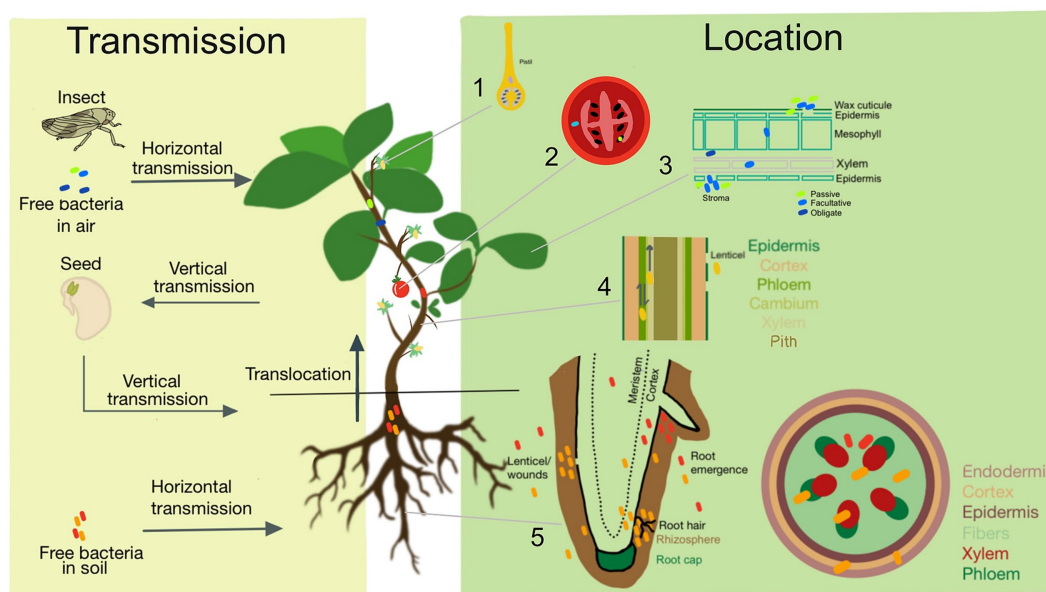


FIGURE 2

Types of endophyte transmission and endophyte location in plants. The gray arrows indicate different types of transmission of endophytes in the host plant: horizontally and vertically. The endophytes can move through translocation to reach different locations within the plant: the anthosphere (1), the carposphere (2), the phyllosphere (3), the caulosphere (4), and the rhizosphere (5).

## Toward an endophytome profile?

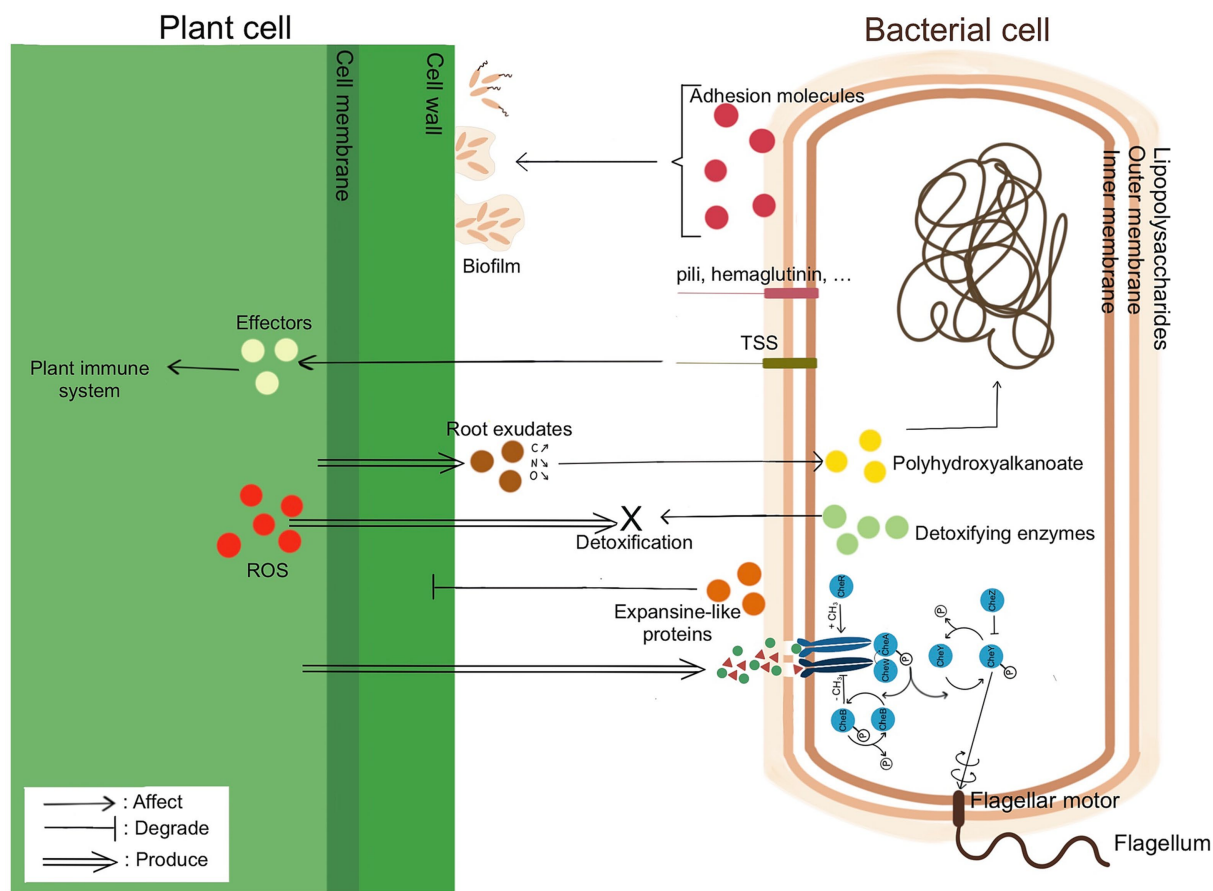
The endophytome comprises various endophytes characterized by genomic differences compared with free-living microorganisms. However, these differences can be difficult to describe because some are facultative (Del Orozco-Mosqueda et al., 2021). Ali et al. (2014) were the first to compare the genomes of endophytes and non-endophytes, thereby identifying the genes involved in secretion and transport activities, polymer degradation or modification, detoxification, and maintenance of redox potential. They suggested that these functions might play a role in endophytic behavior, allowing them to colonize plants.

This review presents the functional characteristics of endophytic bacteria and their involvement in plant colonization and propagation. The soil-to-root colonization steps were divided into: (1) detecting root exudates, (2) motility toward the plant, (3) adhering to root surfaces, (4) penetrating the root surface, and (5) colonizing the plant's internal parts. Each of these stages is mediated by a variety of biomolecules that influence the expression of both bacterial and colonized plant genes (Pinski et al., 2019; Figure 3).

Colonization by endophytic bacteria starts with the chemotaxis of free-living bacteria toward the roots, aided by methyl-accepting chemotaxis proteins (MCPs). These transmembrane sensors detect molecules and direct bacteria toward attractants or away from repellents (Balsanelli et al., 2016). The involvement of MCPs in plant colonization was demonstrated using inactivation mutants of *Herbaspirillum seropedicae* SmR1 and *Azospirillum brasilense* Sp7. In SmR1, one MCP is required to sense the rhizosphere and direct bacteria toward host-secreted compounds. In Sp7, the inactivation of another MCP results in impaired chemotaxis and colonization of plant roots (Greer-Phillips et al., 2004).

At the root surface, bacteria can attach through biofilms, which contain water, proteins, polysaccharides, eDNA, RNA, and ions. Mutants in various species, such as *G. diazotrophicus* PAL, have shown that other polymers, including EPS, glucomannan, and cellulose, also affect attachment and colonization. Adhesion is mediated by the flagella, pili, curli, and hemagglutinins. The upregulation of genes encoding filamentous hemagglutinin proteins suggests their involvement in root attachment (Barak et al., 2005; Williams et al., 2008; Monteiro et al., 2012; Ainele et al., 2017). Bacterial surface components, particularly lipopolysaccharides (LPS), play crucial roles in early attachment and colonization. Mutations in *rfbB* or *rfbC*, which are involved in rhamnose biosynthesis, reduce the attachment to and colonization of maize roots by *H. seropedicae* SmR1, as well as the bacterium's robustness against detergents, antibiotics, and phytohormones. Similarly, mutations in the *rfbD* gene of *A. brasilense* impair attachment and colonization efficiency. O-antigen ligase, involved in O-antigen biosynthesis, was upregulated during colonization, indicating its involvement in plant-endophyte interactions. Bacterial LPS binds to maize root lectin proteins leading to agglutination, which is impaired when the O-antigen ligase is inactive, resulting in reduced attachment and colonization efficiency (Jofré et al., 2004; Balsanelli et al., 2013).

After attachment to the root surface, bacterial endophytes enter the plant through natural openings or wounds or by producing plant cell wall-degrading enzymes (e.g., pectinase or cellulase) that facilitate entry and spread within plants. For example, *Azoarcus* sp. BH72 requires endoglucanase for rice root colonization and spreads to the aboveground parts, whereas *Bacillus mycoides* EC18 upregulates hydrolases and chitin-binding proteins in response to root exudates (Badri and Vivanco, 2009; Reinhold-Hurek and Hurek, 2011; Baetz and Martinoia, 2014).



**FIGURE 3**  
Principal drivers involved in bacterial endophyte colonization of plant host. Adhesion molecules (●) and hemagglutinin, curli protein, pili IV, and pili I (—) facilitate the attachment of endophytic microorganisms to the plant's surfaces, promoting biofilm formation and providing a stable environment for colonization, nutrient exchange, and interactions within the plant tissues. Type 3 and 6 secretion systems (—) produce effectors (●), which play a role in manipulating the host plant's cellular processes, suppressing immune responses, and promoting colonization. Plant cell wall degrading enzymes (●) enable endophytes to break down and penetrate the plant cell wall, facilitating colonization. Expansin-like proteins (●) promote cell wall loosening and expansion, allowing endophytes to access nutrients and establish symbiotic interactions within plant tissues. Detoxifying enzymes (●) can neutralize reactive oxygen species (●) generated by plants as a defense response and metabolize phytoalexins, aiding in the plant's protection against oxidative damage and enhancing its resistance against pathogens or stressors. Root exudates (●) influence the production of polyhydroxyalkanoate (●), which affects the expression of specific genes involved in the colonization process, nutrient acquisition, and establishment of interactions with the host plant. Attractants (●) or repellents (▲) play a role in endophyte motility through the action of methyl-accepting chemotaxis proteins (—) and chemoreceptors (●), which detect the presence of specific chemical signals released by plants, guiding endophytes toward attractive compounds or repelling them from harmful substances. The motility of endophytes is influenced by the differential expression and activity of methyl-accepting chemotaxis proteins and chemoreceptors, allowing them to navigate toward favorable environments or avoid hostile conditions within the plant.

During colonization, specific endophytic genes, such as genes encoding membrane-associated proteins belonging to the resistance nodulation and cell division (RND) efflux systems, actively contribute to successful establishment. Among them, the Membrane Fusion Protein (MFP) subunit of the RND family efflux systems has been shown to have a significant role in the successful colonization of the host plant, as observed in the case of the endophyte *Erwinia amylovora* in apple trees (Taghavi et al., 2010). Detoxification mechanisms such as glutathione synthesis and reductase-related genes have been identified as crucial factors for competent endophytes, as they protect their host against oxidative stress induced after host infection (Compant et al., 2010). Thus, these genes play a potential role in the protective response of endophytic bacteria to oxidative stress resulting from the infection of plant hosts (Alquéres et al., 2013).

After entering the plant, certain endophytes spread systemically throughout the plant, eventually reaching the flowers, fruits, and seeds through the xylem vessels of their host plants, taking advantage of their flagella and the plant's transpiration stream (Compant et al., 2005).

Transport proteins, including various genes associated with the major facilitator superfamily (MFS) transporter system, play a crucial role in the endophytic lifestyle by facilitating the uptake of plant-synthesized nutrients. These proteins are essential for acquiring nutrients found internally within plants or released into the rhizosphere. Their primary function involves the exchange of diverse carbohydrates and amino acids, enabling efficient nutrient transfer between the endophyte and its host plant (Taghavi et al., 2010; Ali et al., 2014). Certain endophytic genes appear responsible for bacterial nutrition within the plant, including non-plant-cell-wall-breaking hydrolases found in the genomes of plant growth-promoting bacterial

TABLE 1 Conserved classes of genes responsible for endophytic behavior, including various transcriptional regulators.

Abbreviation	Function	Reference
AraC	Involved in carbon metabolism, stress responses, and virulence management	Gallegos et al. (1997); Martin and Rosner (2001)
FrmR	Involved in the global transcriptional regulator and negatively controls cellular carbohydrate metabolism	Hyeon et al. (2012)
AsnC	Activate asnA, a gene involved in the synthesis of asparagine	Thaw et al. (2006)
LrgB	Controlling hydrolase activity	Groicher et al. (2000)
LysR	LysR family proteins control a diverse set of genes that are mainly involved in bacterial virulence, metabolism, quorum sensing, and motility	Maddocks and Oyston (2008)
DeoR	DeoR family of transcriptional regulators contains proteins that negatively control genes involved in carbohydrate metabolism	Elgrably-Weiss et al. (2006)
WrbA	WrbA flavoproteins have been documented to act as RpoS-dependent stationary phase proteins	Yang et al. (1993); Lacour and Landini (2004)

endophytes, such as *Enterobacter* spp. 638 and *Serratia proteamaculans* 568 (Taghavi et al., 2010). The widespread presence of these enzymes among different endophytes suggests their potential involvement in the versatile utilization of sugars, which could be a valuable characteristic of proficient endophytes.

Endophytic bacteria possess various secretion systems that differentiate them from free-living bacteria. Among these, the type VI secretion system (T6SS) appears to be involved in utilizing plant carbon sources (Del Orozco-Mosqueda et al., 2021). Bacterial endophytes commonly exhibit type I and II secretion systems (Reinhold-Hurek and Hurek, 2011), whereas type III and type IV secretion systems are predominantly found in pathogenic bacteria and are typically absent in endophytes (Downie, 2010). The type V secretion system, also known as an autotransporter, is primarily observed in endophytes. Additionally, T6SS may benefit plant-microbe interactions (Mattinen et al., 2008) and have been detected in certain bacterial endophytes (Reinhold-Hurek and Hurek, 2011).

Some groups of genes have been identified as conserved and potentially responsible for endophytic behavior, including various transcriptional regulators involved in metabolic adaptation and quorum sensing, such as AraC, FrmR, AsnC, LrgB, LysR, DeoR, and WrbA (Table 1). Many of these regulators play a role in modulating carbohydrate metabolism, which is crucial when cells enter the stationary phase of growth. The presence of these regulatory proteins suggests their likely function, specifically in the non-invasive breakdown of the plant cell wall, which occurs when endophytes meet plant hosts during infection. Additionally, some of these transcriptional regulators are involved in communication pathways that are vital for altering the behavior of an organism when it adapts to its physiology (Ali et al., 2014). The gene encoding a lysine biosynthesis enzyme, specifically diaminopimelate decarboxylase, along with the gene encoding a lysine exporter protein, may also be involved in the transition of the bacterium from a free-living state in the soil to an endophytic state within the plant (Maddocks and Oyston, 2008; Ali et al., 2014).

## Endophyte community variation drivers

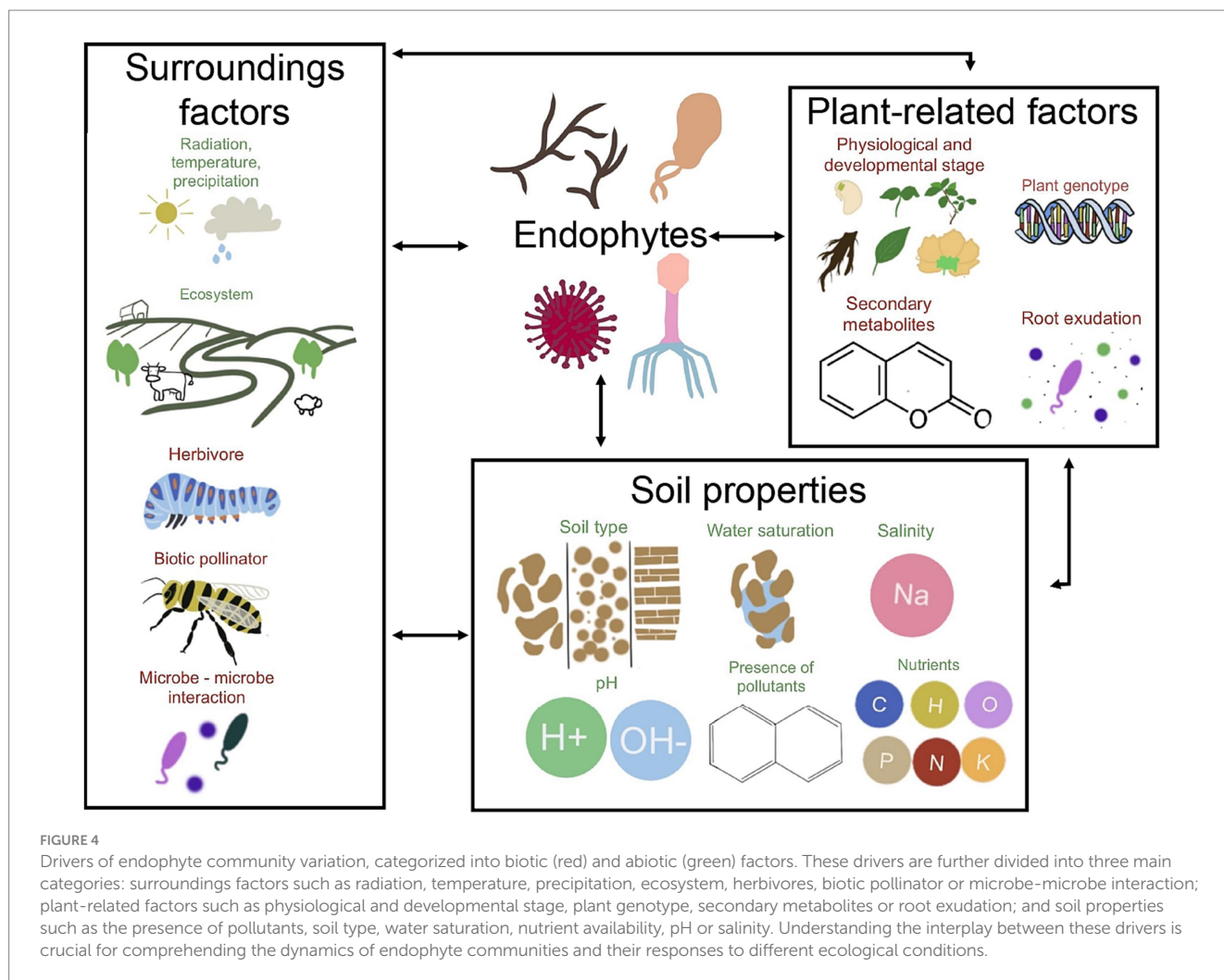
A holobiont is the assemblage of a host, its microbiome, and any other organism that contributes to the functioning of the host and

forms an ecological niche through mutual interconnections (Vandenkoornhuysse et al., 2015). The evolutionary history of the holobiont may be shaped significantly by the response of microorganisms to environmental changes, as well as the host organism itself (Occhipinti, 2013; Vandenkoornhuysse et al., 2015; Rosenberg and Zilber-Rosenberg, 2016; Hassani et al., 2018). Endophytic bacteria are typically defined as individual microorganisms rather than communities, whereas plants are influenced mainly by microbial communities. A microbial community can be defined as an assemblage of co-occurring and potentially interacting microbes present in a defined habitat in space and time (Compant et al., 2010). In this section, we review the effects of biotic and abiotic stresses on these communities and their effects on plants.

During the colonization of the endosphere, osmotic pressure, oxygen availability, carbon sources, and pH of the environment change, and bacteria must quickly adapt (Singh et al., 2021). Soil type and plant development stage appear to be the most important drivers of bacterial endophytic communities, whose composition is influenced by biotic factors and abiotic factors (Figures 2, 4).

Biotic factors include (1) plant genotype (Hardoim et al., 2011; Yu et al., 2015; Ding and Melcher, 2016), developmental, and physiological stage (Jin et al., 2014; Yang et al., 2017); (2) composition of the root exudate and secondary metabolites (Aulakh et al., 2001; Shaw et al., 2006; Zhang et al., 2006; Dennis et al., 2010; Philippot et al., 2013; Vandenkoornhuysse et al., 2015; Henning et al., 2016; Musilova et al., 2016; Sasse et al., 2018); (3) biotic pollination; and (4) microbe-microbe interactions (Vandenkoornhuysse et al., 2015; Rosenberg and Zilber-Rosenberg, 2016).

Plant genotype, developmental and physiological stage—Plant genotype is one of the main factors. Research on bacterial endophyte communities is facilitated by high-throughput sequencing techniques, especially for root and phyllosphere microbiota. Next-generation sequencing (NGS) has revealed differences in the taxonomic composition of phyllosphere bacterial endophyte communities depending on the nature of the host plant species. Therefore, the core seed microbiome depends on the host genotype (Saikkonen et al., 2012). In addition to this genotypic effect, different plant organs harbor distinctive bacterial endophytes, suggesting that plants play a role in structuring endophytic communities (Jin et al., 2014; Yang et al., 2017). These variations in bacterial endophyte communities can also be explained by different environmental sources or by their ability to colonize different niches *in planta*. The examples are listed in Table 2.



**Root exudation**—Plants can control variations in bacterial endophyte communities through root exudation. Plant exudate photosynthesis-derived compounds in the soil control the composition of microbial communities (Dennis et al., 2010; Philippot et al., 2013). Root exudate composition changes with plant species, cultivars, and developmental stages (Aulakh et al., 2001). For example, variation in phenolic compounds drives interactions between bacteria and plants (Shaw et al., 2006). Beneficial microbes are drawn to the root exudates because of their metabolites. Rhizospheric organisms use carbohydrates, lipids, amino acids, phenolics, phytosiderophores, and flavonoids as carbon sources (Badri and Vivanco, 2009). These metabolites modulate gene expression patterns in microorganisms to modify bacteria-host interactions (Mark et al., 2005; Yi et al., 2017). Due to the limited number of studies focusing on its impact on the composition of the bacterial endophyte community, the mechanisms underlying this influence are still poorly understood. Examples of the effects of root exudation on endophytic communities are listed in Table 2.

**Plant secondary metabolites**—Plant secondary metabolites (PSM), such as luteolin, quercetin, daidzein, and steviol glycosides (Papik et al., 2020), are another one of the most important factors influencing the structure and function of the endophyte community (Musilova et al., 2016; Sasse et al., 2018). PSM are a potential carbon

source for rhizosphere and endophyte communities. They exhibit antimicrobial activity and induce the selection of microorganisms in the rhizosphere (Musilova et al., 2016). The more PSM are present in the rhizosphere, the higher the probability of microorganisms being capable of degrading pollutants because PSM can serve as primary substrates and/or enzyme inducers for the growth of microorganisms (Singer et al., 2003, 2004). Secondary metabolites can influence gene expression, modulate host immunity, alter primary and secondary metabolism, and morphology of the host plant, which can result in plant growth promotion, increased stress tolerance, or reduced rates of herbivory during endophyte colonization (Zhang et al., 2006; Henning et al., 2016). Microorganisms found in the soil are primarily influenced by the rhizosphere, which constitutes the first plant-influenced habitat they encounter. Plant metabolism profoundly affects the thin layer of soil surrounding the roots through the release of oxygen and secretion of exudates, including carbon-rich molecules and antimicrobial compounds. Consequently, the rhizospheres between roots and soil are highly dynamic environments, resulting in differentiated microbial rhizosphere and endosphere communities (Vandenkoornhuyse et al., 2015).

**Microbe-microbe interactions**—Microbe-microbe interactions play an important role in endophyte variation. Interspecies interactions can affect the diversity and productivity of communities.



TABLE 2 Examples of biotic factors driving variation in endophytic communities.

Biotic factors	Description	Plant species, endophyte	Reference
Plant genotype	Influences of plant species on leaf endophytic bacterial communities of non-cultivated plants	<i>Ambrosia psilostachya</i> DC., <i>Asclepias viridis</i> Walt., <i>Panicum virgatum</i> L., <i>Sorghastrum nutans</i> (L.) Nash and <i>Ruellia humilis</i> Nutt	Ding and Melcher (2016)
	Determination of the different bacterial communities' composition across cultivars by rice genotype	<i>Oryza sativa</i> subspecies <i>indica</i> , <i>japonica</i> , and <i>aromatica</i>	Hardoim et al. (2011)
	Conservation of a core microbiota in maize seeds across evolution with variations in relation to plant host phylogeny from teosinte to corn	<i>Zea mays</i>	Johnston-Monje and Raizada (2011)
Root exudation	Attraction of rhizobial endophytes and <i>Serratia</i> sp. thanks to flavonoids during colonization of rice roots	<i>Oryza sativa</i> , <i>Rhizobial endophytes</i> , <i>Serratia</i> sp.	Balachandar et al. (2006)
	Attraction of endophytes thanks to exudates composed of citric acid and oxalate from the tricarboxylic acid flux and promotion of biofilms	<i>Cucumis sativus</i> , <i>Bacillus amyloliquefaciens</i> SQR9	Zhang et al. (2014)
Microbe - microbe interaction	Mutualistic interactions between salt-tolerant endophytes enhancing the fitness of the plant	<i>Bacillus subtilis</i> <i>Mesorhizobium cicero</i> <i>M. cicero</i>	Egamberdieva et al. (2017)
	Application of keystone species theory to plant-associated microbiota for the first time	Inoculation of <i>Enterobacter</i> sp. E5, <i>Kosakonia</i> sp. S1 and <i>Klebsiella</i> sp. Kb on banana endosphere increase resistance to the <i>Fusarium</i> wild disease;	Liu et al. (2019); Macedo-Raygoza et al. (2019); Zhang et al. (2019)

Even if often described to be rare, positive interactions between microorganisms of soil microbiome often occur in coculture primarily as parasitisms (18%), commensalisms (12%) and mutualisms (5%; Kehe et al., 2021). Microorganisms and host plants form a mutually inclusive ecosystem, which has recently been discussed regarding their mutual interconnections (Occhipinti, 2013; Vandenkoornhuys et al., 2015). Endophytic bacteria can antagonize phytopathogens (Hu et al., 2009; Fürnkranz et al., 2012; Khalaf and Raizada, 2018; Zhao et al., 2018). Fungi and bacteria can interact in the endosphere, which is crucial for the development of endophytic communities. Identifying the major endophytic taxa of certain crops and clarifying their unique roles in plants would contribute significantly to developing the aforementioned agricultural applications of endophytes and deepen our knowledge of the microbial composition in the endosphere. Some examples of microbe-microbe interactions are listed in Table 2.

Abiotic factors influencing endophytic communities include (1) radiation and temperature (Redman et al., 2002; Ju et al., 2006; Nissinen et al., 2012); (2) precipitation and moisture (Rolli et al., 2015; Ullah et al., 2019); (3) soil type (Buyer et al., 1999; Hinsinger et al., 2009; Polivkova et al., 2018); (4) pH (Hayman and Tavares, 1985; Wang et al., 1993; Anyango et al., 1995; Lafay and Burdon, 1998; Cornelissen et al., 2011); (5) nutrients (Hermans et al., 2017); and (6) presence of pollutants (Vergani et al., 2017; Yergeau et al., 2018).

Radiation/temperature—Radiation and temperature affect endophytic communities, mostly by influencing host plant colonization (Redman et al., 2002; Ju et al., 2006; Nissinen et al., 2012). An important increase in temperature decreases shoot endophytic density because of reduced endophytic colonization (Pillay and Nowak, 1997). In contrast, a slight increase in temperature (+ 5°C) in temperate forests results in higher endophytic bacterial population (Rahman et al., 2021). It has been shown that climate change treatments, represented by elevated temperatures and/or increased

CO<sub>2</sub> concentrations shift leaf-associated bacterial communities (Ren et al., 2015) and could impact bacterial functions such N<sub>2</sub> fixation (Nissinen et al., 2012; Rahman et al., 2021; Table 3).

Water and oxygen availability—precipitation, and soil moisture are also important factors affecting endophyte diversity. One common perturbation is drought stress, which impacts root bacterial communities directly by changing moisture availability and indirectly by altering soil chemistry and plant phenotypes. Many putative causes of endophytic bacterial community shifts have been hypothesized (Table 2). First, naturally selected bacteria are directly resistant to drought stress. Some physiological mechanisms improve drought tolerance, including sporulation and thick cell walls, which are primarily found in bacteria belonging to gram-positive phyla, such as Actinobacteria and Bacilli (Cherif et al., 2015; Tocheva et al., 2016). Differences in survival could also be explained by the ability to produce and accumulate osmolytes, such as amino acids (proline, glutamine, and glycine betaine) and carbohydrates (trehalose and ectoine). Gram-negative bacteria produce osmolytes only when they are constitutively produced (Schimel et al., 2007). Second, slow-growing microbes could be selected according to the nutrient-poor (less labile organic carbon and nitrogen) but oxygen-rich characteristics of drought environments. These characteristics favor oligotrophic bacteria with high metabolic activity, mostly gram-positive bacteria (Curiel Yuste et al., 2014; Hartmann et al., 2017). The third hypothesis is that drought stress may induce the production of various compounds by bacteria, thereby affecting community stability. A high antibiotic content was found in drought environments, probably produced by drought stress-tolerant bacteria that outcompete other bacteria for limited resources (Bouskill et al., 2016). Taxa selected by drought stress and plants can be in the rhizosphere or endosphere and improve drought stress resistance in plants by maintaining host functions and fitness (Rolli et al., 2015; Ullah et al.,

TABLE 3 Examples abiotic factors driving variation in endophytic communities.

Abiotic factors	Description	Plant species, endophyte	Reference
Radiation and temperature	Elevated temperatures and CO <sub>2</sub> concentration impacted the leaf-associated bacterial communities of rice	<i>Oryza sativa</i> , <i>Enterobacteriaceae</i> , <i>Xanthomonadaceae</i>	Ren et al. (2015)
	Temperature affects the key enzymes used to fix N <sub>2</sub> by bacteria	<i>Azotobacter chroococcum</i>	Miller and Eady (1988)
	Many psychrotolerant endophytic bacteria were found in plant tissues of Arctic plants species	Endophytes of <i>Oxyria digyna</i> , <i>Diapensia lapponica</i> and <i>Juncus trifidus</i> ,	Nissinen et al. (2012)
Water and oxygen availability—drought	Gram-positive phyla are favored thanks to their thick cell and spores	Actinobacteria and Bacilli	Schimel et al. (2007); Tocheva et al. (2016)
	Plants modulate their cell wall components in response to drought with components that are usable by Actinobacteria	Actinobacteria	Naylor et al. (2017)
	Enrichment of Actinobacteria ( <i>Streptomyces</i> genera) in the endosphere was related to drought resistance in plants	Actinobacteria, Streptomyces	Fitzpatrick et al. (2018)
	Enrichment of Actinobacteria in roots of <i>Poaceae</i> and rice plants	<i>Poaceae</i> , <i>Oryza sativa</i> , Actinobacteria	Naylor et al. (2017); Santos-Medellín et al. (2017)
Water and oxygen availability—flooding	Depletion of Actinobacteria, Firmicutes, and Alphaproteobacteria phyla and enrichment of Gammaproteobacteria phylum after flooding of wheat phyllosphere microbiota	<i>Triticum aestivum</i> , Actinobacteria, Firmicutes, Alphaproteobacteria, Gammaproteobacteria phyla	Francioli et al. (2022)
	Dominance of Gammaproteobacteria and Betaproteobacteria in a diazotrophic community of rice roots submitted to flooding stress	<i>Oryza sativa</i> , Gammaproteobacteria, and Betaproteobacteria phyla	Ferrando and Fernández Scavino (2015)
pH <i>Note: Soil pH can be influenced by metal toxicity, soil structure and texture, and water sources.</i>	Abundance of members of <i>Pirellulaceae</i> is favored in neutral soil pH	<i>Pirellulaceae</i>	Hermans et al. (2017)
	<i>Pseudomonas oryziphobans</i> and <i>Rhizobium radiobacter</i> are favored in neutral-pH soil, whereas in low-pH soil, <i>Enterobacter</i> -like and <i>Dyella ginsengisoli</i> are dominant	<i>Oryza sativa</i> , <i>Pseudomonas oryziphobans</i> ; <i>Rhizobium radiobacter</i> ; <i>Enterobacter</i> -like; <i>Dyella ginsengisoli</i>	Sessitsch et al. (2012)
	Acidic soil is a major driver of diazotroph communities' assembly	In qinghai-tibet alpine plant, <i>Bradyrhizobium</i> and <i>Mesorhizobium</i> had different pH-relative abundance patterns	Wang et al. (2017)
	Alkaline soils display reduced microbial activity due to low soil organic biomass and nutritional content	Reduction of <i>Bradyrhizobium</i> communities	Rahman et al. (2021)
Pollutants	Increase of Proteobacteria phylum after graphene and graphene oxides application	Proteobacteria phylum	Rong et al. (2017)
	Firmicutes and Actinobacteria phyla colonize heavy metals polluted soils	Firmicutes and Actinobacteria phyla	Pires et al. (2017)
	Aluminum reduces the abundance of members of the <i>Chitinophagaceae</i>	<i>Chitinophagaceae</i>	Hermans et al. (2017)
Nutrients	The carbon-nitrogen ratio influence soil bacterial population	<i>Gaiellaceae</i> , <i>Bradyrhizobium</i>	Hermans et al. (2017)

2019). Several studies have reported a correlation between drought stress resistance in plants and a shift in their microbiome in response to stress (Naylor et al., 2017; Santos-Medellín et al., 2017; Fitzpatrick et al., 2018). Flooding also affects endophytic communities, favoring the growth of anaerobic and aerotolerant bacteria. In this environment, endophytic bacteria may play an essential role in fixing nitrogen as reported in rice (Ferrando and Fernández Scavino, 2015). Indeed, as

oxygen irreversibly inhibits nitrogenase, N<sub>2</sub> fixers are favored in oxygen-poor environment (Smercina et al., 2019; Table 3).

Soil type—Soil type is described by Hinsinger et al. (2009) as one of the major abiotic drivers of endophyte community diversity. Multiple studies have shown that soil type strongly influence the endophytic bacterial and fungal communities (Buyer et al., 1999; Polivkova et al., 2018; Hou et al., 2019; Adeleke et al., 2022). Soil

fertility, physicochemical properties, pH, porosity, water and oxygen content and soil organic carbon are interlinked to influence soil microbial density and activity (Rahman et al., 2021). The primary features of the soil, such as water-holding capacity, cation-exchange capacity, hydraulic conductivity, oxygen diffusion and humidity directly or indirectly influence soil bacterial communities and, indirectly influence endophytic bacterial communities. The relationship between the soil characteristics and bacterial taxonomic groups reflects the ecological functions of these organisms (Hermans et al., 2017). For example, soil with a high clay content has smaller interparticle spaces and, therefore, a lower oxygen content, which favors nitrogen-fixing bacteria.

pH—pH has been shown to affect microbial communities in the rhizosphere, but its impact also extends to the endosphere (Hayman and Tavares, 1985; Wang et al., 1993; Anyango et al., 1995; Lafay and Burdon, 1998; Cornelissen et al., 2011). A slight change in pH promotes the growth of more adapted species by lowering the original community (Rahman et al., 2021; Table 3).

Pollutants—The presence of pollutants in the soil selects microorganisms capable of using and/or degrading them as sources of carbon and energy (Vergani et al., 2017; Yergeau et al., 2018). Heavy metals, naturally present in soils but also used in fertilizers, pesticides, and wastewater irrigation, explained a portion of the variability in the abundance of bacterial phyla and classes (Table 3).

Nutrients—Nutrients are essential for bacterial survival. The carbon-nitrogen ratio and the level of P may influence soil bacterial populations (Hermans et al., 2017).

## Conclusion and future perspectives

This review aims to establish a refined and enhanced understanding of endophytes and endophytomes, considering the rapid technological advancements that have deepened our understanding of this concept. Additionally, we extensively examined the profile, colonization pathway, and various drivers responsible for the diversity and variation observed in the bacterial endophytome.

The urgent need for sustainable agriculture arises from the imperative to ensure global food security, mitigate environmental degradation, and build resilience in the face of climate change. Embracing sustainable practices is not merely an option but an essential strategy for safeguarding the well-being of present and future generations (Espinosa-Leal et al., 2018; Raza et al., 2019; Qaim, 2020; Delitte et al., 2021). The colonization of plants, animals, and humans by countless microorganisms has sparked a significant shift in the study of the effects of these microorganisms on the biology and well-being of their hosts (Drew et al., 2021). Numerous cases of microbial evolution causing transition across the ‘parasite-mutualist continuum’ have been reported both in human and plant health and will further emerge through research. For example, a healthy gut microbiome is now considered crucial for human growth, development, and immune system establishment, underscoring the importance of maintaining balance for optimal health (Kartjito et al., 2023). Recent data show that early-life gut microbiome development can protect against diseases linked to an imbalanced gut microbiome in later stages of life (Barone et al., 2023; Sabino et al., 2023). These findings support the idea that targeted therapies can restore the gut microbiome during infancy, potentially promoting long-term infant health (Charbonneau et al.,

2017). Thus, modifying early colonization or addressing early-life gut dysbiosis may be strategies for enhancing well-being (Kapourchali and Cresci, 2020). The importance of microbiota in animal health has also been demonstrated in numerous studies, for example, in honeybees, where the genetic modification of a core gut bacterium improves resistance to viral infection (Leonard et al., 2020). In the future, engineering a microbiome or symbiont community via direct genetic modification of key transition loci in microbiome members could be used to improve human health. Future therapeutic and prophylactic modalities may be used to treat cancer and obesity (Sekirov et al., 2010).

In plant health, endophytes play a crucial role in alleviating both abiotic and biotic stresses. They enhance plant tolerance to adverse environmental conditions such as drought, salinity, and extreme temperatures. They stimulate the production of stress-related compounds and regulate plant hormone levels, thereby improving water and nutrient uptake efficiencies. Additionally, endophytes promote root development and enhance plant defense mechanisms against abiotic stressors (Khare et al., 2018; Ullah et al., 2019; Nadarajah, 2020; Singh et al., 2022). In response to biotic stress, endophytes shield against pathogens and herbivores by producing antimicrobial compounds, inducing systemic resistance, and activating plant defense pathways. These symbiotic microorganisms confer resistance to a wide range of pathogens, including bacteria, fungi, and nematodes, thereby ensuring plant health and productivity in the face of biotic challenges (Hardoim et al., 2008; Bulgarelli et al., 2013; Compant et al., 2019; Papik et al., 2020; Oukala et al., 2021). Overall, endophytes hold great promise for enhancing plant resilience and mitigating the negative impacts of abiotic and biotic stresses.

Drawing parallel to the human microbiota, there is a growing trend toward exploring endophytes in a similar manner. However, using a definition that targets only beneficial endophytes has prevented research from advancing as quickly as in the medical field. Moreover, studies of endophytes have been plagued by several limitations: (1) properties are studied in a single species or within closely related genotypes, but rarely across a taxonomically wide range of species; (2) the environmental conditions in which plant-endophyte interactions are investigated are often similar; (3) consortia are not often explored and bacterial and fungal endophytes are often considered separately (Elasri et al., 2001; Andreote et al., 2009; Hardoim et al., 2015). Consequently, our understanding of the modes of action of endophytes and their use in agriculture is limited.

The multiple interactions between endophytome, plants and environmental factors highlighted in this review reveals that endophytes need to be studied in terms of their endophytome as a community of microorganisms that share a common space. Using new technologies available in metagenomics, we argue that the dynamics of evolution of endophytic communities in plants during plant development and in response to biotic and abiotic stresses need to be explored using metatranscriptomics, metaproteomics, and metabolomics. Until now, the adoption of these technologies has been limited owing to their high cost and the complexity of the experimental and analytical procedures involved. However, the rapid evolution of technologies and price and cost decrease of these technologies promise for providing a more comprehensive perspective of the microbiome (Liu et al., 2021). This knowledge will allow the

underlying mechanisms to be elucidated and products derived from well-adapted endophytes to be developed. Understanding the intricacies of endophytic communities can pave the way for sustainable agricultural practices.

## Author contributions

SL: Writing – original draft, Writing – review & editing. LP: Writing – original draft, Writing – review & editing. CB: Writing – review & editing. AL: Writing – review & editing.

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## Supplementary material

The Supplementary material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fsufs.2024.1378436/full#supplementary-material>

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