



# Multitrophic interactions of entomopathogenic fungi in BioControl

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**Abstract** Biocontrol with hypocrealean entomopathogenic fungi (EF) is a key tool to develop Integrated Pest Management (IPM) programs for the progressive replacement of synthetic chemical insecticides with more environmentally friendly pest control measures. These fungi stand out among entomopathogens not only for their contact mechanism of infection through the arthropod integument, but also for developing close associations with plants including the endophytic lifestyle and rhizosphere competence that can enable them to make broader contributions to IPM and crop production. Anyhow, the interaction of EF with the plants incorporates multitrophic complexity at different levels including insect pests, plants, and their natural enemies. The aim of the present review was to gather and summarize all available data on multitrophic interactions of EF. These fungi can influence both the chemical ecology of host-plant selection by insect pests and the host or prey selection by parasitoid or predators, respectively. Moreover, EF treatments are compatible with natural enemies in terms of safety and effectiveness, which could allow

biocontrol strategies for their synergistic application in IPM programs. A comprehensive understanding of the impact of these multitrophic interactions in longer term, farm-level real-life biocontrol implementation studies will provide new opportunities in plant protection and production.

**Keywords** Epiphyte · Endophyte · Rhizosphere competent · Natural enemies · Parasitoids · Predators, Beauveria · Metarhizium

## Introduction

Hypocrealean entomopathogenic fungi (EF) stand out among microbial control agents not only because their mode of infection by direct penetration through the cuticle and relatively easy mass production, but also because the newly described EF plant-interacting lifestyles, which place them at the forefront of crop protection and production tools (Quesada-Moraga et al. 2020). The current knowledge of the primary mode of action of EF and the molecules involved in different steps of their infection pathway has been extensively reviewed (Vega et al. 2012; Mannino et al. 2019). Besides, newly described modes of action of EF have also been discovered such the accidental death caused by stress in the insects through oral infection (Butt et al. 2013; Garrido-Jurado et al. 2015) and indirect mortality related to EF associations with the plants (Akello et al. 2008; Butt et al. 2013; Vidal and Jaber

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2015; Klieber and Reineke 2016; Garrido-Jurado et al. 2017, 2020; Resquín-Romero et al. 2016; Vega 2018; Zhu et al. 2018; Russo et al. 2019).

Particularly noteworthy are the associations of EF with plants as epiphytic (with the plant surface), endophytic (inside the plant), and rhizosphere competent microorganisms described mainly in the twenty-first century. As epiphytic microorganisms, EF propagules can become part of the phylloplane microbiota of different types of vegetation in natural and transformed habitats (Meyling and Eilenberg 2006; Ormond et al. 2010; Meyling et al. 2011; Garrido-Jurado et al. 2015). Recent studies on the adaptation and evolution of EF towards epiphytic, endophytic, or rhizosphere lifestyles reveal passive or active dispersal of EF soil conidia by wind or arthropods, respectively (Meyling and Eilenberg 2006; Garrido-Jurado et al. 2015; Fernández-Bravo et al. 2017; González-Mas et al. 2021b).

The endophytic behavior of EF with biocontrol potential, first described in corn in 1991 (Bing and Lewis 1991), has been thoroughly and widely reported in numerous cultivated and non-cultivated plant species, both naturally colonized and artificially inoculated (Quesada-Moraga et al. 2014; Vidal and Jaber 2015; Vega 2018; Quesada-Moraga 2020). Moreover, it has been proposed that entomopathogenic fungal endophytes may be important bodyguards having negative effect on polyphagous and sucking insect pests (Gange et al. 2019). Entomopathogenic fungi asymptotically colonize plant tissues (Saikkonen et al. 2006; Arnold and Lutzoni 2007) and can even promote growth and protect the plant against biotic stresses, pests, and diseases, or abiotic ones such as water deficit, nutritional deficiencies, etc. (Quesada-Moraga, 2020). The degree of EF colonization of the different tissues and organs of the plant and fungal persistence over time vary according to the plant species and fungal strain, from local to systemic colonization of the plant tissues, with even vertical transmission detected (Landa et al. 2013; Quesada-Moraga et al. 2014; Garrido-Jurado et al. 2017; Quesada-Moraga, 2020).

The persistence and biological activity of EF are also promoted in the rhizosphere (Hu and St Leger 2002; Pava-Ripoll et al. 2011; Wyrebek et al. 2011; Barelli et al. 2016; McKinnon et al. 2018) (Fig. 1). The rhizosphere is the narrow zone of soil that is influenced by root secretions that can contain an

enormous diversity of microbes (Mendes et al. 2011). The rhizosphere is an important niche for soil-borne fungal entomopathogens in which EF may be developed both to soil dwelling pest control and to provide additional ecosystem services such as plant growth promotion and direct disease antagonism (Bruck 2010). Indeed, an adaptation mechanism as a rhizosphere competent organism has been reported for *Metarhizium anisopliae* (Mets.) Sorokin (Ascomycota: Hypocreales), which expresses a specific subset of genes induced by plant root exudates different from the one expressed during infection of the arthropod hosts (Bruck 2005; Hu and St Leger 2002; Pava-Ripoll et al. 2011).

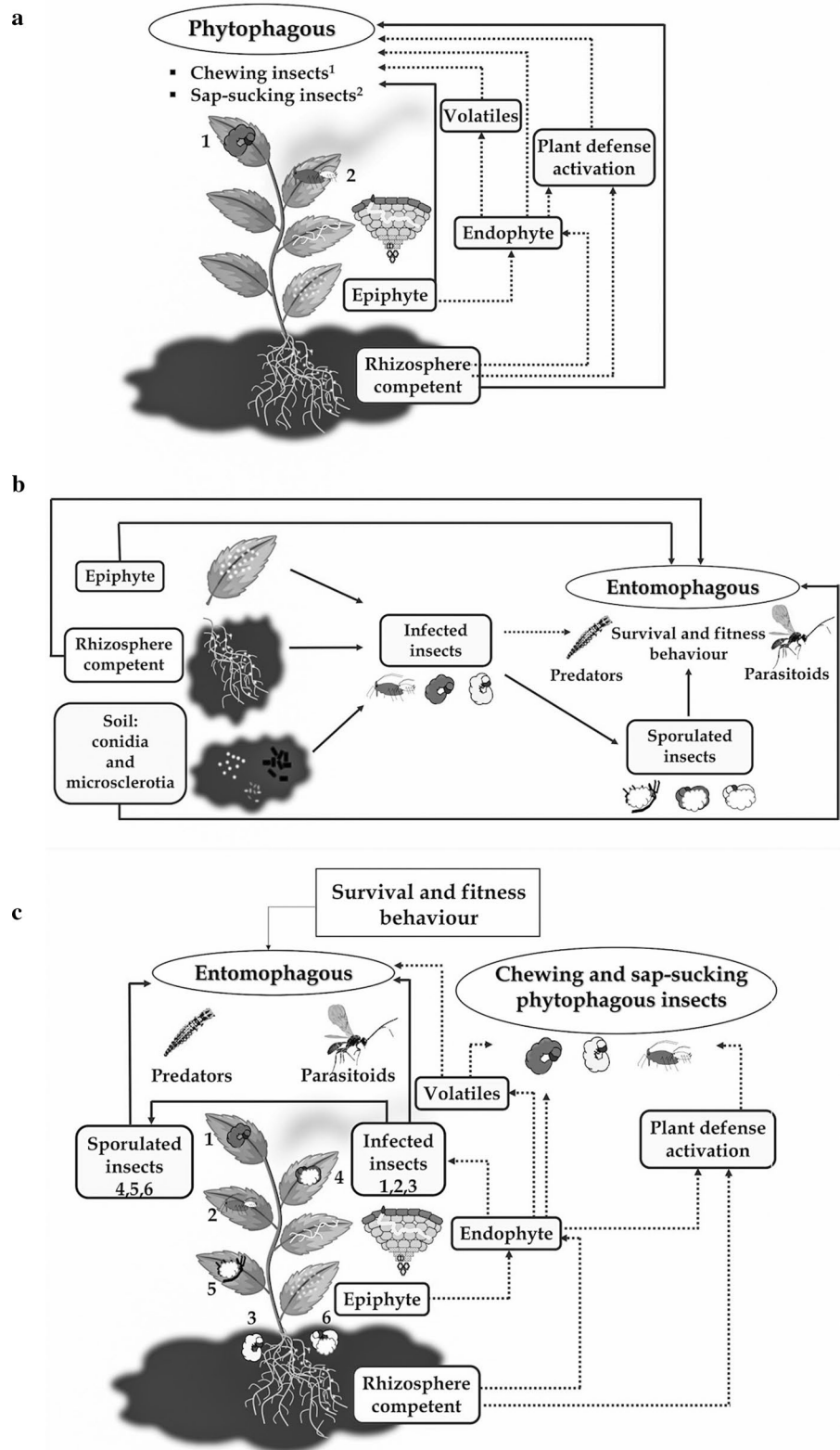
The role of EF on plant-mediated effects, insect population dynamics in crop ecosystems and semi-natural habitats and communities and the ecological principles of community interactions have been reviewed (Cory and Ericsson 2010; Hesketh et al. 2010; Meyling and Hajek 2010). New and noteworthy works indicate that EF are entomopathogens to insects through direct infection and toxin production but also indirectly through metabolite production in plants or plant defense activation (Gange et al., 2019). However, it is now necessary to expand on this previous work to examine how the trophic complexity created by the close association of EF with plants might influence multitrophic insect-plant and insect-natural enemy relationships, to take advantage of this EF-plant association to develop new crop protection and crop production strategies (Fig. 1a, b, c).

The aim of this review was to update the relatively scant data available on EF-mediated trophic interactions of plants, insect pests, and their natural enemies (hereafter natural enemies are predators and parasitoids). Trophic interactions are considered as two or three trophic levels interactions between EF and plants or between EF-infected insects and predators or parasitoids while interactions of more than three trophic levels are defined as multitrophic, such as the one including EF-colonized plants, insect pests, and their natural enemies.

Entomopathogenic-fungi-mediated trophic interactions between insects and plants

It is known that various host plant species can modify the susceptibility of insect pests to EF (Santiago-Álvarez et al. 2006; Cory and Ericsson, 2010;

**Fig. 1** Increasing complexity in the multi-trophic relationships of entomopathogenic fungi (EF). **a** EF-mediated trophic interactions between insects and plants. **b** EF-mediated trophic interactions between insects and their natural enemies either predators or parasitoids. **c** Multitrophic interactions involving entomopathogenic fungi. Solid connecting arrows represent direct effect while stippled connecting arrows represent an indirect effect. In Fig. 1a, 1 and 2 represent respectively a chewing or a sap-sucking insect feeding on a plant challenged by an epiphyte, endophyte, or rhizosphere competent entomopathogenic fungus. In Fig. 1c, 1, 2 and 3 represent respectively aerial chewing, aerial sap-sucking and soil dwelling insects infected by entomopathogenic fungi. Numbers 4, 5 and 6 represent cadavers of the same insects with fungal outgrowth



Ocampo-Hernández et al. 2019). Even, it has been shown that the behavior of insects can be indirectly affected by both EF propagule infestation of the plant surface or endophytic colonization (Pell and Vandenberg 2002; Meyling and Pell 2006; Lam et al. 2010; Yanagawa et al. 2011; Davis et al. 2013; Mburu et al. 2013; Rashki and Shirvani 2013; Gange et al., 2019). However, this section aims to examine in greater depth the possible behavioral responses of insects to EF-colonized plants, which might be indirectly related to metabolite secretion in plants or plant defense activation (Gange et al., 2019) (Fig. 1a). Most of the behavioral responses in insects, such as foraging, mating, preference for an oviposition site, or interaction with natural enemies, are regulated by olfactory chemical signals produced by plants, insects and natural enemies (Dicke and Grostal 2001; Sigsgaard 2005; Bruce et al. 2005; Xu and Turlings 2018). In addition, the volatile profile emitted by plants can be altered by their colonization by microorganisms, which can modify the insect-plant and insect-natural enemy relationships (Yue et al. 2001; Hempel et al. 2009; Shikano et al. 2017; Contreras-Cornejo et al. 2018; Tasin et al. 2018) (Fig. 1a). Thus, it has been shown that *Beauveria bassiana* (Balsamo) Vuillemin (Ascomycota: Hypocreales) influences the choice of host plant by the cotton aphid *Aphis gossypii* Glover (Hemiptera: Aphididae), which selects non-colonized over *B. bassiana*-colonized plants (Rashki and Shirvani 2013). In this regard, the limited knowledge available on the ability of plant-associated EF to influence plant-feeding insects is not conclusive, with reports on repellency (Sword et al. 2017; Rondot and Reineke 2017) or attraction (Kepler and Bruck 2006). Anyhow, unraveling whether endophytic EF colonization can cause alterations in the chemical signals produced by plants, and therefore in insect-plant relationships, or even in those of phytophagous insects with their natural enemies, is a key research goal. Hence, *Lygus hesperus* Knight (Hemiptera: Miridae) and *Nezara viridula* (Linnaeus) (Hemiptera: Pentatomidae) bugs can detect and subsequently avoid flowers and fruits developed in plants whose tissues are endophytically colonized by *B. bassiana* and prefer control plants in selection experiments (Sword et al. 2017). In addition, *B. bassiana* endophytic colonization led to a deterrent effect in adults of the vine weevil *Otiiorhynchus sulcatus* (Fabricius) (Coleoptera: Curculionidae), which preferred the control plants (Rondot and

Reineke 2017). In contrast, the larvae of this weevil were shown to be attracted to pots containing plants with *M. anisopliae* (Kepler and Bruck 2006).

These studies reveal the ability of insects to detect EF endophytic colonization of plant tissues, a behavior that could be regulated by variations in the profile of plant volatile compounds (González-Mas et al. 2021a) (Fig. 1a). It has been noteworthy shown that endophytic colonization by *B. bassiana* influences volatile emissions by melon and cotton plants, either unharmed or after being damaged by sap-sucking aphids or leaf-chewing caterpillars (González-Mas et al. 2021a). Some of the emitted compounds have been previously reported to be released in response to herbivory and have been implicated in natural enemy attraction, or even to have antimicrobial properties. Hence, colonization by *B. bassiana* might help not only to directly control insect pests but also to increase the resistance of plants against agronomically important pests and phytopathogenic microorganisms (González-Mas et al. 2021a). By using an axenic consortium of *B. bassiana* and *Trichoderma asperellum* Samuels, Lieckf. & Nirenberg (Ascomycota: Hypocreales) against *Ostrinia furnacalis* (Guenée) (Lepidoptera: Crambidae), it has been demonstrated that colonization by EF may have a positive effect on increasing herbivory-induced defenses and restricting pest survival and growth (Batoool et al. 2022). This effect on increasing herbivory-induced defenses and restricting pest survival and growth has also been observed by Cotes et al. (2020), who demonstrated that root-associated entomopathogenic fungi indirectly influence herbivorous insect performance by causing an increase in the production of jasmonic, (+)-7-iso-jasmonoyl-l-isoleucine and salicylic acid in certain parts of the host plant. The above examples illustrate that EF can influence the chemical ecology of host-plant selection by insect and mite pests.

Entomopathogenic-fungi-mediated trophic interactions between insects and their natural enemies

Whilst the use of natural enemies and entomopathogenic microorganisms in biological control reduces the effects on the environment and non-target organisms compared to the use of conventional insecticides, it is necessary to evaluate the compatibility between them for developing IPM programs

(Roy et al. 2010). In general, it has been found that EF treatments can be considered to be of low-risk for predators and parasitoids and therefore compatible with them in the light of the numerous investigations on the safety and effectiveness of the combined use of EF and other biocontrol agents (Roy and Pell 2000; Acevedo et al. 2007; Labbé et al. 2009; Ansari et al. 2010; Martins et al. 2014) (Fig. 1b). Indeed, infection of phytophagous insects by EF, initiated either by direct contact with the fungal inoculum or by the insects feeding or developing in EF endophytically colonized tissues, can affect their behavior, and therefore their intra- and interspecific relationships (Meyling and Pell 2006; Roy et al. 2006) (Fig. 1b). Table 1 summarizes the works done so far by different authors on EF-mediated tritrophic interactions. In this section, we highlight recent advances in the knowledge about direct effects of entomopathogenic fungi on predator/parasitoid survival and fitness and indirect effects on natural enemy behavior/capacity (Fig. 1a).

#### Direct effects of entomopathogenic fungi on natural enemy survival and fitness

In unlikely scenarios in real situations (worst-case scenarios), by spraying or immersion of high doses of different fungal strains (Castillo et al. 2009; Da Silva et al. 2016; Miranda-Fuentes et al. 2021), the direct application of EF suspensions to Hymenoptera parasitoid braconids and eulophids can decrease their longevity (Labbé et al. 2009; Tamayo-Mejía et al. 2015; Miranda-Fuentes et al. 2020) (Table 1). In general, the compatibility of EF with parasitoids and predators is influenced, among other factors, by the species involved, the application technique, the fungal dosage, the degree of prey/host infection, and the time interval between the fungal application and the release of the predators or parasitoids (Mesquita and Lacey 2001; Aqueel and Leather 2013; Ibarra-Cortés et al. 2018). Decreasing the doses and applying the natural enemy before EF inoculation minimize the possible negative effects on various groups of predators such as predatory coccinellids (James et al. 1995; Pingel and Lewis 1996; Todorova et al. 1996; Smith and Krischik 2000; Roy and Pell 2000; Pell and Vandenberg 2002; Roy et al. 2008), lacewings (Portilla et al. 2017), and several species of aphid parasitoids (Brodeur and Rosenheim 2000; Mesquita and Lacey

2001; Jeong et al. 2005; Aqueel and Leather 2013; Oreste et al. 2016; Shrestha et al. 2017) (Table 1).

Regarding predators, it has also been shown that *B. bassiana* and *M. anisopliae* are compatible with the generalist predator *Coccinella septempunctata* L. (Coleoptera: Coccinellidae) (Rizwan et al. 2021) (Table 1). Neither fungus induced any significant changes in the development time (egg-adult), fecundity rate, adult preoviposition period, total preoviposition period, or mean generation time as compared to control treatment (Rizwan et al. 2021). When evaluating *B. bassiana* and phytoseiid mites that can independently contribute to suppressing the two-spotted spider mite, *Tetranychus urticae* Koch (Acari: Tetranychidae), it was demonstrated that although several *B. bassiana* strains displayed a high virulence in *T. urticae*, there was no evident pathogenicity to phytoseiid mites (Wu et al. 2016) (Table 1). In worst-case scenarios, by direct spraying of *Phytoseiulus persimilis* Athias-Henriot (Acarina: Phytoseiidae) with *B. bassiana* conidia at high dosages, significant negative effects on fecundity and life table parameters (net reproductive rate, intrinsic rate of natural increase, mean generation time, finite rate of increase, and doubling time) were found when *B. bassiana* was applied to the adult stage (Ullah and Lim 2017). Indeed, laboratory and potted plant investigations on the predatory behavior of the predatory mite *P. persimilis* against *T. urticae* indicated that *P. persimilis* showed significant aversion behavior to the initial fungal spray, but gradually dispersed over the entire bean plants, with no significant differences between the treatments in the number of *T. urticae* consumed (Wu et al. 2018). Fungal spray did not affect the predation capability of *P. persimilis* and poses a negligible risk to its behavior (Wu et al. 2018) (Table 1).

Regarding parasitoids, some studies have shown a high level of compatibility between EF and parasitoids (Polanczyk et al. 2010; Rossoni et al. 2016; Shrestha et al. 2017; González-Mas et al. 2019a; Miranda-Fuentes et al. 2020), while others have shown antagonistic interactions (Oreste et al. 2015; Tamayo-Mejía et al. 2015) (Table 1). Despite this, most studies have demonstrated that combining EF and parasitoids in IPM programs is always beneficial when release times are adjusted appropriately, with emphasis on which agent is administered first and whether the treatments are timed correctly (Da Silva et al. 2016; Jarrahi and Safavi 2016; Shrestha

**Table 1** Tritrophic interactions involving Hypocrealean entomopathogenic fungi, insect and mite pests and their natural enemies. References are listed in chronological order

Entomopathogenic fungal species	Insect and mite pest	Predator	Parasitoid	Reference
<i>Nomuraea rileyi</i> (Farlow) Samson = <i>Metarhizium rileyi</i> (Farlow) Kepler	Corn Earworm, <i>Helicoverpa</i> (= <i>Heliothis</i> ) <i>zea</i> (Boddie)	–	<i>Microplitis croceipes</i> Cresson	(King and Bell, 1978)
<i>Beauveria bassiana</i> (Balsamo) Vuillemin	Pea aphid <i>Acyrtosiphon pisum</i> Harris	<i>Hippodamia convergens</i> Guérin- Ménéville	–	(James et al., 1995)
<i>Beauveria bassiana</i> (Balsamo) Vuillemin	European corn borer; <i>Ostrinia</i> <i>nubilalis</i> (Hübner)	<i>Coleomegilla maculata</i> De Geer	–	(Pingel and Lewis, 1996)
<i>Beauveria bassiana</i> (Balsamo) Vuillemin	Colorado potato beetle <i>Leptino-</i> <i>tarsa decemlineata</i> (Say)	<i>Coleomegilla maculata lengi</i> (Schneider)	–	(Todorova et al., 1996)
<i>Isaria fumosorosea</i> Wize	Russian wheat aphid; <i>Diuraphis</i> <i>noxia</i> (Mordvilko)	–	<i>Aphelinus asychis</i> Walker	(Mesquita et al., 1999)
<i>Beauveria bassiana</i> (Balsamo) Vuillemin	–	<i>Hippodamia convergens</i> (Guérin- Ménéville), <i>Coleomegilla</i> <i>maculata</i> (DeGeert), <i>Harmonia</i> <i>axyridis</i> Pallas, and <i>Cryptolae-</i> <i>mus montrouzieri</i> Mulsant	–	(Smith and Krischik, 2000)
<i>Isaria fumosorosea</i> Wize	Russian wheat aphid; <i>Diuraphis</i> <i>noxia</i> (Mordvilko)	–	<i>Aphelinus asychis</i> Walker	(Mesquita and Lacey, 2001)
<i>Isaria fumosorosea</i> Wize	Russian wheat aphid; <i>Diuraphis</i> <i>noxia</i> Kurdjumov	<i>Hippodamia convergens</i> Guérin	–	(Pell and Vandenberg, 2002)
<i>Lecanicillium lecanii</i> (Zimm.) Zare and Gams	Cotton aphid <i>Aphis gossypii</i> Glover	–	<i>Aphidius colemani</i> Viereck	(Jeong et al., 2005)
<i>Beauveria bassiana</i> (Balsamo) Vuillemin	Nettle aphid <i>Microlophium carno-</i> <i>sum</i> (Buckton)	<i>Anthocoris nemorum</i> L.	–	(Meyling and Pell, 2006)
<i>Beauveria bassiana</i> (Balsamo) Vuillemin	Nettle aphid <i>Microlophium carno-</i> <i>sum</i> (Buckton)	<i>Anthocoris nemorum</i> (L.)	–	(Meyling et al., 2006)
<i>Beauveria bassiana</i> (Balsamo) Vuillemin	–	<i>Harmonia axyridis</i> Pallas, <i>Coc-</i> <i>cinella septempunctata</i> L. and <i>Adalia bipunctata</i> L.	–	(Roy et al., 2008)
<i>Beauveria bassiana</i> (Balsamo) Vuillemin	Coffee berry borer; <i>Hypothenemus</i> <i>hampei</i> (Ferrari)	–	<i>Phymastichus coffea</i> LaSalle	(Castillo et al., 2009)
<i>Beauveria bassiana</i> (Balsamo) Vuillemin	<i>Trialeurodes vaporariorum</i> Westwood	<i>Dicyphus hesperus</i> Knight	<i>Encarsia formosa</i> Gahan	(Labbé et al., 2009)
<i>Beauveria bassiana</i> (Balsamo) Vuillemin	Green peach aphid <i>Myzus persicae</i> Sulzer	–	<i>Aphidius matricariae</i> Haliday	(Rashki et al., 2009)
<i>Beauveria bassiana</i> (Balsamo) Vuillemin	Green peach aphid <i>Myzus persicae</i> Sulzer	–	<i>Diaeretiella rapae</i> McIntoch	(Polanczyk et al., 2010)

**Table 1** (continued)

Entomopathogenic fungal species	Insect and mite pest	Predator	Parasitoid	Reference
<i>Beauveria bassiana</i> (Balsamo) Vuillemin	–	<i>Coccinella septempunctata</i> L	–	(Ormond et al., 2011)
<i>Beauveria bassiana</i> (Balsamo) Vuillemin	Green peach aphid <i>Myzus persicae</i> Sulzer	<i>Harmonia axyridis</i> (Pallas)	–	(Zhu and Kim, 2012)
<i>Lecanicillium lecanii</i> (Zimm.) Zare and Games	Cereal aphids <i>Rhopalosiphum padi</i> (L.) and <i>Sitobion avenae</i> (F.) killed	<i>Harmonia axyridis</i> (Pallas) (Petri plate)	<i>Aphidius colemani</i> Viereck	(Aqueel and Leather, 2013)
<i>Beauveria bassiana</i> (Balsamo) Vuillemin	Green peach aphid <i>Myzus persicae</i> Sulzer	–	<i>Aphidius colemani</i> Viereck	(Emami et al., 2013)
<i>Beauveria bassiana</i> (Balsamo) Vuillemin	Green peach aphid <i>Myzus persicae</i> Sulzer	–	<i>Diaeretiella rapae</i> McIntoch	(Martins et al., 2014)
<i>Beauveria bassiana</i> (Balsamo) Vuillemin	Mediterranean fruit fly (medfly), <i>Ceratitis capitata</i> (Wiedemann)	–	<i>Psytalia concolor</i> (Szepliget)	(Oreste et al., 2015)
<i>Beauveria bassiana</i> (Balsamo) Vuillemin	Mediterranean flour moth, <i>Anagasta kuehniella</i> Zeller	–	<i>Trichogramma pretiosum</i> Riley	(Potrich et al., 2015)
<i>Beauveria bassiana</i> (Balsamo) Vuillemin and <i>Metarhizium brunneum</i> Petch	Cabbage root fly, <i>Delia radicum</i> L	–	<i>Trybliographa rapae</i> Westwood	(Rännbäck et al., 2015)
<i>Beauveria bassiana</i> (Balsamo) Vuillemin	<i>Bactericera cockerelli</i> (Sulc.)	–	<i>Tamarixia triozae</i> (Burks)	(Tamayo-Mejia et al., 2015)
<i>Beauveria bassiana</i> (Balsamo) Vuillemin and <i>Metarhizium anisopliae</i> (Metschnikoff) Sorokin	Sugarcane moth borer <i>Diatraea diatraea</i> flavipennella (Box)	–	<i>Cotesia flavipes</i> (Cam.)	(Da Silva et al., 2016)
<i>Metarhizium anisopliae</i> (Metschnikoff) Sorokin	Cotton bollworm, <i>Helicoverpa armigera</i> (Hübner)	–	<i>Habrobracon hebetor</i> Say	(Jarrahi and Safavi, 2016)
<i>Beauveria bassiana</i> (Balsamo) Vuillemin	<i>Trialeurodes vaporariorum</i> Westwood	–	<i>Encarsia formosa</i> Gahan	(Oreste et al., 2016)
<i>Beauveria bassiana</i> (Balsamo) Vuillemin and <i>Metarhizium anisopliae</i> (Metschnikoff) Sorokin	Sugarcane borer, <i>Diatraea saccharalis</i> (Fabricius)	–	<i>Palmistichus elaeisis</i> Delvare and LaSalle, <i>Tetrastichus howardi</i> (Olliff), and <i>Trichospilus diatraeae</i> Chertan and Margabandhu	(Rossoni et al., 2016)
<i>Beauveria bassiana</i> (Balsamo) Vuillemin	Lettuce aphid <i>Nasonovia ribisnigri</i> (Mosley)	–	<i>Aphelinus abdominalis</i> Dalman	(Shrestha et al., 2016)
<i>Lecanicillium muscarium</i> Zare and Gams	Green peach aphid <i>Myzus persicae</i> Sulzer	–	<i>Aphidius colemani</i> Viereck	(Mohammed and Hatcher, 2017)

Table 1 (continued)

Entomopathogenic fungal species	Insect and mite pest	Predator	Parasitoid	Reference
<i>Beauveria bassiana</i> (Balsamo) Vuillemin and <i>Metarhizium anisopliae</i> (Metschnikoff) Sorokin	<i>Diaphorina citri</i> (Kuwayama)	–	<i>Tamarixia radiata</i> (Waterston)	(Ibarra-Cortés et al., 2018)
<i>Beauveria bassiana</i> (Balsamo) Vuillemin	Wax moth <i>Galleria mellonella</i> (L.)	–	<i>Habrobracon hebetor</i> (Say)	(Kryukov et al., 2018)
<i>Metarhizium brunneum</i> Petch	Cotton leafworm, <i>Spodoptera litoralis</i> (Boisduval)	<i>Chrysoperla carnea</i> Stephens	–	(Ríos-Moreno et al., 2018)
<i>Beauveria bassiana</i> (Balsamo) Vuillemin	Two-spotted spider mite, <i>Tetranychus urticae</i> Koch	<i>Phytoseiulus persimilis</i> Athias-Henriot	–	(Wu et al., 2018)
<i>Beauveria bassiana</i> (Balsamo) Vuillemin	The fruit fly <i>Anastrepha obliqua</i> (Macquart)	–	<i>Coptera haywardi</i> (Ogloblin)	(Martínez-Barrera et al., 2020)
<i>Metarhizium brunneum</i> Petch	Cotton leafworm, <i>Spodoptera litoralis</i> (Boisduval)	–	<i>Hyposoter didymator</i> (Thunberg)	(Miranda-Fuentes et al., 2020)

et al. 2017). Emami et al. (2013) found that extending the release interval of the parasitoid *Aphidius colemani* Viereck (Hymenoptera: Braconidae) following *B. bassiana* application for control of the green peach aphid, *Myzus persicae* (Sulzer) (Hemiptera: Aphididae), decreased the quantity of parasitoid pupae growing and the percentage emerging as adults. It has even been reported that using commercial isolates of EF had no influence on the survival rates and enhanced parasitism rates of the parasitoid *Encarsia formosa* Gahan (Hymenoptera: Aphelinidae) (Labbé et al. 2009). Mohammed and Hatcher (2017) observed that, when *M. persicae* treated with the fungus *Lecanicillium muscarium* (Petch) Zare & W. Gams (Ascomycota: Hypocreales) were offered to the parasitoid *A. colemani* 3–4 days after fungal infection, they were less likely to be parasitized than when offered 1–2 days after fungal infection. In whiteflies, Labbé et al. (2009) discovered that applying *B. bassiana* after parasitism by *E. formosa* had no influence on parasitoid numbers or parasitism rates. Furthermore, (Mohammed and Hatcher 2017) found that applying the fungus *L. muscarium* to *M. persicae* 3–7 days after *A. colemani* parasitism had no effect on the proportion of aphids parasitized. It should be noted that the use of parasitoids as vectors of EF has recently been documented, showing that the presence of *Habrobracon hebetor* (Hymenoptera: Braconidae) females significantly (1.5–13 fold) increased the mycoses level in clusters of *Galleria mellonella* L. (Lepidoptera: Pyralidae) (Kryukov et al. 2018), revealing not only compatibility of EF with natural enemies but also a synergistic interaction (Table 1). *Beauveria bassiana* caused no negative effects either on the development of the immature stages of the parasitoid *Coptera haywardi* (Ogloblin) (Hymenoptera: Diapriidae) or on female fecundity during the first 18 days of adult life, and it is therefore possible to develop management strategies using these two natural enemies in biological control against *Anastrepha obliqua* (Macquart) (Diptera: Tephritidae) (Martínez-Barrera et al. 2020) (Table 1).

Hymenopteran eulophid *Tamarixia triozae* (Burks) adults may die prematurely if *B. bassiana* is used to suppress *Bactericera cockerelli* (Šulc) (Hemiptera: Triozidae), without affecting their overall reproductive potential (Tamayo-Mejía et al. 2015). Other researchers have found that previous inoculation with EF can impact fitness of the parasitoid



wasp *Trybliographa rapae* (Westw.) (Hymenoptera: Eucolidae), shortening its lifetime while raising oviposition rates as a response to fungal presence (Rännbäck et al. 2015). Under controlled conditions, Potrich et al. (2015) described negligible effects of *M. anisopliae* on the biological parameters of *Trichogramma pretiosum* Riley (Hymenoptera: Trichogrammatidae) on *Anagasta kuehniella* Zeller (Lepidoptera: Pyralidae). The potential of *M. brunneum* applied by direct contact and/or as an endophyte to control *S. littoralis* larvae alone or in combination with the solitary endoparasitoid *Hyposoter didymator* (Thunberg) (Hymenoptera: Ichneumonidae) in melon plants has also been investigated (Miranda-Fuentes et al. 2020, 2021). In contact treatments, when applied at high concentrations, the fungus significantly reduced the parasitoid's longevity, but had no effect on the parasitoid female's reproductive potential during the three days after treatment. Indeed, in several simultaneous use scenarios (inoculation of *S. littoralis* larvae with the fungus before being exposed to parasitoid females and vice versa), the combinations of the two agents to control *S. littoralis* were explored, with additive impact in all cases (Miranda-Fuentes et al. 2020). Martínez-Barrera et al. (2020) found similar results when they investigated several techniques for controlling *Anastrepha obliqua* (Macquart) (Diptera: Tephritidae) with *B. bassiana* and the parasitoid *Coptera haywardi* Loíacono (Hymenoptera: Diapriidae) (Table 1).

Effect of prey or host infection by entomopathogenic fungi on natural enemy behavior/capacity.

In the case of predators, it has been detected that lacewings quite frequently do not completely consume *S. littoralis* larvae when they are infected by the *M. brunneum* fungus, either to avoid mycosed areas of the body or because the fungal infection can reduce the nutritional quality of the prey (Ríos-Moreno et al. 2018) (Table 1). Other studies also indicate the ability of predators to discriminate between healthy and EF-infected prey (Pell and Vandenberg 2002; Meyling and Pell 2006; Ríos-Moreno et al. 2018). Indeed, it should be noted that several predators have been observed to prefer control prey over *B. bassiana*-infected one, such as *Anthocoris nemorum* (L.) (Hemiptera: Anthocoridae) (Meyling and Pell 2006) or *C. septempunctata* (Ormond et al. 2011), although the specific mechanisms that give rise to this behavior are as yet unknown (Table 1).

The number of *A. gossypii* females consumed by *C. carnea*, as well as the consumption time, were not significantly affected after direct exposure to a *B. bassiana* conidia suspension, compared to what was observed with the control aphids (González-Mas et al. 2019a). However, lacewings did not completely consume aphids that showed signs of fungal infection, as described when *C. carnea* consumed larvae of *S. littoralis* infected by *M. brunneum* (Ríos-Moreno et al. 2018), in what is presumably a lacewing safety mechanism (Table 1).

There are very few studies investigating the parasitoid's influence on host susceptibility to the fungus. It has been reported that parasitism by *H. didymator* improved EF infection of *S. littoralis* larvae, with parasitization dramatically reducing the total hemocytes in *S. littoralis* hemolymph, encouraging fungal infection (Miranda-Fuentes et al. 2020). Therefore, the combined use of EF and predator or parasitoids can enhance the effect of the entomopathogen that might be relevant for biocontrol in terms of both the direct effect of the fungus on the target insect population and the dissemination and spread of the fungal inoculum to uninfected insect hosts.

#### Multitrophic interactions involving entomopathogenic fungi

Another question that arises is whether prey or host feeding on plants endophytically colonized by EF alters predator or parasitoid behavior/capacity in multitrophic systems with a crop plant colonized by an entomopathogenic fungus on which a pest is feeding and becomes a prey or a host for a predator or parasitoid, respectively (Fig. 1c). There are few studies investigating whether endophytic colonization of the plant by EF can influence natural enemies at the third trophic level, and the few that exist have focused on its effect on predators or parasitoids. Table 2 summarizes the works done so far by different authors on multitrophic interactions involving entomopathogenic fungi.

It has been shown that there is no effect on the predatory efficacy of *C. carnea* when feeding on *A. gossypii* aphids that had previously fed on melon plants endophytically colonized with *B. bassiana*, although a reduction in the consumption of prey was detected and an increase in consumption time compared to the control (González-Mas et al. 2019a)

**Table 2** Multitrophic interactions involving plants, Hypocrealean entomopathogenic fungi, insect and mite pests and their natural enemies. References are listed in chronological order

Entomopathogenic fungal species	Plant	Insect pest	Predator	Parasitoid	Reference
<i>Beauveria bassiana</i> (Balsamo) Vuillemin	Broad bean <i>Vicia faba</i> L	Pea leafminer <i>Liriomyza huidobrensis</i> Blanchard	–	<i>Phaenodrotoma scabriventris</i> Nixon and <i>Diglyphus isaea</i> Walker	(Akutse et al., 2014)
<i>Beauveria bassiana</i> (Balsamo) Vuillemin and <i>Metarhizium brunneum</i> Petch	White cabbage <i>Brassica oleracea</i> var. <i>capitata</i> f. <i>alba</i> cv. Castello	Cabbage root fly, <i>Delia radicum</i> L.,	–	<i>Trybliographa rapae</i> Westwood	(Cotes et al., 2015)
<i>Beauveria bassiana</i> (Balsamo) Vuillemin	Common bean <i>Phaseolus vulgaris</i> L. var. Red Rose Coco	Pea leafminer <i>Liriomyza</i> species [ <i>L. huidobrensis</i> Blanchard, <i>L. sativae</i> Blanchard and <i>L. trifolii</i> (Burgess)]	–	<i>Opius dissitus</i> Muesebeck, <i>Phaenodrotoma scabriventris</i> Nixon, <i>Diglyphus isaea</i> Walker, <i>Neochrysocharis formosa</i> Westwood, <i>Hemiptarsenus varicornis</i> Girault and <i>Halticoptera arduine</i> (Walker)	(Gathage et al., 2016)
<i>Beauveria bassiana</i> (Balsamo) Vuillemin and <i>Metarhizium brunneum</i> Petch	Sweet pepper <i>Capsicum annum</i> L. cv Castro	Green peach aphid <i>Myzus persicae</i> Sulzer	–	<i>Aphidius colemani</i> Viereck	(Jaber and Araj, 2018)
<i>Beauveria bassiana</i> (Balsamo) Vuillemin	Melon ( <i>Cucumis melo</i> L. var. Galia)	Cotton aphid <i>Aphis gossypii</i> Glover	<i>Chrysoperla carnea</i> Stephens	<i>Aphidius colemani</i> Viereck	(González-Mas et al., 2019a)
<i>Beauveria bassiana</i> (Balsamo) Vuillemin	Broad bean <i>Vicia faba</i> L. cv. Vertigo	Black bean aphid <i>Aphis fabae</i> Scopoli	–	<i>Aphidius colemani</i> Viereck	(Jensen et al. 2020)
<i>Metarhizium brunneum</i> Petch	Melon ( <i>Cucumis melo</i> L. cv. Galia)	Cotton leafworm, <i>Spodoptera littoralis</i> (Boisduval)	–	<i>Hyposoter didymator</i> (Thunberg)	(Miranda-Fuentes et al., 2021)

(Table 2). A significant preference of lacewings for *A. gossypii* aphids that feed on *B. bassiana*-colonized melon plants was observed, compared to the control plants. This could be related to compounds detected in the plants that were endophytically colonized affecting the behavior of the insects by acting as attractants (i.e., beta-ionone) (Obata et al. 1983; Flath et al. 1994; González-Mas et al., 2019b). In another choice assay, the number of aphids parasitized by *A. colemani* and their sex ratio were not influenced by whether or not the aphids had been feeding on *B. bassiana*-colonized plants (González-Mas et al. 2019a) (Table 2).

In a multitrophic system consisting of the endophytic fungus *M. brunneum* colonizing the melon plant offered to *S. littoralis* together with the parasitoid *H. didymator*, the presence of the parasitoid had a substantial impact on total mortality of *S. littoralis* larvae in all tests (Miranda-Fuentes et al. 2021). Treatments including the parasitoid had the highest death rates both *in vitro* and *in planta*. The total mortality of *S. littoralis* larvae was not significantly increased by simultaneous exposure to the fungus and the parasitoid when compared to the parasitoid alone (Miranda-Fuentes et al. 2021). Jaber and Araj (2018) also report that EF endophytic colonization of plants had no effect on *A. colemani* parasitism rates. Akutse

et al. (2014) discovered that feeding EF-colonized plants to *Liriomyza huidobrensis* (Blanchard) (Diptera: Agromyzidae) larvae had no effect on the parasitoids *Phaeditoma scabriventris* (Hymenoptera: Braconidae) and *Diglyphus isaea* (Walker) (Hymenoptera: Eulophidae) (Table 2).

Whilst in the *M. brunneum*–*S. littoralis*–melon–*H. didymator* system neither the application mode (contact or endophytic) nor the fungal exposure period had a significant effect on *S. littoralis* mortality (Miranda-Fuentes et al. 2020, 2021), other authors have reported that fungal exposure time was a significant factor affecting performance of the combined use of EF with the parasitoid *A. colemani* against *M. persicae* (Emami et al. 2013; Mohammed and Hatcher 2017). In the *M. brunneum*–*S. littoralis*–melon–*H. didymator* system, the parasitoid demonstrated a substantial preference for larvae fed on control plants compared to larvae fed on fungus-colonized plants (Miranda-Fuentes et al. 2021). This preference for untreated hosts is thought to be due to the parasitoid's ability to recognize and avoid the fungus. Mesquita and Lacey (2001) found that the parasitoid *Aphelinus asychis* Walker (Hymenoptera: Aphelinidae) probed the ovipositors of infected aphid hosts for a shorter period, followed by rejection and absence of oviposition, due to strong internal cues. González-Mas et al. (2019a) discovered that offering aphids fed on EF-colonized plants had no effect on the oviposition preference of the parasitoid *A. colemani*. It is unknown what the preference outcomes would be in a similar scenario if EF and *H. didymator* were used together to control *S. littoralis* in the field. According to Mesquita and Lacey (2001), parasitoids will avoid possible hosts that have been exposed to fungus and will look for those that have not, which is good for parasitoid survival in the long term. Indeed, the histological investigation of *S. littoralis* larvae simultaneously parasitized by *H. didymator* and infected with *M. brunneum* revealed that both agents coexisted within the same host and even parasitoid larvae grew inside the host despite fungal invasion (Miranda-Fuentes et al. 2020). Although the fungus may outcompete immature parasitoids within the host, there have been no reports of the fungus invading parasitoid tissues when they are both attacking the same host (Furlong and Pell 2005; Miranda-Fuentes et al. 2020, 2021).

There are very few works investigating whether endophytic colonisation by EF can change secondary

metabolites or trigger different plant defense pathways that could affect natural enemies. Jensen et al. (2020) investigated how the endophytic colonization of broad beans by *B. bassiana* influences the fitness and host-choice of the aphid parasitoid *A. colemani*, as well as differences in the plant defense responses to aphid infestation. Their study revealed that there are changes in the plants' initial defense response to the aphids in the EF-treated plants compared to non-fungus treated control plants by measuring changes in the expression of the specific marker genes PR1 and PR2 involved in the salicylic acid pathway, as well as ERF-1, involved in the ethylene pathway (Table 2).

## Conclusions and future perspectives

The potential uses of EF are going beyond their conventional function of controlling insect pests due to their plant-interacting lifestyles, mainly as plant endophytes and rhizosphere competent microorganisms. However, the close association of EF with plants incorporates trophic complexity because it can influence multitrophic relationships. Our comprehensive review of the scant data available on multitrophic relationships of EF shows that plant associated EF can influence the insect-plant interaction mainly by altering both the chemical ecology of host-plant selection by insect pests and insect pest selection by natural enemies, predators and parasitoids. Overall, EF treatments directly targeting the insect pest or indirectly via endophytism do not compromise predator and parasitoid fitness and behaviour, an important compatibility that should be further explored and utilized in biocontrol strategies for a synergistic application in IPM programs. Nonetheless, the fact that the available data summarized in the present work is mainly based upon short term and small-scale experiments makes necessary much more longer-term farm level real-life implementation research to fully understand the biocontrol impact of the multitrophic interactions of EF. Indeed, it remains unknown whether the newly described lifestyles of EF can also impact other key beneficial arthropods such as pollinators.

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#### Declarations

**Conflict of interest** The authors declare that there are no conflicts of interest associated with this publication.

**Ethical approval** There are no ethical concerns regarding the organisms and the topic of this research.

**Research involving animal rights** This article does not refer to any studies with human participants or animals (vertebrates) performed by any of the authors.

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