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INVITED REVIEW

Bidirectional plant-mediated interactions between rhizobacteria and shoot-feeding herbivorous insects: a community ecology perspective

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Abstract. 1. Plants interact with various organisms, aboveground as well as belowground. Such interactions result in changes in plant traits with consequences for members of the plant-associated community at different trophic levels. Research thus far focussed on interactions of plants with individual species. However, studying such interactions in a community context is needed to gain a better understanding.

2. Members of the aboveground insect community induce defences that systemically influence plant interactions with herbivorous as well as carnivorous insects. Plant roots are associated with a community of plant-growth promoting rhizobacteria (PGPR). This PGPR community modulates insect-induced defences of plants. Thus, PGPR and insects interact indirectly via plant-mediated interactions.

3. Such plant-mediated interactions between belowground PGPR and aboveground insects have usually been addressed unidirectionally from belowground to aboveground. Here, we take a bidirectional approach to these cross-compartment plant-mediated interactions.

4. Recent studies show that upon aboveground attack by insect herbivores, plants may recruit rhizobacteria that enhance plant defence against the attackers. This rearranging of the PGPR community in the rhizosphere has consequences for members of the aboveground insect community. This review focusses on the bidirectional nature of plant-mediated interactions between the PGPR and insect communities associated with plants, including (a) effects of beneficial rhizobacteria via modification of plant defence traits on insects and (b) effects of plant defence against insects on the PGPR community in the rhizosphere. We discuss how such knowledge can be used in the development of sustainable crop-protection strategies.

Key words. Belowground-aboveground interactions, community ecology, inducible defence, insect-plant interactions, plant growth promoting rhizobacteria.

Introduction

Plants are members of a diverse community that includes micro-organisms and macro-organisms, aboveground and belowground. The most speciose groups consist of micro-organisms and insects (Van der Putten *et al.*, 2001;

Stam *et al.*, 2014; Cordovez *et al.*, 2019). Plants have evolved various defences that have extensive consequences for the plant-associated community (Ohgushi, 2005; Stam *et al.*, 2014). In this review, we focus on interactions between plants, rhizobacteria, and herbivorous insects. Most rhizobacteria-plant-insect interactions so far have been studied from a single-species approach (Pineda *et al.*, 2010; Pangesti *et al.*, 2013; Biere & Goverse, 2016; Gadhawe & Gange, 2018). Yet, these studies pave the way for a community approach.

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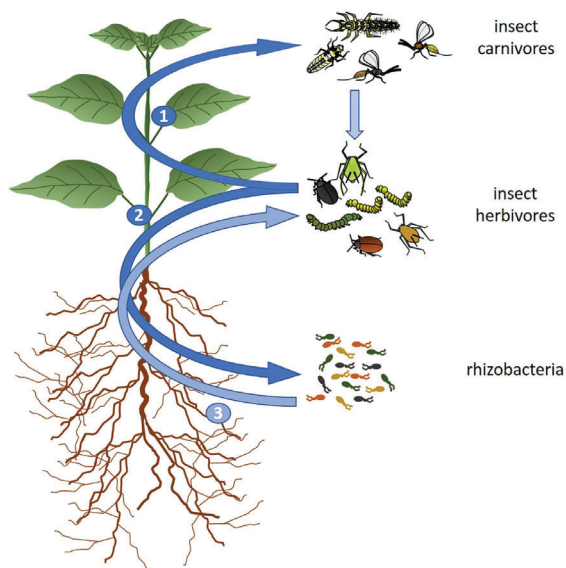


Fig. 1. Plants may recruit other organisms that assist them in their defence. Upon insect herbivory on the shoot, (1) plants produce herbivore-induced volatiles that attract parasitoids or predators that attack the herbivore (Stam *et al.*, 2014; Turlings & Erb, 2018) and (2) alter their root exudates thus recruiting rhizobacteria from the bulk soil to the rhizosphere. These rhizosphere microbes (3) alter the plant's phenotype thus affecting the performance of shoot-feeding insect herbivores (Hu *et al.*, 2018). [Colour figure can be viewed at wileyonlinelibrary.com].

Community approach to plant defence

Plant defence has long been considered an intrinsic plant trait that is expressed independent of interactions with other organisms. However, it has become clear that plant-associated organisms can be a component of plant defence as well (Price *et al.*, 1980). For instance, upon damage by herbivorous insects plants can actively recruit the enemies of insect herbivores, such as carnivores that thereby act as an indirect defence (Stam *et al.*, 2014; Turlings & Erb, 2018). As a result of the modification of the plant's phenotype, this induced indirect defence leads to changes in the plant-associated insect community, which has mostly been studied for aboveground communities (Ohgushi, 2005; Poelman *et al.*, 2008; Stam *et al.*, 2014). In addition, communities belowground, including the microbiome around the roots, may also be an important component of plant defence (Berendsen *et al.*, 2012; Rasmann & Turlings, 2016). For instance, soil microbes that assist the plant in the defence against pathogens or herbivorous insects may be recruited to the rhizosphere (Berendsen *et al.*, 2018; Hu *et al.*, 2018) (Fig. 1). This involves a rearrangement of the microbial community belowground (Berendsen *et al.*, 2018).

Thus, plant responses to attack influence the micro-organisms and macro-organisms in the associated community of beneficial organisms aboveground as well as belowground, thereby enhancing plant defence against various attackers. Although microbes and insects colonise both plant roots and shoots, we focus on cross-compartment plant-mediated interactions between root-associated microbes and shoot-associated insects.

Previous reviews have addressed such cross-compartment interactions especially by focussing on unidirectional effects of rhizosphere microbes on aboveground insects (Pineda *et al.*, 2010; Pangesti *et al.*, 2013; Biere & Goverse, 2016; Gadhave & Gange, 2018). Here, we focus on bidirectional plant-mediated interactions.

Bidirectional nature of plant-mediated interactions between rhizobacteria and shoot-associated insects

Studies on the effects of rhizosphere bacteria on plant defence initially focussed mainly on the effects of individual bacterial species or strains on plant and insect performance (Pineda *et al.*, 2010; Hol *et al.*, 2013; Pangesti *et al.*, 2013; Gadhave & Gange, 2018) (Table S1). During recent years, the focus has shifted by taking into consideration the full microbial community (Pineda *et al.*, 2017; Dini-Andreote & Raaijmakers, 2018; Cordovez *et al.*, 2019). Similarly, studies on the effects of insect herbivores have long focussed on effects of individual species, but now shift to a community approach as well (Van Zandt & Agrawal, 2004; Utsumi *et al.*, 2013; Stam *et al.*, 2014; Poelman & Kessler, 2016; Ando *et al.*, 2017). After initial studies on effects of belowground microbes on aboveground insect herbivores (Pineda *et al.*, 2010; Pangesti *et al.*, 2013; Gadhave & Gange, 2018), the reverse direction gains momentum in recent years (Berendsen *et al.*, 2018; Hu *et al.*, 2018). Thus, the unidirectional focus is being replaced by a bidirectional approach to plant-mediated interactions between the belowground microbial community and the aboveground insect community. Here, we take a bidirectional approach and address the effects of (1) beneficial rhizobacteria via alterations in plant defence traits on the insect community as well as (2) the effects of plant defence against insects on the bacterial community in the rhizosphere. Building blocks for this review consist of studies on effects of individual bacteria and insect species. These will be integrated to present a community perspective towards these bidirectional cross-compartment interactions.

Microbial community associated with roots

The rhizosphere harbours a species-rich microbial community that influences plant traits such as growth and defence (Mendes *et al.*, 2011; Berendsen *et al.*, 2012). Plants influence the composition of this microbial community. They are especially known to influence the bacterial community, much more than the fungal community. Therefore, this review focusses especially on the bacterial community of the rhizosphere and its interactions with plants and foliage-feeding insects. For plant-mediated interactions between belowground fungi and aboveground insects, we refer to various reviews on that topic (Hartley & Gange, 2009; Jung *et al.*, 2012; Biere & Goverse, 2016).

Beneficial effects of rhizobacteria on plant growth and defence against insect herbivores

Beneficial rhizobacteria, among which *Bacillus* spp. and *Pseudomonas* spp. have been most extensively studied (Table S1),

are known to promote plant growth and enhance plant defence (Pineda *et al.*, 2010; Pieterse *et al.*, 2014) and have, therefore, been termed plant growth-promoting rhizobacteria (PGPR). In addition to physical contact between plant and bacteria also rhizobacterial volatiles alone can influence plant traits (Ryu *et al.*, 2004; Zhang *et al.*, 2008).

Table S1 provides a literature review of the effects of rhizobacteria on herbivorous insects. Most studies (52 out of 74) have been conducted with species and strains of the genera *Bacillus* and *Pseudomonas*. The effects on aphids (39 studies) and caterpillars (31 studies) are best studied and in most cases effects of rhizobacteria on insect performance are negative. These effects are plant-mediated and result from changes in plant traits. Most studies addressed the effects of individual microbes. Among the 74 studies, only five assessed the effects of the natural microbiome on insect performance. Yet, it is likely that interactions of a plant with individual rhizobacterial species influence interactions of the plant with other rhizobacterial species. Such indirect effects of rhizobacteria on plant traits may subsequently affect insect herbivores. Such indirect effects should be studied through investigating the effects of combinations of rhizobacteria and, finally, the effects of the full rhizobacterial community. This literature analysis (Table S1) highlights the need for studies of systems that represent the wide bacterial and insect diversity in nature, including community approaches to understand how the belowground rhizobacterial community composition influences the aboveground insect community.

Root exudation influences rhizosphere bacterial community

Plant roots produce exudates (Berendsen *et al.*, 2012; Sharifi & Ryu, 2017), that contain many compounds, including primary metabolites such as sugars and amino acids as well as secondary metabolites, such as flavonoids, coumarins, glucosinolates, or plant hormones (Sasse *et al.*, 2018). These exudates represent a considerable cost to plants because they can represent up to 40% of a plant's photosynthates (Bais *et al.*, 2006; Berendsen *et al.*, 2012). The exudates can be released through both passive and active mechanisms (Badri & Vivanco, 2009; Huang *et al.*, 2014) and influence the composition of the microbial community in the rhizosphere (Smalla *et al.*, 2001; Bulgarelli *et al.*, 2013; Huang *et al.*, 2014), because bacteria are attracted to the rhizoplane through chemotaxis (Neal *et al.*, 2012; Zhang *et al.*, 2014; Wu *et al.*, 2015; Yuan *et al.*, 2015). Plant exudates influence microbial densities and density-dependent processes in the microbial community of the rhizosphere (Hassan & Mathesius, 2012).

Thus, plants influence the recruitment of bacteria to the rhizosphere as well as density-dependent processes that subsequently influence plant phenotype.

Insect community associated with plants

An individual plant may face the attack of hundreds of insect species, each of which is attacked by a diversity of carnivorous

insects (Schoonhoven *et al.*, 2005; Poelman *et al.*, 2008). Moreover, two-thirds of angiosperm plants interact with insect pollinators (Schoonhoven *et al.*, 2005; Bascompte & Jordano, 2007). Thus, plants are members of a diverse insect community consisting of species at different trophic levels (Stam *et al.*, 2014; Ikemoto *et al.*, 2017). This community is dynamic. For instance, early-season herbivory influences community composition throughout the season. On plants exposed to early-season herbivory, the community of insect herbivores is characterised by a higher proportion of specialists than generalists (Poelman *et al.*, 2010). Plants interact with this community both directly and indirectly (Morris *et al.*, 2007; Rasmann *et al.*, 2011; Stam *et al.*, 2014; Turlings & Erb, 2018). For instance, plant traits such as toxic secondary metabolites may negatively affect herbivores, whereas herbivore-induced plant volatiles affect the herbivores and subsequently the plants indirectly via the attraction of their natural enemies (Stam *et al.*, 2014; Turlings & Erb, 2018).

Induced plant defences against herbivorous insects modify plant phenotype both locally and systemically. These phenotypic changes are regulated by plant hormones (Pieterse *et al.*, 2012; Stam *et al.*, 2014). The two main phytohormonal pathways involved in regulating induced defences are the salicylic acid (SA) pathway and the combined jasmonic acid (JA) - ethylene (ET) pathway (Pieterse *et al.*, 2012; Verma *et al.*, 2016). The feeding mode of the insect herbivore affects the signalling pathway that is activated: the JA pathway is generally induced in response to biting-chewing insects, such as caterpillars or beetle larvae, whereas the SA pathway is especially induced by piercing-sucking phloem feeders. Cross-talk between the JA and SA signalling pathways allows plants to fine-tune defence responses (Pieterse *et al.*, 2012; Verma *et al.*, 2016). As a result of phytohormone induction, insect herbivory alters physical and chemical plant traits in a species-specific manner both locally and systemically. Such phenotypic changes may have consequences for the belowground microbial community.

Insect-induced changes in plant phenotype affect rhizobacterial community

Changes in root exudates induced by insect herbivores

One of the phenotypic changes induced by insect herbivory is the composition of plant root exudates (Tsunoda & van Dam, 2017; Hoysted *et al.*, 2018; Hu *et al.*, 2018). For instance, maize plants increase their carbon allocation to roots and root exudates upon feeding by the lubber grasshopper *Romalea guttata* (Holland *et al.*, 1996) and *Spodoptera littoralis* infestation of maize seedlings increases the release of benzoxazinoids by the roots (Marti *et al.*, 2013; Hu *et al.*, 2018). Herbivore-induced changes in root exudate composition result from phytohormonal induction and root exudation may also include phytohormones (Li *et al.*, 2016b; Kong *et al.*, 2018). The importance of phytohormonal signalling pathways for root exudation has been demonstrated in mutants. For instance, the *A. thaliana* mutants *myc2* and *med25*, which are impaired in the JA-signalling pathway, had different exudate compositions compared to

wildtype plants (Carvalhais *et al.*, 2015). *Arabidopsis thaliana* mutants defective in particular defence signalling pathways had rhizobacterial communities that differed from that of wildtype plants (Kniskern *et al.*, 2007; Hein *et al.*, 2008; Doornbos *et al.*, 2009; Lebeis *et al.*, 2015). Because root exudates influence microbiome composition, this suggests that herbivory may affect the rhizosphere microbial community.

Herbivory-induced changes in root-associated microbial community

Herbivore infestation of plants indeed results in changes in the root-associated microbiome (Hu *et al.*, 2018; Cordovez *et al.*, 2019). For instance, in response to attack by the whitefly *Bemisia tabaci*, the diversity of bacteria associated with the roots of pepper (*Capsicum annuum*) plants was lower than for roots of control plants. Roots of whitefly-infested plants were colonised most abundantly by *Achromobacter*, *Janthinobacterium*, and *Stenotrophomonas* rhizobacteria (Kong *et al.*, 2016). The latter bacterial genus was also found in higher density in the rhizosphere of *A. thaliana* plants in response to plant infection with the pathogen *Hyaloperonospora arabidopsidis* (Berendsen *et al.*, 2018). Moreover, herbivores may even affect root-microbe interactions before the herbivores initiate feeding. In an interesting experiment, the exposure of alder (*Alnus spp.*) plants to woolly alder aphids (*Prociphilus tessallatus*) that had not yet initiated feeding, resulted in increased nitrogen-fixing activity within a day (Zekveld & Markham, 2011).

Even when the total number of rhizobacteria remains the same, different bacterial groups may be differentially affected by insect herbivory-mediated changes in plant phenotype, thus resulting in a change in community composition (Hu *et al.*, 2018). For instance, the density of gram-positive bacteria, but not the total density of bacteria, on pepper roots increased upon feeding by the whitefly *Bemisia tabaci* (Yang *et al.*, 2011) and the green peach aphid *Myzus persicae* (Kim *et al.*, 2016). Single bacterial species may be specifically supported by the plant after insect attack (Kong *et al.*, 2016). For instance, the density of the PGPR *Bacillus subtilis* increased on pepper roots upon infestation by the shoot herbivore *M. persicae* (Lee *et al.*, 2012).

These effects of herbivory on root-associated microbes may be mediated by root exudates (Rudrappa *et al.*, 2008). Maize roots release benzoxazinoids that attract *Pseudomonas putida* (Neal *et al.*, 2012). Enhanced exudation of benzoxazinoids by maize roots in response to caterpillars feeding on the leaves of the plant influenced the rhizosphere bacterial community composition; this effect was mediated by the benzoxazinoid breakdown product 6-methoxy-benzoxazolin-2-one (MBOA) as was shown by comparing wildtype plants and benzoxazinoid mutants in combination with complementation of MBOA (Hu *et al.*, 2018).

Thus, insect herbivory may alter the rhizosphere microbial community through changes in root exudate composition. Because many individual species of rhizosphere microbes are known to affect plant defence to insect herbivores, the effects of the altered rhizosphere microbial community on

plant defence are an interesting next step in understanding microbe-plant-insect interactions.

Effects of herbivory-induced changes in rhizobacterial community feed back on the performance of aboveground insect herbivores

Plant-mediated effects of rhizobacteria on individual insect herbivore species

Rhizobacteria are known to modulate induced plant defence through a mechanism called priming (Conrath *et al.*, 2006; Gange *et al.*, 2012; Hilker *et al.*, 2016; Martinez-Medina *et al.*, 2016), which may have lower fitness costs than immediate activation of defence upon herbivore attack (van Hulten *et al.*, 2006), the costs of which can be considerable (Balmer *et al.*, 2015). Rhizobacterial priming of induced systemic resistance (ISR) is commonly dependent on intact JA signalling (Pieterse *et al.*, 2014). However, other phytohormonal signalling pathways may also be involved: *Pseudomonas fluorescens* strain SS101 can mediate ISR via the SA-pathway in *A. thaliana* (van de Mortel *et al.*, 2012). Rhizobacteria-mediated priming of plant defence has been especially reported for defence against plant pathogens (Pieterse *et al.*, 2014; Mauch-Mani *et al.*, 2017), but can also be effective against insect herbivores (Kim & Felton, 2013; Pangesti *et al.*, 2015a,b; Hilker *et al.*, 2016). Studies on rhizobacterial priming of defence against insect herbivores are rapidly gaining interest (Gadhve & Gange, 2018).

Rhizobacterial colonization of plant roots may affect oviposition preference of insect herbivores. For instance, the European corn borer moth *Ostrinia nubilalis* prefers to oviposit on control plants compared to plants with rhizobacterial colonization (Disi *et al.*, 2018). Rhizobacteria can also influence shoot-feeding herbivores (Pineda *et al.*, 2010). The effect of rhizobacterial colonization of plant roots on an insect herbivore feeding on a plant can be either positive, negative, or neutral. For instance, aphid performance can be enhanced on plants with rhizobacterial colonization of the roots (Dean *et al.*, 2009; Pineda *et al.*, 2012; Megali *et al.*, 2014; Naluyange *et al.*, 2014; Kim *et al.*, 2016), but also negative (Gadhve *et al.*, 2016a; Howard *et al.*, 2020) or neutral effects (Herman *et al.*, 2008; Dean *et al.*, 2014) have been recorded.

An interesting study on insect-maize-microbiome interactions showed that changes in rhizosphere microbial communities as a result of feeding by *S. littoralis* caterpillars on maize plants enhanced plant resistance to *S. littoralis*. This effect is mediated by *S. littoralis*-induced benzoxazinoid secretion by the maize roots and JA signalling in the plant (Hu *et al.*, 2018). This elegant study used mutant plants that are impaired in benzoxazinoid exudation in combination with supplementation of soil with benzoxazinoids. This mechanism of how herbivore-induced changes in the rhizosphere microbial community feed back to plant resistance against an insect herbivore is an example of the bidirectional interaction between a shoot-feeding insect species and the rhizosphere microbial community. This raises the question whether such plant-soil feedback effects influence the community of insects associated with plants.

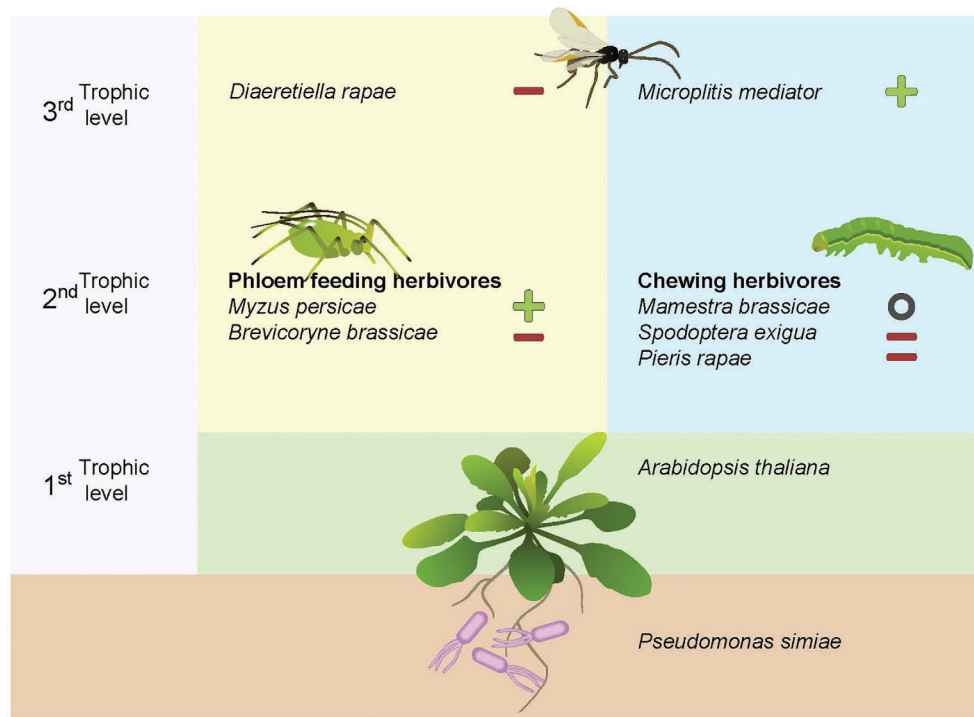


Fig. 2. Differential effects of the Plant-Growth Promoting Rhizobacterium *Pseudomonas simiae* WCS417 on insect herbivores and their parasitoids on the host plant *Arabidopsis thaliana*. Green + indicates beneficial effect on insect performance, red - indicates detrimental effects on insect performance and grey O indicates neutral effects on insect performance. Figure based on Van Oosten *et al.* (2008), Pineda *et al.* (2012), Pineda *et al.* (2013) and Pangesti *et al.* (2015a,b). [Colour figure can be viewed at wileyonlinelibrary.com].

Effects of rhizobacteria on the plant-associated insect community

A single rhizobacterial species can differentially influence various insect herbivores. For instance, colonization of *A. thaliana* roots by *Pseudomonas simiae* WCS417 (formerly *P. fluorescens* WCS417) resulted in negative effects on the performance of the generalist caterpillars *Spodoptera exigua* and *Mamestra brassicae*, whereas positive effects on the generalist aphid *M. persicae* were recorded, and neutral effects on the specialist aphid *Brevicoryne brassicae* and the specialist caterpillar *Pieris rapae* (Van Oosten *et al.*, 2008; Pineda *et al.*, 2012; Pangesti *et al.*, 2015a) (Fig. 2). These differential effects on different insect species suggest that rhizobacteria influence the insect herbivore community associated with plant shoots.

Rhizobacteria can also influence tritrophic interactions via herbivore-induced plant volatiles (Pineda *et al.*, 2010; Rasmann *et al.*, 2017). These effects also appear to be species-specific. For instance, adding *Bacillus spp.* to the soil increases the parasitism rates of the cabbage aphid *Brevicoryne brassicae* by the parasitoid wasp *Diaeretiella rapae* on *Brassica oleracea* plants, but did not increase ladybird beetle *Coccinella septempunctata* and syrphid fly feeding on the aphids (Gadhav *et al.*, 2016a). In contrast, natural parasitism levels of cabbage aphids (*B. brassicae*) correlated negatively with the abundance of *Bacillus ssp.* when broccoli plants were grown in soils with naturally different densities of bacteria (Blubaugh *et al.*, 2018). *Pseudomonas simiae* WCS417 colonization of *A. thaliana*

roots resulted in reduced attraction of the aphid parasitoid *D. rapae* in response to infestation with the aphid *M. persicae*, whereas it enhanced the attraction of the parasitoid *Microplitis mediator* upon feeding damage by *M. brassicae* caterpillars (Pineda *et al.*, 2013; Pangesti *et al.*, 2015b) (Fig. 2). Thus, colonization by a single rhizobacterial species differentially affected shoot-associated insects not only at the second but also at the third trophic level. Part of these effects is caused by modification of herbivore-induced plant volatile emission as a result of plant-root-microbe interactions, with consequences for insect behaviour (Ballhorn *et al.*, 2013; Pineda *et al.*, 2013). In a field experiment, rice plants treated with *P. fluorescens* harboured increased numbers of natural enemies of herbivores, especially hymenopteran parasitoids and spiders (Commare *et al.*, 2002). It remains to be investigated what caused this effect.

Altogether, these findings show that rhizobacterial colonization of plant roots differentially affects different herbivore species and, consequently, may influence the composition and dynamics of the insect community. In this context, it is interesting that the interaction of soybean plants with symbiotic rhizobia influences various characteristics of the associated insect community, including herbivore species richness and abundance as well as taxonomic richness, diversity, and abundance of predatory insects (Katayama *et al.*, 2011). Such community analyses should serve as a guideline for similar studies on the effects of PGPR on insect community composition and dynamics.

Concluding remarks and future perspectives

Plants are known to recruit the enemies of insect herbivores by emitting herbivore-induced plant volatiles in response to attack (Dicke & Baldwin, 2010) with consequences for the insect community (Stam *et al.*, 2014). The current review highlights the emerging view that plants may also recruit rhizosphere microbes that enhance plant defence against insect herbivores. Maize plants respond to shoot feeding by *S. littoralis* caterpillars with the emission of herbivore-induced root exudate that alters the rhizosphere microbiome, thus enhancing plant resistance to the caterpillars in previously undamaged plants (Hu *et al.*, 2018). This plant–soil feedback is even more complex than indirect plant defence mediated by herbivore-induced plant volatiles because it not only involves the recruitment of soil microbes but also involves the plant's response to these recruited microbes. Knowledge on the ecology of PGPR–plant interactions advances rapidly (Balmer *et al.*, 2015; Sharifi & Ryu, 2017; Hu *et al.*, 2018; Carrion *et al.*, 2019; Howard *et al.*, 2020; Liu *et al.*, 2020). With new data showing that plants may recruit rhizobacteria that contribute to their defence (Pineda *et al.*, 2017; Berendsen *et al.*, 2018; Hu *et al.*, 2018), just like they recruit predators and parasitoids aboveground (Dicke & Baldwin, 2010; Turlings & Erb, 2018), plant defence against insects appears to be a participatory activity involving selected members of the associated community.

Emerging knowledge that plants can respond to foliar herbivory by insects with recruiting a microbial community to their rhizosphere that aids in the defence against insect attack raises various questions.

- 1 Insect-herbivore-related specificity of plant response. It is known that plant responses to insect herbivory, as documented for foliar changes in defence metabolites have a certain degree of specificity (Kessler & Baldwin, 2002; Mithofer & Boland, 2012). This specificity is exhibited especially in terms of phytohormonal signalling pathways being induced (Bidart-Bouzat & Kliebenstein, 2011). The reports on the effects of phytohormonal signalling on root exudate composition suggest that phytohormonal signalling may also underlie specificity in microbial community recruitment. Yet, it remains important to include the effects of aboveground insect herbivory on induced responses in plant roots that may differ from induced responses in shoot tissues (Biere & Goverse, 2016). We hypothesise that the phytohormonal response of plants influences root exudate composition and the community composition of the recruited microbial community.
- 2 Soil-related specificity of the recruited microbial community. The bulk soil provides the reservoir from which the plant can recruit its rhizosphere microbial community in response to aboveground insect herbivory. Thus, we hypothesise that the composition of the microbial community in the bulk soil influences microbial recruitment by a particular plant–insect–herbivore combination and thus, that rhizosphere-mediated plant defence against foliar herbivores varies with bulk soil microbiome composition.
- 3 Insect-community effects on the recruitment of the soil microbial community. Studies on the above-ground insect community associated with plants show that this community is influenced by prior herbivore damage by single herbivores (Van Zandt & Agrawal, 2004; Poelman *et al.*, 2010) or by the sequence of herbivores feeding on the plant (Li *et al.*, 2016a; Stam *et al.*, 2018). We hypothesise that the effects of herbivores feeding in sequence or simultaneously on a plant has consequences for the microbial community recruited by root exudates, just like has been recorded for the effects on the aboveground herbivore community (Stam *et al.*, 2014).
- 4 Correlation of effects on aboveground community and belowground community as a result of foliar-feeding insect herbivores. Plant species differ in their effects on the above-ground insect community (Poelman *et al.*, 2010; Aartsma *et al.*, 2020): some plant species have stronger effects than others. We expect that plant species also differ in effects on the recruited belowground microbial community. It will be interesting to investigate whether differences in effects on the aboveground community are reflected in differences in effects on the belowground community. To investigate this, a comparative approach is needed with plant species that are well characterised for their relative effects on the aboveground community (Poelman *et al.*, 2010; Aartsma *et al.*, 2020).
- 5 So far, evidence for plant-mediated effects of rhizobacteria on more than one insect species on the same plant is limited (Gadhavé *et al.*, 2016a; Blubaugh *et al.*, 2018). Yet, plants are commonly infested by a diversity of insect herbivores from various feeding guilds (Van Zandt & Agrawal, 2004; Stam *et al.*, 2014; Stam *et al.*, 2019). Thus, this represents an important knowledge gap. Investigating such effects with a focus on the underlying mechanisms to understand how rhizobacteria influence insect community composition, diversity, and dynamics and the consequences for plant performance will be important to enhance our understanding of the ecological effects of herbivory-induced changes on rhizobacteria-mediated effects on the plant-associated insect community. Yet, most of the current knowledge relates to the mechanisms underlying the effects of a single rhizobacterial species (but see Blundell *et al.*, 2020; Pineda *et al.*, 2020). Taking this to the next level, i.e. by investigating the effects of a rhizobacterial community on the aboveground insect community presents an important challenge.
- 6 Recent studies showing that herbivory may influence soil PGPR community composition with effects on plant defence against insect herbivores also raise questions on how this plant–soil feedback affects other aboveground insect community members, such as pollinators. Gaining information on this is relevant because pollinators directly contribute to reproductive success of many plant species (Rusman *et al.*, 2019). Phenotypic plasticity in plants as a result of interactions with community members such as insect herbivores may influence pollinator activity. It is plausible that phenotypic plasticity resulting from interactions with herbivory-induced changes in rhizosphere microbes does

so as well. Indeed, other soil microbiota, such as arbuscular mycorrhizal fungi are known to affect aboveground flower traits such as number of flowers per plant, inflorescence size, or nectar content with consequences for pollinator behaviour (Gange & Smith, 2005). Investigating whether herbivory-induced changes in PGPR also influence plant-pollinator interactions is important to understand the consequences of herbivore-plant-PGPR interactions for plant fitness.

Overall, new information indicates that plants actively recruit and retain specific bacterial groups to enhance plant defence. Therefore, the increase of specific rhizobacteria associated with insect attack might be regarded as part of the plant's inducible defence. Investigating such plant-mediated interactions between root-associated insect herbivores and shoot-associated microbes in the phyllosphere will be an interesting extension (Liu *et al.*, 2020). This review highlights that the rhizosphere is influenced by individual herbivore species feeding on a plant. In nature, plants are commonly attacked by a diversity of insect species (Stam *et al.*, 2014). The effects of multiple attackers on a single plant interact, e.g. via crosstalk of plant signal-transduction pathways. This may lead to synergistic or antagonistic effects on the plant's phenotype, with consequences for the members of the associated insect community (Stam *et al.*, 2014). How multiple attack on plants influences the rhizosphere microbiome deserves to be investigated at the level of the underlying mechanisms, including the dynamics in gene transcription in the shoot and roots, phytohormonal signalling, and root exudate composition (Liu *et al.*, 2020).

Most studies on the effects of PGPR on plant defence concern artificial conditions addressing the effects of a single or a simple mixture of bacterial species. PGPR, especially *Bacillus* species, have been used to develop biological control products to protect crops (Gadhav *et al.*, 2016b). However, the effectiveness of such biological control products as alternatives for chemical pesticides is limited under field conditions. Extrapolating from studies on potted plants to plants in the field is not straightforward (Heinen *et al.*, 2018). Moreover, the application of one or a few bacteria into the soil leads to interactions with resident bacteria (Gadhav *et al.*, 2016b) and the outcome of such interactions likely influences the biological control result. Thus, a community approach to rhizobacteria is needed for a true understanding of rhizobacteria-plant-insect interactions. Indeed, a community approach to protect crops is gaining momentum (Mendes *et al.*, 2011; Carrion *et al.*, 2019; Blundell *et al.*, 2020; Pineda *et al.*, 2020). Methods to steer the microbial composition of the soil to suppress aboveground insect pests are being developed (Pineda *et al.*, 2017, 2020; Blundell *et al.*, 2020). Moreover, the ability of plants to steer such processes via induced changes in root exudates (Hu *et al.*, 2018) may be exploited in breeding for crops with enhanced capacities of doing so. Especially the latter option may take the context-dependence into account because it exploits the natural capacity of plants to combat their enemies, similar to the interaction of plants with the carnivorous enemies of herbivorous insects (Hairston *et al.*, 1960; Dicke, 1996). For successful application, it is important that community processes that result from direct and

plant-mediated interactions between community members are taken into account because these result in indirect effects of community members on plant defence against insect herbivores. Thus, taking context dependence into account is important to gain true understanding of rhizobacteria-plant-insect interactions from both a fundamental and applied point of view.

As plants are central members of a diverse community including insects and microbes aboveground and belowground, plant attackers, and their antagonists, plant-mediated interactions are important forces shaping plant-associated community ecology and influencing plant performance (Stam *et al.*, 2014; Biere & Govers, 2016). Incorporating bidirectional effects of beneficial rhizobacteria and herbivorous insects on plant-mediated interactions within the plant-associated community will increase our understanding of plant community ecology. Such knowledge may be used to develop agricultural practices that exploit ecological interactions to produce crops without input of chemical pesticides.

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Author contributions

JF executed the literature analysis, prepared figures and tables, and wrote the first draft of the paper. MD, JvL and AP significantly contributed to the final manuscript. All authors read and approved the manuscript.

Data availability statement

This paper is a review and does not contain data.

Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1: Overview of the effects of individual rhizobacteria on insect herbivores, both directly and indirectly via plant-mediated effects.

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