Entomologia Generalis, Vol. 44 (2024), Issue 4, 797–811
Published online August 16, 2024

Review Article

The potential and limitations of entomopathogenic fungi as biocontrol agents for insect pest management

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With 3 figures and 1 table

Abstract: Agricultural productivity is frequently threatened by a range of insect pests and pathogens that cause damage to crops. The use of chemical insecticides for control has raised concerns due to negative environmental effects, potential risks to animal and human health, and the emergence of insecticide resistance. Such issues pose threats to the future crop generations. To address these challenges, the application of biological control agents, particularly fungal insect pathogens, has shown promise in effectively managing crop pests and disease vectors. In recent years, significant progress has been made in harnessing the potential of entomopathogenic fungi (EF) for insect pest management. These advancements encompass the discovery and characterization of new fungal isolates, a better understanding their ecological effects in plants, integration of fungal agents within Integrated Pest Management (IPM) strategies, and improvements in their efficacy, formulation, and range of applications. Efforts to overcome limitations in the use of EF under natural conditions and for large-scale applications have also yielded substantial advancements. Here, we provide an overview of recent successes achieved using EF as biocontrol agents, while also addressing their continued limitations, identifying promising areas for further research and challenges associated with utilizing EF. Progress in enhancing the safety and effectiveness of biocontrol methods using EF has led to important breakthroughs. These advancements have the potential to improve food security and safety while reducing adverse environmental impacts associated with pests.

Keywords: application; genetic improvement; pest management; entomopathogenic fungi; biocontrol agent

1 Introduction

Invertebrate insects are the largest group of animals in nature and pose one of the most significant threats to agricultural crops, human health, and indigenous flora and fauna. Economic losses caused by various insects surpass tens of billions of dollars worldwide each year (Oerke 2006; Savary et al. 2019; Douglas 2018). Factors such as climate change and rapid globalization contribute to the increasing colonization and occurrences of insect pests (Deutsch et al. 2018; Maxmen 2013). While chemical insecticides are commonly used for insect control, the long-term and overuse have led to detrimental effects on the environment and human (Wang et al. 2022a). These chemicals also extend to detrimental impacts on non-target organisms and natural enemies of pests (Desneux et al. 2007; Siviter et al. 2021; Zattara & Aizen 2021). Additionally, excessive use of chemical pesticides has led to the development of resistant insect populations, necessitating the development for potent alternatives (Bendis & Relyea 2016). Therefore, there is a need to explore effective alternatives to chemical insecticides for pest control in crop production and beyond (Wilson et al. 2013).

Entomopathogenic fungi (EF), which are naturally occurring and abundant, play important roles in regulating insect populations in the environment (Islam et al. 2021), and therefore have the potential to be effective alternatives to chemical pesticides with fewer environmental risks. Some countries have already developed certain EF as biocontrol agents for pests (Peng et al. 2021; Senthil Kumar et al. 2022). Recent advancements in technology, formulation, life-history, and applications, have revealed not only high potency in their ability to infect and kill insect pests, but also a range of beneficial effects on the microecological environment of plants (Quesada-Moraga 2020; Yerukala

DOI: 10.1127/entomologia/2024/2498
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0171-8177/2024/2498 $ 6.75

et al. 2022). EF can also enhance integrated pest management (IPM) by synergistically acting with natural enemies of pests and promoting plant growth (Quesada-Moraga 2020; Quesada-Moraga et al. 2023a). These discoveries expand our understanding of EF and offer new insights for their use in insect and disease management in agriculture, forestry, and other applications, providing a plant-based approach to biological pest control.

Recent findings in the field of EF have resulted in significant progress towards developing these organisms as sustainable and environmentally friendly agents. Studies have focused on discovering new fungal strains (Gutierrez et al. 2019; Zhao et al. 2023), understanding their ecological benefits with plants, and developing formulation and best application practices (Quesada-Moraga et al. 2023a). In addition, research has elucidated the important aspects of the mechanisms of EF-insect infection (Hong et al. 2023; Ortiz-Urquiza & Keyhani 2013), including strategies for improvement and integration with other pest control methods (Meirelles et al. 2023; Gu et al. 2023). Efforts have also been made to enhance production methods (Sala et al. 2023; Lopes et al. 2019) and utilize genetic engineering and mutant isolation for strain improvement (Wang & Wang 2017; Lovett & St Leger 2018). These research endeavors have significantly contributed to a better understanding of the function and application of fungal pesticides.

Despite the advancements in research, there are still limitations and challenges associated with the use of EF in pest control. These limitations include stability, susceptibility to environmental stresses, efficiency in the field, ability and cost to mass produce, quality control and contamination of commercialized products, and field application challenges (Whipps & Lumsden 2001; Lacey et al. 2015). For example, one limitation is the relative low resistance of EF to environmental factors such as UV radiation (Braga et al. 2015). EF also have specific requirements for humidity levels (typically > 50%) and temperature ranges (best between 20–30 °C), which can limit their viability and effectiveness in natural conditions (Quesada-Moraga et al. 2023b). Additionally, the host range of some EF can be limited, with different strains showing significant variation in their effectiveness against different insect species. In the case of some Hypocreales, their host range can be narrow and restricted (Du et al. 2023), however, *Beauveria* and *Metarhizium* sp. which represent the two main commercialized genera typically have broad host ranges. Overall, these factors have collectively hindered large-scale applications of EF and increased the overall cost of implementation, although the demand of “green” alternatives and the compatibility of EF with organic farming practices is beginning to offset many of these previous impediments (Islam et al. 2021). Efforts are ongoing to address some of these challenges and develop strategies to improve the stability, efficiency, and field application of EF in pest management.

2 The potentials of entomopathogenic fungi as biological control agents

2.1 Natural occurrence and potential applications of entomopathogenic fungi

Entomopathogenic fungi are diverse and can be found in various environments worldwide. Over 1,000 species from approximately 100 different genera have been identified, distributed within the phyla *Ascomycota, Basidiomycota, Glomeromycota, Oomycota*, and *Zygomycota* (Vega et al. 2012; Barra-Bucarei et al. 2019). Among these, more than 750 species are known to be pathogenic to insects (Rabindra & Ramanujam 2007). Some recent studies have tested new isolates of fungal entomopathogens for control of specific insect pests. For example, *Cladosporium* sp. has been tested against the longhorn beetle, *Osphranteria coerulescencs* (Farrokhzadeh et al. 2024), *M. indicum* against *Busoniomimus manjunathi* (Senthil Kumar et al. 2023) and *B. bassiana* against *Diaphorina citri* (Cisneros et al. 2022). However, less than 5% of EF have been developed into around 170 commercial products, and amongst those that have been commercialized, most belong to the *Beauveria, Metarhizium*, and *Isaria* genera (Du et al. 2023; Nawaz et al. 2022; de Faria & Wraight 2007) (i. g., *M. anisopliae, B. bassiana* and *I. fumosorosea*; Table 1). In particular, *B. bassiana, B. brongniartii, M. anisopliae*, and *M. acridum* within the Hypocreales, Cordycipitaceae, have been extensively studied and widely used for pest control (Ortiz-Urquiza & Keyhani 2016; Mascarin & Jaronski 2016; Zimmermann 2007a). These species, known for their ease of cultivation, high virulence, and broad spectrum of activities, popular choices for pest control in agriculture and forestry, targeting insects including *Spodoptera littoralis, Rhynchophorus ferrugineus* and *Chaetoptelius vestitus*.

Metarhizium sp. have a long history of use in agricultural pest control and have the ability to parasitize over 900 species of insects, as well as mites and ticks (Nawaz et al. 2022; Zimmermann 2007b). The wide range of insecticidal abilities has made *Metarhizium* a valuable tool in IPM strategies. Numerous studies have demonstrated its effectiveness against various pests in agriculture and forestry, such as *Oxycarenus hyalinipennis, Sogatella furcifera* and *Nilaparvata lugens* (Shaukat et al. 2023; Wang et al. 2022b; Peng et al. 2020b). As research in biopesticides progresses, *Metarhizium* and its applications are expected to play increasingly important roles in sustainable pest management practices in agriculture and forestry.

Aside from *Beauveria* and *Metarhizium* species, *Isaria fumosorosea* is a widely used entomopathogenic fungus known for its efficacy against more than 40 species of insects across eight orders (Zimmermann 2008). It has shown high virulence against piercing-sucking insects like aphids and whiteflies (Ghulam et al. 2018; Hussein et al. 2016). Other Ascomycete entomopathogens, such as *Verticillium lecanii*

Table 1. The entomopathogenic fungi *M. anisopliae, B. bassiana* and *I. fumosorosea* used for the control of various insect pests. F: field, L: laboratory, PH: polyhouse, SM: semi-field, GH: glasshouse, GRH: greenhouse.

Entomopathogenic fungi	Fungal isolate	Target insect	Exp. condition	References
M. anisopliae	*M. anisopliae* NA-01299	*B. tabaci* nymph	PH / F	(Sain et al. 2021)
	M. anisopliae Ma41/Ma22	*S. frugiperda* larvae	L	(Cruz-Avalos et al. 2019)
	M. anisopliae Ma-002/003	*D. neivai* adult	L / SM	(Martínez et al. 2022)
	M. anisopliae Ma-M2	*O. hyalinipennis* nymph	L	(Shaukat et al. 2023)
	M. anisopliae ARSEF 925	*A. glabripennis* adult	L	(Clifton et al. 2020)
	M. anisopliae CEP591	*L. botrana* larvae and adult	L / F	(Aguilera-Sammaritano et al. 2021)
	M. anisopliae CQMa421	*F. occidentalis* adult	L / F	(Li et al. 2021)
	M. anisopliae CQMa421	*Rice Planthopper*	F	(Peng et al. 2020b)
	M. anisopliae CQMa421	*C. medinalis*	F	(Hong et al. 2017)
B. bassiana	*B. bassiana* JEF-158/484	*R. ferrugineus* larvae	L	(Yang et al. 2023)
	B. bassiana EABb 07/06-Rf	*R. ferrugineus* adult	L / SF	(Dembilio et al. 2018)
	B. bassiana EABb 04/01-Tip	*S. littoralis* larvae	L	(Sánchez-Rodríguez et al. 2018)
	B. bassiana EABb 90/2-Dm	*D. maroccanus* adult	L	(Valverde-Garcia et al. 2018)
	B. bassiana ACP18001/18002	*D. citri*	F	(Cisneros et al. 2022)
	B. bassiana Bb9	*S. frugiperda* larvae	L	(Cruz-Avalos et al. 2018)
	B. bassiana Bea111	*D. fovealis* larvae	L / GRH	(Amatuzzi et al. 2018)
	B. bassiana Bb-0018/0025	*D. neivai* adult	L / S	(Martínez et al. 2021)
	B. bassiana B12: MT610917	*A. gossypii* adult	L	(Mseddi et al. 2022)
	B. bassiana GHA	*B. tabaci* nymph	GH	(Bohatá et al. 2024)
	B. bassiana ARSEF 6444 GHA	*A. glabripennis* adult	L	(Clifton et al. 2020)
	B. bassiana MT-4511	*B. tabaci* nymph	PH / F	(Sain et al. 2021)
	B. bassiana CFCC81428	*C. lapathi L.* larvae	L / F	(Niu et al. 2022)
	B. bassiana FUM 01	*O. coerulescens* larvae & adult	L	(Mohammadyani et al. 2016)
	B. bassiana Bea111	*D. fovealis* larvae	L	(Baja et al. 2020)
	B. bassiana GHA	*P. chrysocephala* adult	L	(Price et al. 2024)
	B. bassiana FIN1-B	*B. tabaci* pupae	L	(Topuz et al. 2016)
	-	*T. cinnabarinus* adult	L	-
	B. bassiana Bb03	*A. stephensi* adult	L	(Blanford et al. 2012)
	B. bassiana IGE3	*S. nonagrioides larvae*	L / F	(Mantzoukas et al. 2020)
I. fumosorosea	*I. fumosorosea* Ifu13a	*A. gossypii* and *J. formosana* adult	L	(Ghulam et al. 2018)
	I. fumosorosea CCM 8367	*L. decemlineata* larvae	L	(Hussein et al. 2016)
	I. fumosorosea PFR 97	*B. tabaci* nymph	GH	(Bohatá et al. 2024)
	I. fumosorosea PF49	*C. curvignathus* adult	L	(Jessica et al. 2019)
	I. fumosorosea Ag. Stefanos	*S. nonagrioides* larvae	L / F	(Mantzoukas et al. 2020)

(Ghaffari et al. 2017), *Nomuraea rileyi* (Zhang et al. 2022), *and Aschersonia spp* (Zhang et al. 2017), have also been utilized in commercial pest control attempts including targeting insects such as *Planococcus citri, Spodoptera frugiperda* and *Bemisia tabaci*. These examples highlight the wide range of hosts targeted by EF and their effectiveness in specific pests, making them valuable contributors to sustainable pest management in agriculture.

2.2 Beneficial effects of entomopathogenic fungi on plant

Certain entomopathogenic fungi, particularly *Beauveria* and *Metarhizium* sp., have been found to positively impact plant growth and enhance plant resistance to both abiotic and biotic factors, including plant pathogens (Quesada-Moraga et al. 2022, 2023a; Vega et al. 2009). Fungal colonization of plant roots (rhizosphere) and other structures, with *M. anisopliae* and *B. bassiana*, has been shown to direct impact plant growth in various beneficial aspects (González-Pérez et al. 2022). *B. bassiana* and *M. brunneum* have been shown to regulate plant "immune"-related hormonal synthesis and thereby affect the growth of *Triticum aestivum* (González-Guzmán et al. 2022). *M. anisopliae* demonstrates a selective attachment to the root of test plants in soil, resulting in a significant increase in root hair density and length, as well as an earlier onset of root hair growth (Sasan & Bidochka 2012). The colonization of EF in the rhizosphere is an important aspect of their biology, impacting soil health, nutrient transfer, persistence, and potential insect control (Qiao et al. 2023; Quesada-Moraga et al. 2022, 2023a) (Fig. 1).

As mentioned, in addition to such rhizosphere competence, both *Metarhizium* and *Beauveria* can establish epiphytic or endophytic associations with various plants, including maize, arabidopsis, and rice. These associations have shown to positively affect plant health and provide protection against herbivorous insects (Quesada-Moraga et al. 2022; Rondot & Reineke 2017). The endophytic presence of *B. bassiana* in melon even affects pollinator behavior by modifying the host plant's flowering phenology and floral volatile profile (González-Mas et al. 2023). As part of this interaction, colonization by EF can also induce the production of secondary metabolites both plants and fungi, which can impact plant growth (Quesada-Moraga et al. 2022; González-Pérez et al. 2022; Quesada-Moraga et al. 2023a) (Fig. 1). Furthermore, priming Cucurbits with *M. brunneum* has been found to significantly affect the survival and fitness of *Spodoptera littoralis*, indicating an interaction between host resistance and fungal colonization (García-Espinoza et al. 2023). These findings highlight the potential of fungal-plant interaction to contribute to pest control through metabolic perspective.

Entomopathogenic fungi have also been shown to induce plant resistances to various diseases, such as gray mold (Sui et al. 2023). Fungal entomopathogen-plant interactions can reduce or slow down pathogen damage, potentially through mechanisms like nutrient competition and ecological niche competition (e.g., *Beauveria* against *Rhizoctonia solani, Lecanicillium* spp against powdery mildew) (Ownley et al. 2010). Leveraging the endophytic nature of EF can help overcome challenges faced by traditional application methods (Yerukala et al. 2022). For example, tomato plant inoculated with *Metarhizium brunneum*, showed increased resistance to spider mites (Rasool et al. 2023), while tomato plants inoculated with *B. bassiana* exhibited increased resistance to gray mold caused by *B. cinerea* (Sui et al. 2023). These findings suggest that the presence or inoculation of EF can enhance plant growth, stimulate the production of defensive compounds, and confer resistance to pests and diseases, thus promoting plant health and protection (Fig. 1).

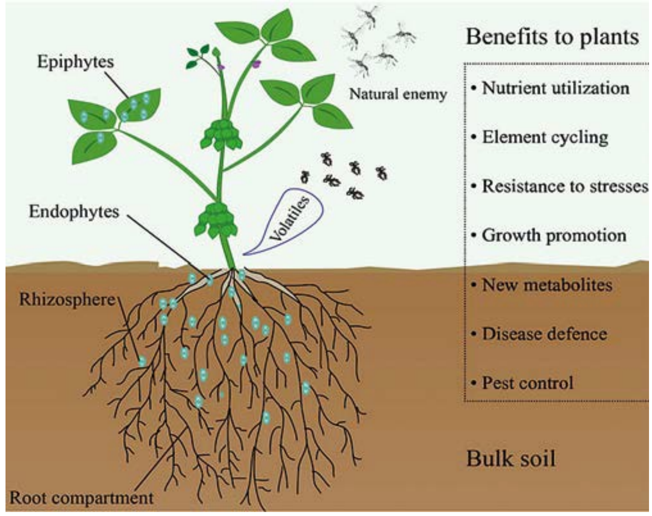

Fig. 1. The important ecological roles of entomopathogenic fungi and their potential to provide beneficial effects on plant growth and enhance resistance.

The promotion of plant growth by EF is the result of interactions of various factors, including improved nutrient and water uptake, stimulation of plant defenses, induction of resistance to biotic and abiotic stressors, and antagonisms plant pathogens through an endophytic and mycorrhiza-like relationship (García-Espinoza et al. 2023; Quesada-Moraga et al. 2023a) (Fig. 1). However, it is important to note that many of these associations appear to be temporary, which can impact the long-term efficacy of plant inoculations with EF. There are still significant gaps in our understanding of how these associations occur and persist. To fully harness the potential of EF in biological control, future research should focus on elucidating the mechanisms that mediate interactions between EF and plants.

2.3 Utilization of entomopathogenic fungi as biopesticides for pest management

Entomopathogenic fungi play a unique role in the biological control of pests as they can infect insects by penetrat-

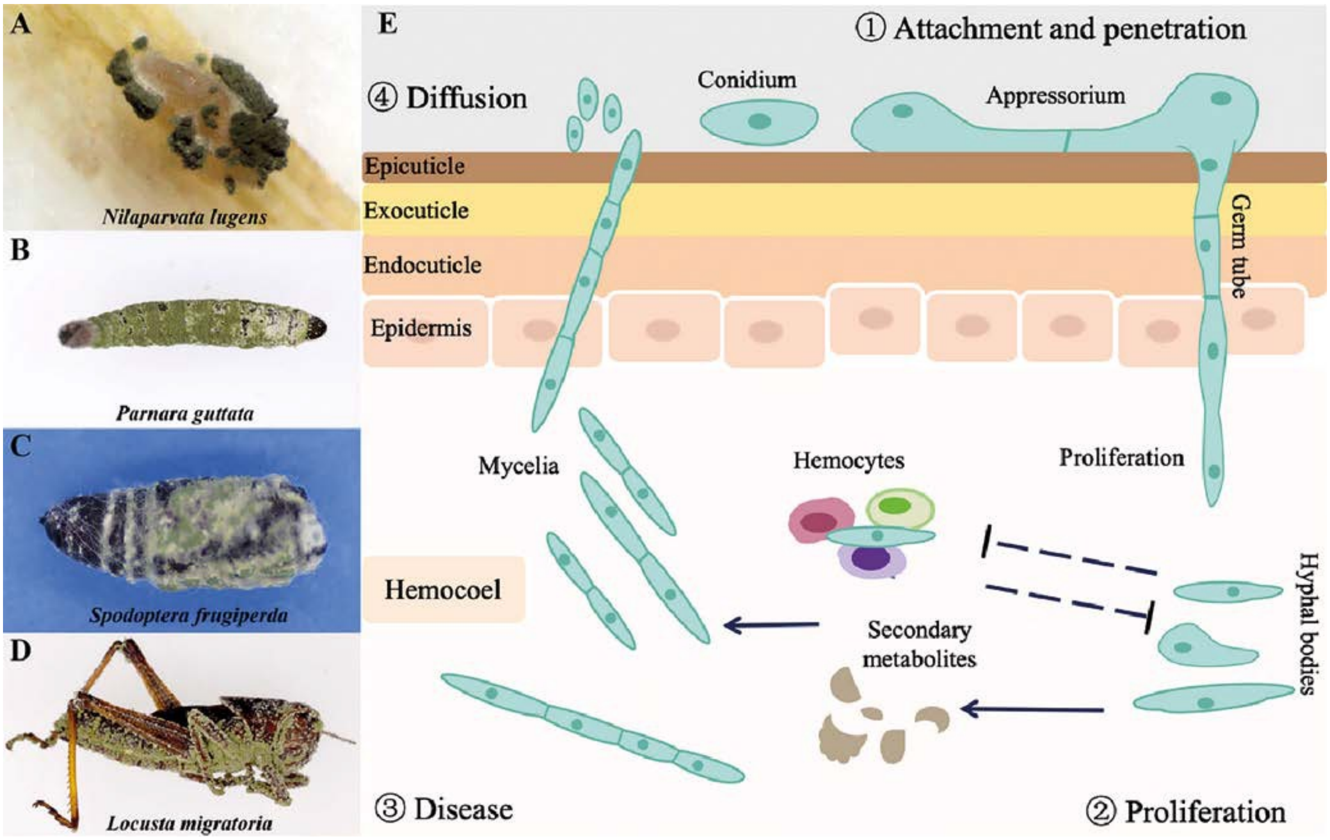

Fig. 2. The insect pests after *M. anisopliae* infection at different stages and typical processes of fungal infection to host insect. A, the egg of rice planthopper *N. lugens* after *M. anisopliae* infection. B, the larva of *P. guttata* after *M. anisopliae* infection. C, the pupa of *S. frugiperda* after *M. anisopliae* infection. D, the adult of *L. migratoria* after *M. anisopliae* infection. E, the infection cycle of entomopathogenic fungi is completed under mainly four stages, including attachment and penetration, proliferation and disease in host body, and diffusion from host insect's body.

ing their cuticle (Du et al. 2023). This makes them effective against a wide range of pests (Fig. 2 and Table S1), including sap-sucking insects, e.g., *N. lugens* and *B. tabaci* (Peng et al. 2021; Topuz et al. 2016). For most entomopathogenic fungi there are two modes of infection: namely cuticular, where the fungal spore penetrates the insect's exoskeleton, and *per os* infection, where the fungus infects gut after being ingested (Zhang et al. 2011; Ortiz-Urquiza & Keyhani 2013). During cuticular infection, the fungal conidium attaches, germinates, and the growing hyphae subsequently penetrate the host exoskeleton (Fig. 2E). Once inside the insect, the fungal cells overcome the host immune system, proliferate within the insect body and tissues, and ultimately kill the host, sporulating on the cadaver (Fig. 2).

While entomopathogenic fungi have shown promise in laboratory conditions for infecting insect pests, their translation to field use has yielded mixed results (Table 1 and Table S1). Some specific isolates of EF, such as *M. anisopliae* targeting *Nilaparvata lugens, Cnaphalocrocis medinalis, Chilo suppressalis* and *Frankliniella occidentalis* (Li et al. 2021; Peng et al. 2021), *M. acridum* targeting *Locusta migratoria* (Hu & Xia 2019), and *B. bassiana* targeting *Cryptorhynchus lapathi* (Niu et al. 2022), have been successfully employed as biological agents for pest control in greenhouse and field conditions. However, the virulence of different fungal species and even different strains within the same species can vary significantly (Table S1). Among the fungi studied (Table S1 and Fig. 3A), *B. bassiana* and *M. anisopliae* has one of the broadest infection spectra, capable of infecting a wide range of insect species, including Hemiptera, Lepidoptera, Thysanoptera, Orthoptera, Coleoptera, and others (Fig. 3). While laboratory studies have reported the infection of important insect pests like *A. gossypii* adults and *L. decemlineata* larvae, data on the effectiveness of these fungi in field conditions remains limited (Ghulam et al. 2018; Hussein et al. 2016).

Entomopathogenic fungi (e.g., *M. anisopliae*), have also demonstrated the ability to infect various developmental stages of target insect hosts, including eggs, larvae or nymphs, pupae, and adults (Fig. 2A–2D). The feeding behavior of the target insect can impact the efficacy of control measures. For example, the below-ground feeding hab-

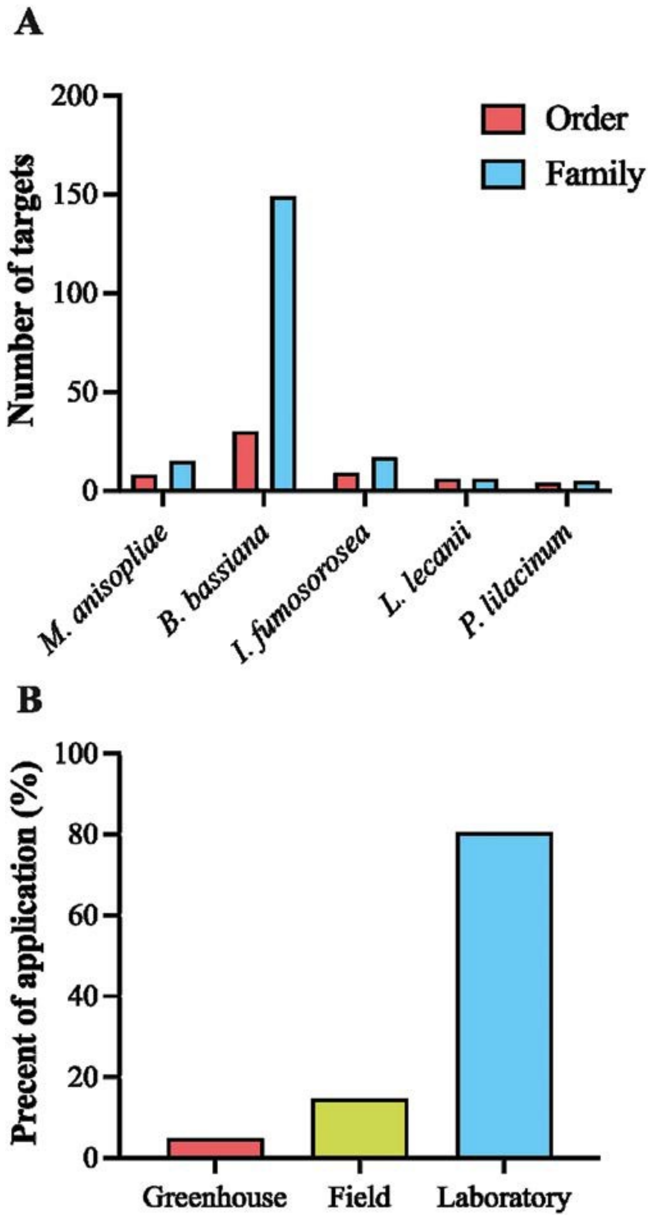

Fig. 3. The major entomopathogenic fungi commonly used for controlling insect pests (Order: family) under different application conditions. A, the five of commonly used entomopathogenic fungi for pest control, including *M. anisopliae, B. bassiana, I. fumosorosea, L. lecacnii* and *P. lilacinum*. B, the major tested scenarios for the use of entomopathogenic fungi in insect infection include various conditions and applications, including laboratory, greenhouse and field conditions.

its of *Adoryphorus couloni* make above-ground insecticide applications ineffective. However, the use of *Metarhizium* fungi in the soil has been found to reduce larval infestation and improve pasture productivity (Berg et al. 2014). These findings are significant as they offer an opportunity to target soil-borne insects that are difficult to control using chemical insecticides. Furthermore, the limited development of insect immunity to these fungi further underscores their potential as effective tools in pest management (Dubovskiy et al. 2013; Hong et al. 2023; Pedrini et al. 2015).

Entomopathogenic fungi have evolved complex infection strategies to overcome insect resistance as seen in experiments examining the infection of mosquitoes (Wei et al. 2017). In addition to agricultural pests, research suggests that fungal biopesticides can be effectively used for the control of populations of mosquitoes, including *Anopheles*, which have developed resistance to chemical pesticides (Farenhorst et al. 2009). By not only killing the target, but also contributing to reducing the likelihood of resistance formation to any chemical pesticide, EF offer a valuable tool for sustainable and effective pest control, particularly in the case of disease vectors like mosquitoes (Blanford et al. 2012; Qin et al. 2023). Furthermore, fungal biopesticides can also be to target agricultural pests, e.g., *Spodoptera frugiperda* varieties which have developed resistances to various chemical pesticides (Gu et al. 2023). Importantly, the development of insect resistance to EF appears to be limited, with no defined reports of resistance occurring due to their application (Gao et al. 2017). However, it is essential to continue monitoring and researching their efficacy and potential resistance development to ensure their long-term effectiveness.

In addition to naturally occurring strains, genetically engineered fungal strains have demonstrated high pathogenicity and significant potential in targeting chemical-resistant mosquito populations and the pathogens they carry (Lovett et al. 2019). More broadly, a range of approaches at genetic improvement of EF exploiting a variety of insect targets have been employed (Fan et al. 2012; Ortiz-Urquiza et al. 2015). These strategies for improving EF strains offer promising solutions for combating not only agricultural pests, but also the spread of vector diseases of both plants and animals (e.g., tick and mosquito-borne regarding the latter). Furthermore, EF have the ability to proliferate in natural environments, providing long-term pest control and contributing to the reduction of chemical insecticide resistance (Islam et al. 2021).

2.4 Entomopathogenic fungi contributing to IPM practices

The viability of EF strains can maintain and even enhanced in response to deleterious environmental factors through formulation, soil application, or treatment of seeds and plant (Quesada-Moraga 2020; Quesada-Moraga et al. 2023a). In addition, combining EF with other control methods, ranging from other biological agents such as parasitoids to low doses of chemical pesticides, can enhance its effectiveness in targeting pests (Jaber & Ownley 2018; Gu et al. 2023). These approaches can help overcome limitations associated with traditional fungal insecticides in practical applications. Thus, integrating biological control agents with other pest management strategies, has shown significant promise (Tang et al. 2019; Salem et al. 2023). Studies have shown that adding low doses of chemical pesticides, e.g., nitenpyram, dinotefuran, pyriproxyfen and thiamethoxam to fungal preparations enhances the effectiveness of *M. anisopliae* against pests like *Aphis gossypii* and rice planthopper (Nawaz et al. 2022; Tang et al. 2019). In the case of mosquitoes, *B. bassiana* can expedite the mosquito mortality when interacting with the mosquito intestinal microbiota (Wei et al. 2017). These findings highlight the potential of leveraging the interactions between EF and other factors, such as the host microbiome, to enhance biocontrol strategies.

Utilizing a combination of interventions with different modes of action is gaining attention as a management strategy (Farenhorst et al. 2010). As mentioned, another approach involves using predatory and parasitic insects that can carry and transmit EF to regulate pest populations (de Bekker et al. 2021; Kryukov et al. 2018a). For instance, the parasitoid *Hyposoter didymator* can be used in conjunction with endophytic entomopathogenic Ascomycetes for controlling *Spodoptera littoralis* in a multitrophic system with melon plants (García-Espinoza et al. 2024). Studies have demonstrated that the simultaneous use of natural enemies and pathogenic fungi can have synergistic effects on pests *Aedes aegypti* and *Myzus persicae* (Alkhaibari et al. 2018; Mohammed & Hatcher 2017). When EF pose a risk (albeit substantially lower than chemical pesticides) to beneficial insects or natural enemies of the target pest, considerable biological control effects can still be achieved by staggering the application time of the two agents (Rashki et al. 2009; Wakil et al. 2017). The combined application of EF and natural enemies, along with careful risk assessment and strategic planning, holds promise for effective pest control within IPM framework.

The compatibility and synergistic application of EF with other control agents is becoming increasingly important (Quesada-Moraga et al. 2022; Tavoosi Ajvad et al. 2020). Factors such as the specific species involved, the timing of application, and environmental conditions can influence the outcomes of these interactions. Further research is needed to gain a better understanding of the dynamics and potential conflicts between EF and other control methods, as well as to identify optimal strategies for their combined use.

3 The limitations of entomopathogenic fungi as biological control agents

3.1 Abiotic factors impact the efficacy of entomopathogenic fungi

The insecticidal effect of fungal biocontrol agents is influenced by various environmental stress factors, with temperature and humidity being key factors (Peng et al. 2020a; Barra-Bucarei et al. 2019). Relative high humidity (> 50%) is crucial for the germination of fungal spores, their invasion into insect hosts, and the subsequent formation of spores necessary for successful mycosis (Quesada-Moraga et al. 2023b). Different temperatures have a significant impact on the fitness of fungal biocontrol agents. For example, *M. acridum* exhibits greater fitness at temperatures above 27 °C, while the *B. bassiana* is better adapted to the temperature range of 10–25 °C (Valverde-Garcia et al. 2018). In addition, an optimal temperature range of 18–30 °C is typically required for infection fungal biocontrol agents, as it influences their growth rate, nutrient utilization efficiency, and ability to evade the insect immune system (Kryukov et al. 2018b).

Furthermore, the exposure to UV irradiation in the environment can have detrimental effects on the survival and efficacy of biocontrol agents, including fungal biopesticides (Tong & Feng 2022). For instance, the germination rate of *M. rileyi* isolates decreased to below 40% after 3 h exposure to UV-B radiation (Licona-Juárez et al. 2023). The UV-B radiation also significantly affected the virulence of the *M. brunneum* against *C. capitata* adults, with the effect being dependent on the exposure time rather than the fungal dosage (Fernández-Bravo et al. 2017). Although irradiation led to a significant loss of conidial viability in three isolates of *B. bassiana*, their virulence was not significantly affected compared to non-irradiated treatments when exposed to 6 hours before or after the inoculation of *C. capitata* (Fernández-Bravo et al. 2023). Therefore, it is important to consider the response of fungal biocontrol agent in terms of virulence and conidial susceptibility to UV-B radiation when selecting environmentally competent isolates, regardless of the results obtained from in vitro assays on conidial germination.

The type of media used to produce *M. anisopliae* conidia can also have an impact on its virulence (Maldonado-Blanco et al. 2014). For instance, when cultured in casein amino acid medium, *M. anisopliae* exhibits significantly higher mortality rates against *Aedes aegypti* larvae compared to conidia harvested from unamended media (Maldonado-Blanco et al. 2014). The culture media can further influence the production of insect toxins and the resulting conidia (Fan et al. 2015; Ortiz-Urquiza et al. 2013). Understanding these factors and their interactions is crucial for optimizing the efficacy of EF in pest management strategies. Ongoing research aiming to further enhance the resistance and overall performance of biological control agents, addressing the limitations and improving their effectiveness in practical applications is warranted.

3.2 Possible risks posed by entomopathogenic fungi to non-target organisms

The application of fungal biocontrol agents like EF in agricultural fields can potentially expose to non-target organisms to these pathogenic microorganisms, leading to various levels of infection, lethality, or sub-lethality (Roy & Pell 2000; Matos Franco et al. 2022). Although these effects are far lower with EF as compared to chemical pesticides, it is crucial to consider both direct and indirect effects on non-target organisms (Mullié et al. 2021). Therefore, before using biopesticidal microorganisms, they are typically tested against beneficial species (e.g., natural enemies of pests such as parasitoid wasps) and species closely related to the non-target. Experiments conducted on foraging bee larva, *Hippodamia convergens* using *B. bassiana, M. anisopliae*, and *P. fumosoroseus*, have shown potential negative effects on their survival (Goettel et al. 2021).

The effects of EF on parasitic natural enemies can manifest in various ways in some cases, including resulting in mortality, altering development, e.g., eclosion rates of pupae, and impacting the ability of the parasitoid to successfully infect target hosts (Yan et al. 2023). For example, the presence of *M. brunneum* on melon plants significantly increased the parasitism rate of *Spodoptera littoralis* by parasitoid wasps (Miranda-Fuentes et al. 2021). This suggests a positive effect of *M. anisopliae* on enhancing the effectiveness of natural enemies in controlling pest populations. However, *B. bassiana*, has been reported to exhibit selective insecticidal effects and mild to moderate toxicity to the Eastern honeybee, *Apis cerana*, whereas *Nomuraea rileyi* was found to be harmless to *A. cerana* (Challa et al. 2019).

The dispersal of entomopathogenic fungi through wind and rain during the sporulation period can also have effects on non-target organisms. Although rare, such dispersal can reduce the survival of exposed social wasp workers on their natal colonies, impair the reproductive ability of foundresses, and induce the removal of exposed brood, ultimately leading to premature colony failure (Lacey et al. 2015; Maute et al. 2017). Considering environmental factors, both in terms of agricultural yield and the selective toxicity to non-target organisms, is crucial when using fungal pesticides in the field (Cappa et al. 2024). It is important to take a holistic approach when assessing the effects of pesticides on non-target organisms (Skrzecz et al. 2024). To ensure the safety of apiculture, fungal candidate strains with low pathogenicity to bees can be considered. An example of such a strain is the locust-specific mycopathogen, *M. acridum*. By considering these factors and conducting comprehensive evaluations, we can gather important information for assessing the environmental safety of entomopathogenic fungi.

3.3 Challenges associated with the practical applications in entomopathogenic fungi

The application of fungal insecticides in practical production poses significant challenges (Jaronski & Mascarin 2017). To enhance the effectiveness and competitiveness of EF as biocontrol agents, several limitations need to be addressed, including cost-benefit analyses, toxicology and registration (Whipps & Lumsden 2001). Compared to chemical insecticides, fungal insecticides have a longer reaction time, i.e., require a longer time to kill the target insect, which can be a disadvantage, especially when dealing with large-scale insect infestations (Fang et al. 2012). This increases the risk of economic losses and may hinder the adoption of biological control agents in certain situations (Bamisile et al. 2021). For example, in Kenya, although there is a considerable number of registered biopesticide products, the demand and local supply of these products remains low. Farmers perceive biopesticides as slow in terms of effectiveness, and cost is also a concern (Constantine et al. 2020). Therefore, optimizing the efficacy and developing strategies to reduce the time required for effective control are crucial areas for improvement.

The insecticidal effects of EF can also be influenced by the host plant/crop examined. Different plant species may affect the efficacy of fungal biocontrol agents against insect pests (Tian et al. 2016; Ocampo-Hernández et al. 2019). For example, when whiteflies were exposed to *Isaria fumosorosea* at concentrations $\leq 5 \times 10^6$ conidia/ml, the mortality rate of whiteflies reared on bean and tomatoes had a shorter median lethal time (LT_{50}) of 4 to 5 days, which was significantly higher compared to whiteflies reared on cucumber and eggplant (5 to 7 days) (Tian et al. 2016). Similarly, *Bactericera cockerelli* nymphs maintained on tomato were more susceptible to *B. bassiana* than nymphs maintained on potato or chili peppers (Ocampo-Hernández et al. 2019). These variations in effectiveness can be attributed to factors such as the plant surface composition, the presence of natural defense mechanisms, and variations in insect physiology when feeding on the plant. It is important to consider these factors when designing pest management strategies using fungal biocontrol agents.

The stability and shelf life of fungal formulations present additional concerns. It is crucial to ensure the viability and efficacy of EF during storage and transportation for their practical application (Ayala-Zermeño et al. 2023; Mascarin et al. 2016). Contamination of commercial products is also a major issue that can lead to a lack of confidence among end users. The handling and storage conditions of microsclerotia (MS) produced by certain *Metarhizium* species can affect their survival, germination, and conidia yield (Yousef-Yousef et al. 2022). Research efforts should focus on developing more stable formulations that maintain the virulence of the fungi over extended periods, while ensuring stringent quality control, particularly in relation to contamination issues.

Furthermore, there are important gaps in our knowledge about the infection process of EF on pests, the mechanisms of action of fungal toxins, and the epidemiological mechanisms of insect epidemics. In-depth research in these areas can provide valuable insights into the development of more targeted and efficient biocontrol strategies. The actual impact of EF in the field can be influenced by various factors, including environmental conditions, interactions with other organisms, and the complexity of natural ecosystems (Leite et al. 2022). Therefore, it is essential to conduct field assessments under conditions that closely resemble larger-scale applications to gain a more comprehensive understanding of the effects of these biocontrol agents.

4 Summary

Entomopathogenic fungi exhibit dual characteristics of preventing plant disease and prompting plant health, while also serving as effective agents in pest control. Future studies should aim towards more fully exploiting the multiple functions of EF, thereby further contributing to plant protection and the sustainable development of agriculture. EF are also often compatible with other biocontrol agents. When combined with other approaches, their application can result in important synergistic effects in controlling plant diseases and insect pests. Moreover, EF are considered "green" and compatible with organic farming practices. By exploring the potential of EF in conjunction with other pest management approaches, we can harness their benefits and develop comprehensive strategies to address agricultural challenges. This approach holds great promise for achieving sustainable and environmentally friendly agricultural practices. Continued research and innovation in this area will enable us to better understand the complexities of EF and maximize their potential for enhancing plant health and agricultural sustainability. Although there may be challenges in use EF, such as formulating and applying them effectively, ongoing research is continually advancing our understanding in this field. This integrated approach would enhance the overall effectiveness of pest management strategies, leading to more sustainable and environmentally friendly agricultural practices.

Acknowledgments: We appreciate our lab members, Yanru Du and Baicheng Li, for providing pictures of the infected insects. Dr. Jiaqin Xie acquired the grants from the National Natural Science Foundation of China (Project No. 31801798) and the Fundamental Research Funds for the Central Universities with project No. 2023CDJXY-009 and 2024CDJXY016.

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Manuscript received: February 2, 2024
Revisions requested: March 22, 2024
Revised version received: June 17, 2024
Manuscript accepted: June 19, 2024

The pdf version (Adobe JavaScript must be enabled) of this paper includes an electronic supplement:
Supplementary Table S1