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REVIEW

Disentangling arbuscular mycorrhizal fungi and bacteria at the soil-root interface

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Abstract

Arbuscular mycorrhizal fungi (AMF) are essential components of the plant root mycobiome and are found in approximately 80% of land plants. As obligate plant symbionts, AMF harbor their own microbiota, both inside and outside the plant root system. AMF-associated bacteria (AAB) possess various functional traits, including nitrogen fixation, organic and inorganic phosphate mobilization, growth hormone production, biofilm production, enzymatic capabilities, and biocontrol against pathogen attacks, which not only contribute to the health of the arbuscular mycorrhizal symbiosis but also promote plant growth. Because of this, there is increasing interest in the diversity, functioning, and mechanisms that underlie the complex interactions between AMF, AAB, and plant hosts. This review critically examines AMF-associated bacteria, focusing on AAB diversity, the factors driving richness and community composition of these bacteria across various ecosystems, along with the physical, chemical, and biological connections that enable AMF to select and recruit beneficial bacterial symbionts on and within their structures and hyphospheres. Additionally, potential applications of these bacteria in agriculture are discussed, emphasizing the potential importance of AMF fungal highways in engineering plant rhizosphere and endophyte bacteria communities, and the importance of a functional core of AAB taxa as a promising tool to improve plant and soil productivity. Thus, AMF and their highly diverse bacterial taxa represent important tools that could be efficiently explored in sustainable agriculture, carbon sequestration, and reduction of greenhouse gas emissions related to nitrogen fertilizer applications. Nevertheless, future studies adopting integrated multidisciplinary approaches are crucial to better understand AAB functional diversity and the mechanisms that govern these tripartite relationships.

Keywords Bacterial-fungal interactions · Hyphosphere · Tripartite interactions · Core microbiome · Plant growth–promoting bacteria · Sustainable agriculture

Introduction

Microbes and higher organisms closely coexist, forming beneficial, neutral, and antagonistic relationships. The plant microbiome consists of a variety of microorganisms, including archaea, bacteria, and fungi, which inhabit different plant niches, such as the rhizosphere (soil around roots affected by root exudates), rhizoplane (root surfaces), endosphere (root interior), and phyllosphere (aboveground parts) (Fig. 1). Plants and microorganisms depend on one another to maintain their ecological fitness and ability to adapt to environmental changes and have been considered holobionts (Parniske 2008; Zilber-Rosenberg and Rosenberg 2008; Vandenkoornhuyse et al. 2015; Lee et al. 2019). Arbuscular mycorrhizal fungi (AMF), which colonize approximately 80% of plants, form the oldest known symbiosis and help plants to adapt to their land environment (Parniske 2008; Bonfante and Genre 2010).

Arbuscular mycorrhizal (AM) symbiosis is established upon a nutrient economy in which host plants dedicate a portion of their photosynthates to feed AMF colonizing their roots in exchange for mineral nutrients, especially phosphorus and nitrogen. These are supplied through the extraradical hyphae, which serve as an extension of the root system to form an alternative route for nutrient uptake

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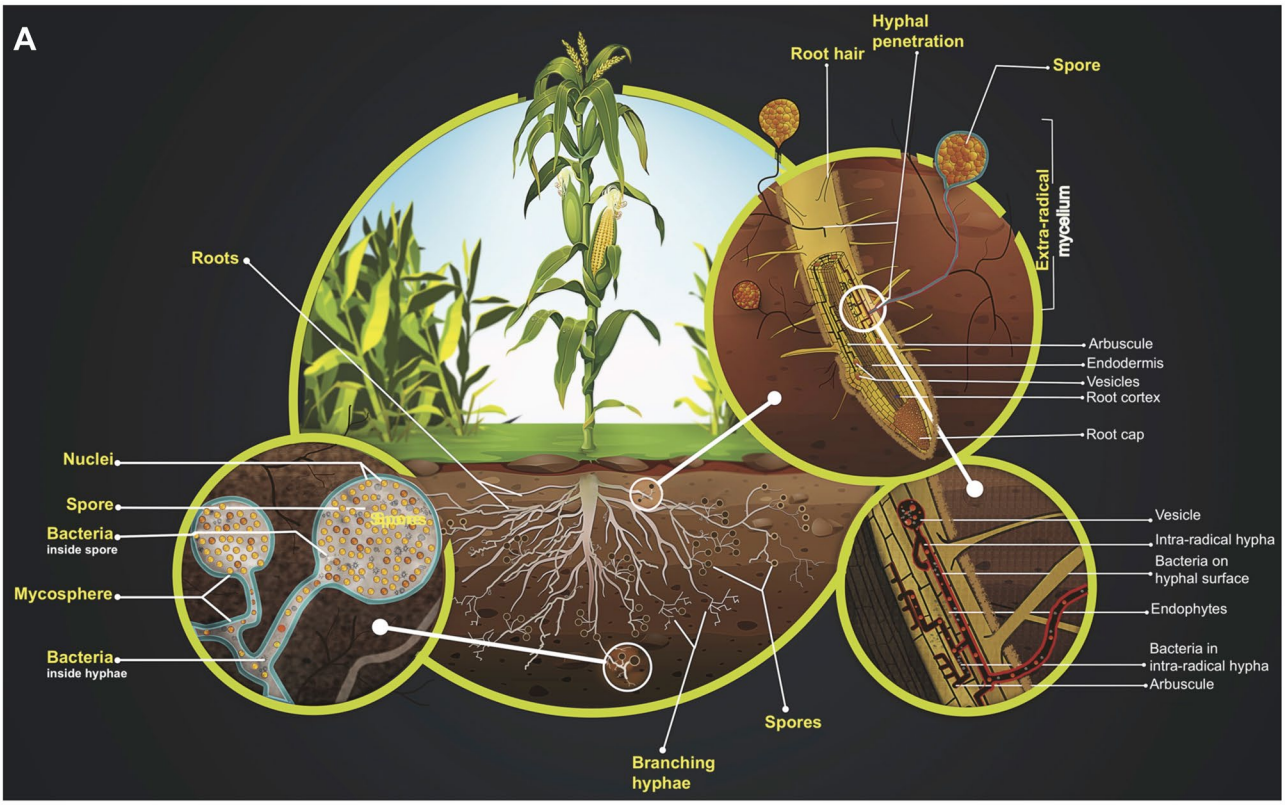
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Endodermis
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Mycosphere
Bacteria inside hyphae
Vesicle
Intra-radical hypha
Bacteria on hyphal surface
Endophytes
Bacteria in intra-radical hypha
Arbuscule
Spores
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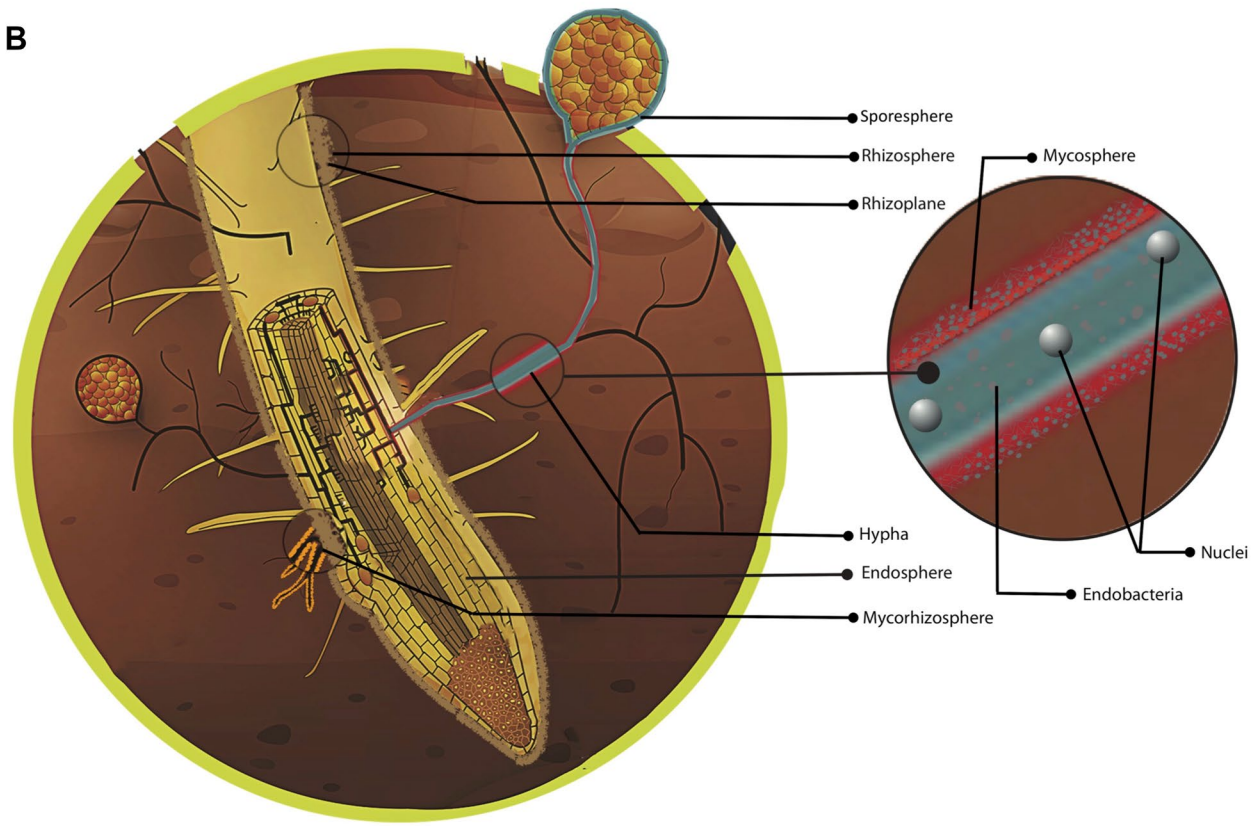
B
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◂**Fig. 1** **A** Presents an overview of the multipartite interactions between plant roots, the rhizosphere, arbuscular mycorrhizal fungi (AMF), and the bacteria living both inside and outside of AMF spores and mycelium. Endofungal bacteria can be found residing within spores and hyphae, while mycorrhizal helper bacteria are borne on spore and hyphal surfaces within the mycorrhizosphere and hyphosphere. **B** Is a closeup of the microbial habitats that can be found on AMF spores and hyphae both in the soil and root cortex. **B** Also shows the rhizosphere, rhizoplane, endosphere, mycorrhizosphere, and hyphosphere biotopes

called the mycorrhizal pathway (Smith and Read 2008; van der Heijden et al. 2015; Diagne et al. 2020). AMF also enhance plant resilience under abiotic stresses such as salinity, drought, extreme climate events like heat, elevated CO_2, and biotic stress involving bacterial and fungal pathogens (van der Heijden et al. 2015).

Arbuscular mycorrhizal fungi bridge between the plant root internal environment and the surrounding soil, extending beyond the root's influence zone, and at the same time interacting with diverse microbial communities along this continuum of the soil-root system. After successful root colonization, the extra-radical mycelium in the rhizosphere not only creates a new biotope that serves as an ecological hotspot for microbial interactions but also exerts tremendous impacts on the assembly and structure of the rhizosphere microbial community. While the rhizosphere microbiome is primarily affected by the roots, the hyphosphere microbiome —the microbial community thriving in the soil region surrounding the hyphae—is largely influenced by the AMF. The hyphosphere is a sub-region of the mycorrhizosphere, which encompasses the entire soil region occupied by mycorrhizal roots, as opposed to the rhizosphere, which refers to the soil region surrounding non-mycorrhizal roots (Priyadharsini et al. 2016; Wang et al. 2022a). The AMF hyphosphere consists of the hyphal surface (hyphoplane) and the surrounding soil spanning from 0 to 2 mm from the hyphal surface and extending as much as 120 mm from the root surface (Fig. 1B), and reaching depths of up to 1 m beneath the soil surface (Priyadharsini et al. 2016; Wang et al. 2022a).

Several bacterial communities interact directly or indirectly with AMF in the hyphosphere, with many of them serving as helpers or bioenhancers to AM symbiosis. The hyphosphere microbiome possesses several functional traits, such as organic phosphate (e.g., phytate) and inorganic phosphate mineralization, phytohormone production, nitrogen fixation, and pathogen suppression (Frey-Klett et al. 2007; Taktek et al. 2015, 2017; Zhang et al. 2016; Sangwan and Prasanna 2021). Understanding the physical, chemical, and biological interplay occurring at this biotope is essential to decipher the various mechanisms underlying soil-related functions performed by AMF, such as nutrient cycling, carbon sequestration and turnover, soil micro- and macro-aggregation and weathering, and nitrous oxide emission mitigation (Okiobe et al. 2022; Wang et al. 2022a, b, c). In addition to the hyphosphere microbiome, a large variety of bacterial species thrives directly upon or within fungal structures, such as spores, intraradical mycelium, and vesicles. Recently, Zhang et al. (2021) reviewed the hyphosphere microbiome, emphasizing the important role played by AMF chemical exudates in bacterial recruitment and how these bacteria can influence AMF fitness through the mediation of nutrient cycling, especially organic nutrient mobilization. Knowledge about AMF-associated bacteria is still fragmented, however, despite the growing recognition of their crucial role in AM symbiosis. Fortunately, advances in high throughput sequencing technologies, including next- and third-generation sequencing, have enabled scientists to execute state-of-the-art experimental designs that have allowed exploration of the metagenome, metatranscriptome, metaproteome, and metabolome of the three components (plants, fungi, bacteria) of AM symbioses, revealing key molecular signatures that underpin host-symbiont interactions. Essentially, several ecosystem services rendered by AMF are orchestrated by the AMF microbiome acting as a "second genome" (Turrini et al. 2018; Giovannini et al. 2020; Zhang et al. 2021).

This review critically appraises the diversity of AMF-associated bacteria (AAB), focusing on how these bacteria have been studied and characterized across different AMF species and ecosystems. We highlight the physical and ecological interplay occurring between AAB and AMF across various fungal microniches and discuss the various factors influencing AAB community composition, structure, and function. Furthermore, we provide insights into the potential application of these bacteria in agriculture and how the functional diversity of the AMF-associated bacteria together with AM fungal highways could be used to engineer the plant microbiome for improved ecosystem services.

Diversity of AMF-associated bacteria

Arbuscular mycorrhizal fungal structures, such as spores, sporocarps, extra- and intra-radical hyphae, and vesicles, are home to a large and diverse population of bacterial species, ranging from 2.5 to 6.1×10^6 CFU/ml (Agnolucci et al. 2019). These fungal-bacterial interactions differ in both strength and specificity; bacteria can loosely or strictly colonize fungal surfaces or cytoplasm as either facultative or obligate symbionts. The biology of obligate endobacteria has been studied in detail. Obligate bacterial endosymbionts colonize AMF cytoplasm or intracellular structures such as vacuoles and belong to either *Burkholderiaceae* (Proteobacteria) or *Mycoplasmataceae* (Tenericutes) (Araldi-Brondolo et al. 2017; Arora and Riyaz-Ul-Hassan 2019). Because

obligate endobacteria are biotrophic and rely on their hosts for carbon, nitrogen (amino acids, nucleic acids, and vitamins), and phosphorus, they are difficult to study in vitro (Jargeat et al. 2004; Lumini et al. 2007; Alabid et al. 2019). Although, multiple OMICS studies involving metagenomics, metatranscriptomics, and metabolomics have revealed important details about the influence of obligate endobacterial symbionts on hosts' pre- and post-symbiotic lifestyles (Dearth et al. 2018; Venice et al. 2020a, b; Kuga et al. 2021; Venice et al. 2021), the possible roles in plant growth remain unclear.

In contrast, the bulk of AMF-associated bacteria is non-obligate biotrophs and can be cultivated without fungus hosts, although a sizeable proportion remains uncultivable in standard media. Several studies have demonstrated through in vitro culture and a functional assay that these bacteria play an important role in AM symbiosis that confers fitness advantages to both fungi and plants. Beneficial traits such as nitrogen fixation, phosphate solubilization, growth hormone production, and biocontrol against plant pathogens are among the several traits positioning this category of AMF-associated bacteria as a third component of the tripartite symbiosis (Bonfante and Anca 2009). Thus, understanding the factors that influence these functions as well as the bases of AMF interactions with these diverse bacterial groups may be crucial for the successful deployment of AMF bioinoculants in agroecosystems (Gopal et al. 2012; Basiru et al. 2021). In vitro co-culturing of AMF in transformed roots which allows artificial recreation of tripartite symbiosis has been instrumental to studying resource flows (from plant to AMF and vice versa), and how these resources are deployed in recruiting beneficial bacteria microbiomes (St-Arnaud et al. 1996; Zhang et al. 2018a, b; Pandit et al. 2022b). By coupling in vitro bicompartmental cultivation techniques with advanced microscopy, such as transmission and scanning electron microscopy as well as high-resolution secondary ion mass spectrometry, a great deal of information can be revealed concerning AAB colonization and interaction with spores and hyphal structures. AMF-associated bacteria may appear as single cells, aggregates, or biofilms (Roesti et al. 2005; Cruz and Ishii 2012; Iffis et al. 2016; Steffan et al. 2020; Pandit et al. 2022a, b). Recently, Pandit et al. (2022a) demonstrated that in vitro-propagated AMF mycelium harbors a wider variety of cultivable exo- and endobacteria than in situ cultures in pots. Of the 109 bacterial isolates cultivated, 69 were identified as ectobacteria, while 40 isolates were endobacteria.

Many studies have investigated AMF-associated bacteria but often reported only a few cultivable strains with certain functional traits. To assess the diversity of AAB, we examined 15 studies containing data on the diversity of bacteria hosted by AMF structures. Table 1 summarizes the different AMF types and their associated bacterial taxa, as well as the method used to identify these species. Most studies used crude DNA extracts to identify bacterial taxa, while a few used cultivation methods, and two employed both approaches (Fig. 2A). Among these studies, profiling techniques were the most common, such as polymerase chain reaction-denaturing gradient gel electrophoresis (PCR-DGGE), BOX-PCR, and fatty acid methyl ester (FAME). Four studies utilized next-generation sequencing (Fig. 2B). Nine phyla (*Proteobacteria*, *Firmicutes*, *Actinobacteria*, *Bacteroidetes*, *Cyanobacteria*, *Plantomycetes*, *Verrucomicrobia*, *Acidobacteria*, and *Chloroflexi*) comprised about 95% of all genera of AAB reported (Fig. 2C). The 15 genera most frequently mentioned across all studies were *Bacillus*, *Pseudomonas*, *Sphingomonas*, *Paenibacillus*, *Arthrobacter*, *Rhizobium*, *Streptomyces*, *Variovorax*, *Lysobacter*, *Achromobacter*, *Burkholderia*, *Chryseobacterium*, *Leifsonia*, *Massilia*, and *Microbacterium*, occurring in at least five studies (Supplementary Table S1).

As expected, high-throughput sequencing identified numerous taxa compared to profiling methods, although a significant portion of those bacteria is uncultured, belonging to candidate phyla (microbial dark matter) (Agnolucci et al. 2019; Emmett et al. 2021). Discrepancies in the number of taxa identified also could be attributed to the methods used to prepare fungal propagules before bacterial culture or DNA extraction. Typically, AMF propagules are cleaned with sterile water or disinfectants such as 5% chloramine-T (Walley and Germida 1995) or supplied with antibiotics such as streptomycin and chloramphenicol to remove spore wall-dwelling bacteria, leaving presumably endobacteria (Xavier and Germida 2003; Budi et al. 2013). To isolate endobacteria, cultivation in growth media is necessary to ascertain that there has been complete removal of the surface-dwelling bacteria and to avoid confusion regarding the niches of AAB as either exo- or endo-bacteria. For example, *Bacillus* sp. (KTCIGM01), *Bacillus thuringiensis* (KTCIGM02), and *Paenibacillus rhizosphere* (KTCIGM03) were reported as "probable" endobacteria because of a lack of definitive evidence supporting endofungal colonization (Cruz and Ishii 2012). The choice of culture media is another possible source of bias because different media could lead to the cultivation of different bacterial isolates. For example, Xavier and Germida (2003) reported that yeast extract agar and water agar supported the growth of a few bacteria, while tryptic soy agar, nutrient agar, and Luria–Bertani agar supported diverse bacterial communities. Instructively, the combinations of multiple growth media, culture conditions, atmospheres, and times of incubation have improved the recoverability of human gut bacterial species by 50% (Sarhan et al. 2019). High-throughput culture approaches such as culturomics rely on a diversity of culture media coupled with varied environmental conditions and prolonged incubation periods in order to increase the recovery of cultivable AAB. This approach also is gaining ground in plant microbiome studies, for which

Table 1 Summary of AMF-associated bacterial phyla by study, AMF type and parts, and the method used for characterization

AMF					Bacteria			
AMF	**AMF niche**	**Probable location of bacteria**	**Source/plant host**	**Growth condition**	**Method for determining bacteria community composition**	**Molecular techniques**	**Phyla**	**References**
Funneliformis mosseae (IMA1, IN101C, AZ225C), *Rhizophagus intraradices* (IMA5 and IMA6), *Funneliformis coronatum* (IMA3)	Spores	Spore surface, wall, and endospore	*Trifolium alexandrinum* L. and *Medicago sativa* L	Inoculum were maintained in pot cultures for 15 years	Culture-independent	PCR-DGGE Analysis	Acidobacteria, Bacteroidetes, Protebacteria Actinobacteria, Firmicutes	(Agnolucci et al. 2015)
Rhizophagus irregularis BEG72 (AEGIS)	Whole inoculum	Spore wall and endospore	*Allium ampeloprasum* var. Porrum L	Commercial inoculum consisting of substrates, trap plant, AMF spores, and extraradical mycelium	Culture-independent	16S rRNA metabarcoding (Illumina MiSeq)	Acidobacteria, Actinobacteria, Armatimonadetes, Bacteroidetes, Chlamydiae, Chloroflexi, Cyanobacteria, Deinococcus-Thermus, Dependentiae, Elusimicrobia, Fibrobacteres, Firmicutes, Gemmatimonadetes, Hydrogenedentes, Nitrospirae, Patescibacteria, Planctomycetes, Proteobacteria, Verrucomicrobia	(Agnolucci et al. 2019)
Rhizophagus intraradices, Funneliformis mosseae	Spores	Spore wall and endospore	*F. ovina* L and *L. vulgare* Lam	AMF spores (yellow and white spores) obtained from rhizosphere of two plants F. ovina L and L. vulgare Lam grown in monoculture	Culture-dependent	PCR-FAME analysis	Actinobacteria, Chordata, Firmicutes, Proteobacteria, Tenericutes	(Bharadwaj et al. 2008)
Gigaspora margarita (Centra Glass Co. Ltd Tokyo, Japan	Spores	Endospore	Bahiagrass culture	G. margarita spores from culture collection (Centra Glass Co. Ltd Tokyo, Japan	Culture-dependent	16S rRNA Sequencing (Sanger)	Firmicutes, Proteobacteria	(Cruz et al. 2008)

Table 1 (continued)

AMF					Bacteria			
AMF	**AMF niche**	**Probable location of bacteria**	**Source/plant host**	**Growth condition**	**Method for determining bacteria community composition**	**Molecular techniques**	**Phyla**	**References**
Gigaspora margarita (Centra Glass Co. Ltd Tokyo, Japan	Spores	Endospore		G. margarita spores from culture collection (Centra Glass Co. Ltd Tokyo, Japan	Culture-dependent	16S rRNA Sequencing (Sanger)	Firmicutes	(Cruz and Ishii 2012)
Glomus versiforme and *Rhizophagus irrgeularis*	Extraradical hyphae	Hyphal surface (Hyphoplane) and endohyphal	Brachypodium distachyon	AMF spores was propagated in pot installed with in-growth cores filled with unsterilized soils, and allowing hyphae colonization	Culture-independent	16S rRNA metabarcoding (Illumina MiSeq)	Acidobacteria, Actinobacteria, Armatimonadetes, Bacteroidetes, Chlamydiae, Chloroflexi, Cyanobacteria, Deinococcus-Thermus, Dependentiae, Diapherotrites, Entotheonellaeota, Euryarchaeota, Fibrobacteres, Firmicutes, Gemmatimonadetes, Halanaerobiaeota, Hydrogenedentes, Kiritimatiellaeota, Latescibacteria, Lentisphaerae, Nanoarchaeaeota, Nitrospirae, Omnitrophicaeota, Patescibacteria, Planctomycetes, Proteobacteria, Rokubacteria, Spirochaetes, Tenericutes, Thaumarchaeota, Verrucomicrobia, Zixibacteria,	(Emmett et al. 2021)

Table 1 (continued)

AMF					Bacteria			
AMF	**AMF niche**	**Probable location of bacteria**	**Source/plant host**	**Growth condition**	**Method for determining bacteria community composition**	**Molecular techniques**	**Phyla**	**References**
Archaeospora schenckii, Claroideoglomus sp., Claroideoglomus sp., Diversispora eburnean, Glomus sp., Rhizophagus irregularis	Intraradical vesicles and spores	Endophytic	*Solidado Rugosa*	Propagules from microdissected *Solidado rugosa* growing in petroleum hydrocarbon conatinated sites	Culture-independent	Whole Genome Annotation and Sanger Sequencing	Actinobacteria, Firmicutes, Proteobacteria	(Iffis et al. 2014)
Diversispora, Rhizophagus, Glomus sp, Glomus versiforme, Entrophospora infrequens, Unclassified Rhizophagus, Glomus sp, Acaulospora, Glomus irregulare, Claroideoglomus luteum	Spores	Spore wall and endospore	*Solidado canadensis*, *P. balsamifere* and *L. europaeus*	Spores were obatined from the rhizosphere soil of plants growing in Petroleum hydrocarbon decantation basin	Culture-independent	16S rRNA Roche 454 FLX1 pyrosequencing	Actinobacteria, Bacteroidetes, Myxococcota, Proteobacteria	(Iffis et al. 2016)
Rhizophagus irregualaris	Spore	Spore wall	*Agrostis stolonifier*		Culture-dependent and culture-independent	PCR-DGGE, 16S rRNA metabarcoding	Actinobacteria, Firmicutes, Proteobacteria	(Lecomte et al. 2011)
Gigaspora margarita MAFF, *Gigaspora rosea*	Spore	Spore wall	*Medicago sativa* (alfafa), *Nicotiana tabacum*	Pot cultures using sand/soil mixture or vermiculite	Culture-independent	PCR-DGGE-band sequencing	Actinobacteria, Bacteroidetes, Proteobacteria	(Long et al. 2008)
Gigaspora margarita MAFF	Spore	Spore wall and endosphere	*Medicago sativa*, *Sorghum bicolor*, *Zea mays*	AMF was propagated in four plant-substrate system: *Medicago sativa*, *Sorghum bicolor*, *Zea mays* in sand/soil mixture; and *Medicago sativa* in Vermiculite in four months	Culture-dependent	16S rRNA Sequencing	Actinobacteria, Firmicutes, Proteobacteria	(Long et al. 2017)

Table 1 (continued)

AMF					Bacteria			
AMF	**AMF niche**	**Probable location of bacteria**	**Source/plant host**	**Growth condition**	**Method for determining bacteria community composition**	**Molecular techniques**	**Phyla**	**References**
Rhizophagus irregularis *Rhizophagus intraradices* *Funneliformis coronatus* *Claroideoglomus etunicatum* *Glomus deserticola* *Rhizophagus custos* *Dentiscutata heterogama* *Gigaspora margarita* *Gigaspora decipiens* *Rhizophagus prolifer*	Spores and Extraradical mycelium	Spore wall and endosphere		Samples obtained from in vitro and in situ propagules	Culture-dependent and culture-independent	Illumina Hiseq 16S amplicon sequencing	Actinobacteria, Bacteroidetes, Firmicutes, Proteobacteria	(Pandit et al. 2022a, b)
Glomus Constrictum, *Glomus geosporum*	Spore	Spore wall and endospore	*Plantago lanceolata* and *Hieracium pilosella*	AMF originate from calcareous grass land in Switzerland and maintained in pots culture under same condition	Culture-independent	PCR-DGGE	Bacteroidetes, Cyanobacteria, Fibrobacteria, Proteobacteria	(Roesti et al. 2005)
Funneliformis caledonium, *Racocetra alborosea*, and *Funneliformis mosseae*	Spores	Spore wall and endospore	Reclaimed land dominated by plants such as *Phragmites australis*, *Cyperus polystachyos* and *Miscanthus sinesis*	Spores retrieved from salt affected reclamation area dominated by natural grasses	Culture-independent	BOX-PCR Fingerprinting	Actinobacteria, Bacteroidetes, Firmicutes, Proteobacteria	(Selvakumar et al. 2016)
Rhizophagus clarum NT4 (basiodionym Glomus luteum	Spores	Spore wall and endospore	*Zea mays*	Spores retrieved from 14-month old monospecific culture	Culture-dependent	FAME	Actinobacteria, Bacteroidetes, Firmicutes, Proteobacteria	(Xavier and Germida 2003)

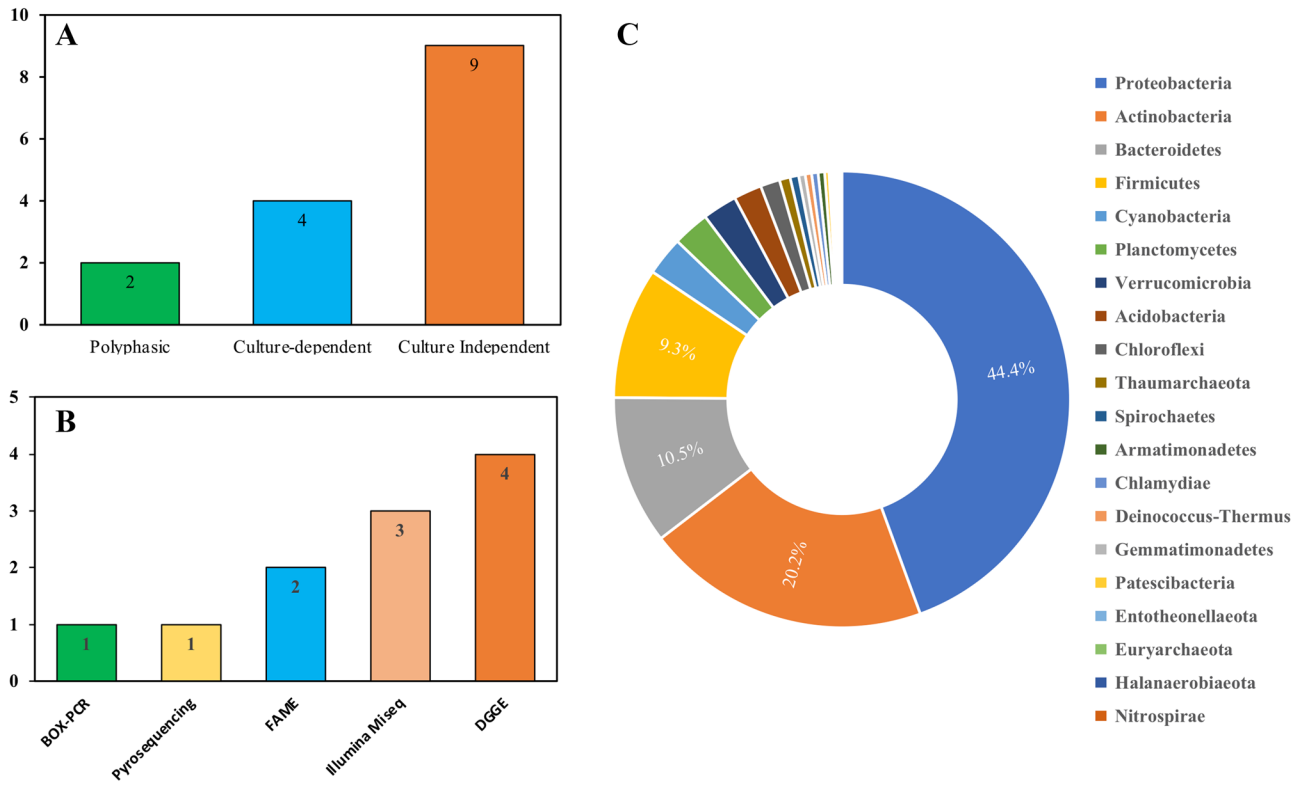

Fig. 2 **A** and **B** Provide insight into the different approaches and methods applied to genotype AMF-associated bacteria in diverse studies, while **C** displays the percentage breakdown of AMF-associated bacterial genera within each phylum

natural culture media based on plants and their inhabiting microbes in the form of juices, saps and/or dehydrated powders, and pellets have improved recovery and isolation of the plant microbiomes that once were considered microbial dark matter (Sarhan et al. 2018, 2019).

Factors driving the community composition of AMF-associated bacteria

Substrate conditions

The soil comprises the microbial "seed bank" for the recruitment of the plant root microbiome and constitutes a major factor influencing the community assembly and functions of the bacterial communities associated with both plant roots and AMF mycelia (Vandenkoornhuyse et al. 2015; Goldmann et al. 2020; Yuan et al. 2021). Although obligate endobacteria are inherited or acquired through vertical or horizontal transmissions (Anca et al. 2009; Di Fossalunga et al. 2017), most AMF-associated bacteria are recruited from the soil microbial reservoir; therefore, both taxonomic and functional diversity may be influenced by soil type and physicochemical properties. The composition and structure of the plant microbiome can be affected especially by soil conditions, particularly under stress conditions such as low P-availability (Bulgarelli et al. 2022). AMF community composition are influenced by soil physicochemical properties (i.e., moisture condition, pH, salinity, and contamination concentrations), agricultural practices, and geography (Davison et al. 2015; Sturmer et al. 2018; Higo et al. 2020; Yang et al. 2021a). Similarly, AMF-associated bacterial community composition is affected by the substrate in which AMF are propagated (Bharadwaj et al. 2008; Long et al. 2017; Zhang et al. 2018a; Emmett et al. 2021). It was reported, for example, that AMF-associated bacteria harbored by *Gigaspora margarita* spores differed among three substrate types, i.e., sand, soil, and vermiculite, or a mixture employed for AMF production (Long et al. 2017).

The functional diversity of AAB could reflect prevailing conditions of the substrate, with AMF selecting bacterial strains able to degrade certain contaminants or facilitate tolerance of an abiotic stress (Sato et al. 2019; Wang et al. 2022a). *Massilia* sp. RK4 isolated from saline coastal reclamation land increased maize plant growth and alleviated salinity stress by reducing plant proline concentration (Krishnamoorthy et al. 2016). Similarly, Selvakumar et al. (2018) found that AAB isolated from a salt-affected reclamation area displayed improved salinity tolerance in a corn field trial in which co-inoculation with *Pseudomonas*

koreensis, *Gigaspora margarita*, and *Claroideoglomus lamellosum* resulted in increased corn dry weight and elevated nutrient concentrations (N, P, K, Ca, Mg, and Na) in shoots and roots at all levels. The combined treatment of AMF and bacterial symbionts decreased proline and stimulated the genes involved in sodium and potassium homeostasis ((Selvakumar et al. 2018). High petroleum hydrocarbon contaminants shifted the community composition of spore-associated bacteria to favor Actinobacteria species, such as *Streptomyces*, which are tolerant to high contaminant concentrations, while Proteobacteria species (mainly *Pseudomonas*) that are less tolerant to petroleum hydrocarbon contaminants were enriched at lower contaminant concentrations (Iffis et al. 2016, 2017).

Plant identity

The plant rhizosphere is the first micro-environment encountered by soil microorganisms including AMF, and it can act as a microbial filter in which competition occurs (Vandenkoornhuyse et al. 2015). For example, crosstalk between AMF and potential plant hosts before symbiosis is mediated by diffusible compounds, such as strigolactones originating from the plant, and *Myc* factors secreted by presymbiotic mycelia (Genre et al. 2005; Bonfante and Genre 2010). Breakdowns in this crosstalk result in the failure of the colonization process. Similarly, plants can influence the assembly of their root microbiota through root exudates, comprising a cocktail of chemical substances such as sugars, amino acids, and other organic compounds which serve as nutrients, signals, growth hormones, and inhibitors that allow plant roots to coordinate a deterministic assembly of the plant root microbiome (Beckers et al. 2017; Stringlis et al. 2018; Huang et al. 2019). For example, differential resource allocation to AMF species co-colonizing the same plant roots has been reported regarding *Funneliformis mosseae* and *Claroideoglumus claroideum*; under drought conditions, the former received more carbon from the host plant than *C. claroideum* (Forczek et al. 2022). Thus, it is expected that plant identity exerts a stronger influence on community assembly of the root microbiome both in the soil and inside roots than do soil chemical properties, such as mineral nutrients or contaminant concentrations (Dagher et al. 2019; Bulgarelli et al. 2022). The influence of plant identity on the rhizosphere microbiome also extends to AMF-associated bacteria. Long et al. (2008) reported that *Gigaspora margarita* propagated colonizing tobacco and alfalfa roots under the same soil conditions harbored distinct AAB communities. The Shannon diversity indices of the bacterial operational taxonomic units (OTUs) inhabiting AMF spores obtained from the rhizosphere of three plant species were affected by plant species: *Lycopus europaeus* and *Populus balsamifera* supported a greater diversity of AAB than *Solidago canadensis* (Iffis et al. 2016).

Interactions between substrate and plant host identity also could play an important role in AMF-associated bacterial assembly and composition. Different root exudation patterns expressed by distinct plant genotypes can influence the composition of AMF-associated bacteria under different plant-substrate conditions. Nevertheless, the substrate may be most influential in the absence of roots, especially in the bulk soil colonized by extraradical hyphae. According to a report by Floc'h et al. (2022), *Funneliformis mosseae* and *Rhizophagus iranicus* found in a field of canola—a non-mycorrhizal plant—shared 90% similar bacterial cohorts dominated by *Vicinamibacteraceae* after 10 years of canola monocropping. In this case, the host of the AMF was unknown since canola is not mycotrophic, and it also is unclear whether the bacteria were harbored on fungal structures or just thriving in their proximity. It was hypothesized that these bacteria could have contributed to the survival of associated AMF in the absence of a mycotrophic plant by supplying carbon compounds to the fungi through the decomposition of soil organic matter. Additionally, studies by Emmett et al. (2021) concluded that *R. irregularis* and *R. clarus* shared similar bacterial profiles on their extraradical hyphae that reflect host-symbiont adaptation to the physicochemical conditions of the substrate, but not fertilization.

AMF identity

Host genetic identity is a strong driver of microbial community composition in diverse hosts and different ecosystems (Dal Grande et al. 2018; Kivlin et al. 2019; Dove Nicholas et al. 2021; Smee et al. 2021). Although AMF physiology and functions vary between extraradical and intraradical components, the genetic identity of AMF nevertheless is expected to play an important role in the assembly of AMF-associated bacterial communities. Considering that AMF-bacterial interaction involves different fungal structures, i.e., spores and extraradical hyphae occupying multiple biotopes along the soil-root continuum, the effect of host identity on the assembly of microbial communities along the dynamics of these niches and biotopes can differ, just as the specificity of the interactions. Multiple lines of evidence indicate that spore identity is a stronger predictor of spore-associated bacteria than plant and substrate types. Using denaturing gradient gel electrophoresis (DGGE) profiling and 16S rDNA sequencing to study the AMF-associated bacterial community harbored by spores of six AMF species cultured for 15 years with the same substrate and environmental conditions, Agnolucci et al. (2015) reported that AMF identity explained 50% of the variation observed in AAB community composition. Furthermore, in a petroleum

hydrocarbons contaminated site, Iffis et al. (2016) found that AMF identity which explained up to 13.3% of the variation observed in the spore-associated bacterial community composition was more influential than both plant identity (7.4%) and contaminant level (6.7%). The composition of 385 AAB isolates harbored on the spores of *Rhizophagus intraradices* and *Funneliformis mosseae* colonizing *Festuca ovina* and *Leucanthemum vulgare* were largely influenced by AMF identity compared with plant identity despite significant interactions between both factors (Bharadwaj et al. 2008). Bacterial 16S rDNA genotyping also revealed significant differences in the diversity of AAB harbored by in vitro root organ cultures of *Septoglomus deserticola* and *Rhizophagus irregularis*, with the former having just 11 OTUs that were far less than the 115 OTUs hosted by *R. irregularis* (Pandit et al. 2022a).

The abundance and community composition of AMF-associated bacteria can be influenced by the size, morphology, and chemical composition of the spore wall. AMF spore wall structures typically consist of two or three layers, with the outer hyaline layer and, to some extent, the inner laminated layer providing a preferred habitat for several exobacterial symbionts (Maia and Kimbrough 1998; Roesti et al. 2005). The outer layer is believed to be particularly attractive to bacteria, owing to its high chitin concentration which provides a rich source of carbon and nitrogen to bacterial colonizers. This layer may be absent in old or mature spores, however, or otherwise replaced with mucilaginous substances resulting in a low diversity of bacteria in old spores (Ames et al. 1989; Sbrana et al. 1995; Filippi et al. 1998; Maia and Kimbrough 1998; Roesti et al. 2005). Additionally, large spores tend to host more abundant AAB than small spores, as evidenced by *Racocetra alborosea*, whose large spore size (400 µm) compared to *Funneliformis caledonium* and *F. mosseae*'s smaller sizes resulted in abundant spore-associated bacteria. AMF extraradical mycelium also releases exudates consisting of various chemical groups including amino acids, amines, nucleic acids, and organic acids among other compounds, which can serve as effectors, chemo-attractants, and carbon sources, thereby enabling AMF to filter bacteria interacting with them (Filion et al. 1999; Toljander et al. 2007; Scheublin et al. 2010; Gahan and Schmalenberger 2015; Luthfiana et al. 2021; Zhang et al. 2021). Plant secondary metabolites transported by AMF also are known to affect the composition and abundance of the hyphal bacterial community in the bulk soil (Babikova et al. 2013; Duhamel et al. 2013). The quality and quantity of extraradical mycelial exudates can vary significantly according to different AMF types and plant hosts, as well as substrate conditions which allow each AMF type to interact in a distinct way with the soil bacterial community (Filion et al. 1999; Kaiser et al. 2015; Zhou et al. 2020; Luthfiana et al. 2021).

Although a large portion of the variation in the community composition of AMF-associated bacteria can be explained by AMF identity, AMF genotypes within the same genus or species can harbor distinct AAB communities unrelated to their taxonomic position (Lecomte et al. 2011; Selvakumar et al. 2016). AMF taxa growing in long-term pot culture under the same substrate and environmental conditions harbored distinct AAB assemblages (Agnolucci et al. 2015). While the composition of AAB harbored by *Funneliformis mosseae* AZ225C clustered with that of *Rhizophagus intraradices* IMA6 by only 45%; two conspecific isolates of *F. mosseae*, i.e., AZ225C and IMA1, displayed drastic heterogeneity (Agnolucci et al. 2015). Two conspecific isolates of *Rhizophagus irregularis*, i.e., MUCL 41,833 and 43,914, also responded differently to phosphorus stress (Wang et al. 2022b). Whereas *R. irregularis* MUCL 41833 produced a greater density of extraradical hyphae and increased the expression of phosphate transporter genes in response to low P availability; isolate 43914 recruited an abundant alkaline phosphatase-expressing *Betaroteobacteriaceae* community that mediated organic matter mineralization, releasing phosphate for hyphal absorption. Comparative genome analysis of the genomes of five *Rhizophagus irregularis* DAOM197198 revealed striking genome variations, with less than 50% of the genes shared among conspecific isolates as core genes, while about 11–25% of the genes are lineage-specific genes (Chen et al. 2018; Reinhardt et al. 2021). Foreign genes purportedly acquired from either plants or bacteria have been detected in the genome of *Rhizophagus irregularis* (Lee et al. 2018; Li et al. 2018) suggesting that horizontal gene transfer events could occur between AMF and bacterial symbionts, contributing to satellite genes (non-lineage-specific genes), although studies investing such events are scarce. Taken together, the large discrepancies occurring in the genomes of conspecific isolates can have tremendous phenotypic implications for physiology, growth, and reproduction (Mathieu et al. 2018) which also could explain the differential behavior displayed towards other soil microbial communities under specific host plant and environmental conditions.

Bacterial-fungal interactions along the soil-root interface

Extraradical spores

In addition to providing long-term reproductive capacity, AMF spores also serve as hotspots for bacterial colonization. Studies have shown that co-inoculation of *R. irregularis* with spore-associated bacteria such as *Bacillus filamentosus* (BF311), *Phyllobacterium myrisinacearum* (Bf54), *Izhakiella australiensis* (BF372), *Bradyrhizobium japonicum* (1RS), *Terribacillus saccharophilus* (BF4A4), and *Bacillus*

filamentous (BF370) can improve reproductive fitness, resulting in increased spore density (Pandit et al. 2022b). Moreover, volatile compounds produced by some bacteria may be able to stimulate spore production. For example, *Paenibacillus validus* induced secondary (asymbiotic) sporulation in *R. irregularis* in the absence of a host plant (Hildebrandt et al. 2006). The compound was later identified as (S)-12-methyltetradecanoic acid, or (S)-anteiso-C15:0. This could potentially have implications for future inoculant production by eliminating the need for the presence of a live plant root (Kameoka et al. 2019) but the ability of these secondary spores to colonize host plant roots requires further investigation. Furthermore, hydrolytic enzymes, such as chitinase, cellulase, and pectinase, produced by spore-associated bacteria promote germination and and hyphal penetration of roots by facilitating the breakdown of fungal and plant cell walls (Budi et al. 2013).

In exchange for the beneficial services rendered to AMF, spore-associated bacteria obtain their nutrition through extracellular necrotrophy by feeding on the outer hyaline layers, extracellularly relying on chemical exudates, and by endocellular biotrophy, or a mix in some cases (Toljander et al. 2006; Bonfante and Anca 2009). AAB dwelling on spore walls can derive nutrients from the outer hyaline layer, which is rich in nutrient sources such as chitin, protein, and fatty acids (Roesti et al. 2005; Cruz et al. 2008; González-Chávez et al. 2008; Selvakumar et al. 2016). The mode of feeding among the cultivable endobacteria, however, has yet to be studied, although studies have confirmed endocellular biotrophy among obligate endobacteria (Ghignone et al. 2012; Kuga et al. 2021). The colonization of fungal cytoplasm by cultivable bacteria other than heritable obligate endobacteria raises questions about mechanisms that govern invasion as well as the integrity of the fungal immune system. It also remains unclear whether these bacterial symbionts are transferred vertically within fungal generations, although that seems to be common among the obligate bacterial symbionts of Mucoromycotan fungi (Mondo et al. 2017; Ingrid et al. 2020; Takashima et al. 2020). Studies have shown that AAB possesses the machinery required for fungal invasion including cellulolytic, chitinolytic, pectinolytic, and proteolytic enzyme activities and secretion systems, but the processes leading to active invasion of fungal cytoplasm are poorly understood (Roesti et al. 2005; Budi et al. 2013; Moebius et al. 2014; Gahan and Schmalenberger 2015). Nevertheless, the possibility of passive invasion cannot be ruled out, which is likely to occur at hyphae tips and points of damage on the walls of hyphae or lytic holes (Levy et al. 2003; Boer et al. 2005).

Extraradical hyphae

The extra-radical hyphae (ERH) are the life support system for the AM symbiosis, with the primary function of supplying nutrients in soluble form to both fungi and plant hosts. Its effectiveness and efficiency to scavenge soil nutrients, however, are hampered by the absence of the saprophytic ability necessary to decompose soil organic matter, the primary reservoir of mineral nutrients such as phosphorus and nitrogen (Frey 2019). AMF hyphae also have a limited ability to mobilize insoluble phosphate (Taktek et al. 2015). This deficiency alone could force AMF to form symbiotic relationships with other soil organisms possessing such traits. Harboring phosphate-solubilizing bacteria enables AMF to gain access to recalcitrant phosphate reserves in the hyphosphere, such as phytate (Jiang et al. 2021). These hyphae-associated phosphate solubilizing bacteria (PSB) are more proficient phosphate mobilizers than PSB from other soil environments (Taktek et al. 2015). Intriguingly, interactions between AMF and these bacteria often result in better plant growth when inoculated, resulting in increased plant biomass and phosphorus content in *Zea mays* (Battini et al. 2017), and *Solanum lycopersicum* (Sharma et al. 2020).

The current understanding of extraradical hyphae-associated bacteria has been enabled by a range of techniques, encompassing both culture-dependent and culture-independent approaches as well as a novel experimental design that allowed for the separation of plant roots from fungal hyphae, making it possible to identify and characterize hyphobacterial communities. Scheublin et al. (2010) employed in vitro propagation of AMF with *A. rhizogenes* transformed carrot-roots in bicompartmental Petri dishes to identify numerous soil bacteria with the capability of colonizing fungal hyphae, including members of the *Oxalobacteriaceae* family such as *Duganella*, *Janthinobacterium*, and *Massilia*. Furthermore, Lecomte et al. (2011) highlighted the potential for spore-associated bacteria to colonize hyphae using *R. irregularis* in vitro and identified *Bacillus*, *Kocuria, Microbacterium, Sphingomonas*, and *Variovorax* that were able to grow on hyphae with no additional nutrients. Although the in vitro establishment of tripartite symbiosis can provide invaluable insight into the mechanisms driving bacterial-fungal interactions, it should be noted that the growth conditions may be biased towards highly competitive or rapidly growing taxa. This, as Toljander et al. (2007) have demonstrated, can result in an estimation of bacterial abundance and community composition that is not necessarily reflective of real-world dynamics.

To study the bacteria directly colonizing extra-radical hyphae in the soil, one must overcome the tiny (2–10 µm) and delicate nature of hyphae with an innovative technique such as laser microdissection approaches. For instance, Artursson and Jansson (2003) employed immunocapture of bromodeoxyuridine-containing DNA to study the bacteria interacting with AMF in the hyphosphere of a natural fallow soil. They also utilized green fluorescent gene tagging (with plasmid *pnf8*) of one hyphobacterium (*Bacillus cereus* strain VA1) to demonstrate a strong attachment of

the bacteria to fungal hyphae. To trap phosphate-solubilizing bacteria growing on the hyphae of *R. irregularis*, Taktek et al. (2015) employed Turface clay for the propagation of AMF using leek (*Allium ampeloprasum*). Furthermore, Gahan and Schmalenberger (2015) employed density gradient centrifugation to separate the hyphosphere and hyphoplane microbiome revealing significant shifts in the bacterial community composition and functions between bulk soil and hyphosphere. While the hyphosphere was enriched in sulfonate-desulfurizing bacteria compared to bulk soil, the study failed to detect any significant differences between hyphosphere and hyphoplane microbiome community composition. Recently, Emmett et al. (2021) used next-generation sequencing for the first time to study the microbiome harbored on the extra-radical hyphae of *R. irregularis* and *D. versiformis* in different soils. Diverse bacterial taxa were found on hyphae of both AMF including Proteobacteria (50%), Actinobacteria (10%), Chloroflexi (9%), Acidobacteria (7%), Bacteroidetes (6%), and Fibrobacteres (4%). Interestingly, members from Betaproteobacteriales, Myxococcales, Fibrobacters, Cytophagales, Chloroflexales, Cellvibrionales, Alphaproteobacteria, and Gammaproteobacteria were enriched on hyphae regardless of AMF type and soil sources.

Intraradical structures

Highly diverse endophytic bacteria reside inside plant roots, contributing to the hosts' physiology and phenology (Santos and Olivares 2021). Some endophytic bacteria have been demonstrated to colonize intraradical structures such as spores, hyphae, and arbuscules in the pioneering work carried out by Iffis et al. (2014). The authors micro-dissected mycorrhizal roots of *Solidago rugosa* growing under petroleum hydrocarbon pollution to collect intraradical propagules. Phylogenetic analysis of the total DNA extracted from isolated intraradical spores and vesicles of diverse AMF (*Diversispora eburnea*, *Archaeospora schenckii*, *Claroideoglomus* sp., and *Rhizophagus irregularis*) led to the identification of several bacterial taxa affiliated with *Sphingomonas*, *Pseudomonas*, *Massilia*, and *Methylobacterium*. The occurrence of these bacteria also was confirmed by scanning electron microscopy, which identified bacteria having coccoid or biofilm structures attached to AMF inside the root cortex. Overall, the most abundant bacteria were *Shingomonas* sp. (28.2%), followed by *Pseudomonas* sp. (15.7%), *Massilia* sp. (14.4%), *Methylobacterium* sp. (11.7%), and unidentified bacterial species (9.8%), whereas *Bradyrhizobium*, *Bacillus*, *Bosea*, and *Paenibacillus* were the least abundant. The rationale for this intraradical bacterial-fungal interaction is not clear, although intraradical vesicles are spore-like storage structures that contain lipids and could serve as a carbon source for these bacteria. Moreover, the functional role of these bacteria to AMF and plant hosts is yet to be identified; it also remains elusive whether these bacteria were imported by the AMF into plant roots or whether they were recruited from plant endophytic bacteria already present in host roots (Ujvari et al. 2021).

Harnessing the functional diversity of the AMF microbiome for sustainable agriculture

The obligate biotrophy of AMF has been attributed principally to the absence of saprophytic traits for carbon assimilation, such as lignocellulose degradation and synthesis of fatty acids, secondary metabolites, and thiamin (Tisserant et al. 2013; Morin et al. 2019; Sun et al. 2019; Venice et al. 2020a, b, c). Moreover, the AMF genome lacks genes encoding some key extracellular enzymes such as phytases and secreted phosphatases, essential to mineralize insoluble nutrients and soil organic matter (Frey-Klett et al. 2011; Tarkka et al. 2018; Turrini et al. 2018; Emmett et al. 2021). These deficiencies can explain the context-dependency of the outcomes of introducing commercial AMF inoculants in new fields (Basiru and Hijri 2022). AMF-associated bacteria affect AMF fitness by facilitating pre-symbiotic processes such as sporulation, germination, mycelia growth and branching, and root system branching to support AMF colonization (Fernández Bidondo et al. 2016; Ordonez et al. 2016). Supplementing AMF isolates with already adapted growth-promoting bacteria can enhance the establishment of AMF inoculants in plant roots. Furthermore, these microbes also promote plant growth through nutrient fixation, solubilization/mobilization of minerals, biocontrol of fungi and plant pathogens, phytohormone production, biofilm production, and cellulose/toxics degradation (Bharadwaj et al. 2012; Battini et al. 2016; Ordonez et al. 2016; Lasudee et al. 2018; Pandit et al. 2022a, b). Therefore, understanding AMF-bacterial interactions is essential for the successful deployment of AMF inoculants. In the following sub-sections, we discuss the importance of AMF and associated bacteria as a tool to engineer the plant microbiome and enhance ecosystem services.

Potential role of an AMF core microbiome in improving agroecosystem functions

Core microbiomes are increasingly recognized as an important tool for promoting plant health and physiology, compared to direct pair-wise microbe-plant inoculation (Ahmed et al. 2021a, b; Ahmed and Hijri 2021; Ahmed et al. 2021a, b). Keystone taxa of the plant microbiome that are consistently associated with hosts or under certain environmental conditions can be used to organize the

resident plant microbiome and increase plant fitness (Toju et al. 2018). Core bacterial taxa that are shared among diverse AMF taxa and soil conditions will not only facilitate AMF function but also play a key role in the recruitment and structuring of health-promoting microbiomes. One study found that adding core bacterial taxa and AMF promoted host growth and nutrient acquisition more than when separate trials of AMF or core bacteria were used (Xu et al. 2022). Nevertheless, the core microbiome must be functional regardless of taxonomic diversity especially that genes (replicators) encoding specific functional traits can be carried on different vehicles (bacteria) whose taxonomic identity are preselected by the soil microbial reservoir or the frequency of transfer of such genes among soil microbes, i.e., horizontal gene transfer (Lemanceau et al. 2017). Advances in next-generation sequencing have enabled the identification of core taxa across several AMF strains (Emmett et al. 2021; Pandit et al. 2022a, b; Wang et al. 2022a, b, c) but the functional relevance of these core taxa is yet to be explored. Core hyphosphere microbiomes from three fields across different climatic conditions were identified using network analysis, and their abundance was correlated with increased phosphatase activity (Wang et al. 2022c). Pandit et al. (2022a) used 16S rDNA metabarcoding to identify 16 OTUs shared by eight AMF genotypes from different continents. Hierarchical clustering of cultivable bacteria from in vitro and in situ co-culture of AMF from different parts of the world generated nine functional clusters based on 10 functional traits, the taxa of which were highly varied, although a certain bacterial taxon usually dominated each cluster (Pandit et al. 2022a). In some cases, isolates of the same species occupied different clusters. Some clusters had very high functional diversity and included bacteria such as *Rhodococcus jialingiae* (BF317) and *Terribacillus saccharophilus* BFA4 which displayed all 10 functional traits examined. A functional cluster could be deployed as a bioinoculant, together with AMF, to target specific or multiple plant traits. Nevertheless, compatibility among these strains first must be determined. Compatibility among several AAB using the same fungal niche is possible (Palla et al. 2018), as gram-positive bacteria associated with AMF spores (e.g., *Bacillus* and *Fictibacillus*, quorum negative) tolerated their gram-negative neighbor (*Sinorhizobium meliloti* strain, quorum positive). It still is unknown, however, whether compatibility would be possible between AAB from different AMF sources. Lastly, the consequences of long-term domestication (i.e., in vitro co-culture) have been documented on AMF genetics and function (Kokkoris and Hart 2019), however, trials are still needed to explore the effects this could have on the selection and recruitment of functional core microbiomes in the field.

The AMF highway as a tool for engineering the plant root microbiome

The potential significance of extraradical hyphae—or "fungal highways"—as a tool for engineering both rhizosphere and endophytic bacteria recently has been given significant attention. Fungal hyphal networks can facilitate the dispersal of beneficial bacteria through unsaturated soils where their active movement is limited (Or et al. 2007; Jansa and Hodge 2021). These networks also help bacteria move to organic patches, aided by the exudates of the fungal highways, which provide an environment containing water and energy for swimming movement (Jiang et al. 2021). AMF fungal highways have been shown to facilitate the movement of beneficial bacteria between two plants connected via the same mycorrhizal network (de Novais et al. 2020). In addition, they can improve nodulation of leguminous crop roots by nitrogen-fixing bacteria, through increased phosphorus supply. Selvakumar et al. (2018) have further raised the prospect of engineering plant endophytic bacterial communities, after confocal scanning laser microscopy revealed several spore-associated bacteria colonizing corn roots in a co-inoculation experiment. Mechanisms governing bacterial colonization of the root endosphere under AMF influence, however, deserve further investigation.

Conclusions

Considering our discussion, it is reasonable to conclude that AMF, despite being an important member of the plant mycobiome, harbor their own set of microbiomes of which community assembly and functions are majorly driven by the AMF genotypes, host plant identity, and the conditions of the substratum. The AMF microbiome encompasses both obligate and non-obligate exo- and endobacterial symbionts occupying fungal microniches that span the soil-root continuum. Although different techniques, including culture-dependent and culture-independent approaches, have been employed to study AAB diversity, consistently, most AMF-associated bacteria belong to the major four phyla, comprising Proteobacteria, Actinobacteria, Bacteroidetes, and Firmicutes. AMF-associated bacteria serve as an AMF "second genome," filling important functional gaps occurring in the AMF genome. It thus comes as no surprise that many services rendered by AMF are choreographed by their bacterial partners. The multiple functional traits such as nutrient fixation, inorganic and organic P (phytate) solubilization, biocontrol, plant growth promotion, and polymer-degrading properties make AAB indispensable for the success of AMF in delivering mutualistic benefits to plant hosts. No doubt, the next generation of AMF inoculants could benefit a great deal from the study of AMF and their associated microbiome

as well as the factors driving its community assembly and functions. The prospect of an AMF core microbiome, especially with respect to functional guilds, remains promising as shown by recent studies, but compatibility among strains will need testing.

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Data availability Data are available in Supplementary Table S1.

Declarations

Conflict of interest The authors declare no competing interests.

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