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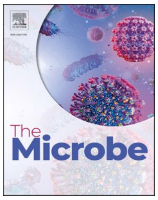

Trichoderma-bacterial network: A balance inter-kingdom interaction for agricultural relevance

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ABSTRACT

Exploring the potential of fungal-bacterial interactions holds great promise as this inter-kingdom association has coexisted and been ubiquitous. Benefiting from an enhanced comprehension of microbial community structure and assembly allows us to understand how this bipartite interaction can be manipulated for maintaining the agricultural balance. Given the complexity of their relationships, it is necessary to understand their ecological role in biocontrol applications. In this mini-review, we provide an overview of the intricate interplay between *Trichoderma* and bacteria, encompassing both physical and chemical interactions. We highlight their beneficial effects and the multifaceted nature of this relationship in both natural and laboratory settings. Critical discussion on the need for having compatible and stable consortia is covered, emphasizing their effect on the biocontrol consistencies. Future studies should utilize advanced techniques to address research gaps, such as the need for simple model in eukaryotes-bacteria interaction, the hidden novel *Trichoderma*-bacteria-derived metabolites, the impact of omics technologies for deciphering mechanisms and the development of cost-effective bioformulations. Leveraging the microbial crosstalk has shown a great potential in agricultural sustainability that allows for the development of future intervention strategies.

1. Introduction

Microbes are the most abundant life forms on earth, having a close association with all living organisms and playing a central role in many biogeochemical cycles towards ecosystem functioning. Although microbial communities form complex and dynamic yet diverse ecosystems, their predictive understanding based on interspecies interactions among different community members remains challenging even though sharing a similar ecological niche (Martiny et al., 2015). In a shared microhabitat, the co-occurrence of fungi and bacteria leads to dynamic yet coevolved communities while promoting key selective forces towards diversity. Such fungal-bacterial communities' interaction has been described to exist and exploited by humans for centuries in many biotechnological applications, with more than 600 studies dealing with within the last five years. The establishment of such interactions is driven not only by their close physical associations but also through chemical communication that is broadly studied under the socio-microbiology field. Noteworthy to mention, this inter-kingdom interaction produces a wide range of relationships that affect the ecology of both fungal and bacterial partners at different levels with respect to growth, nutrition, pathogenicity and even stress modulation/adaptation (Wagg et al., 2014). Regarding the latter, their beneficial interactions relatively remain poorly uncovered, despite their contributions to the stabilization of environmental settings. Exploration of fungal-bacterial interaction grants a novel avenue towards contributing to plant growth promotion for meeting a sustainable global demand (Zhou et al., 2022; Rashid et al., 2016; Chen et al., 2024). Nevertheless, the fungal-bacterial interactions may be difficult to interpret as always yielding into competition outcomes due to reciprocal antagonism to both partners. Such intricate yet complex interactions are often considered as a chemical warfare for their own survival advantage.

Whatever the environment considered, a suite of adaptive mechanisms can be modulated during fungal-bacterial interactions, shifting from antagonism to mutualism, via cell wall modification and ROS metabolism in enabling selective symbiosis with specific bacteria. Among the various fungal-bacterial interactions occurring in nature,

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those involving biocontrol and plant disease prevention are of particular interest due to their significant impact on agriculture. Members of *Trichoderma* spp. and *Bacillus* spp., represent one of the emerging studied fungal-bacterial groups based on their capability to improve plant growth and prevent disease incidence. Use of *Trichoderma* as a means of biocontrol agents has been considered effective in combating phytopathogens by limiting the virulence properties, thereby enhancing host plant health (Dutta et al., 2022). Under certain circumstances, their prior energy-consuming antagonistic interactions can be shifted to mutualism for the success of biocontrol capabilities. The development of cooperative behavior has been recently reported for *Trichoderma* and *Bacillus*, which resulted in forming a more effective barrier against *Fusarium* wilt disease by a microbiome engineering approach. Fungal antagonist *Trichoderma* evolved into mutualists with *Bacillus* after mitigation of bacterial toxins uptake by modulating the expression of bacilysin transmembrane transporter (*Tg*MFS4) protein, potentiating plant immune response (Li et al., 2025). In addition to producing efficacious biocontrol properties, an understanding mechanistic underpinning of fungal-bacterial mutualism is of importance for agricultural relevance, as exogenous application through bio-inoculants is subjected to different abiotic stresses. Theoretically, applying a combination of beneficial microbes gives a positive effect, but somehow in practice, overlooking the compatibility between strains has led to the failure of biocontrol strategies. Irrespective of the interaction, fungi and bacteria need to be recognized prior to initiating any kind of greater likelihood of targeted-biocontrol mode of action. Thus, more effective efforts should be extensively applied, encompassing the exploration of *Trichoderma*--bacterial communities as an important feature for proper agroecosystem balancing, in which establishing mutualistic associations with plant roots, enhancing nutrient uptake and safeguarding plant health (Tyśkiewicz et al., 2022). Although they remain one of the least attention inter-kingdom interactions so far compared to the well-studied mycorrhizal fungal-bacterial system, this approach can be further enhanced by utilizing existing beneficial microbes and strategically altering their interactions, thereby circumventing the challenges of time-consuming strain selection and the constraints of functional microbial cultivation.

An important example of such general principles governing this reciprocal relationship is the fungal ability to perceive the secreted metabolite signals from bacterial counterparts, where an interacting bacteria can directly acquire a carbon source pool in return, named facilitation. Fester et al. (2014) demonstrated that mycelial fungus is able to mobilize entrapped polycyclic aromatic hydrocarbons (PAHs) via hyphal pipelines and render them for bacteria consumption. While some bacteria such as *Burkholderia* sp. can prey on fungal-derived metabolites of family *Mucoromycota*, this association has resulted in significant genome reductions for bacterial counterparts that tightly coevolved over millions of years (Jung et al., 2018). Importantly, the possibility of trade-off metabolites between fungi and bacteria as an outcome of intimate relationships represent a fitness cost experienced by interacting species. Altogether, this interplay between bacteria and fungi is something similar to what has been described for plants and animals in microbiota-assisted host nutrition. An ecological balance between microbiome and host homeostasis has been extrapolated to be fundamental to maintaining the health of plant host. Zhou and co-workers thus identified the native microbiome cultivation, together with crop rotation practice, has brought the disease suppression capacity against the *Fusarium* pathogen (Zhou et al., 2023). Such positive associations revealed non-random relationships, reflecting commonalities of microhabitat as compared to negative ones. Therefore, we present an updated review showcasing how this inter-kingdom interaction evolves relying on a suite of physical and chemical associations, with particular emphasis on *Trichoderma* and bacterial species. When possible, relevant examples of *Trichoderma*-bacterial interactions are provided in this mini-review, however, referencing interactions between other fungi and bacteria is sometimes unavoidable. We also shed light on the environmental benefit of a simple pairwise intertwined combination as a means of a good exemplary model for obtain deeper comprehension and prediction of co-occurrence microbial networks. This provides emerging possibilities to manipulate these bipartite interactions for optimal implementation in agricultural balance.

1.1. *Trichoderma*

Trichoderma, whose belongs to the phylum *Ascomycota,* which includes more than 260 species, are found in almost all ecological climatic areas of various niches (Bissett et al., 2015). They are also capable of producing large quantities of conidia for rapid colonization, which are dispersed by the wind. Commonly known as rhizosphere inhabitants, these organisms hold significant economic importance in agriculture as a biological control (biocontrol) agent owing to their ability to produce enzymes and antibiotics (Bononi et al., 2020). Of 35 established species of *Trichoderma*, their core mechanisms for biocontrol have been associated with mycoparasitism, antibiosis, induction of plant systemic resistance and competition for resources (Manzar et al., 2022). Adding more, *Trichoderma* species are known to be successful wood decayers and organic matter decomposers with a number of potent secondary metabolites, of which those most studied are peptaibols, polyketides, terpenes and diketopiperazine-like compounds (Leylaie and Zafari, 2018). These metabolites are being chemically exchanged in nature through communication crosstalk signals with all forms of microbial species. Some species of *Trichoderma* have a high xylanolytic activity, but their effectiveness is not high enough. This genus can also form a close association with other microorganisms with complementary effects in pathogen antagonism. Attention has been drawn for their wide range secretions of important biological control-related-compounds properties (Marcías-Rodríguez et al., 2020). The ability of *Trichoderma* to produce secondary metabolites with diverse bioactivities, while possessing inherent defensive mechanisms, makes them valuable candidates for inducing activation of antibiotic-related genes with any bacterial strains.

Morphologically speaking, visual features were used to classify the species of *Trichoderma*. These fungi usually appeared to be white cottonish, developing into rapid yellowish-green to deep green compact tuft growth, especially at the center of a growing spot or in concentric ring-like zones on the agar surface under ideal conditions (Druzhinina et al., 2018). The conidial pigment commonly observed in the asexual morphs is typically associated with the *Hypocreaceae* family, aiding in the dispersal of fungal spores. In fact, all *Trichoderma* species were reclassified from the *Hypocrea* genus as early as 2005. Rifai (1969) initially classified the genus into nine ’aggregate’ species based on morphological characteristics. Later, Bisset (1991) revised Rifai’s work by incorporating the conidiophore branching system into the species concept, leading to the classification of *Trichoderma* into five sections. However, relying on morphological and physiological features is not enough in discriminating taxonomic identification at the species level due to the high degree of similarities among strains. Therefore, molecular techniques are necessary together with a polyphasic approach for the correct identification of species (Zin and Badaluddin, 2020). Instead of using a universal fungal barcode, the internal transcribed spacer (ITS) region, which possesses low resolution, alternative molecular approaches with different barcode regions (genes encoding RNA polymerase II subunit B; *rpb*2, transcription elongation factor 1-alpha; *tef*1-α and ATP citrate lyase; *acl*1) have been applied either individually or in combination for accurate *Trichoderma* identification (Błaszczyk et al., 2014). Despite the increasing number of the importance of different *Trichoderma* species used in the biocontrol efforts, studies that consider *Trichoderma* and bacterial partners are still limited in number. Given those gaps, providing crucial information on the environmental performance of *Trichoderma* will assist in justifying the selection of partnership strategies. It has been known that *Trichoderma* species grow optimally at temperatures between 25°C and 30°C. These soil-derived mesophilic fungi are known for their ability to utilize a wide range of substrates, exhibit rapid growth, and act as environmental opportunists. Notably, *Trichoderma* can efficiently utilize various rhizodeposits, including both simple sugars and polymeric carbohydrates from cell wall components. Their remarkable nutritional versatility allows them to feed on fungal biomass through mycophagy and degrade plant debris, including microcrystalline cellulose, via phytophagy (Druzhinina et al., 2011). This adaptability not only makes *Trichoderma* ubiquitous across diverse ecological conditions but also enables them to produce a variety of glycoside hydrolase enzymes responsible for hydrolyzing hemicellulose biomass (Andberg et al., 2015).

Although the genus *Trichoderma* was first found in 1794 when Persoon introduced their generic name, the proof of their biocontrol capability was only discovered in 1932 by Weindling (1934) through *Trichoderma lignorum* experimentation against *Rhizoctonia solani*. As a fungal biocontrol agent, *Trichoderma* do not cause any harm towards environment as they are capable of integrating or even replacing synthetic fungicides to maintain an allowable threshold limit of pest populations (Zeilinger et al., 2016; Ons et al., 2020). A key aspect of *Trichoderma*'s biocontrol ability is its production of antifungal compounds through G-protein-coupled receptors (GPCRs) and mitogen-activated protein kinase (MAPK) pathways (Hinterdobler et al., 2020; Wang et al., 2017). These signal transduction proteins play a crucial role in various physiological functions, particularly in secondary metabolism related to mycoparasitism. In this context, *Trichoderma* regulates mycoparasitism-related genes, enabling it to penetrate the host's cell wall and confer biocontrol properties. While the interaction between *Trichoderma* species and bacteria is an important area of focus, it is equally important to investigate the compatibility of *Trichoderma* with multi-kingdom microorganisms and consider the potential unintended consequences for non-target organisms, including soil microbial populations, plants, and even humans. Interestingly, Xu et al. (2011) have outlined a mathematical model to predict the relationship outcomes based on the number of interactions, which is named the Bliss independence model. In fact, the cooperative effect between the pairwise interaction of *Trichoderma* and other bacterial strains is a key determinant for enhancing biocontrol efficacies, as individual strains are likely not enough to deliver consistencies. On the contrary, concerns associated with antifungal capacity posed by bacterial partners such as *Bacillus subtilis* against *Trichoderma* spp. are among the major threats in the development of efficacious biocontrol agents (Li et al., 2005). Noteworthy to mention, there is an increasing body of evidence under the pairwise relationships between fungi and their bacterial symbionts, highlighting the co-occurrence network effects (Tarkka et al., 2009; Deveau et al., 2018). In a recent study, co-occurrence analysis between fungi and bacteria revealed a positive correlation with the soil enzymatic activity. These fungal-bacterial associations, under the mixed pine tree species, suggest that the adoption of a cooperative strategy has a greater impact on maintaining soil fertility and biodiversity, thereby mediating plant coexistence (Hu et al., 2024). Moreover, integrating interrelationship network-inferred prediction with ecosystem functioning is always a way forward to validate the role of involved synergistic microbial interaction. Mounting evidence suggests that mechanisms leading to that fungal-bacterial homeostasis are likely involved via molecular interaction of cross-feeding, metabolic mutual maintenance and functional complementarity. For example, Wong et al. (2019) in their studies demonstrated that combination of *Trichoderma harzianum* CBF2 and *Pseudomonas aeruginosa* DRB1 in the bioformulation of talc powder is more efficient at weakening *Fusarium*-related disease symptoms by a 58 % reduction with higher viability. A recent finding from Xie et al. (2023) mentioned that the *Trichoderma*--seed coating strategy may serve as a key role for rhizosphere microbial recruitment and assembly, which positively contributse to reducing the disease occurrence rate. Adding to the list, *Trichoderma* application, by which after fumigation not only accelerates the recovery of soil microbial community to rebuild but also increases the abundance of beneficial microorganisms and keeps pathogens below economic thresholds (Wu et al., 2022). An important beneficial effect that can be obtained through *Trichoderma*-bacterial consortia is the stimulation of new bacterial niches, thus resulting the modification of soil micro community-level behavioral activities. In this regard, Zhang et al. (2020) reported that increased bacterial abundances of *Sphingomonas*, *Pseudomonas*, *Actinomadura* and *Rhoanobacter* genera, which were obviously noted after *Trichoderma asperellum* application. Putting an example for biocontrol context, the use of *Trichoderma harzianum* - *Pseudomonas fluorescens* combination is just as effective in reducing disease severity as the use of the broad-spectrum chemical fungicide with greater effect (Sandheep et al., 2013). All those beneficial effects primarily depend on the metabolic interdependencies of both *Trichoderma* and their counterparts, across distinct ecosystems. Collectively, *Trichoderma*-bacterial consortia can be considered as a green and environmentally feasible approach for agricultural productivity with multiple benefits.

2. Understanding *Trichoderma*-bacterial interaction

Currently, the application of *Trichoderma*-bacterial consortia has gained increasing attention as an approach to increase the sustainability of agricultural systems, together with the emerging analytical tools used. These consortia support the environmentally friendly farming practices, which benefit agricultural ecosystems (Pastor et al., 2023; Rodrigues et al., 2023). A different phenomenon with a similar encounter has shown that *Trichoderma*-bacterial consortia's great capability in bioremediation endeavours, which taking part in the breakdown of contaminants through the presence of microbial biofilm-matrix assemblages that allow them to survive under nutrient-restricted conditions. To a certain extent, this interspecies interaction intrinsically modulates the behavior of either or both interacting organisms. On one end of the spectrum, co-occurrence patterns of fungi and bacteria lead to intimate biophysical and metabolic interactions in which they interdependently evolve. Based on the Black Queen hypothesis, positive correlations in fungal-bacterial interaction may be explained by the beneficial of leaky traits, inter-kingdom horizontal gene transfer and moderation of positive loops (Morris et al., 2012). Depending on the species involved, their interactions can be specific or can involve a broad spectrum of bacterial species irrespective of their taxonomic associations. As a consequence, a shift in understanding bipartite fungal-bacterial interaction has taken place towards complex networks of multiple interacting partners with regards to microbial diversity in maintaining ecological functions. In this regards, knowledge on the microbial assembly and functioning is indispensable for unravelling those microbial interactions that most likely occur in natural environments.

Here, functional potential of *Trichoderma*-bacterial species does matter even when facing changing environmental conditions. In our context, the functional potential (read: biocontrol properties) for the required ecosystem process can be achieved completely if interaction between two or more microbial species takes place. Most conventional practice in preparing biocontrol agents now focuses on a limited number of single-strain cultivation. However, mimicking the way microbes exist naturally as members of complex communities will be able to drive better ecosystem processes, as they likely have a higher number of unique functional traits as a result of the combined metabolic capabilities. An approach that has garnered attention involves the purposefully combined multiple microorganisms, enabling the synergistic effects in the plant disease prevention. Predicting the contribution of each microbial partner to ecosystem process can be determined by genomic connectivity information, linking to the reactions involved in the pathway of interest. A successful example of *Trichoderma* and rhizobia co-inoculation effectiveness has been reviewed extensively from previous studies with special reference to yield improvement of legumes (Barbosa et al., 2022). On the other hand, *Trichoderma lixii* NAIMCC-F-01760 not only builds a synergistic interrelationship with bacteria, *Bacillus velezensis* MB101, but also has a close cooperation with actinobacteria *Streptomyces atrovirens* N23 in reducing disease incidence caused by *Rhizoctonia solani* (Solanki et al., 2019).

Taking into account the importance of *Trichoderma*-bacterial interaction, this bipartite relationship is seemingly difficult to circumvent under a complex soil environment, potentially due to the spatial heterogeneity of soil particles. Recent studies by Xie et al. (2024) delved into co-culture reliable system to capture these two microorganisms interacting. Aiming to alleviate the competitive pressure, *Bacillus velezensis* SQR9 interestingly attached to *Trichoderma guizhouense* NJAU4742, contrary to the antagonistic behavior observed in the plate medium as evidenced by using fluorescence microscopy visualization. Importantly, *B. velezensis* was suggested to strongly exert their beneficial effects under the condition of biofilm matrix association with fungal hyphae. Over the last decades, our effort in the visualization of microbial interactions at the soil microscale has dramatically changed. From the classical agar-based co-culture experiment until the artificial matrixes up to the fungal highway column approach, such as iChip *in situ* cultivation, none of these methods has proven possible to elucidate the microbial interdependency (Harvey et al., 2020; Ingham et al., 2011; Nichols et al., 2010). In recent years, fabricated microfluidic arrays allow for the precise monitoring of small heterogeneous microbial populations with various technical parameter manipulations and real-time dynamic observation. Gimeno et al. (2021) proposed an investigation on the versatility of a microfluidic platform focusing on fungal-fungal interaction. The study showed that the spatiotemporal output of tracking fungal hyphal advancement in a time-lapse experiment can be resolved using live-cell imaging. Different visualization techniques including non-specific stains such as live-dead staining can be deployed to define topographical features of spatially bacterial-fungal organisms in close proximity. However, the problem remains as microbial samples get physically altered and chemically fixed, as it is impossible to visualize cell dynamics. A more exciting technique to capture a simultaneous detection of microbial species in multiple organisms *in situ* and *in vivo* is the is the use of red-green fluorescent protein. With regards to non-invasively studies on bacterial-fungal interaction in structured environments, several techniques are being proposed, combining the taxa-specific target probes via fluorescence in situ hybridization (FISH) and stable isotope probing (SIP) with nanoSIMS. This remarkable technique gives both physical and molecular information on the respective interaction down to the single-cell scale. This type of approach is adopted for investigation of nutrient exchange between bacterial cells and fungal hyphae at high spatial resolution under nutrient-poor microhabitat circumstances (Worrich et al., 2017).

Molecular dialogue between interacting organisms is a feature integral to all interspecific interactions. Many chemical crosstalk-guided interactions have been deciphered through ‘omics’ approaches. A multitude of ‘omics’ technological applications are ideally suited to address magnitude responses and metabolic exchanges in complex interspecies signaling, taking into account the spatiotemporal scales. To put these advantages in perspective, techniques not only have the ability to detect spatial small molecule signal distribution but can also directly map between detected compounds and the observed phenotypes of the sample substrate. LC-QTOF/MS can be considered a high-throughput mass spectrometry technique that straight-forward suits particularly well for studying fungal-bacterial interaction. Their application is gradually increasing, especially for the detection of new antibiotic compounds in co-culture experiment. Using co-culture extract from *Trichoderma* pairwise fungal-bacterial culture, Zohair et al. (2024) exclusively discovered Trichodermarin N and Trichodermatide D, adding to the list of 21 unique chemical entities. These newly compounds have to be linked to the presence of bacteria *Bacillus* in cryptic biosynthetic gene activation in *Trichoderma*. Moreover, the antifungal activity was way stronger than the separate monoculture extracts. The combination of mass spectrometry and NMR spectroscopy, together with genome mining provide a novel chemodiversity compound as *Trichoderma* sp. has a greater role in affecting the production of specialized metabolic chemistry and regulatory responses during the microbial crosstalk. Finally, another promising tool for volatile organic compounds (VOCs) detection which is proton transfer reaction-MS (PTR-MS) and GC-MS. Such a platform allows the profile characterization of the volatile metabolic fingerprints from four *Trichoderma* spp. with high mass resolution, aiming to access the biologically driven changes of volatile in real time (Guo et al., 2020).

As highlighted before, important progress concerning this model multi-kingdom interactions confers a biocontrol benefit, assuring consistent efficiency under open field conditions, thereby aiding in ecological sustenance. In general, the colonizing-effect ability after *Trichoderma*-bacterial application in the plant rhizosphere not only benefits both multi-kingdom organisms but also enhances the host plant development synergistically. A better understanding of these bipartite interactions is needed to assist in identifying the crucial drivers of their assembly, or even greater in engineering synthetic microbiome consisting of for optimal biocontrol approaches. Table 1 shows the proven efficacy of the *Trichoderma*-bacterial network, highlighting agricultural benefits along with the mode of application from the year 2010 onwards.

2.1. Physical interaction

Bacteria form an intimate association with *Trichoderma*, mutually benefitting from their cumulative ecological success. Physical interactions are recognized as the simplest relationships in which bacteria use fungal surfaces and secretory factors as anchorage (Steffan et al., 2020). This interaction can be classified into highly specific symbiotic associations of fungal hyphae and bacterial cells, which are known as ectosymbionts and endosymbionts. A recent study leveraged endobacterial-fungal association is the mutualism between *Bacillus velezensis* and *Rhizophagus irregularis*. First, bacteria migrate along the hyphal network of fungus, whereby forming the biofilms in a compatible interaction. Remarkably, fungus modulates the biosynthesis of specialized metabolites in *B. velezensis* as the mechanism to safeguard host plant health. Moreover, studying this physical interaction revealed that the bacteria attenuates fengycin production in order to accommodate hyphosphere, shifting the interaction from antagonistic into mutualistic (Anckaert et al., 2024). Another example portraying the intimate physical interaction has profound effects on other interacting partners, including cell-cell communication-based electromagnetic signal radiation that can be converted into sound spectra waves, enabling transferablility faster than chemical signals due to less diffusion limitation (Reguera, 2010). Knowledge of physical contact examples has gone beyond into the migration of bacterial cells on fungal hyphae. In response to this, surface fungal hyphae are used as a highway platform to mobilize bacteria towards plant roots or air-filled soil particles, facilitating their entry into plant tissue or rhizospheric vicinity areas. This mycelium-driven bacterial dispersal has been suggested as a mechanism contributing to the long-term soil fertility in the context of oxalate-carbonate pathway. Using a simple method of agar co-culture, Bravo et al. (2013) experimentally demonstrated bacterial dispersal of *Stenotrophomonas* sp. to access targeted Schlegel AB-calcium oxalate (Caox) as a carbon source by using *Trichoderma* hyphae network. Additionally, growing fungal networks are known to disseminate bacterial survival and resistance over environmental antibiotic and contaminant hotspots (Nazri et al., 2017) As the growth of fungal hyphae is becomes instrumental, active bacterial motility by the fungus is certain. In fact, motile bacteria use the physical network created by fungal hyphae for dispersal. Zhang et al. (2018) concentrated their attention on the interactive dynamic of cheese bacterial motility on physical fungal hyphae. Employing a time-lapse microscopy of *Serratia*-*Mucor* on a thin layer of agar, they demonstrated that *Serratia* species rapidly disperse on fungal network via active flagella-mediated motility.

Table 1
Trichoderma-bacterial interactions and their agricultural-related effects.

***Trichoderma* sp.**	**Interacting partner**	**Interaction**	**Mechanism**	**Application**	**References**
Trichoderma viride	*Pseudomonas fluorescens*	Mycoparasitism	• Reduced the disease incidence through secretion of lysis enzymes	Field evaluation	Radjacommare et al. (2010)
Trichoderma viride Tv1	*Pseudomonas fluorescens* Pf1, *Bacillus subtilis* Bs16	Mycoparasitism	• Reduction the collar and root rot disease incidence through production of antibiotics	Glasshouse and field experiment	Latha et al. (2011)
Trichoderma harzianum RU01	*Bacillus subtilis* CA32	Mycoparasitism	• Protection bean seedlings from Fusarium solani through seed bacterization	Greenhouse pot experiment	Abeysinghe (2012)
Trichoderma asperellum T42	*Pseudomonas fluorescens* OKC*, Rhizobium* sp. RH4	Synergism	• Enhanced seedling growth	Glasshouse experiment	Yadav et al. (2013)
Trichoderma harzianum	*Azospirillum brasilense*	Synergism	• Nitrogen supply (*Azospirillum brasilense*) • Chitinase, β−1,3-glucanase, carboxymethyl cellulase xylanase and polygalacturonase activity (*T. harzianum*)	Greenhouse application	El-Katatny and Idres (2014)
Trichoderma virens, Trichoderma atroviride	*Bacillus subtilis. Pseudomonas pseudoalcaligens, Pseudomonas chlororaphis*	Mycoparasitism	• Induced a delay at the onset of disease	Greenhouse application	Ruano-Rosa et al. (2014)
Trichoderma citrinoviride (MBAAT)	*Pseudomonas aeruginosa* (MBAA1), *Bacillus cereus* (MBAA2), *Bacillus amyloliquefaciens* (MBAA3)	Mycoparasitism and synergism	• Lower disease incidence with increased plant growth parameters	Laboratory and greenhouse experiment	Thakkar and Saraf (2015)
Trichoderma harzianum TNHU27	*Bacillus subtilis* BHHU100, *Pseudomonas aeruginosa* PJHU15	Mycoparasitim	• Increased plant growth promotion with enhanced protection against plant pathogen	Greenhouse and field experiment	Jain et al. (2015)
Trichoderma virens	*Pseudomonas fluorescens*	Mycoparasitism	• Reduction in nematode reproduction	Greenhouse application	Moradi et al. (2015)
Trichoderma harzianum	*Pseudomonas aeruginosa*	Mycoparasitism	• Antagonistic effect against soil-borne diseases	Screenhouse experiment	Shafique et al. (2015)
Trichoderma viride	*Pseudomonas fluorescens* CHA0	Mycoparasitism	• Enhanced biocontrol effect against *Meloidogyne javanica*	Greenhouse experiment	Saeedizadeh (2016)
Trichoderma harzianum	*Serratia proteamaculans*	Synergism	• Increased tomato seedling growth with increasing ROS-scavenging enzymes and bursting *Rhizoctonia solani* cells	Greenhouse experiment	Youssef et al. (2016)
Trichoderma harzianum strain Th3	*Pseudomonas fluorescens* RRb11	Mycoparasitism with synergistic relationship	• Enhanced rice plant growth and reduced rice blast severity	Laboratory and field application	Jambhulkar et al. (2018)
Trichoderma harzianum	*Pseudomonas fluorescens*	Mycoparasitism	• Induced defense related enzyme leading to systemic resistance	Open field	Madhavi et al. (2018)
Trichoderma harzianum	*Glomus fasciculatum, Mesorhizobium ciceri*	Mycoparasitism	• Improving plant growth and decreasing the root-knot development	Farm field application	Rizvi et al. (2018)
Trichoderma spp. AA2	*Pseudomonas fluorescens, Bacillus subtilis*	Mycoparasitism	• Antagonistic effect against *Ralstonia* spp.	Open field	Yendyo et al. (2018)
Trichoderma viride	*Pseudomonas fluorescens*	Synergism	• Increased mycorrhizal fungi-root colonization: increased water absorption and P supply	Greenhouse experiment	Saini et al. (2019)
Trichoderma harzianum (Th)	*Brevibacterium haloterans* (Sd−6)	Synergism	• Increased plant growth, oil content, photosynthetic pigment with protection from phytopathogens	Greenhouse and field experiment	Singh et al. (2019)
Trichoderma harzianum CGMCC7861	*Bacillus subtilis* CGMCC7850	Mycoparasitism	• Suppressed common scab disease with increased tuber yield	Field study	Wang et al. (2019)
Trichoderma viride	Arbuscular mycorrhizal fungi	Synergism	• Improved onion growth parameters	Glasshouse experiment	Metwally and Al-Amri (2020)
Trichoderma harzianum	*Bradyrhizobium spp.*	Synergism	• Enhanced effect on growth development	Greenhouse experiment	Neelipally et al. (2020)
Trichoderma harzianum	*Achromobacter xylosoxidans* (Fd−2)	Synergism	• Better photosynthetic efficiency with improved nutrient uptake and increased the accumulation of proline	Glasshouse experiment	Singh et al. (2020)
Trichoderma sp.	*Bacillus* sp.	Antagonism	• Incompatibility issue	Controlled (*in vitro*) and natural (in greenhouse)	Poromarto et al. (2022)
Trichoderma harzianum MZ025966	Arbuscular mycorrhizal fungi	Mycoparasitism	• Suppressive against root-knot nematodes with great potentiality to produce growth promoting compounds	Greenhouse experiment	Nafady et al. (2022)

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Table 1 (*continued*)

***Trichoderma* sp.**	**Interacting partner**	**Interaction**	**Mechanism**	**Application**	**References**
Trichoderma afroharzianum T22	*Azotobacter chroococcum* 76 A	Synergism	• Increased tomato yield with enhanced soil microbial abundance	Field experiment	Cirillo et al. (2023)
Trichoderma harzianum (Th47)	*Pseudomonas fluorescens* Pf27	Mycoparasitism	• Effective in reducing disease incidence and increasing growth promotion	Glasshouse, experimental field and open farmer field	Kabdwal et al. (2023)
Trichoderma asperellum (Th−11)	*Pseudomonas fluorescens*, arbuscular mycorrhizal fungi	Mycoparasitism	• Effectively reduced root rot and wilt disease with enhanced plant growth	Laboratory and on-station field trials	Sain et al. (2023)
Trichoderma album	*Bacillus megaterium*	Synergism	• Increased photosynthetic pigment levels in leaves, mineral contents, antioxidant properties, and nutritional values • Reduced the accumulations of reactive oxidative species (ROS) products	Field experimentation	Younes et al. (2023)
Trichoderma velutinum, Trichoderma tomentosum, Trichoderma gamsii, Trichoderma harzianum	*Sinorhizobium meliloti* BL225C, *Sinorhizobium meliloti* 1021	Synergism, antagonism	• Symbiosis is based on strain-specific and genotype-to-genotype interaction	Laboratory experiment	Vaccaro et al. (2024)

This dispersal facilitation not only affected to single bacterium of *Serratia* group but also went beyond the range of other *Gammaproteobacteria* species, shaping the relatively simple cheese model microbiome assembly. Characterizing *Trichoderma*-mediated bacterial migration has been recorded by Reis et al. (2021), who mentioned that extended *Trichoderma longibrachiatum* hyphae has been suggested to be used as microhabitats that harbor *Serratia marcescens* bacterial fitness, leading to compatible biofilm-type formation structures. At the microscopic level, their partnership effect has been evidenced by the ability to increase biosolubilisation activity and improve tomato and papaya growth response. On the other hand, bacterial intrahyphal colonization is used as a vector for bacteria for easy transferability into inaccessible nutrient sources. This synergy between bacteria and fungi has been attributed to their complementary action, which has a crucial role in breaking the complex substrates in the soil. Most biofilms primarily facilitate inter-kingdom interactions by the formation of extracellular polymeric substances (EPS), in which are considered as a shared space of the encased microbial cells. Intimate biophysical and collaborative interaction in achieving biofilm homeostasis normally emerges as a way of efficient cell-to-cell communication. Using plant-adhered biofilm-related tripartite association as an example, fungal hyphae play a key role in biofilm formation by creating the necessary ecological conditions, such as regulating gene expression during root colonization and providing protection from toxic compounds (Stopnisek et al., 2016; Nazir et al., 2014). Stabilized cell-to-cell contact is commonly observed in mixed fungal-bacterial assemblages within biofilm matrices. Bacteria with S-layer proteins (SLPs) on their outer surfaces are particularly adept at adhering to other microbial cells. Kouzuma et al. (2015) noted that the FliC protein, responsible for flagellar movement, and the cap protein FliD of *Pelotomaculum thermopropionicum*, a propionate-oxidizing bacterium, are involved in the adherence to methanogenic archaeon cells. Adhesin protein or complementary receptors on the other cells and even eDNA filaments are seen to be key elements in biofilm co-aggregation, thus mediating fungal-bacterial interactions. Compatible interaction was suggested by Izquierdo-García et al. (2020) as the adhesion of *Bacillus velezensis* spores causing no physical damage on the surface of *Trichoderma viride*. Alongside the physical interactions, Yang et al. (2016) demonstrated that the bacterial type 3 secretion system (T3SS) in *Burkholderia terrae* BS001 has facilitated the migration in the mycosphere of *Trichoderma asperellum* 302. This movement ability is a kind of motility appendage that connects bacteria to fungal surfaces before biofilm formation. External biotic cues such as plant roots and exudates produced by fungal hyphae can act as chemoattractants for bacteria to be attached to. Further evidence of bacterial attachment to fungal surfaces was provided by Haq et al. (2016), who identified ceramide monohexoside (CMH) moieties as anchoring structures for *Burkholderia terrae* BS001. As shown by Guennoc et al. (2018), *Pseudomonas fluorescens* BBc6 exhibited a wide range of physical associations, forming biofilms on the hyphal surface of tested fungi, indicative of their broad specificity. By contrast, free-living fungi *Tuber melanosporum* secretes DNAse to avoid any bacterial biofilm on their hyphal surface. In this regard, certain fungi have developed a systemic approach to restrain the formation of biofilms, causing their ecological fitness to be jeopardized. Triveni et al. (2013) reported that the development of multispecies biofilms comprised of *Trichoderma* with agriculturally important bacteria (*Azotobacter chroococcum*, *Pseudomonas fluorescens* and *Bacillus subtilis*) has shown a significant effect on plant growth-promoting attributes. Similar studies conducted by Triveni et al. (2015) showed that the deployment of *Trichoderma-Anabaena*-based microbial biofilms has provided a benchmark setting in the biocontrol effort of pathogen-infected crops. The presence of *Trichoderma viride* as a co-partner with *Azotobacter* in the biofilm establishment has been evidenced to be a mediator in the nutrient solubilization via the acidification process as reported by Velmourougane et al. (2019). All these aforementioned physical contact features have made them an ideal complementary consortium to be employed in biocontrol phytopathogen infection.

2.2. Chemical interaction

Several chemical associations have been reported to be involved in fungal-bacterial communication, ranging from antibiosis, metabolic exchange and chemotaxis for their survival. Mycoparasitism is a well-established mode of biocontrol related to *Trichoderma* against a diverse range of phytopathogenic fungi, with plenty of studies being recorded (Velázquez-Robeldo et al., 2011; Contreras-Cornejo et al., 2016). Antibiotics (broadly encompassing both antibacterial and antifungal compounds) and volatile organic compounds are some commonly biochemical groups being released for biocontrol reasons, particularly in triggering antagonism activities with fungal-interacting partners (van der Meij et al., 2017; Zhao et al., 2019). Some examples of the antagonistic effect possessed by the *Trichoderma* species are directly related to the secretion of antimicrobial metabolites against *Escherichia coli* and *Staphylococcus aureus* as reported by Leylaie and Zafari (2018). Besides, the biocontrol effectiveness of *Trichoderma* against various phytopathogens such as *Penicillium oryzae, Aspergillus fumigatus and Botrytis cinerea*, primarily attributed to the presence of the Trichodermin compound. One notable exemplary bidirectional volatile-mediated interaction between *Trichoderma* and rhizosphere bacteria was recorded by Li et al. (2019), mentioning a significant growth inhibition for 48 soil bacteria tested due to production of esters, trichorzianines and sesquiterpenes by *Trichoderma*. From the perspective of crosstalk communication, their interactions in the microbial ecosystem were regulated by chemically signalling molecules. Chemical signals of *Trichoderma* often secrete in conjunction with observed phenotypes based on the specificity of their interacting bacterial partners (Zeilinger and Omann, 2007). For example, *Trichoderma virens* PS1–7 produced carot-4-cn-9,10-diol, a sesquiterpenes-type signal molecule that attenuates the virulence development caused by *Burkholderia plantarii* (Wang et al., 2013). That inter-kingdom molecule was putatively produced by *T. virens* PS1–7 whenever co-cultured with *B. plantarii*. Owing to tropolone synchronously mediating biofilm formation, carot-4-cn-9,10-diol was mimicry functioned to repress AHL-QS of *B. plantarii*, leading to abnormal and defective biofilm development. Likewise, volatile organic compounds (VOCs) released by *Trichoderma atroviride* have contributed into the enhanced expression of biocontrol genes, *phlA* encoding 2,4-diacetylphloroglucinol (DAPG) in *Pseudomonas fluorescens* (Lutz et al., 2004). As for consequences, a mutual benefit can result in a bidirectional dialogue as shown by increasing the production of the ECH42 endochitinase enzyme responsible for the biocontrol activity of *T. atroviride*. For the first time, they demonstrated that metabolites from both antagonistic microbial species, fungi and bacteria, can influence biocontrol gene expression in both positive and negative directions.

Numerous studies regarding synergistic effects have been documented through the combined complementarity of *Pseudomonas* and *Bacillus* with *Trichoderma* isolates in an attempt to enhance pathogen-inhibition ability (Alizadeh et al., 2013; Poveda and Eugui, 2022). A field experiment demonstrated that a significant reduction in disease was achieved by the combined application of *Trichoderma hamatum* THSW13 and *Pseudomonas aeruginosa* BJ10–86 against damping off chili caused by *Phytophthora capsici* (Chemeltorit et al., 2017). *Trichoderma*, when combined with *Pseudomonas fluorescens*, appears to be a particularly compatible and complementary pairing for biological control efforts (Woo et al., 2002; Dugassa et al., 2021; Pereira et al., 2022). As mentioned earlier, although both species are known to display good biocontrol against phytopathogenic fungi, that bilateral dialogue needs to be facilitated to produce controllable chemical compounds concerning to growth rate and culture conditions. It would be very beneficial to establish a proper co-culture growing condition in relation to metabolic dependency, along with required harvestable novel biocontrol compound properties. A recent study demonstrated a bilateral crosstalk in which both cross-feed to modulate lipopeptide production. When *Bacillus velezensis* GA1 was co-cultured with *Trichoderma harzianum* IHEM5437, the bacteria overgrew *Trichoderma* in a rich medium due to its antifungal lipopeptide production. However, this condition was reversible when co-cultured in a minimal medium, which inhibited the expression of *Bacillus* genes encoding lipopeptide synthetases. Interestingly, the bacterium's growth returned to normal upon replacement with the fungal supernatant. In this case, the fungal supernatant ensured a high production yield of lipopeptides, acting as the exchanged signal between the two species (Fifani et al., 2022). Similarly, a comparable homeostasis loop may occur in the interaction between *Trichoderma atroviride* T23 and *Bacillus amyloliquefaciens*, where the *Vel*1 gene of strain T23 plays a role in regulating their compatibility (Karuppiah et al., 2020). In terms of effector molecules during *Trichoderma*-bacterial interaction, Guzmán-Guzmán et al. (2024) pinpointed the upregulation of *epl*1 and *tatrx*2 gene expression in response to the presence of *Pseudomonas fluorescens,* thereby promoting plant health. As for the record, *epl*1 gene is vital in modulating plant- induced systemic resistance systems. They also demonstrated that the biocontrol capacity of *Trichoderma atroviride* and *Rouxiella badensis* SER3 consortia was more effective at inhibiting *Fusarium brachygibbosum* growth. Additionally, Iturralde et al. (2020) revealed the role of nitrate-inhibition relief mediated by the auxin molecule in the interaction between *Trichoderma harzianum* and *Bradyrhizobium japonicum*. Auxin, an efficient growth factor, was supplied by *T. harzianum* to *B. japonicum* during their coexistence in the soybean rhizosphere. Owing to cadmium biosorption capability, the combination of *Trichoderma harzianum* and *Azotobacter chroococcum* shows a promising result to manifest the resilience effect of heavy metal toxicity. Their synergistic interaction helps to attenuate the toxic effects by accumulating most metal in their biomass extracellularly, resulting in higher phytotoxic adaptability in sunflowers (Abeed et al., 2022). From all these above-mentioned findings, for the first time, *Trichoderma* spp. and bacterial co-partners can coexist based on the ecological outcome of each microbe's experience in a pairwise interaction, adapting their metabolisms to grow together without nutrient competition.

Bacteria often synthesize broad-spectrum inhibitory metabolites when co-cultivated with fungi. These metabolic dependencies trigger the mutualism and produce chemically diverse antifungal substances as compared with the monoculture. For instance, *Trichoderma atroviride* SG3403 and *Bacillus subtilis* 22 produce more potent sources of antifungal antibiotics that are effective in reducing *Fusarium graminearum* by 54.22 % (Li et al., 2020). Zhang et al. (2017) in their explanatory research were able to isolate two novel sesquiterpenes compounds with potent inhibitory effects when *Trichoderma* sp. 307 was co-cultivated with an aquatic pathogenic bacterium, *Acinetobacter johnsonii* B2. Similarly, metabolites derived from *Trichoderma* spp., *Pseudomonas putida* and *Bacillus subtilis* were found to have several antimicrobial compounds from various chemical classes, effective in suppressing *Gnomoniopsis smithogilvyi* virulence (Silva-Campos et al., 2022). Xu et al. (2023) has extensively summarized all fungal co-cultures and their derived metabolites from the intricate relationship. Cross-antagonism was also found as *Trichoderma harzianum* M10 and *Streptomyces microflavus* AtB-42 encountered, producing a variety of secondary metabolites to protect their own territorial niches. However, they contradictorily exerted a synergistic effect on tomato seedlings as explained by Prigigallo et al. (2023) in their transcriptomic analysis. Based on the works reviewed above, they concluded that these silent biosynthetic gene clusters responsible for antifungal production can be activated if bacterial co-culture is employed, mimicking to naturally occurring conditions.

Apart from mutual benefits from the fungal-bacterial relationship, their partnership is usually extended into a tripartite context through the provision of enhanced protection to the host plant via the induction of systemic resistance mechanisms (Fig. 1). Not only does *Trichoderma harzianum* OTPB3 promote the extensional support of *Bacillus subtilis* OTPB1, but they also cooperate in inducing systemic resistance through antibiosis in tomato plants (Chowdappa et al., 2013). Co-cultivation of *Trichoderma longibrachiatum* with *Bacillus amyloliquefaciens*, can induce coexistence benefits in protecting tomatoes although it reduces their biocontrol effectiveness in nutrient-competitive environments (Ma et al., 2021). It is noticeable as *Trichoderma*-bacterial consortia have an ability to induce salicyclic acid (SA)-mediated defense system with regards to plant response to pathogen attack. Despite the effect on plant health, the presence of *Trichoderma* with other bacteria promotes such a morphological defect. Based on recent RNA-seq analysis, the crosstalk interaction with *Bacillus subtilis* HG1 has a strong impact on gene expression levels in *Trichoderma asperellum* TpB55 (Li et al., 2024). Strain HG1 modulated *T. asperellum* genes related to cell homeostasis, carbon metabolism, cell membrane fluidization, and spore formation. The study suggested that the fungal physiology was significantly altered, accompanied by mycelium shrinkage, upon contact with the bacterium. Previously, similar microbial interconnectedness driven by chemical interactions was experimentally demonstrated by Zhang et al. (2022). Their findings revealed that reciprocal gene expression led to the production of the anti-oomycete metabolite dodecadienal (DDA), which effectively inhibited *Phytophthora nicotianae*.

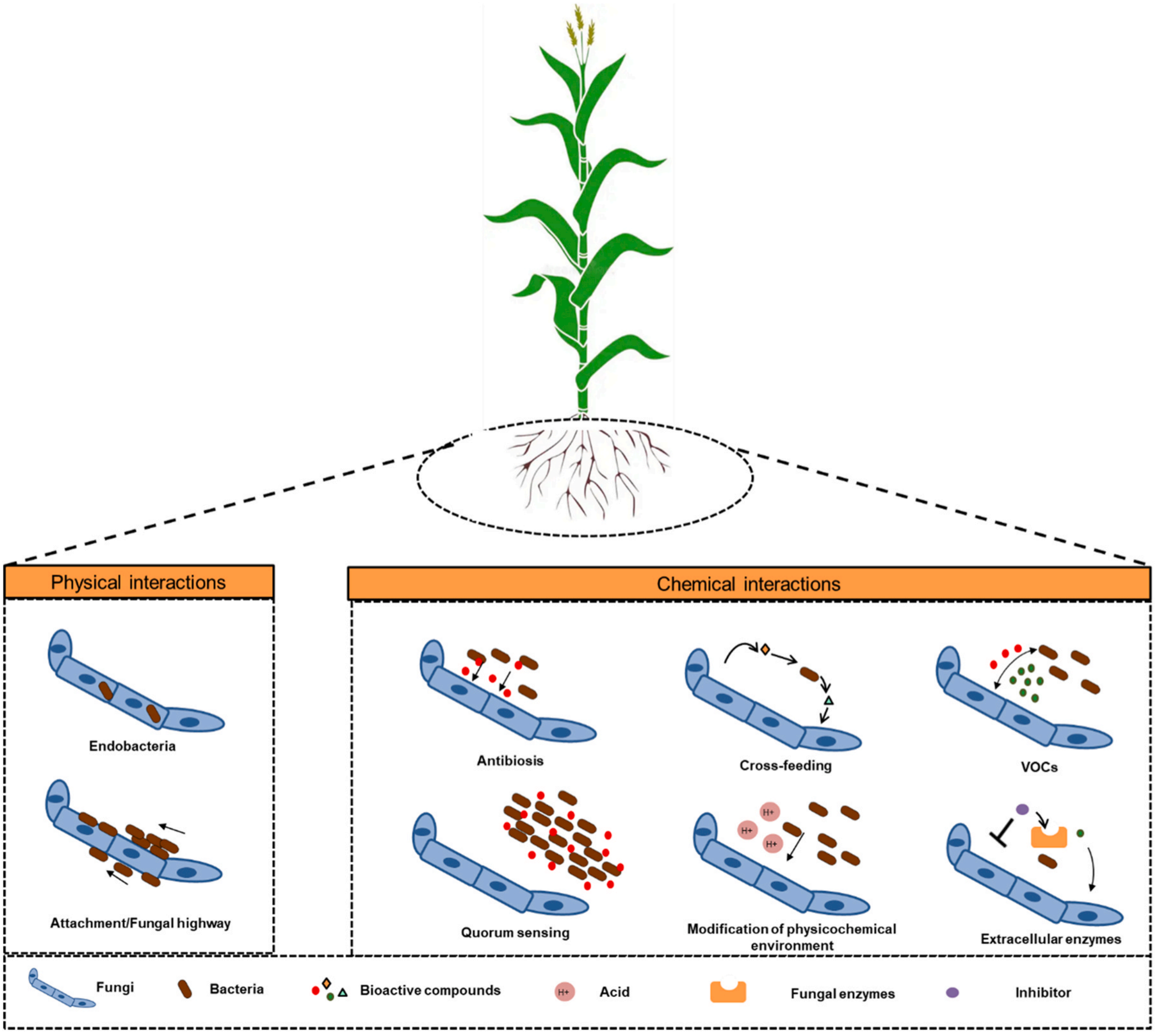

Fig. 1. Implication of *Trichoderma*-bacterial interaction on agriculture. Fungi and bacteria can perform various mode of interactions that promote agricultural benefit effects in which extending to tripartite plant-bacterial-fungal associations. Physical interactions involve bacterial endosymbionts of fungi or attachment to the fungal hyphae surface. Chemical interactions include metabolite crosstalk, production of small molecules (volatile metabolites, bioactive compounds, quorum sensing) to affect their bacterial counterparts involving growth, nutrition, pathogenicity and stress adaptation.

Acknowledging the multifaceted nature of the *Trichoderma*-bacterial relationship, the strategies for genome-wide fitness profiling of a given microbial consortium can be employed to provide predictive understanding using libraries of rhizosphere bacterial mutants. Combining high-throughput genetic screening and bacterial cytological profiling analysis, Pierce and his team deciphered the fitness factor of 16 different bacterial-fungal pairwise combinations that lead to their structures and functions (Pierce et al., 2021). Recent advancements include the use of random barcode transposon-site sequencing (RB-TnSeq) to identify bacterial genes critical for fitness in the presence of *Trichoderma atroviride* exudates. Furthermore, purine-mediated microbial communication has been proposed as a mechanism that promotes coexistence, offering functional benefits by enhancing the metabolic processes within the *Trichoderma*-bacteria symbiotic network (Villalobos-Escobedo et al., 2023).

3. Research gaps and future directions

Based on the above-mentioned studies, it is apparently obvious that *Trichoderma*-bacterial consortia are one of the valuable bioresources for biological control reasons. However, *Trichoderma* and bacterial co-inoculation so far have been reported to have inconsistent results before it can be fully harnessed for their potential. One of the reasons for such failure could be that consortia may not proliferate as fast as they likely encounter resource competition from soil indigenous microbes. To design inoculation success for field application, the approach has focused on the construction of tractable synthetic fungal-bacterial consortia based on compatibility and stability traits, uncovering an in-depth view of microbial community assembly rules (Hao et al., 2022). To be honest, construction minimal and stable consortia with less complexity, whereby the collaborative strains have enriched from a naturally occurring ecosystem, is a key determinant to promote synergistic effect. Top-down studies by Wang et al. (2021) clearly demonstrated the efficiency with which a tripartite bacterial-fungal consortium can support various metabolic tasks, with the fungus *Coniochaeta* sp. 2T2.1 playing a key role in lignocellulosic degradation. Similarly, *Trichoderma reesei* and its co-partner utilize the released monomers from cellulose degradation to produce itaconic acid (Schlembach et al., 2020). By mimicking natural conditions, this synthetic consortium can be experimentally applied to incorporate a desired set of microbial traits for agricultural purposes (Che and Men, 2019). Despite these advantages, elucidating the underlying mechanisms and regulations of inter-kingdom interaction remains poorly understood, as coexisting strains are not commonly found growing together in natural environments, which genetically lack communicative dialogues among them. Therefore, employing *in silico* methodology such as metabolic modelling approaches can be developed to design synthetic consortia by finding the ideal division of labor between strains to avoid potential competitive behavior (García-Jiménez et al., 2021). Traditional genome-scale metabolic models assume that all interacting members maximize biomass instantaneously as a collective objective function. However, this assumption is flawed, as microbes exhibit diverse phenotypes influenced by community interactions. These interactions involve known rate-yield trade-offs, where maximizing biomass production may not always be the primary objective. Consequently, predicting emergent properties of microbial communities remains a key challenge in systems biology. At the same time, examining coexistence profiles under varying spatiotemporal heterogeneity between fungal and bacterial species is a tipping point in validating the positive relationship out of the stereotypical competitive ones. In other studies, fungi and bacteria can shift into positive interactions if concerned about resource and environmental stress (Lee et al., 2022). Engineering synthetic *Trichoderma*-microbial consortia within a bioreactor is even possible using an oxygen gradient to spatially arrange different compositions. This gradient allows for *Trichoderma reesei* to coexist with *Lactobacillus pentosus* and *Clostridium tyrobutyricum* capable of converting biomass into relevant chemicals (Shahab et al., 2020). In addition, Basiru et al. (2023) provided insights into the core arbuscular mycorrhizal fungi-associated bacteria that can be used to engineer the plant microbiome for improved ecological functions. Essentially, the success of agroecosystem services provided by this core microbiome is primarily driven by keystone taxa associated with plant hosts, regardless of environmental condition differences. On a practical note, reference genomics-available datasets, recruitment of functional core microbiome and programming mutualistic interaction offer great potential to minimize the work during the construction process of synthetic fungal-bacterial consortia (Fig. 2).

The rapid emergence of omics technologies and genome editing tools in recent years offers opportunities to decipher the bilateral dialogue of fungal-bacterial interactions. It is important to note that the responses of interacting organisms are likely influenced by the type of interaction, with the magnitude of these responses varying according to the specific nature of the interaction itself. By using *Trichoderma atroviride* IMI206040 transcriptome as an example, Reithner and team examined the localized expression genes at various phases of interaction with different phytopathogens. Interestingly, they found a correlative transcription of several genes responsible for fungal cell wall degradation, indicating the successive biocontrol treatment during mycoparasitism (Reithner et al., 2011). Furthermore, in another study conducted by de Lima et al. (2017), secretomes (analysis of secreted proteins) from *Trichoderma harzianum* were responsible for inhibiting the growth of *Guignardia citricarpa*. In another context, using proteomics analysis helps to understand *Trichoderma*-mediated defense response in mycoparasitism. Combination of MALDI-TOF and liquid chromatography mass spectrometry proteomics, Suárez et al. (2005) successfully profiled a novel aspartic protease P2681 secreted by *Trichoderma harzianum* CECT 2413 upon treatment with fungal cell walls. The increase in sequencing depth technologies provides accurate insights into microbial community structure while enhancing the capability of distinguishing subcommunities from sequencing errors. Advances in single-cell sequencing coupled with species-level functional profiling of metagenomes and spatiotemporal variability consideration allow a greater in-depth understanding of complex microbial communities. Godin et al. (2022) proposed a computationally tractable modelling framework that links spatiotemporal patterning to consortia dynamics on the synthetic communities' construction. Even O'Leary et al. (2018) highlighted the importance of different spatial heterogeneity for fungal coexistence, which in the real world emulates decomposition processes. Answering fundamental questions: Who is there?', 'What are they capable of?', 'Who is actively doing what?' and 'What are the determinant factors contributing to interaction output?' really needs technological advances

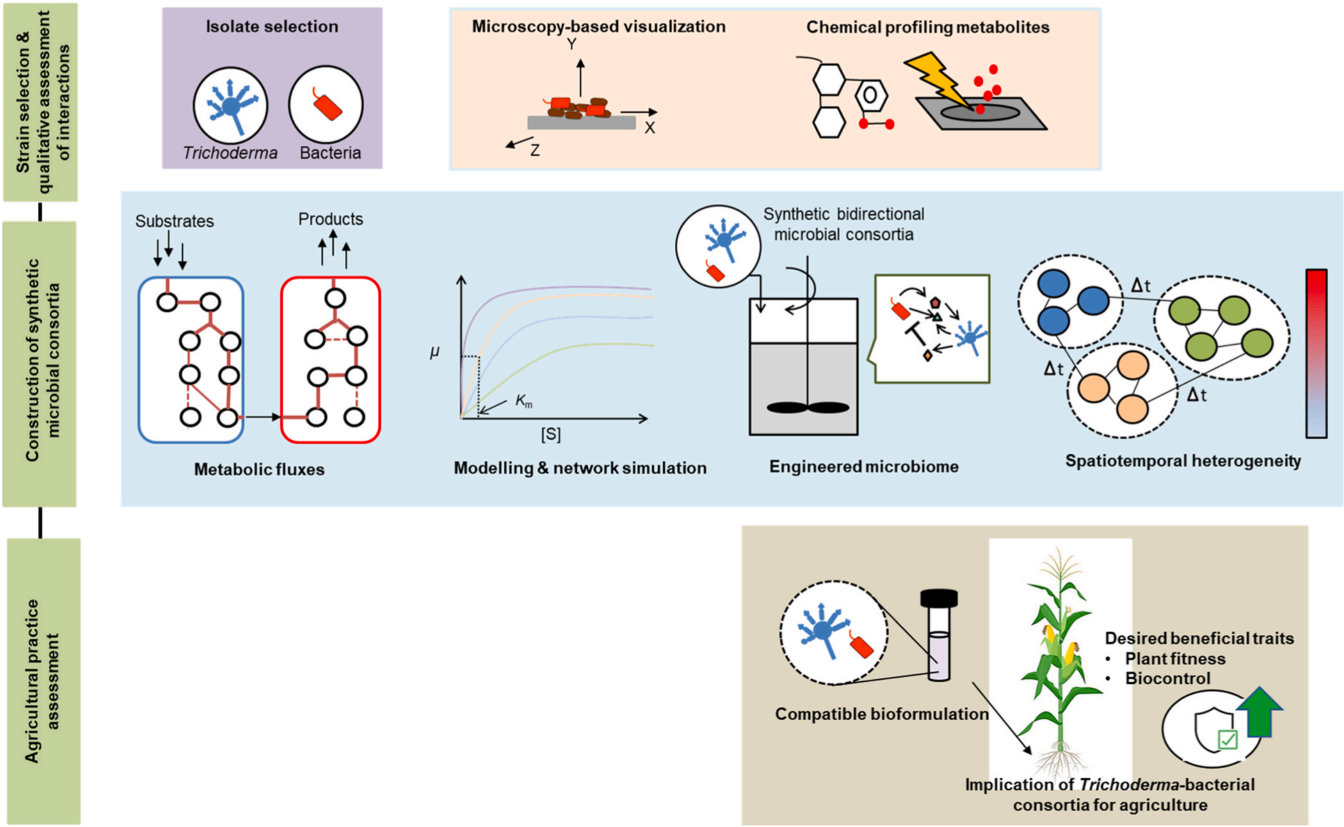

Fig. 2. Schematic illustration of the construction of stable *Trichoderma*-bacterial consortia for agricultural productivity with a description of characterized microbial interactions.

to simultaneously resolve the host-bacterial-fungi interactions at the tissue level. Recently, Saarenpää et al. (2024) presented spatial metatranscriptomics (SmT), a sequencing-based approach that leverages 16S/18S/ITS/poly-d(T) arrays, allowing simultaneous spatial interrogation of bacterial and fungal communities at the leaf scale of *Arabidopsis thaliana* and how these microbial hotspots locally impact host response. Thus, our understanding of fungal-bacterial intertwined interaction is heavily dependent on the advancement of system biology as well as high-advanced analytical and modelling tools.

Despite bacteria tends to be the focal point for microbiome studies, the biosynthetic potential production of biologically active metabolites from fungi is greatly underestimated. In fact, co-culture of *Trichoderma* and compatible bacterial strain strategies are prerequisites to induce hidden new metabolites encoded by silent biosynthetic genes that are not being explored before when cultured under single cultivation. It is generally assumed that fungal-bacterial inter-kingdom interaction under species coexistence state has led to abundant specialized chemical diversity (Schroeckh et al., 2009; Luu et al., 2023). In some cases, an intimate physical interaction is required in the fungal-bacterial mutualism rather than diffusible chemical signals to synthesize unprecedented polyketide metabolites. γ-aminobutyric acid (GABA) was produced in much higher quantities by *Trichoderma-Bacillus* co-cultures, as this molecule helps enhance resistance to abiotic stresses (Karuppiah et al., 2019). Additionally, Kossuga et al. (2013) reported the production of two novel polyketides, (*Z*)-2-ethylhex-2-enedioic acid and (*E*)-4-oxo-2-propylideneoct-7-enoic acid, during the co-cultivation of *Trichoderma* sp. Gc(M2)1 and *Penicillium* sp. Ma(M3)V, both of which exhibited novel bioactivity. All these examples mentioned surmise the fungal-bacterial co-cultivation can be a promising tool to produce structurally diverse secondary metabolites with respect to discover new potentially biocontrol compounds. Therefore, the ecological role of fungal-bacterial symbiosis can be leveraged further to unlock the wealth of biocontrol-related silent biosynthetic genes for biotechnology relevance as well. Moreover, elucidating the chemical mediator metabolites that link fungal-bacterial mutualism will be a primary focus in the years to come.

Another overlooked aspect to deliver biocontrol efficiencies is bioformulation along with persistent functions in agricultural settings. Indeed, up to 90 % of microbial inoculants can be deteriorated during field application (Qiu et al., 2019). Martinez et al. (2023) critically reviewed the potential state-of-the-art innovations related to bioformulation containing *Trichoderma*. Nunes et al. (2024) have reported approximately 246 registered marketable biocontrol products containing *Trichoderma* and bacterial symbionts. Additionally, many studies regarding *Trichoderma*-bacterial bioformulation development and their effects on biocontrol efficiencies (Upamanya et al., 2020; Comite et al., 2021; Wong et al., 2021). While improving efficiency and viability, the nano-encapsulation approach of fungal-bacterial inoculation with novel carrier materials can be a promising tool in facilitating their survival and improving the delivery system. Even Fakhrullin et al. (2009) encapsulated *Saccharomyces cerevisiae* cells and *Trichoderma asperellum* conidia with metal nanoparticles as they found that approach was stable and gave cell protection against inert toxicity. Given the substantial economic reason, it is important to identify the biodegradable carrier substances with respect to maintaining its functional properties (viability, high survival rates, prolonged shelf life, lower susceptibility to contamination and harmless to fungal cells) under adverse climatic conditions (Turgeman et al., 2016). In this regard, Marghoob et al. (2023) developed mud-based bioformulations comprised of three bacterial strains together with *Trichoderma harzianum* for wheat crops and have found their ability to exhibit significant improvement in agronomic traits under saline soils. One of the key findings highlighted by Namasivayam et al. (2024) that evaluates the compatibility of the *Trichoderma viride* bioformulation and its impact on the biocontrol efficacy against *Fusarium oxysporum*. The nanoparticle treated-formulation (1000 μg/ml) was found to be effective in the disease management with high fungal viability. Of equal importance are studies on the progressive adaptability of active ingredients encapsulation including cell-wall-degrading enzymes and bioactive metabolites into bioformulations to tackle spore dormancy issues. For example, Tewari et al. (2020) amalgamated exopolysaccharides from *Bradyrhizobium* spp. when dealing with target pathogens. Some of the relevant fields that need to be taken into consideration are the biosafety of introduced microbial consortia as these bioformulations potentially a pose risk to both the environment and human health. In response to that, Vilchez et al. (2016) have outlined the guideline procedure named as the Environmental and Human Safety Index (EHSI) to access any pathogenicity and potential risk associated with newly indigenous microbial species. Overall, although the development of *Trichoderma*-based bioformulation products is relatively well-established, integrating innovative approaches with a strong commitment to sustainability is essential to unlocking their full potential as an effective biological control solution.

4. Conclusion

A growing number of studies have proven that the *Trichoderma*-bacterial network is an essential subcommunities of the microbial ecosystem and plays a crucial role in agricultural productivity. It thus comes as no surprise that many biocontrol success stories rendered by *Trichoderma* are choreographed by the bacterial symbionts. Understanding the molecular mechanisms of fungal-bacterial inoculation in the provision of biocontrol is a key in delivering mutualistic benefits in the open field implementation. Standardizing qualitative and quantitative methods can facilitate mechanistic and reproducible exploration of *Trichoderma*-bacterial interactions. No doubt, deciphering the spoken communication language between this bipartite interaction helps us to strategize advanced molecular tools intervention to improve the next generation of bioformulation reproducibility. To this end, the fungal-bacterial relationship can be portrayed as a relatively simple model for the study of eukaryotes-bacteria interactions. This interaction also serves as a practical example for the study of evolutionary theory which can in turn influence ecosystem functioning. Query on how interaction remains metabolically stable and resilient along spatiotemporal environmental disturbances remains unfulfilled. The fungal-bacterial partnership research not only needs a better understanding but also harnesses them as a foundational model system for future microbial reprogramming approaches.

CRediT authorship contribution statement

Mohd Din Abd Rahman Jabir: Writing – original draft, Visualization, Resources, Project administration, Investigation, Conceptualization. **W.H. Yong Jean:** Writing – review & editing. **Othman Nor Zalina:** Writing – review & editing, Supervision, Resources, Project administration, Funding acquisition. **Mohamad Azam Zaheda:** Investigation, Conceptualization.

Declaration of Competing Interest

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

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Data availability

No data was used for the research described in the article.

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