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REVIEW
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Microbial Biocontrol Strategies for Ambrosia Beetles and Their Associated Phytopathogenic Fungi

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Ambrosia beetles and their symbiotic fungi are causing severe damage in natural and agro-ecosystems worldwide, threatening the productivity of several important tree crops such as avocado. Strategies aiming at mitigating their impact include the application of broad-spectrum agrochemicals and the incineration of diseased trees, but the increasing demand for environment-friendly strategies call for exploring biological control for the management of ambrosia beetles and their phytopathogenic fungal symbionts. The aim of this review is to examine the existing knowledge on biocontrol approaches using beneficial microorganisms and microbial natural products with entomopathogenic and antifungal activity against ambrosia beetles and fungi. We show that biocontrol has been mainly focused on the insect, using entomopathogenic fungi (EPF) such as *Beauveria* spp. or *Metarhizium* spp. However, recent studies have been integrating EPF with mycoparasitic fungi such as *Trichoderma* spp. to simultaneously challenge the vector and its fungal symbionts. Novel approaches also include the use of microbial natural products as insect lures or antifungal agents. Contrastingly, the potential of bacteria, including actinobacteria (actinomycetes), as biocontrol agents of ambrosia fungi has been little investigated. We thus suggest that future research should further examine the antifungal activity of bacterial strains, with an emphasis on harsh environments. We also suggest pursuing the isolation of more effective microbial strains with dual biocontrol effect, i.e., exhibiting fungicidal/insecticidal activities. Moreover, additional efforts should aim at determining the best application methods of biocontrol agents in the field to ensure that the positive effects detected *in vitro* are sustained. Finally, we propose the integration of microbiome studies in pest and disease management strategies as they could provide us with tools to steer the beneficial host plant microbiome and to manipulate the beetle microbiome in order to reduce insect fitness.

Keywords: antifungal activity, bioactive microbial products, entomopathogenic fungi, microbiome engineering, *Trichoderma*

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INTRODUCTION

Ambrosia beetles (Coleoptera: Platypodinae and Scolytinae) are a group of wood-boring insects that characteristically colonize stressed or recently dead trees, burrowing galleries into their hosts where they inoculate and culture their fungal symbionts as a food source for their larvae and maturing adults (Farrell et al., 2001; Biedermann and Taborsky, 2011; Huang et al., 2019). In turn, ambrosia fungi depend on their beetle vectors for dispersal (Ranger et al., 2021), as their spores are transported by the beetles in specialized sac-like structures named mycangia, thus facilitating fungal propagation among host trees (Batra, 1963). Fungi in the ambrosia symbiosis have been identified in at least seven families (Ophiostomataceae, Ceratocystidaceae, Nectriaceae, Bionectriaceae, Saccharomycetaceae, Peniophoraceae, and Meruliaceae) and dominantly belong to the genera *Ambrosiella, Fusarium*, and *Raffaelea* (Harrington et al., 2010; Huang et al., 2019; Ranger et al., 2021).

Exotic ambrosia beetle species have been recently acknowledged as potential pests, as some of their fungal symbionts may act as plant pathogens (Hulcr and Dunn, 2011; Cruz et al., 2021). By shifting from colonizing dead or declining trees to attacking living ones, these exotic beetles can become highly invasive (Hulcr and Dunn, 2011). Invasive ambrosia beetles that have inflicted serious damage to tree crops and forest ecosystems include those of the *Euwallacea fornicatus* species complex, native of Southeast Asia, which form an association with fungi from the ambrosia *Fusarium* clade (Kasson et al., 2013). Among them, *Fusarium euwallaceae* and *F. kuroshium* are responsible for Fusarium dieback (Lynch et al., 2016; Na et al., 2018), a disease that has been reported in the U.S.A. (California and Florida), Israel, and South Africa, infecting more than 58 plant families (Eskalen et al., 2013; Freeman et al., 2013; Carrillo et al., 2016; Paap et al., 2018). By invading the plant vascular tissues, fungi responsible of Fusarium dieback block the transport of nutrients and induce wilting, branch dieback, potentially leading to tree mortality (Eskalen et al., 2013). Another invasive ambrosia beetle with a large economic impact is *Xyleborus glabratus*, which symbiotic fungus *Raffaelea lauricola* has been causing extensive mortality of Lauraceae species in the Southeastern part of the U.S.A., including avocado (*Persea americana* Mill.), by triggering laurel wilt (Lira-Noriega et al., 2018). The development of this disease involves xylem dysfunction and disturbed water transport (Inch and Ploetz, 2012). Other species of *Raffaelea* are also found in the ambrosia beetle *Platypus cylindrus*, causing severe harm to *Quercus* (Fagaceae) trees in the Mediterranean basin (Freeman et al., 2019).

Both Fusarium dieback and laurel wilt, vectored by ambrosia beetles, have hampered avocado production in several regions of the word (Carrillo et al., 2015; Freeman et al., 2019). Moreover, one of the vectors of Fusarium dieback, the ambrosia beetle *Euwallacea kuroshio*, also known as Kuroshio Shot Hole Borer (KSHB), was recently detected in Tijuana, Mexico, representing a serious threat for the world largest producer and exporter of avocados (García-Ávila et al., 2016). Other crops which production has been hindered by ambrosia beetles and their fungal symbionts include orange (*Citrus sinensis* (L.) Osbeck), grapevine (*Vitis vinifera* L.), cacao (*Theobroma cacao* L.), coffee (*Coffea* spp.), macadamia (*Macadamia integrifolia* Maiden & Betche), peach (*Prunus persica* L. Stokes), and tea (*Camellia sinensis* (L.) Kuntze) (Gadd and Loos, 1947; Eskalen et al., 2013; Kagezi et al., 2015; Paap et al., 2018; Rugman-Jones et al., 2020; Asman et al., 2021). It is therefore critical to find efficient control strategies for these economically important pests and diseases (Báez-Vallejo et al., 2020).

The application of broad-spectrum agrochemicals is currently the main management practice for the mitigation of the impact caused by ambrosia beetle/fungi complexes. The cryptic habit of the beetles warrants the repeated application of contact insecticides to avoid infestation and of systemic insecticides with long residual efficacy to kill those beetles already inside the trees (Paine et al., 2011; Castrillo et al., 2016; Eatough Jones and Paine, 2018). Early detection and sanitation measures are also implemented to dispose of infested wood and limit the spread of wood borers (Eatough Jones and Paine, 2015; Avery et al., 2018). A wide array of systemic fungicides has been tested to reduce the spread of ambrosia fungi, propiconazole being one of the most promising active ingredients so far (Mayfield et al., 2008; Freeman et al., 2012). The current agrochemical restrictions for the export of crops such as avocado and the increasing demand for environment-friendly strategies call for exploring biological control for the management of ambrosia beetles and their fungal symbionts (Dunlap et al., 2017; Reverchon et al., 2019; Castrejón-Antonio et al., 2020). Here, we define biological control as the use of microorganisms and their natural products as natural antagonists for controlling the populations of pests and plant pathogens. The objective of this review is to examine the current state of biological control approaches aiming at mitigating the damages caused by ambrosia beetles and their associated phytopathogenic fungi, focusing on beneficial microorganisms and microbial natural products with entomopathogenic and antifungal activity. Furthermore, we aim at proposing a new, integrated approach to steer the plant microbiome and enhance the potential benefits of the native microbiota for plant health and protection against ambrosia beetles and their fungal symbionts (**Figure 1**).

ENTOMOPATHOGENIC MICROORGANISMS FOR THE CONTROL OF AMBROSIA BEETLES

Entomopathogenic fungi (EPF) represent a promising sustainable alternative to chemical pesticides and have been used against a broad range of agricultural and forest insect pests (Ocampo-Hernández et al., 2011; Verma et al., 2021). Their use is particularly interesting for the control of ambrosia beetles, as the cryptic nature of these insects effectively protect them from conventional insecticides during most of their life cycle (Castrillo et al., 2016). Several

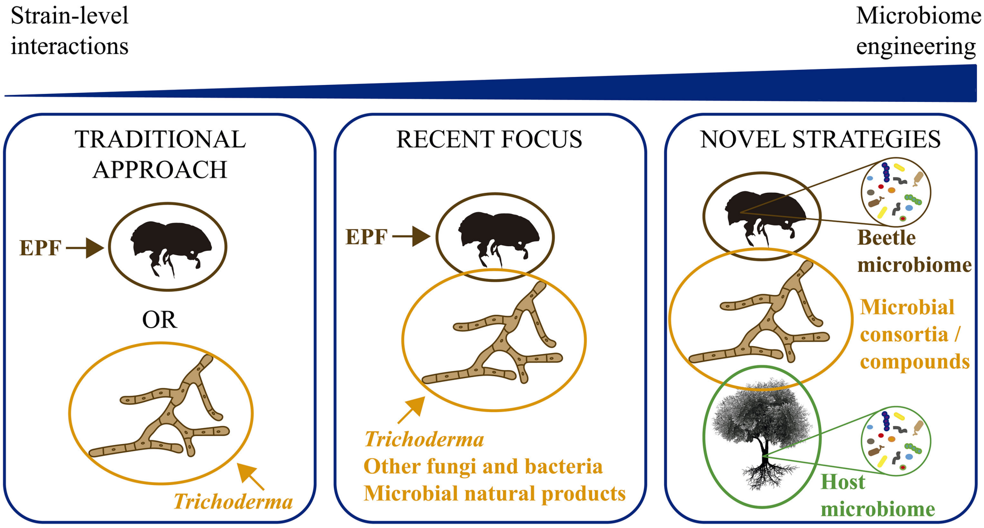


FIGURE 1 | Overview of the different microbe-based approaches for the biocontrol of ambrosia beetles and their pathogenic fungi. The traditional approach has been focused on studying the antagonism displayed by single strains of entomopathogenic fungi (EPF) or *Trichoderma* spp. against ambrosia beetles or their associated fungi. Recent works have been integrating both strategies to tackle ambrosia fungi and their vectors at the same time, exploring other sources of biocontrol agents. Novel, cutting-edge strategies aim at manipulating the beetle microbiome in order to reduce its fitness, or the host microbiome in order to steer beneficial microorganisms.

species of EPF have been used against ambrosia beetles with encouraging results, the most commonly tested ones being *Beauveria bassiana* and *Metarhizium brunneum* (Ascomycota: Hypocreales; **Table 1**).

Beauveria bassiana is a widely distributed fungus with a broad host range and has been used as the basis for the development of many commercial bioformulations aiming at pest control (Zimmermann, 2007a). The mode of infection of *B. bassiana* is similar to that of other EPF, and initiates with the attachment of hydrophobic conidia to the insect cuticle, where germination starts. The formation of germ-tubes allows fungal penetration through the cuticle, further favored by the evasion from the insect host immune response. The subsequent fungal proliferation and invasion of insect tissues, coupled with the production of toxins, is followed by outgrowth from the dead host and production of new infective fungal spores (Zimmermann, 2007a; Wang and Wang, 2017; Xu et al., 2019). This EPF has already been described for its potential use in the biological control of several bark beetle species, such as *Dendroctonus valens* (Zhang et al., 2011; Xu et al., 2019), *D. rufipennis* (Davis et al., 2018), *Ips typographus* (Kreutz et al., 2004), or *Scolytus amygdali* (Batta, 2007). Regarding ambrosia beetles, the entomopathogenic effect of *B. bassiana* has been successfully tested against the redbay ambrosia beetle *X. glabratus* with mortality rates ranging from 55 and 71%, where the fungus prevented the reproduction of adult beetles and inhibited the establishment of their pathogenic fungal symbiont, although not affecting their initial boring activity (Carrillo et al., 2015). Similar findings were found in studies where *B. bassiana* was used to mitigate the impact of *Xylosandrus crassiusculus, Xyleborus volvulus, Xyleborus bispinatus,* and *Xyleborus affinis* (Castrillo et al., 2013; Avery et al., 2018; Castrejón-Antonio et al., 2020).

In the reviewed studies reporting the potential of *B. bassiana* for mitigating the impact of ambrosia beetles, several recommendations were made for an adequate selection of EPF and their optimum application under field conditions. Castrejón-Antonio et al. (2020) highlighted that EPF selection is key to the successful development of commercial biocontrol formulations and recommended that EPF strains be selected for their virulence, enzymatic profile, and adaptation to harsh environmental conditions, the latter to ensure a proper viability and persistence of fungal propagules in the field. This is particularly important since microbial biocontrol agents such as EPF are easily inactivated by natural environmental factors, especially ultraviolet radiation (ultraviolet A; UVA, 320 to 400 nm) and high temperatures (≥35°C), which consequently limit their effectiveness and persistence in open field conditions. Castrejón-Antonio et al. (2020) also emphasized the relevance of considering initial fungal growth parameters, such as mycelial growth, sporulation, and germination rates, since these are key aspects for subsequent massive production. Moreover, it is essential to consider the time elapsed between the application of EPF spores and the substantial mortality and mycosis of the treated beetles under laboratory conditions (especially the time until sporulation on cadavers and spores produced per specimen). This time parameter is key since EPF strains which are capable of producing abundant spores could cause horizontal transmission from an infected beetle (secondary inoculum source) to another within the galleries. Avery et al. (2018) recommended the development of oil-based emulsions as they seem to enhance spore adhesion to the insect

TABLE 1 | Existing microbe-based strategies for the biocontrol of ambrosia beetles and their phytopathogenic fungal symbionts.

Microbial biological control agents	Targeted organisms	Antagonistic mechanisms	References
Beauveria bassiana	*Xyleborus affinis, X. bispinatus, X. glabratus, X. volvulus, Xylosandrus crassiusculus*	Fungal penetration through the insect cuticle, invasion of insect tissues and toxin production, negative effect on associated fungal symbionts	Castrillo et al., 2013; Carrillo et al., 2015; Avery et al., 2018; Castrejón-Antonio et al., 2020
Metarhizium spp.	*Xyleborus bispinatus, X. volvulus, Xylosandrus crassiusculus, X. germanus*	Fungal penetration through the insect cuticle, invasion of insect tissues and toxin production, negative effect on associated fungal symbionts	Castrillo et al., 2011, 2013, 2016; Avery et al., 2018; Tuncer et al., 2019
Trichoderma spp.	*Ambrosiella grosmanniae, A. roeperi*	Niche and nutrient competition, antibiosis, cell wall degrading or inhibiting enzyme production and induction of the plant systemic resistance	Castrillo et al., 2013, 2016
Acaromyces ingoldii	*Raffaelea lauricola*	Reduction of mycelial growth and inhibition of spore germination by fungal secondary metabolites	Olatinwo and Fraedrich, 2019
Granulobasidium vellereum	*Raffaelea* sp.	Antifungal activity of fungal VOCs	Robles et al., 2018
Bacillus spp.	*Fusarium euwallaceae, F. kuroshium, Graphium euwallaceae, G. kuroshium, Raffaelea lauricola*	Inhibition of mycelial growth by bacterial lipopeptides and VOCs	Dunlap et al., 2017; Guevara-Avendaño et al., 2018, 2019, 2020; Báez-Vallejo et al., 2020
Paenibacillus spp.	*Fusarium euwallaceae, Raffaelea lauricola*	Reduction of mycelial growth	Dunlap et al., 2017
Streptomyces blastmyceticus	*Raffaelea quercus-mongolicae*	Inhibition of mycelial growth, sporulation and spore germination	Hong et al., 2018

cuticle, protect them against UV radiation, and thus favor germination and penetration. Likewise, the microencapsulation of entomopathogenic fungi through the use of different techniques (such as complex coacervation, liquid phase coating, and spray drying) could improve their entomopathogenic action; microencapsulation is commonly applied using different coating materials to effectively improve the stability of fungal spores and to regulate their release (Qiu et al., 2019). Biopolymers like starches, maltodextrins, and gums can be used as covering materials for biopesticides based on EPF because they favor the spore persistence, increasing the resistance to wash-off by rain and dew, and conferring thermo- and photo-tolerance to the active agent (Camacho et al., 2015). Despite the potential of microencapsulation, its use to improve EPF-based formulations is still scarce and, to the best of our knowledge, has not yet been explored for the control of ambrosia beetles. Finally, Castrillo et al. (2013) and Carrillo et al. (2015) emphasized the importance of optimizing the delivery system of EPF in the field to increase beetle mortality rates, suggesting that, for *X. glabratus*, trunk sprays or treated bait stations could be implemented for fungal delivery. Given the complexity of controlling ambrosia beetles, due to the insect cryptic habits and the cost of protecting large scale plantations, it is also important to conduct studies aimed at finding strains of endophytic EPF that are capable of successfully colonizing tissues of the entire plant (roots, stems, and leaves), where they could exert their bioinsecticidal action (Behie et al., 2015). Brownbridge et al. (2012), for example, proposed using seed coating and root dip as methods to successfully establish *B. bassiana* as an endophyte in *Pinus radiata* seedlings, to counteract the negative impact of bark beetles in pine plantations.

Fungi of the genus *Metarhizium* have also been evaluated as EPF against bark and ambrosial beetles (Castrillo et al., 2011; Tuncer et al., 2019; Mann and Davis, 2021). *Metarhizium* spp. exhibit several characteristics that are distinctive of successful EPF, such as easy isolation and culture, a large spore production, a broad host range and an efficient infection mechanism through the direct penetration of the cuticle (Zimmermann, 2007b; Mann and Davis, 2021). The entomopathogenic activity of commercial strains of *M. brunneum* has been reported against *X. crassiusculus* and *Xylosandrus germanus* in laboratory and field studies (Castrillo et al., 2011, 2013, 2016), where the authors reported an effect not only on adult females (with mortality rates higher than 50%) but also on their offspring. As with *B. bassiana*, negative interactions also seemed to occur between *M. brunneum* and the beetle fungal symbionts, thereby reinforcing the biocontrol activity of EPF. *Metarhizium brunneum* was also evaluated in laboratory assays against *X. crassiusculus*, *X. volvulus,* and *X. bispinatus,* significantly reducing beetle mean survival time when compared with that of untreated beetles (controls), more markedly so in *X. bispinatus* (Avery et al., 2018). Finally, *Metarhizium anisopliae* was tested against *X. germanus* with promising results, as 100% mortality rates were registered in laboratory conditions (Tuncer et al., 2019). Most studies emphasized the need to carry out field experiments to confirm the efficiency of *Metarhizium*-based formulations under unfavorable environmental conditions, and to determine the best spore concentration and delivery system for these biopesticides (Gugliuzzo et al., 2021).

The results presented in these studies point to the need to combine EPF with other control strategies for optimal integrated management and control of ambrosia beetle populations. It is thus necessary to examine the compatibility of EPF-based bioformulations with conventional agrochemicals used by the growers to ensure that applied fungicides minimally affect EPF and other potentially beneficial fungi (Avery et al., 2018; Zhou et al., 2018). Prospecting for new native, potentially successful EPF is an approach that still needs to be pursued, as recently recommended by Gugliuzzo et al. (2021), to identify new virulent fungal strains that could be more adapted to their natural conditions than commercial ones. The combination of EPF with mycoparasitic fungi such as *Trichoderma* spp. also seems like a promising approach, which would tackle not only the insect vector but also its fungal symbionts. Work carried out by Carrillo et al. (2016) showed an indirect negative impact of the commercial strain *Trichoderma harzianum* T-22 on brood production, probably through the limitation of their fungal food source. The antifungal effect of *Trichoderma* spp. against ambrosia fungi will be addressed in more detail in the next section of this review. Finally, further exploration of the beetle microbiome may provide new tools to enhance the beneficial effect of EPF, as recently demonstrated by Xu et al. (2019) for the bark beetle *D. valens*. These authors showed that the beetle gut microbiota interacted with *B. bassiana* to accelerate the beetle death and that bacteria from the genus *Erwinia* may be predominantly involved in this interaction. Examining the gut microbiome of ambrosia beetles thus seems like a promising new area of research, as determining shifts in the beetle microbial assemblages following inoculation with EPF could help identify positive feedbacks favoring EPF action (**Figure 1**).

FUNGI WITH ANTIFUNGAL ACTIVITY AGAINST AMBROSIA FUNGI

Fungi are versatile organisms capable of producing a broad range of antimicrobial secondary metabolites and have thus been used as biocontrol agents for a variety of phytopathogenic fungi (Adnan et al., 2019; Segaran and Sathiavelu, 2019). In particular, mycoparasitic fungi, especially those from the genus *Trichoderma*, have been extensively used as biological control agents of other fungi as they can act as antagonists through combining several inhibition mechanisms. These include niche and nutrient competition, antibiosis, cell wall degrading or inhibiting enzyme production and induction of the plant systemic resistance (Contreras-Cornejo et al., 2016; Adnan et al., 2019). However, until now, the use of fungal antagonists to inhibit the growth of ambrosia fungi has been seldomly explored (**Table 1**).

Three *Trichoderma* strains (*Trichoderma koningiopsis*, *T. harzianum,* and *T. viride*), isolated from the rhizosphere of avocado trees, have been recently documented by our research group to reduce the mycelial growth of *F. kuroshium* by more than 50% (Ruiz-Cisneros et al., unpublished data). The overgrowth of the *F. kuroshium* colony was observed immediately after both fungi came into contact **(Figure 2)**. Based on these results, we are currently aiming at evaluating the antagonistic potential of these *Trichoderma* strains against *F. kuroshium in situ*.

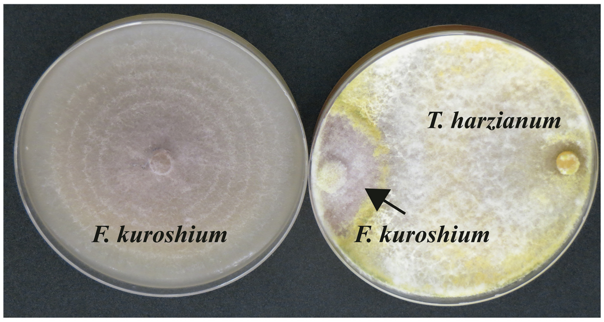


FIGURE 2 | (Left) Culture of *F. kuroshium* in the absence of the antagonistic fungus (control); **(Right)** *in vitro* overgrowth of *Trichoderma harzianum* on *Fusarium kuroshium*.

A commercial strain of *Trichoderma* has been evaluated for its antifungal activity against ambrosia fungi by Castrillo et al. (2013, 2016), with encouraging results. These authors showed that *Trichoderma harzianum* T-22 could successfully outcompete different strains of *Ambrosiella grosmanniae* and *A. roeperi in vitro*, which were isolated from the ambrosia beetles *X. germanus* and *X. crassiusculus*, respectively. Moreover, beetle bioassays showed that *T. harzianum* T-22 could significantly reduce brood production in galleries, most likely through the inhibition of the fungal symbiont growth. The reduction in brood numbers was comparable to that observed when EPF was applied, causing the mortality of female adults before laying eggs (Castrillo et al., 2013, 2016). Future research should also investigate the potential of *Trichoderma* strains as putative biocontrol agents of ambrosia beetles. As recently reviewed by Poveda (2021), *Trichoderma* is capable of controlling insect pests through multiple mechanisms such as parasitism, the production of insecticidal secondary metabolites, antifeedant compounds, and repellent metabolites, the activation of systemic plant defense responses and the attraction of insect natural enemies.

More recently, a basidiomycete species, *Acaromyces ingoldii*, was reported to exhibit antagonism against *R. lauricola* in dual culture plate assays (Olatinwo and Fraedrich, 2019). Interestingly, these authors evaluated the antifungal activity of *A. ingoldii* crude extracts, showing that the produced secondary metabolites completely inhibited mycelial growth of *R. lauricola* and significantly reduced spore germination *in vitro*. These positive biocontrol effects were however not confirmed *in vivo*, which calls for further exploration of the adequate extract dosage and mode of application to overcome the observed resilience of *R. lauricola*. Furthermore, the identity of the antifungal compounds present in these crude extracts should also be determined. The authors suggested that using *A. ingoldii* as a biological control agent instead of its crude extracts could constitute a better alternative to ensure lasting protection against the phytopathogen, as this fungal isolate is capable of growing endophytically within the host tissue (Olatinwo and Fraedrich, 2019). Screening for other endophytic fungal antagonists from different host bark and xylem tissues could therefore offer more alternatives for the biocontrol of ambrosia fungi.

Another potential alternative for the control of phytopathogenic ambrosia fungi is the use of natural products from cultured or wild superior fungi (mushrooms) that could either affect the phytopathogen mycelial growth or reduce its production of phytotoxic compounds (Alves et al., 2013). For example, it has been reported that organics extracts from culture filtrates and basidiomes of *Agaricus subrufescens* (pilei and stipe), *Lentinula edodes* (pilei), and *Pleurotus ostreatus* significantly reduced the mycelial growth and production of fusaric acid in *Fusarium* spp. *in vitro* (Chen and Huang, 2010; Merel et al., 2020). Interestingly, fusaric acid was recently described as one of the potential virulence factors produced by *F. kuroshium* (Gutiérrez-Sánchez et al., 2021) and is capable of inducing *in vitro* foliar damage in avocado, in a similar way to the symptomatology observed in Fusarium dieback. Future research should thus explore the biotechnological potential of crude extracts or pure compounds obtained from mushrooms, as a strategy to tackle the negative effects of ambrosia fungi.

In addition to fungal crude extracts, fungal volatile organic compounds (VOCs) have also been investigated for their antagonistic effect against ambrosia fungi. Robles et al. (2018) demonstrated that *Granulobasidium vellereum*, a wood endophyte of *Platanus acerifolia* (Aiton) Willd (Platanaceae), could successfully inhibit mycelial growth of *Raffaelea* sp. associated with *Megaplatypus mutatus in vitro*, through the emission of fungal VOCs. Chemical analysis of the emitted compounds revealed the presence of esters such as 2-methylpropyl acetate, 2-methylbutyl acetate and 3-methylbutyl acetate, and the sesquiterpene β-caryophyllene, all of which have been previously described for their putative antimicrobial and nematicidal activity (Strobel et al., 2001; Terra et al., 2018; Yalage Don et al., 2020; Hilgers et al., 2021). The use of fungal VOCs as biofumigants seems promising and should be further explored in field experiments in order to determine the best application method to be incorporated into integrated pest and disease management strategies.

Interestingly, the use of fungal VOCs has also been explored as lures for ambrosia beetles (Hulcr et al., 2011; Egonyu and Torto, 2018; Ranger et al., 2021), as beetles showed to be particularly attracted to VOCs emitted by their fungal symbionts. Alcohols such as ethanol, 2-methyl-1-propanol and 3-methyl-1-butanol were detected in the volatile profiles of *Ambrosiella* sp., *R. lauricola*, and *F. solani* associated with *Xylosandrus compactus* (Kuhns et al., 2014; Egonyu and Torto, 2018). Compound β-caryophyllene, previously described as a potential biofumigant, was also dominantly emitted by the ambrosia fungus *F. solani* (Egonyu and Torto, 2018). In particular, ambrosia beetles exhibited a strong attraction to ethanol, which is also emitted by susceptible host trees (Ranger et al., 2021) and has been reported to promote the growth of fungal symbionts *Ambrosiella* spp. while reducing that of other competing fungi (Ranger et al., 2018). Further attention should thus be provided to fungal natural products, as they may constitute a promising source of novel compounds for bioformulations aiming at mitigating the impact of ambrosia beetles and their associated pathogenic fungi.

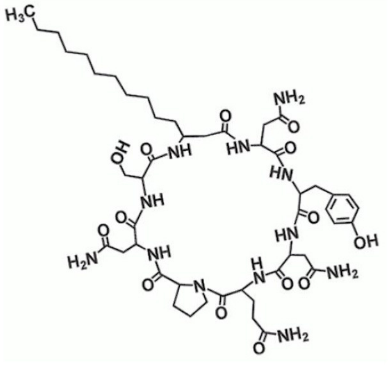
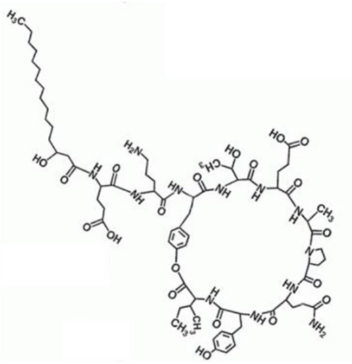
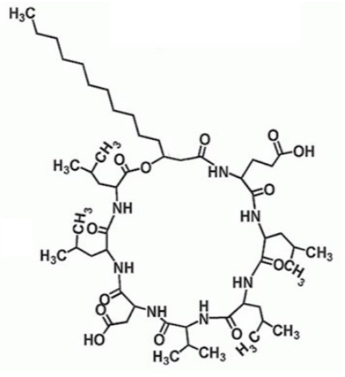
As previously mentioned, identifying fungal strains able to negatively impact ambrosia beetles and their phytopathogenic fungal symbionts is another promising strategy for the biocontrol of ambrosia complexes. In this context, endophytic EPF hold a large potential for the combined biocontrol of insect pests and fungal phytopathogens (Jaber and Alananbeh, 2018; Shapiro-Ilan et al., 2020; Guigón-López et al., 2021). However, to date, no studies have explored the dual efficacy of EPF for the biocontrol of ambrosia beetles and their symbiotic fungi. Recently, we observed *in vitro* inhibitions of *F. kuroshium* mycelial growth, ranging from 38.21 to 42.87%, by three *Metarhizium anisopliae* strains (Rios-Velasco et al., unpublished data). Based on these very promising results, we suggest the continuous exploration of EPF strains with dual antagonistic effects and that are capable of establishing themselves as endophytes to effectively achieve the biocontrol of both ambrosia beetles and their phytopathogenic symbiotic fungi.

BACTERIA WITH ANTIFUNGAL ACTIVITY AGAINST AMBROSIA FUNGI

The use of bacteria as biological control agents of fungal diseases vectored by ambrosia beetles has been seldomly explored (**Table 1**). The first report dates from 2017, when Dunlap et al. investigated the antifungal activity of bacterial strains isolated from different sources against *F. euwallaceae* and *R. lauricola*, causal agents of Fusarium dieback and laurel wilt respectively. They identified three *Paenibacillus* and one *Bacillus* species as successful inhibitors of both avocado fungal pathogens *in vitro*. This initial work called for future research to determine the best application methods in the field that would ensure the effective contact between bacterial antagonists and phytopathogenic ambrosia fungi. Another suggestion made by Dunlap et al. (2017) was to include avocado-associated microorganisms in the search for bacterial biocontrol agents of *F. euwallaceae* and *R. lauricola*.

Guevara-Avendaño et al. (2018) isolated several rhizobacteria from a Fusarium dieback-infested avocado grove in Escondido, California, U.S.A. with antagonistic activity against *F. euwallaceae*, *Graphium euwallaceae,* and *G. kuroshium*, associated with *Euwallacea fornicatus* (Polyphagous Shot Hole Borer) and *E. kuroshio*, respectively. Their dual culture assays evidenced 72 bacterial isolates that were capable of inhibiting the mycelial growth of *F. euwallaceae in vitro*; from these, five isolates, all identified as *Bacillus* spp., successfully reduced the growth of both *Graphium* species. Subsequent investigations determined that crude extracts and fractions obtained from *Bacillus* sp. 4742, the bacterial strain with the strongest antagonism against *G. kuroshium*, also displayed antifungal activity against *F. kuroshium* (Pérez-Molina et al., unpublished results). Chemical profiling of the active extracts and subfractions allowed the identification of cyclic lipopeptidic

TABLE 2 | Antimicrobial cyclic lipopeptides from *Bacillus* spp. (adapted from Gong et al., 2015; Caulier et al., 2019).

Chemical structure and name	Structural features	Antifungal activity
 Iturin	Composed by seven α-aminoacids AC length of C14 to C17	- Induces the formation of pores in fungal membranes altering the electrical conductance. - Interacts with sterols and phospholipids of fungi membranes altering the affinity of ergosterol. - Induces condensation and conglobation along hyphae and severe restriction of branch formation.
 Fengicyn	Composed by 10 aminoacids AC length of C14 to C18	- Provokes perturbation, bending, and micelle formation in fungal membranes. - Causes pore formation of fungal membranes allowing the complete efflux of intercellular content. - Induces vacuolation and conglobation on young hyphae and branch tips.
 Surfactin	Composed by a macrolactone ring of seven aminoacids AC length of C13 to C15	- No significant fungitoxicity

AC refers to acyl chain of the fatty acid.

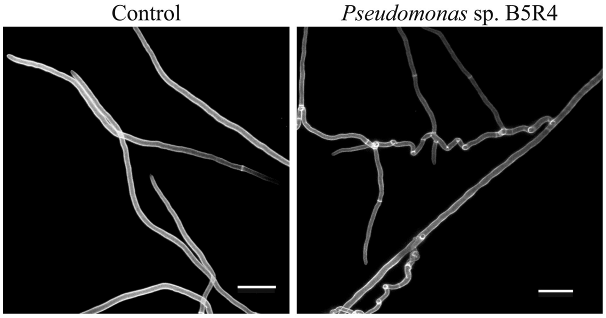


FIGURE 3 | Scanning electron microscopy images of the distortions induced in the hyphal structure of *Fusarium kuroshium* by VOCs emitted by avocado root endophyte *Pseudomonas* sp. B5R4.

compounds from the iturin and surfactin families, which have been previously described for their antifungal activities (Malfanova et al., 2012; Torres et al., 2017; Théatre et al., 2021). The inhibition of *F. kuroshium* by *Bacillus* natural products was further reported by Guevara-Avendaño et al. (2020) and Báez-Vallejo et al. (2020). In both studies, the analysis of bacterial extracts by ultra-performance liquid chromatography coupled to high-resolution mass spectrometry revealed the presence of cyclic lipopeptides from the iturin, surfactin, and fengycin families (**Table 2**) as the putative antifungal compounds. *Bacillus* lipopeptides have been described to alter fungal membranes, produce hyphal damage and vacuolization, and induce the production of resistance structures in pathogenic fungi (Alvarez et al., 2012; Cawoy et al., 2015) and thus constitute a promising source of bioactive compounds. Altogether, these findings call for bacterial natural products to be further investigated for the biological control of phytopathogenic fungi associated with ambrosia beetles.

Cyclic lipopeptides are not the only bacterial compounds to exhibit antifungal activity against phytopathogenic fungi associated with ambrosia beetles. Bacterial VOCs have also been reported to inhibit the growth of *F. kuroshium in vitro* and induce severe hyphal deformations (Guevara-Avendaño et al., 2019, 2020; Báez-Vallejo et al., 2020; **Figure 3**). Bacterial VOCs have been shown to play important roles in plant-microbe interactions, through their antimicrobial activity and the induction of the plant systemic resistance (Gutiérrez-Santa Ana et al., 2020a,b; Reverchon and Méndez-Bravo, 2021). Some of the VOCs responsible for the displayed antifungal activity were identified as 2,3,5-trimethylpyrazine, 2-nonanone, 2-decanone, 2-dodecanone, dimethyl disulfide, and dimethyl trisulfide; they were produced by rhizobacteria isolated from avocado and *Aiouea effusa* (Lauraceae) and belonged to the *Bacillus* and *Pseudomonas* genera (Guevara-Avendaño et al., 2019, 2020; Báez-Vallejo et al., 2020). Similarly, Gutiérrez-Santa Ana et al. (2020a) evaluated different *Bacillus* strains, isolated from different environments (agricultural soils, hydrocarbon-contaminated soils, air, extremophile saline soils), for their antagonistic activity against *Fusarium* spp. The VOCs emitted by these bacterial strains inhibited the growth of *F. solani* by up to 24%, whilst inhibition through direct confrontation ranged from 40 to 76%. The main VOCs identified by these authors were alcohols, ketones and alkenes such as 3-methylbutan-1-ol and 2-methylbutan-1-ol, butane-2,3-diol, 3-hydroxybutan-2-one, pentadeca-5,10-diyn-1-ol, undec-1-ene and hexan-1-ol (Gutiérrez-Santa Ana et al., 2020b). *In vitro* assays showed hyphal deformations and vesicular chlamydospores induced in *F. solani* after incubation with *Bacillus* strain for 5 days, and spore reduction with twisted, thinner or broken hyphae in *F. kuroshium* (**Figure 4**). Despite these promising results, so far, none of these VOCs has been tested *in planta* for the control of Fusarium dieback.

The few available reports investigating the potential of bacteria for the control of ambrosia fungi highlight several future research directions. First, most of these reports have been focused on rhizospheric bacteria, which calls for further exploration of other habitats to identify putative bacterial biocontrol agents. Environments subjected to extreme conditions may be an interesting source of biocontrol agents, as they promote the development of stress resistance mechanisms in microorganisms (Rojas-Solis et al., 2020; Tuesta-Popolizio et al., 2021). In particular, the phyllosphere has been characterized as a harsh and highly fluctuating environment, where microorganisms are exposed to oligotrophic conditions, solar radiation, and limited humidity (Vorholt, 2012). Further studies should thus focus on testing bark and leaf bacteria from ambrosia beetle hosts for their antifungal activity against phytopathogenic fungi. Another striking point from these available studies is the focus on *Bacillus* and *Pseudomonas* isolates. Although these bacterial genera have been extensively reported for their antifungal activity against a wide range of fungal pathogens (Cazorla et al., 2007; Santoyo et al., 2012; Ossowicki et al., 2017), other bacterial genera may also be explored, in particular those from the Actinobacteria phylum. Actinobacteria are known for secreting a wide array of antimicrobial compounds and it is thus surprising that their potential for the biological control of phytopathogenic ambrosia fungi has seldomly been investigated. An exception is the report by Hong et al. (2018), who showed that *Streptomyces blastmyceticus* successfully inhibited mycelial growth, sporulation and spore germination of *Raffaelea quercus-mongolicae*, a close relative of *R. lauricola* causing oak wilt. They attributed the observed antagonistic activity to the antifungal metabolites produced by *Streptomyces*. A subsequent study showed that active fractions obtained from *S. blastmyceticus* induced damage to the plasma membrane of spores and hyphae in several phytopathogenic fungi (Kim et al., 2019). These authors coincidentally mentioned the need for future research to focus on antifungal secondary metabolites and that combined control methods for both pathogenic fungi and insect vectors are necessary for the efficient management of fungal diseases and insect pests in agroecosystems. Preliminary results from our research group also show that actinobacteria of the genus *Streptomyces* were able to significantly inhibit the growth of *F. kuroshium* by 15–20% *in vitro* (Quiñones-Aguilar et al., unpublished). Interestingly, the inoculation of spores from these *Streptomyces* strains into an artificial medium where *Xyleborus ferrugineus* females were

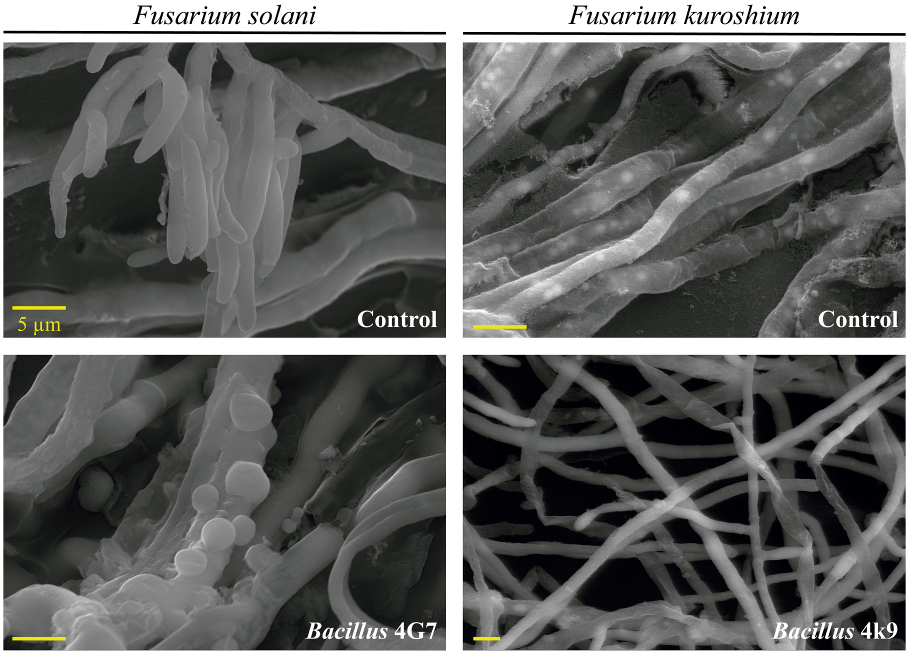


FIGURE 4 | Scanning electron microscopy (SEM) images showing the effect of VOCs emitted by *Bacillus* 4G7 on *F. solani* and *Bacillus* 4k9 on *F. kuroshium*, after 5 days of incubation.

reared significantly decreased (up to 97%) the number of live females at the end of a 38-day experiment (Rincón-Enríquez et al., 2020).

MICROBIOME APPROACHES TO STEER BENEFICIAL MICROORGANISMS

An increasing body of literature has been calling for innovative microbe-based approaches for integrated pest management that would consider managing microbiomes to steer beneficial organisms (Mendes et al., 2011; Orozco-Mosqueda et al., 2018; Zhang et al., 2020). These novel strategies would allow to go beyond strain-level antagonistic interactions and induce a general suppressiveness against diseases vectored by ambrosia beetles (Reverchon and Méndez-Bravo, 2021; **Figure 1**). For example, transplanting new microbiomes into the soil, or steering the existing soil microbiomes to enhance their beneficial effects, could be used to promote plant resistance to ambrosia beetles, following the evidence recently shown by Pineda et al. (2020) for the control of thrips.

Insect and host-plant microbiome studies thus have the potential to shed some light on the complex ecological interactions existing within microbial communities and could consequently help us elucidate how these microbiomes could be manipulated to enhance plant resistance to ambrosia beetles and their associated fungi. Our work on the avocado rhizosphere microbiome has shown that Fusarium dieback decreases the richness and diversity of rhizosphere microbial communities and significantly changed community structure, reducing the abundance of genera such as *Sporocytophaga* and *Cellvibrio*, which have been associated with plant growth promotion and chitinase production (Bejarano-Bolívar et al., 2021). However, some potential biocontrol agents such as *Myxococcus* sp. and *Lysobacter* sp. were exclusively detected in the rhizosphere of infected trees and should be further tested in antagonism assays (Bejarano-Bolívar et al., 2021). The characterization of the avocado bark microbiome has also highlighted the abundance of bacteria with antifungal activity in the bark environment, such as *Sphingomonas* or *Methylobacterium*, which could play a potential role in the biocontrol of Fusarium dieback in avocado trees (Aguirre-von-Wobeser et al., 2021). Collectively, these results could provide a basis for the selection of biocontrol agents that could be used to tackle Fusarium dieback. Finally, the exploration of ambrosia beetle microbiomes could also constitute an initial step for microbiome engineering as a mean to control their associated phytopathogenic fungi, as recently proposed by Ibarra-Juárez et al. (2018). These authors identified bacterial genera *Bacillus*, *Burkholderia, Erwinia, Sphingobacterium,* and *Stenotrophomonas,* among other taxa, as members of the core microbiome of *Xyleborus affinis*, *X. bispinatus,* and *X. volvulus* (Ibarra-Juárez et al., 2018, 2020). These core bacteria are hypothesized to be fundamental drivers of the maintenance of the beetle-fungus farming symbiosis and could thus be targeted in microbiome engineering strategies aiming at reducing pest fitness.

CONCLUSIONS

This review discussed the different biocontrol strategies aiming at decreasing the severe ecological and economic impacts of ambrosia beetles and their associated phytopathogenic fungi. Most studies so far have focused on the control of the insect, using EPF such as *Beauveria* spp. or *Metarhizium* spp. Recent works have suggested to combine EPF with mycoparasitic fungi such as *Trichoderma*, to tackle not only the beetle but also its fungal symbionts. Surprisingly, little emphasis has been made on the potential of bacteria, including actinobacteria, as biocontrol agents of ambrosia fungi, which calls for future research to be directed at finding novel microorganisms with antifungal activity, possibly in little explored, extreme environments. Recent studies have also been tackling the potential of microbial natural products as insect lures or antifungal agents. Additional efforts should be made to determine the best delivery method of potential biological control agents (either microbes or their bioactive compounds) in field conditions, as most studies so far have been implemented *in vitro*. Finally, we propose that microbial engineering methods should be explored in order to steer the plant microbiome and enhance its benefits for plant health and protection against ambrosia beetles and their phytopathogenic fungal symbionts, and to manipulate the beetle microbiomes in order to reduce its fitness.

AUTHOR CONTRIBUTIONS

FR conceived the topic of the research and wrote a draft of the manuscript. All other authors contributed with additional information, data, tables and figures, and revised the final version of the manuscript.

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