Some members of root-associated Bacillus species have been developed as biocontrol agents due to their contribution to plant protection by directly interfering with the growth of pathogens or by stimulating systemic resistance in their host. As rhizosphere-dwelling bacteria, these bacilli are surrounded and constantly interacting with other microbes via different types of communications. With this review, we provide an updated vision of the molecular and phenotypic responses of Bacillus upon sensing other rhizosphere microorganisms and/or their metabolites. We illustrate how Bacillus spp. may react by modulating the production of secondary metabolites, such as cyclic lipopeptides or polyketides. On the other hand, some developmental processes, such as biofilm formation, motility, and sporulation may also be modified upon interaction, reflecting the adaptation of Bacillus multicellular communities to microbial competitors for preserving their ecological persistence. This review also points out the limited data available and a global lack of knowledge indicating that more research is needed in order to, not only better understand the ecology of bacilli in their natural soil niche, but also to better assess and improve their promising biocontrol potential.

Keywords: Bacillus, rhizosphere, bioactive secondary metabolites, microbial interaction, biocontrol, molecular cross-talk, phenotype modulation
been done in the last years to clarify the phylogeny of the phytoolgy of the Bacillus species, such as Bacillus subtilis, B. amyloliquefaciens, B. atrophaeus, B. subtilis subspecies subtilis, B. licheniformis, B. pumilus, and B. siamensis with potential as biocontrol agents (Expósito et al., 2017; Fira et al., 2018; Maksimov et al., 2020), and which led to some confusion in species names but also to misassignments (Dunlap et al., 2016; Fan et al., 2017; Harwood et al., 2018; Du, 2019; Torres Manno et al., 2019). Many isolates, such as strains FZB42, QST713, or SQR9 formerly assigned to the B. subtilis or B. amyloiquiaceicins species have been reclassified as B. velezensis representing the model species for plant-associated bacilli (Dunlap et al., 2016; Fan et al., 2017). A large part of the genome of these species is devoted to the production of antimicrobial compounds with up to 12% annotated as involved in the synthesis of bioactive secondary metabolites (Molinatto et al., 2016; Fan et al., 2017; Pandin et al., 2018).

Non-ribosomal metabolites are synthesized either by polyketide synthases (PKS) or non-ribosomal peptide synthase (NRPS), both acting as assembly lines catalyzing different steps for the incorporation of amino acid residues (Dutta et al., 2014; Winn et al., 2016; Bozhuyuk et al., 2019). The three main families of Bacillus CLPs are surfactins, fengycins, and iturins (Figure 1). According to this limited number of families identified so far, the structural diversity of Bacillus CLPs may appear quite limited compared to other bacterial genera, such as Pseudomonas, for which many more different groups have been discovered (Geudens and Martins, 2018; Götze and Stallforth, 2020). However, reduced specificity of adenylation domains allows substitutions at specific places in the peptide chain and the NRPS machinery can bind different fatty acids with various chain lengths in the initiation step leading to co-production of various homologs within the three families as illustrated in Figure 1 (Kraas et al., 2010; Bozhuyuk et al., 2019). Interestingly, some CLP peptidic variants are synthesized through species-specific clusters, like pumilacidin and lichenysin which are only produced respectively by B. pumilus and B. licheniformis (Figure 1).

The three different types of CLPs retain specific but complementary functions considering biocontrol efficiency and, more generally, ecological fitness of the producing strains. By contributing to motility and biofilm formation, surfactins are involved in colonization of plant tissues which indirectly allow Bacillus to outcompete phytopathogens for space and nutrients. Surfactins are also involved in the molecular cross-talk with the host and it is well-characterized as an elicitor of plant immunity leading to ISR (Ongena and Jacques, 2008; Henry et al., 2011; Garcia-Gutiérrez et al., 2013; Cavoy et al., 2015; Chowdhury et al., 2015a). Direct antibiotic activity of surfactins at biologically relevant concentrations toward soil-dwelling or plant-associated microbes has been only occasionally reported (Qi et al., 2010; Liu et al., 2014). By contrast, fengycins and iturins are best characterized for their antifungal activities against a wide range of plant pathogens (Caulier et al., 2019; Rabbee et al., 2019). This is mainly due to their ability to perturb fungal cell membrane integrity resulting in cytoplasm leakage and finally hyphae death and inhibition of spore germination (Chitarrà et al., 2003; Romero et al., 2007; Delèu et al., 2008; Etchegaray et al., 2008; Gong et al., 2015; Gao et al., 2017; Zhang and Sun, 2018). The three CLPs retain some selectivity but may also act synergistically to inhibit fungal growth (Liu et al., 2014). The lipid composition of the plasma membrane could explain differences in the sensitivity of fungal targets to one or more CLPs (Wise et al., 2014; Fiedler and Heerklotz, 2015).

Besides lipopeptides, most species of the B. subtilis group also produce other non-ribosomal oligopeptide derivatives, such as bacilysin, chlorotetaine, bacitracins, and rhizoxincs which are known to be efficient as antibacterial compounds targeting cell wall biosynthesis (Zhao and Kuipers, 2016). The siderophore bacillibactin is highly conserved in the B. subtilis group (Figure 1)
Bacillus responses to plant-associated microbes

The three main PKs produced by Bacillus are synthesized via hybrid NRPS/PKS systems leading to the condensation of small carboxylic acids mediated by core domains of the corresponding enzyme machinery but some PKs are specifically produced by some species or strains (Brötz et al., 1998; van Kuijk et al., 2012; Arguelles Arias et al., 2013; Scholz et al., 2014; Torres Manno et al., 2019). These BSMs are responsible for growth inhibition of Gram-positive bacteria by acting via different modes of action (Abriouel et al., 2011; Acedo et al., 2018).

**PERCEPTION OF FUNGI TRIGGERS THE PRODUCTION OF APPROPRIATE BSMs**

Several works have illustrated the impact of phytopathogenic fungi on BSMs production by soil bacilli. Some B. amyloliquefaciens, B. velezensis, and B. subtilis strains respond to the presence of antagonistic fungi by stimulating the production of the antifungal CLPs fengycins and/or iturins (Table 1). Not only the production of specific CLPs varies in a species-dependent manner but it is also highly dependent on the interacting fungal species. For example, much higher production of iturins and fengycins by B. subtilis SQR9 was observed in confrontation with *Pythium aphanidermatum* and *Fusarium oxysporum* but not with *Botrytis cinerea* (Cawoy et al., 2015). Further, upon interaction with fungi, some B. velezensis strains (SQR9, FZB42, and S499) overproduced either iturins or fengycins (Li et al., 2014; Chowdhury et al., 2015b; Kulimushi et al., 2017). For instance, Li et al. (2014) showed that when confronted with *Sclerotinia sclerotiorum*, B. velezensis SQR9 overproduces bacillomycin **D** (iturin family), but not fengycins. An overproduction of bacillomycin along with a reduced production of fengycins was also reported by Chowdhury et al. (2015b) upon interaction with *Botrytis cinerea* (Cawoy et al., 2015). Furthermore, interaction with *Fusarium oxysporum* showed that when confronted with *Sclerotinia sclerotiorum*, B. velezensis SQR9 overproduced bacillomycin **D** (iturin family), but not fengycins. An overproduction of bacillomycin along with a reduced production of fengycins was also reported by Chowdhury et al. (2015b) upon interaction with *Botrytis cinerea* (Cawoy et al., 2015). Further, upon interaction with fungi, some B. velezensis strains (SQR9, FZB42, and S499) overproduced either iturins or fengycins (Li et al., 2014; Chowdhury et al., 2015b; Kulimushi et al., 2017). For instance, Li et al. (2014) showed that when confronted with *Sclerotinia sclerotiorum*, B. velezensis SQR9 overproduces bacillomycin **D** (iturin family), but not fengycins. An overproduction of bacillomycin along with a reduced production of fengycins was also reported by Chowdhury et al. (2015b) upon *Botrytis cinerea* interaction with *Rhizoctonia solani* in the rhizosphere of lettuce plants. Differentially, Kulimushi et al. (2017), showed that strains S499 and FZB42 improved production of fengycin but not iturins upon interaction with *Rhizomucor variabilis*. Most of these studies also indicated that fengycins and iturins are the main BSMs responsible for antifungal activities (Table 1). Thus, *Bacillus* cells could specifically sense the presence of fungal competitors and accordingly overproduce appropriate antifungal BSMs to outcompete the interacting fungi. Moreover, besides modulating the production of fengycins and iturins, some strains of *B. velezensis* (SQR9, FZB42, and QST713) and *B. subtilis* (B9-5) may overproduce surfactins when sensing phytopathogenic fungi (Li et al., 2014; Chowdhury et al., 2015b; DeFilippi et al., 2018; Pandin et al., 2019). In support to this hypothesis, surfactin production of *B. velezensis* FZB42 was highly induced in the presence of fungal pathogen *R. solani* in the lettuce rhizosphere where it was found as the main produced compound (Chowdhury et al., 2015b). A similar response was recorded when *B. velezensis* SQR9 was confronted with iron limitation in the environment. It allows *Bacillus* to efficiently acquire Fe$^{3+}$ and other metals (Mietheke et al., 2006, 2008; Li et al., 2014) thereby depriving phytopathogens of this essential element (Miethke et al., 2006; Niewus et al., 2017). Polyketide biosynthesis is performed by successive condensation of small carboxylic acids mediated by core domains of the corresponding enzyme machinery but some PKs are synthesized via hybrid NRPS/PKS systems leading to the integration of amino acid residues (Piel, 2010; Olishhevskaya et al., 2019). The three main PKs produced by *Bacillus* are difficidins, macrolactins, and bacillales, the latter being more widespread across species (Figure 1). The main PKs role is related to their antibacterial activity via the ability to inhibit protein biosynthesis in numerous phytopathogenic bacteria but certain antifungal activity has been reported for bacillales and macrolactins (Caulier et al., 2019; Olishhevskaya et al., 2019).

Rotisomally synthetized BSMs encompass bacteriocins and lantibiotics including plantazolicin, subtilin, ericin, mersacidin, amylosyn, and amylocyclicin that are specifically produced by some species or strains (Brötz et al., 1998; van Kuijk et al., 2012; Arguelles Arias et al., 2013; Scholz et al., 2014; Torres Manno et al., 2019). These BSMs are responsible for growth inhibition of Gram-positive bacteria by acting via different modes of action (Abriouel et al., 2011; Acedo et al., 2018).
S. sclerotiorum and Phytophthora parasitica (Li et al., 2014) or when B. subtilis B9-5 interacted in liquid medium with Rhizopus stolonifer (DeFilippi et al., 2018). In contrast to fengycins and iturins, surfactins are not strong direct antifungal metabolites in biologically relevant concentrations (Raaijmakers and Mazzola, 2012). Thus, it stays unclear why Bacillus responded by surfactin overproduction to the presence of antagonistic fungi. A possible explanation could be rooted in its global role promoting the rhizosphere and thereby, contributing to competition for nutrients and space with the interfering fungi (Ongena and Jacques, 2008; Rabbee et al., 2019).

Even though the siderophore bacillibactin is produced by all members of the B. subtilis species complex (Figure 1), its possible overproduction upon microbial interactions has been poorly investigated. Interestingly, the work of Li et al. (2014) showed that B. velezensis SQR9 overproduces bacillibactin when grown in the presence of a range of fungi including V. dahliae, S. sclerotiorum, F. oxysporum, R. solani, F. solani, and P. parasitica. This may be interpreted as a response of the bacterium to some iron-limitation in the medium caused by the fungi via the release of their own chelatants.

In B. subtilis, the expression of many BSMs biosynthesis genes is transcriptionally fine-tuned by compound-specific regulation but also by global regulators governing the transition to crucial developmental processes like motility, biofilm formation and sporulation (Inaoka et al., 2009; López et al., 2009; Vargas-Bautista et al., 2014). Fungal triggers may affect both types of regulatory systems involved in BSMs production. For instance, upon sensing F. verticillioides, the global stress-related regulator SigB is activated in B. subtilis NCIB3610 which in return enhances surfactin production (Bartolini et al., 2019). In interaction with F. culmorum under biofilm-conducive conditions, B. subtilis Bs12 down-regulates the expression of the sinR gene known as a repressor of biofilm formation which also negatively regulates surfactin production (Kearns et al., 2005; Khezri et al., 2016; Zhi et al., 2017). These observations strongly suggest that specific soluble signals, emitted by fungal pathogens, could be perceived by bacilli which in turn modulate BSMs synthesis. As observed by Bartolini et al. (2019), cells of the Bacillus colony, physically close to the fungal culture, responded to signals by over-expressing genes coding for transcription factors involved in CLPs synthesis regulation. In contrast, colony cells positioned on the opposite side of the fungi did not react to the fungus (Bartolini et al., 2019). This phenomenon indicates that the specific fungal metabolite diffuses on a short distance and has an influence on closely located Bacillus cells. Currently, no fungal compounds have been identified as triggers of BSM stimulation in Bacillus. Nonetheless, few commonly produced metabolites by Fusarium species were suggested to modify Bacillus behavior. It was shown that two cyclic depsipeptides (enniatins B1 and enniatins A1) and a pyrone (lateropyrone) had an antagonistic effect on B. subtilis growth (Ola et al., 2013). Fusaric acid also modified antibacterial activity of B. mojavensis but it was not related to a decrease in the production of specific BSMs (Bacon et al., 2004, 2006; Bani et al., 2014). These metabolites could also play a triggering role at sub-inhibitory concentration and could have an inducible effect on the range of Bacillus responses as has been shown for other signal metabolites (Bleich et al., 2015; Liu et al., 2018).

### Bacillus PhenoType is Modulated Upon Perception of Bacterial Competitors

Some BSMs may also act as molecular determinants driving outcomes of interactions between B. subtilis and bacterial competitors as illustrated for the bacilane polyketide displaying an essential protective role for survival in competition with Streptomyces soil isolates (Straight et al., 2007; Barger et al., 2012). However, there are few direct evidences for enhanced expression of BSMs upon interbacteria interactions. The only convincing examples involve the interaction of plant-associated bacilli with plant pathogens, such asRalstonia solanacearum (Almoneafy et al., 2014) and Pseudomonas fuscovaginae (Kakar et al., 2014). In these two studies, improved expression of surfactin, bacilysin, and iturin biosynthesis genes were observed when Bacillus and pathogens were grown together in dual-cultures. Nevertheless, no clear indication about the enhanced production of the aforementioned BSMs based on their quantification nor improved antibacterial activities of Bacillus was presented as a result of this interaction.

Interestingly, at the phenotypical level, the development of soil bacilli is differentially altered upon sensing other bacteria from the same natural environment. Some of these phenotypical changes can be associated or due to a modulated production of specific BSMs. First, exogenous antibiotics or signals may stimulate biofilm formation which depends, to some extent, on surfactin production (López et al., 2009) and which may be viewed as a defensive response against exogenous toxic compounds and/or infiltration by competitors (Flemming et al., 2016; Townsley and Shank, 2017; Molina-Santiago et al., 2019). For instance, B. subtilis increased its relative subpopulation of biofilm matrix-producing cells in response to small molecules secreted by other bacterial species (López et al., 2009; Shank et al., 2011). The same phenomenon was illustrated for thiazolyl peptides emitted by closely related species, such as B. cereus and putatively formed by other soil microbes, such as Streptomyces isolates (Bleich et al., 2015). However, no change in surfactin production associated with the stimulation of biofilm was reported in these studies.

Besides biofilm formation, other mechanisms drive bacteria to initiate protective responses upon the detection of competitors. The flagellum-independent sliding motility is considered as an adaptive mechanism that allows bacterial cells to physically relocate in the context of a competitive interaction (Wadhams and Armitage, 2004; Jones et al., 2017; McCully et al., 2019). Upon sensing S. venezuelae, the B. subtilis ability to slide was increased (Liu et al., 2018). It depends in part on the production of surfactin (Grau et al., 2015; van Gestel et al., 2015) but a potential boost in lipopeptide synthesis upon the perception of the Streptomyces challenger was not demonstrated. Chloramphenicol and derivatives produced by S. venezuelae were identified as
molecular triggers acting at subinhibitory concentrations for inducing *Bacillus* motility (Liu et al., 2018).

Multiple bacteria promote sporulation in *B. subtilis* which represents another example of alteration of the physiological development of this species. In a context of distant interactions, exogenous siderophores accelerate the differentiation of *Bacillus* cells into spores. It was notably shown for enterobactin from *E. coli* and for ferrioxamine E produced by *Streptomycetes* (Grandchamp et al., 2017). In iron-limited environments, *B. subtilis* cells would thus respond by taking up those "piratable" siderophores and start sporulating. This is not a general response to xenosiderophores since for instance, pyochelin from *Pseudomonas* does not affect *Bacillus* sporulation (Molina-Santiago et al., 2019). Nevertheless, the ability of siderophores

### TABLE 1 | Change in expression and bioactivity of BSMs produced by members of *B. subtilis* group, upon interaction with fungal species.

| BSMs     | Change in expression | Involvement in antifungal activity | *Bacillus* species (strains) | *Fungal* species | References |
|----------|----------------------|-----------------------------------|-------------------------------|-----------------|-----------|
| Fengycins| 0                    | Yes                               | *B. subtilis* (98S)           | *B. cinerea*     | Chowdy et al., 2015 |
| +        | Yes                  |                                   | *B. subtilis* (98S)           | *F. oxyporum*    | Chowdy et al., 2015 |
| +        | No                   |                                   | *B. velezensis* (98S)         | *P. aphanidermatum* | Chowdy et al., 2015 |
| +        | Yes                  |                                   | *B. velezensis* (FZB42)       | *R. variabilis*  | Kulimushi et al., 2017 |
| 0        | Yes                  |                                   | *B. velezensis* (QST713)      | *R. variabilis*  | Kulimushi et al., 2017 |
| +        | Yes                  |                                   | *B. velezensis* (S499)        | *Verticillium dahliae* | Li et al., 2014 |
| +        | Yes                  |                                   | *B. velezensis* (SQR9)        | *F. oxyporum*    | Li et al., 2014 |
| +        | Yes                  |                                   | *B. velezensis* (SQR9)        | *Phytophthora parasitica* var. *nicotianae* | Li et al., 2014 |
| -        | Mediating the plant defense expression |                                   | *B. velezensis* (FZB42)       | *R. solani*     | Chowdy et al., 2015 |
| +        | ND                   |                                   | *B. subtilis* (B9-5)          | *R. stolonifer*  | DeFilippi et al., 2018 |
| +        | ND                   |                                   | *B. subtilis* (B9-5)          | *Fusarium sambucinum* | DeFilippi et al., 2018 |
| +        | ND                   |                                   | *B. subtilis* (B9-5)          | *V. dahliae*     | DeFilippi et al., 2018 |
| +        | ND                   |                                   | *B. velezensis* (QST713)      | *Trichoderma aggressivum f. europeaeum* | Pandin et al., 2019 |
| Iturins  | 0                    | Yes                               | *B. subtilis* (98S)           | *B. cinerea*     | Chowdy et al., 2015 |
| +        | Yes                  |                                   | *B. subtilis* (98S)           | *F. oxyporum*    | Chowdy et al., 2015 |
| +        | No                   |                                   | *B. velezensis* (SQR9)        | *P. aphanidermatum* | Chowdy et al., 2015 |
| +        | No                   |                                   | *B. velezensis* (SQR9)        | *V. dahliae*     | Li et al., 2014 |
| +        | Yes                  |                                   | *B. velezensis* (SQR9)        | *S. sclerotium*  | Li et al., 2014 |
| +        | Yes                  |                                   | *B. velezensis* (SQR9)        | *F. oxyporum*    | Li et al., 2014 |
| +        | Yes                  |                                   | *B. velezensis* (SQR9)        | *P. parasitica*  | Li et al., 2014 |
| +        | Mediating the plant defense expression |                                   | *B. velezensis* (FZB42)       | *R. solani*     | Chowdy et al., 2015 |
| +        | Yes                  |                                   | *B. velezensis* (SQR9)        | *S. sclerotium*  | Li et al., 2014 |
| +        | Yes                  |                                   | *B. velezensis* (SQR9)        | *R. solani*      | Li et al., 2014 |
| +        | Yes                  |                                   | *B. velezensis* (SQR9)        | *Fusarium solani* | Li et al., 2014 |
| +        | Yes                  |                                   | *B. velezensis* (SQR9)        | *P. parasitica*  | Li et al., 2014 |
| +        | Mediating the plant defense expression |                                   | *B. velezensis* (FZB42)       | *R. solani*     | Chowdy et al., 2015 |
| +        | ND                   |                                   | *B. subtilis* (B9-5)          | *R. solani*     | DeFilippi et al., 2018 |
| +        | ND                   |                                   | *B. subtilis* (B9-5)          | *F. sambucinum*  | DeFilippi et al., 2018 |
| +        | ND                   |                                   | *B. subtilis* (B9-5)          | *V. dahliae*     | DeFilippi et al., 2018 |
| +        | ND                   |                                   | *B. velezensis* (QST713)      | *T. aggressivum f. europeaeum* | Pandin et al., 2019 |
| Surfactins| +                    | Yes                               | *B. velezensis* (SQR9)        | *S. sclerotium*  | Li et al., 2014 |
| +        | Yes                  |                                   | *B. velezensis* (SQR9)        | *R. solani*      | Li et al., 2014 |
| +        | Yes                  |                                   | *B. velezensis* (SQR9)        | *Fusarium solani* | Li et al., 2014 |
| +        | Yes                  |                                   | *B. velezensis* (SQR9)        | *P. parasitica*  | Li et al., 2014 |
| +        | Mediating the plant defense expression |                                   | *B. velezensis* (FZB42)       | *R. solani*     | Chowdy et al., 2015 |
| +        | ND                   |                                   | *B. subtilis* (B9-5)          | *R. solani*     | DeFilippi et al., 2018 |
| +        | ND                   |                                   | *B. subtilis* (B9-5)          | *F. sambucinum*  | DeFilippi et al., 2018 |
| +        | ND                   |                                   | *B. subtilis* (B9-5)          | *V. dahliae*     | DeFilippi et al., 2018 |
| +        | ND                   |                                   | *B. velezensis* (QST713)      | *T. aggressivum f. europeaeum* | Pandin et al., 2019 |
| Bacillibactin| +                   | Yes                               | *B. velezensis* (SQR9)        | *V. dahliae*     | Li et al., 2014 |
| +        | No                   |                                   | *B. velezensis* (SQR9)        | *S. sclerotium*  | Li et al., 2014 |
| +        | No                   |                                   | *B. velezensis* (SQR9)        | *F. oxyporum*    | Li et al., 2014 |
| +        | Yes                  |                                   | *B. velezensis* (SQR9)        | *R. solani*      | Li et al., 2014 |
| +        | Yes                  |                                   | *B. velezensis* (SQR9)        | *F. solani*      | Li et al., 2014 |
| +        | Yes                  |                                   | *B. velezensis* (SQR9)        | *P. parasitica*  | Li et al., 2014 |

"0" indicates no changes, "+" enhanced and, "-" decreased BSMs production by *Bacillus* upon interaction with fungi. "Yes" indicates fungitoxic activity, "No" no antifungal activity, "ND" indicates that BSMs with antifungal activity are not detected.
to alter cellular differentiation in *B. subtilis* suggests that those molecules are likely to mediate complex microbial interactions in iron-depleted conditions, as often met in a soil environment. However, induction of *B. subtilis* sporulation by other bacteria may also occur in a cell-to-cell contact situation. Upon interaction with *P. chlororaphis*, its type VI secretion system acted as a trigger for sporulation, independently from its established role as cargo for delivering toxic effectors into the target *Bacillus* cells (García-Bayona and Comstock, 2018; Molina-Santiago et al., 2019).

That said, interspecies interactions may also result in inhibition rather than in stimulation of key developmental processes determining the fate of *Bacillus* multicellular communities. As an example, 2,4-diacetylphloroglucinol, a broad-spectrum antibiotic synthesized by fluorescent *Pseudomonas*, alters colony morphology, inhibits biofilm formation and sporulation in *B. subtilis* populations grown adjacent to *P. protegens* colonies (Powers et al., 2015). This antibiotic seems to act as an interspecific signaling molecule that inhibits bacterial differentiation at subinhibitory concentrations (Powers et al., 2015).

**CONCLUSION**

Here we provide an overview of the phenotypic and molecular responses of plant-beneficial soil bacilli upon sensing signals from other microorganisms that can be encountered in the rhizosphere niche. It is clear that BSMs production by *Bacillus* can be modulated upon interactions with other microbes and that key BSM-driven developmental processes may undergo unsuspected changes. It somehow illustrates the flexibility of these bacteria in re-directing their secondary metabolome to adapt environmental fitness upon sensing the presence of neighboring microorganisms. Nevertheless, the molecular mechanisms integrating the perception of exogenous triggers with a regulatory response leading to enhanced production of BSMs still remain unclear.

A significant boost in BSMs production by soil bacilli has been reported in most cases as an outcome from interactions with plant pathogenic fungi. This is of value in the context of biocontrol of fungal pathogens since direct antagonism is considered as the most powerful mode of action for suppression of plant diseases (Favel, 2005; Frey-Klett et al., 2011; Köhl et al., 2019). By contrast, direct evidence for an impact of interbacteria interactions on the expression of the secondary metabolome in *Bacillus* is still globally missing. Nevertheless, interaction-mediated variations in colony morphology, motility, biofilm formation, or sporulation illustrate how soil bacilli can protect themselves from antimicrobials emitted by bacterial competitors.

Such an impact on those key developmental processes should thus be coupled with significant modulation in the production of specific BSMs underpinning these phenotypes. Depending on the concentration, these BSMs would then act as antimicrobials in interference competition or as signals in cooperative interspecies communication processes not necessarily affecting the growth of the partners (Bleich et al., 2015; Liu et al., 2018). However, this has yet to be thoroughly demonstrated and future examination of developmental controls for BSMs biosynthesis will likely bring light upon the key principles driving environmental fitness of soil bacilli as intrinsically influenced by interspecies competition.

From an ecological viewpoint, further investigations would also help to better understand why soil amendment with selected bacilli, even at high doses, do not durably impact the composition of the rhizosphere microbiome despite their huge arsenal in antimicrobial weapons (Correa et al., 2009; Chowdhury et al., 2013; Kröber et al., 2014; Qiao et al., 2017) and by contrast with some other bacteria and fungi (Buddrus-Schiemann et al., 2010; Chowdhury et al., 2013; Erlacher et al., 2014; Thomas and Sekhar, 2016; Wu et al., 2016). Those bacilli may thus provide protection to their host plant toward microbial pathogen ingress but would avoid detrimental effect on its naturally selected beneficial microbiome which is of prime interest for future application as biocontrol agents.

**AUTHOR CONTRIBUTIONS**

SA, TM, and MO conceived the idea, designed the outlines of the review, and wrote the manuscript. All authors listed have made a substantial, direct and intellectual contribution to the work, and approved it for publication.

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