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Review Article

Effects of Entomopathogenic Fungi on Natural Enemies: A Systematic Review of Their Use in Biological Control

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ABSTRACT

This review evaluates the potential negative impacts of entomopathogenic fungi (EPF) on natural enemies, a key component of sustainable pest management. Literature from Scopus and PubMed, covering 12 countries, 13 EPF species, and 33 natural enemy species, was classified according to the International Organization for Biological Control (IOBC) scale. EPF often caused lethal effects, such as *Lecanicillium muscarium* killing the parasitoid *Diaeretiella rapae*, as well as sublethal effects, including reduced reproduction, shortened longevity, decreased survival rates, and prolonged development. These outcomes varied depending on specific EPF–natural enemy interactions. The findings highlight the need for more field-based and long-term studies to ensure EPF applications do not compromise the ecological role of natural enemies in Integrated Pest Management (IPM).

Key words: Integrated pest management, mortality, predator, parasitoid, sublethal effect

INTRODUCTION

Entomopathogenic fungi (EPF) are important biological control agents that offer an environmentally sustainable alternative to chemical pesticides. Unlike synthetic chemicals, EPF infect and kill insect pests through direct contact and colonization of the host's body, leaving no toxic residues and thus are safer for the environment. EPF have been recognized as effective biological control agents that contribute to sustainable agricultural practices and support the conservation of biodiversity (Bamisile *et al*., 2021).

EPF does not represent a single monophyletic group of fungi but is instead divided across various taxonomic groups. These include approximately 12 species of Oomycetes, 399 of Microsporidia (obligate intracellular pathogens), 65 of Chytridiomycota, 474 of Entomophtoromycota, 283 of Basidiomycota, and 476 of Ascomycota (Kaczmarek & Boguś, 2021; Bihal *et al*., 2023). The most popular species of entomopathogenic including *Beauveria*, *Paecilomyces Metarhizium, Lecanicillium, Isaria, Hirsutella*, and *Lecanicillium* species (Khan *et al*., 2012; Mascarin & Jaronski, 2016; Ríos-Moreno *et al*., 2016; Bamisile *et al*., 2021).

Soil-inhabiting fungi, mostly isolated from arthropod carcasses, are important in controlling pest insects and are often used as commercial biopesticides (Behie & Bidochka, 2014). However, as their use expands, concerns have been raised about their potential non-target effects, particularly on natural enemies like predators and parasitoids, which are important for maintaining ecological balance. These potential non-target effects underscore the need for further research and caution in the use of soil-inhabiting fungi (Panwar & Szczepaniec, 2024).

Natural enemies can be divided into two main groups: predators and parasites. Ladybugs and spiders are predators, preying on various insects throughout their life cycle (Evans, 2009; Mezőfi *et al*., 2020). Parasitoids, such as wasps or flies that lay their eggs on or in other arthropods, are alternatively called parasites (Frago & Zytynska, 2023). The parasitoid eggs develop into immature insects that feed on the host, eventually killing it. Although each developing parasitoid kills only one host during its life cycle, they are generally more specific in the insects they target compared to predators (Memmott *et al*., 2000). Some hosts can have more than one parasite. This phenomenon is known as superparasitism (Heimpel, 2019). Insects can also suffer from diseases caused by bacteria, fungi, or viruses, known as entomopathogens (Kaya & Vega, 2012).

EPF has demonstrated effectiveness in targeting and killing insect pests, yet it also presents potential risks to non-target organisms, including natural enemies. This could disrupt biological control strategies and alter ecosystem dynamics (Panwar & Szczepaniec, 2024). The decline in natural enemy populations could lead to unintended consequences, such as secondary pest outbreaks or shifts in ecological interactions (Cordeiro *et al*., 2014; Sánchez-Bayo, 2021). Additionally, competition between EPF and natural enemies for the same hosts and the potential development of pest resistance could further complicate IPM efforts. Striking a balance between using EPF and preserving natural enemies is crucial for sustainable pest control (Alharbi *et*

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al., 2022). This review aims to identify the potential negative impacts of entomopathogenic fungi on natural enemies that can be used as guidance for biological control, to compile and evaluate existing research on these impacts, categorizing them according to the IOBC scale effect, and to assess the limitations, approaches, and recommendations of the reviewed studies.

This review provides information on the potential risks associated with the use of EPF on non-target organisms, particularly natural enemies like predators and parasitoids that play essential roles in maintaining ecological balance. The findings underscore the necessity of a balanced approach in IPM, emphasizing the preservation of natural enemies while utilizing EPF for pest control. Such information is essential to inform researchers and practitioners in developing strategies that minimize unpredictable ecological consequences, ensuring the long-term success and sustainability of IPM programs.

MATERIALS AND METHODS

Publications associated with the negative impacts of EPF on natural enemies were retrieved from online databases in July 2024 and reviewed. PubMed and Scopus were selected as the databases due to their extensive repositories of full-text research articles and rigorous peer-review processes. The search was restricted to English-language journal articles published between 2014 and 2024.

The following search strings were utilized in the selection of relevant articles in the title, keywords, or abstract: (("Entomopathog* fung*" OR "insect pathog*" OR "disease*" OR "fung*") AND ("Natural enem*" OR "Predator*" OR "Parasit*" OR "Arthropod*" OR "Insect*" OR "Hexapod*") AND ("Negative impact*" OR "Effect*" OR "Implication*" OR "Consequence*" OR "Affect*" OR "Adverse*" OR "Mortalit*" OR "Behavior*" OR "Surviv*" OR "Life cycle*" OR "Parasitism*") AND ("Integrated Pest Management" OR "IPM")). The literature search yielded 1499 records from Scopus and PubMed, which were imported to Rayyan AI (http://rayyan.qcri.org) for data management and screening.

During screening and data extraction, the duplicates, conference proceedings, reviews, book chapters, and editorial material were removed. The remaining records were retrieved in full text and reviewed in detail. The screening was executed by three independent reviewers against the inclusion/exclusion criteria. Three criteria were determined for study inclusion: i) studies with EPF, ii) studies with natural enemies, and iii) studies that evaluated at least one negative impact on natural enemies by the EPF. For study exclusion, criteria include: i) no negative impacts on natural enemies reported; ii) studies of entomopathogens that use bacteria and viruses, in addition to fungi; and iii) studies that are not written in English. This systematic review followed the PRISMA statement and checklist guidelines in excluding or including publications during screening stages (Moher *et al*., 2009). A flow chart for the systematic review is provided in Figure 1.

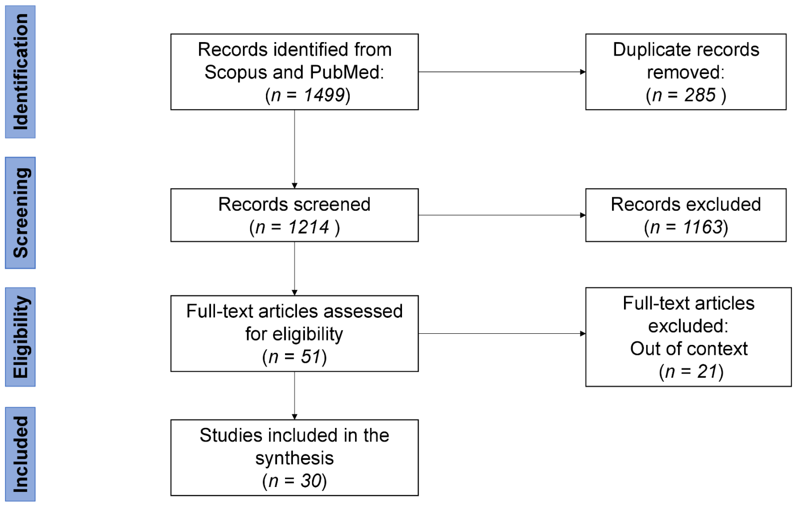

Fig. 1. Preferred Reporting Items for Systematic Reviews and Meta-Analysis (PRISMA) diagram of systematic quantitative literature review selection process.

Potentially relevant articles were downloaded and read in full. Information and data relevant to this review were extracted from the eligible articles. The information included the negative impacts, IOBC levels, target area for inoculation, fungi species, natural enemy species, country where the study was conducted, study setting, and measured parameters. The study settings used in each article were categorized into *in vivo, in vitro*, and combined approaches using more than one methodology (e.g., field & laboratory).

For data analysis, the negative impacts on natural enemies by the EPF were recorded, and their levels were evaluated according to the setting study of the article using scale values from the International Organization for Biological Control (IOBC) (Table 1) (Hassan *et al*., 1991). All figures were constructed using Microsoft Excel 2016, MapChart Version 5.7.5, freepik.com, and VistaCreate.

Table 1. Effect of entomopathogenic fungi on natural enemies based on the International Organization for Biological Control (IOBC) evaluation scale (Hassan *et al*. 1991)

Scale value	Category	Reduction of population in different settings/conditions	
		Laboratory and Greenhouse	Field
1	Harmless	<50%	<25%
2	Slightly harmful	50-79%	25-50%
3	Moderately harmful	80-99%	50-75%
4	Harmful	>99%	>75%

RESULTS AND DISCUSSION

Trends in publications on the negative impact of entomopathogenic fungi on natural enemies over time

The search strategy identified a total of 1214 articles after 285 duplicates were removed, and 1163 articles were dismissed in the first-level screening based on titles and abstracts. Of the 51 full-text articles screened for eligibility, 21 were excluded for being out of context, resulting in 30 articles being included in this systematic review. The number of published studies on the negative impacts of EPF on natural enemies fluctuated between 2014 and 2024 (Figure 2). Only one study was recorded in both 2014 and 2015, but this number increased to three studies in 2016. Following a decline in 2017 (*n*=1 study), the number of publications gradually increased and peaked during 2020 – 2023 (*n*=4 studies, respectively).

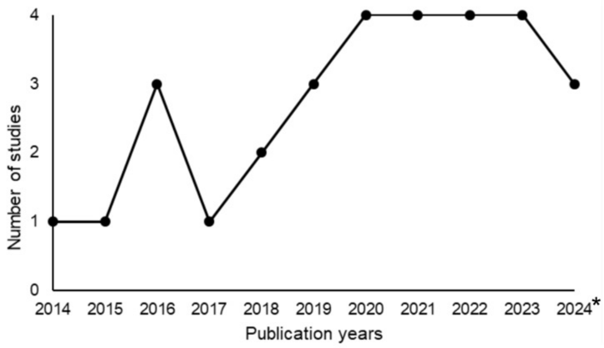

Fig. 2. Temporal trend of published studies on the negative impacts of entomopathogenic fungi on natural enemies during 2014 to 2024. *Indicates studies published until July 2024.

The fluctuation in the number of studies on the negative effects of EPF on natural enemies from 2014 to 2024 can be attributed to shifts in research focus and awareness. Initially, there was limited interest in non-target effects, but this began to grow by 2016 due to rising ecological risk concerns, including potential toxicity to certain plant species and grazing livestock (Bamisile *et al*., 2021). According to the Food and Agriculture Organization (FAO) of the United Nations, approximately 40% of agricultural yield is lost to pests, resulting in $220 million in global losses (FAO, 2021). Staple grains such as rice, maize, and wheat recorded the highest yield losses, at 30.0%, 22.5%, and 21.5%, respectively (Savary *et al*., 2019). This situation likely increased federal funding for biological control research, averaging 42% across the USA's universities, federal, and state levels. Contributions from states range between 29% and 35%, commodity groups provide 19 - 24%, and private sources furnish the balance (Leppla *et al*., 2024). This funding boost likely encouraged researchers to study non-target insects, resulting in two studies in the USA in 2022 and 2023. The growing interest in eco-friendly approaches, driven by the plant pathologist's role in improving agricultural yields and pest management, likely led to more research activity (Collinge *et al*., 2022).

Geographical distribution of studies on entomopathogens causing negative impacts

A total of 13 EPF species that negatively impact natural enemies in these regions from 12 countries (Figure 3). Brazil had the highest number of studies (*n*=7; 23.3% of the total number of studies) (Savi *et al*., 2024), followed by Iran with 6 studies (20.0%) (Atrchian *et al*., 2022). Spain contributed 13.3% (*n*=4) to the total studies (García-Espinoza *et al*., 2024), while the USA comprised 10.0% (*n*=3) of total studies (Pagac *et al*., 2023). China and Denmark each contributed 6.7% (*n*=2) (De Azevedo *et al*., 2018) (Li *et al*., 2024). A single study was recorded in Argentina, Egypt, Greece, New Zealand, South Africa, and Uruguay, respectively (Liu *et al*., 2019) (Corallo *et al*., 2021) (Mama Sambo *et al*., 2022) (Betsi & Perdikis, 2023) (Fergani *et al*., 2023) (Manfrino & Rocca, 2024). *Beauveria bassiana* was the most studied species across nearly all countries. Iran had the highest diversity of EPF species studied (*n*=6), followed by Brazil (*n*=5). *Beauveria bassiana* and *Metarhizium brunneum* were the only species studied in Denmark and Spain. Nine EPF species were examined exclusively in a single country, including *Acremonium sclerotigenum, Akanthomyces muscarius, Cordyceps fumosorosea*, *Hirsutella thompsonii, Isaria fumosorosea, Lecanicillium muscarium, Metarhizium rileyi, Paecilomyces variotii*, and *Simplicillium* species.

Thirty-three species of natural enemies, including predatory and parasitoid insects from six orders, were recorded across the studies (Figure 3B). Approximately 51.5% of the natural enemies recorded were parasitoids, while 48.5% were predators. The order Hymenoptera was the most frequently studied group, with research conducted in countries such as Iran, Denmark, Brazil, Spain, China, Uruguay, Egypt, South Africa, and the United States of America. In contrast, studies involving the order Diptera were limited to Denmark. Among the species, *Diaeretiella rapae* was the most studied (*n*=3), followed by *H. didymator, A. colemani, H. axyridis, C. externa,* and *C. carnea*.

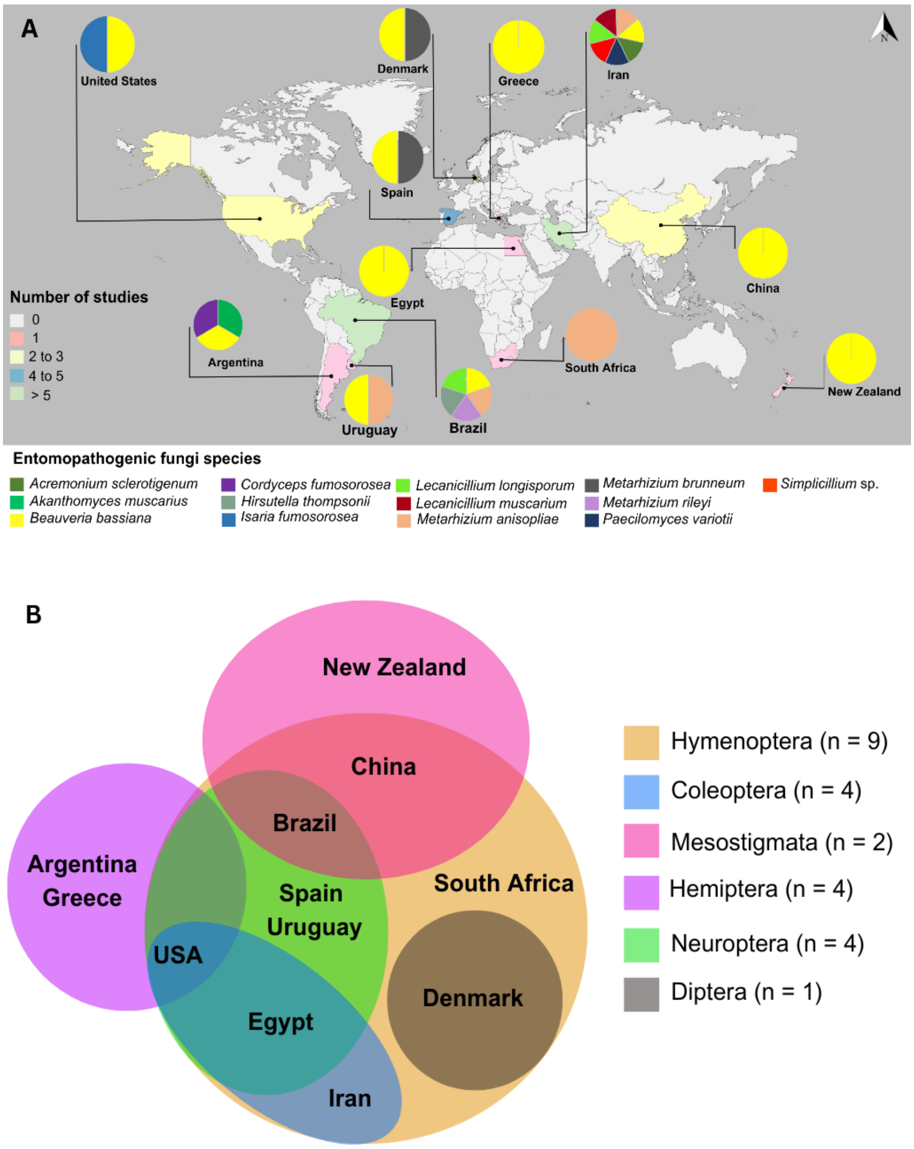

Fig. 3. Geographical distribution of entomopathogenic fungi species and taxonomic variation of natural enemies. A) The geographical distribution of study sites from 30 reviewed articles, highlighting the study frequency and composition of entomopathogenic fungi species by country. B) Venn's diagram illustrates the orders of natural enemies studied across different countries. (n = number of studies per order; the overlaps section represents studies evaluating multiple orders).

South America, Asia, and Europe had the highest representation in the studies, each contributing 23.08%, while Africa contributed 15.38%. North America and Australia each accounted for approximately 7.69% of the geographical distribution of studies. Southeast Asia, despite its tropical climate and rich diversity of entomopathogenic fungi (Rajula *et al*., 2020; Garner *et al*., 2024), did not meet the inclusion criteria for any of the studies. This region's research focus remains more on the benefits of entomopathogenic fungi for plant pests rather than their negative impacts on natural enemies (Rajula *et al*., 2021; Sani *et al*., 2023; Ningrum *et al*., 2024).

Beauveria bassiana is the most commonly used entomopathogenic fungus (Figure 3). *B. bassiana* is an effective entomopathogenic fungus known for its ability to parasitize hundreds of insect species, making it a valuable, environmentally friendly biological control agent. Its effectiveness is largely attributed to its genetic diversity, which enhances its adaptability to different insect hosts and environmental conditions. This genetic diversity allows various strains of *B. bassiana* to adapt to specific environmental conditions and target specific insect species with high virulence. Several mutated genes and positively selected genes reported previously (Zhang *et al*., 2020) may underpin the virulence of *B. bassiana* during the infection process, which provides insights into the potential effects of natural variation on the virulence of *B. bassiana*, which is crucial for identifying potential virulence factors. The selection of highly virulent strains, informed by their genetic diversity, enhances the efficacy of *B. bassiana* as a biological control agent in integrated pest management programs.

The natural enemies from the order Hymenoptera, with 2.5–3.2 times more species than other orders, are the most studied and the largest order among the reviewed articles due to their significant species diversity (Forbes *et al*., 2018). This is because most larvae of the Parasitica infraorder - one of the two infraorders of apocritan Hymenoptera; the other being Aculeata, which includes ants, bees, and stinging wasps- are mandatory parasites of insects and other arthropods, feeding on their host's tissues until the host dies, thereby earning the term "parasitoids." Hymenoptera can thrive in both temperate and tropical regions (Gaston 1991; Stork 1991). They are excellent alternatives to chemical pest control and play a crucial role in biological control programs. Among all natural enemies used for biological control, parasitic Hymenoptera have been particularly successful (Upadhyay *et al*., 2000).

Negative impact of entomopathogens on natural enemies

EPF has been identified to cause mortality (lethal effect) of natural enemies in most studies. This is followed by sublethal effects such as survival rate (Figure 4).

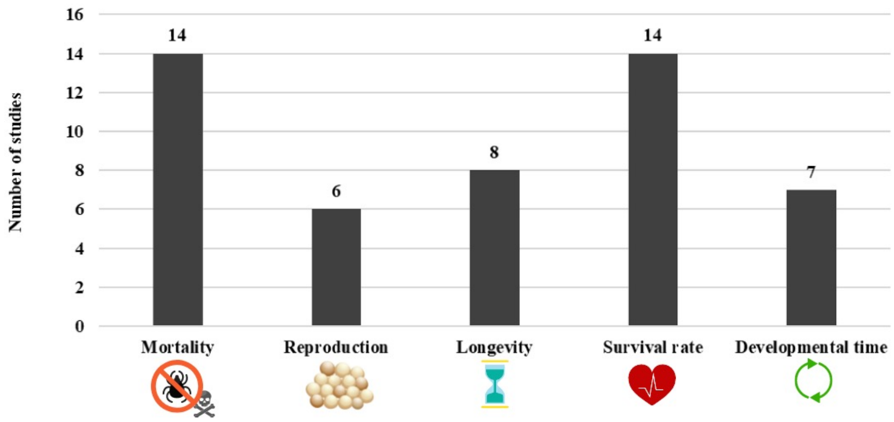

Fig. 4. Negative impact of entomopathogenic fungi identified from 30 reviewed studies, with insect icon illustrations representing different impacts on natural enemies. Numbers on bars indicate the number of studies associated with each impact category.

EPF, while widely used as an alternative method for plant pest control, can have various negative impacts on natural enemies. Direct treatment of predators with EPF at different concentrations has shown detrimental effects across all developmental stages of some predator species (Abbas, 2020) particular, 14 out of 30 reviewed articles (45.1%) reported a decrease in population due to increased mortality. This finding highlights a critical issue: many EPF are currently employed in biological control programs without a comprehensive understanding of their potential impacts on the surrounding ecosystem, including their effects on natural enemies.

Mortality rate of natural enemies caused by entomopathogenic fungi

Ten species of EPF were reported to cause mortality in natural enemies, as documented in 14 laboratory studies and one field study (Table 2). The most severe negative impact of EPF is mortality, which can range from 18–99%. The highest mortality rate (99.9%) was observed for the EPF *L. muscarium* against *D. rapae*, a parasitoid. This variability is influenced by factors such as the species of EPF and the natural enemies involved. For instance, *B. bassiana* caused 40.80% mortality in *C. noackae* and 53.50% mortality in *M. pygmaeus* (Table 2), demonstrating that the same fungus can have varying mortality effects on the different species of natural enemies. This variation is partly due to the heterogeneity of the insect cuticle, which can differ significantly in composition and thickness across various life stages of an insect (Ortiz-Urquiza & Keyhani, 2013). As a member of the order Hymenoptera, *C. noackae* possesses a significantly thicker cuticle (ranging from 1.3 to 109.8 μm) compared to *M. pygmaeus*, which belongs to the order Hemiptera (8.73-10.13 μm) (Lilly *et al*., 2016; Peeters *et al*., 2017).

The IOBC scale was used to assess the mortality effects on natural enemies (van Lenteren, 2012). Of the 25 EPF-natural enemy interactions identified, the majority were classified as moderately harmful (IOBC level 3) with 11 interactions, followed by slightly harmful (level 2) with seven interactions, harmful (level 4) with four interactions, and harmless (level 1) with three interactions. This shows that EPF has a lethal negative impact on natural enemies, with the moderately harmful category being the most prevalent.

Reproductive ability of natural enemies treated with Entomopathogenic Fungi

The fungal treatments significantly influenced the fecundity of various insect species, often prolonging the time required for different life stages compared to controls (Table 3). Specifically, fungi such as *M. anisopliae* and *B. bassiana* affected the pre-pupal and pupal development times, as well as the overall time from oviposition to emergence or mummification in parasitized insects. These sublethal effects include alterations in reproductivity activity, including decreased total fecundity, prolonged pre-oviposition and oviposition periods, and potential reductions in the reproductive success of natural enemies (Table 3). Decrease in reproduction may occur because natural enemies often avoid preying on or parasitizing insects infected by EPF, favouring instead insects that are not exposed to these pathogens (Mesquita & Lacey, 2001). Consequently, the eggs produced by natural enemies exposed to EPF may be lower compared to controls. These findings indicate that a reduction in the reproduction of natural enemies can occur not only when EPF is applied directly to natural enemies but also when EPF is applied directly to the hosts of natural enemies and to leaves treated with EPF (Jarrahi & Safavi, 2016a; De Azevedo *et al*., 2018).

Table 2. Mortality effect of entomopathogenic fungi on natural enemies under different study conditions. % = percentage of mortality; IOBC level = International Organization for Biological Control (IOBC) evaluation scale.

Fungi Species	Natural enemies	Mortality (%)	IOBC level	Setting study	Reference
A. sclerotigenum	*D. rapae*	96.50	4	Greenhouse	Akbari *et al*., 2020
B. bassiana	*D. rapae*	98.60	4		
P. variotii	*D. rapae*	56.60	3		
Simplicillium sp.	*D. rapae*	76.70	4		
L. muscarium	*D. rapae*	99.90	4		
M. anisopliae IRN.1	*M. sexmaculatus*	43.75	2	Laboratory	Atrchian *et al*., 2022
B. bassiana CEP 091	*O. insidiosus*	42.20	2	Laboratory	Manfrino & Rocca, 2024
A. muscarius CEP 182	*O. insidiosus*	55.60	3		
C. fumosorosea CEP 315	*O. insidiosus*	54.40	3		
M. anisopliae 2411	*C. externa*	18.00	1	Laboratory	Corallo *et al*., 2021
B. bassiana	*S. interruptus*	59.96	3	Field	Fergani *et al*., 2023
	C. carnea	56.11	3		
	Formicide ants	65.10	3		
B. bassiana	*C. noackae*	40.80	2	Laboratory	Domingues *et al*., 2020
M. anisopliae	*C. noackae*	22.60	1		
B. bassiana ESALQPL63	*C. externa*	26.00	2	Laboratory	Dias *et al*., 2020
B. bassiana	*M. pygmaeus*	53.30	3	Laboratory	Betsi & Perdikis, 2023
H. thompsonii	*T. evansi*	58.75	3	Laboratory	Savi *et al*., 2024
B. bassiana ICMP 8701	*A. limoniucus*	30.00	2	Laboratory	Liu *et al*., 2019
B. bassiana B4	*A. japonicus*	52.00	3	Laboratory	Li *et al*., 2024
	A. cucumeris	81.20	3		
M. brunneum EAMa 01/58-Su	*H. didymator*	62.50	3	Laboratory	Miranda-Fuentes *et al*., 2019
B. bassiana strain D1-5	*T. dendrolimi*	36.00	2	Laboratory	Wu *et al*., 2022
M. anisopliae sensu lato M14	*H. hebetor*	6.67	1	Laboratory	Jarrahi & Safavi, 2016b

Table 3. Negative impact of entomopathogenic fungi on the reproduction of natural enemies.

Fungi Species	Natural Enemies	Effect on Reproduction of Natural Enemies	References
M. anisopliae	*Habrobracon hebetor*	Treatment of *M. anisopliae* on *H. armigera* larvae with sublethal concentration (LC_{30}): • At time intervals of 48 and 72 hr post-infection, the pre-oviposition to was longer than control with 0.67 ± 0.14 and 1.11 ± 0.26 days, respectively. • At time intervals of 24, 48, and 72 hr post-infection can significantly reduce the oviposition ability of *H. armigera* to 15.53 ± 0.58, 14.08 ± 0.45, and 12.89 ± 0.51 days, respectively. • At time intervals of 24, 48, and 72 hr post-infection can significantly reduce the fecundity total of *H. armigera* to 100.13 ± 3.47, 63.67 ± 3.66, and 45.67 ± 4.39 eggs, respectively. • At time intervals of 0, 24, 48, and 72 hr post-infection, can significantly reduce the net reproductive rate (Ro) of *H. armigera* to 43.895 ± 0.969, 27.767 ± 0.963, 14.235 ± 0.818, and 7.677 ± 0.734, respectively.	Jarrahi & Safavi, 2016a
H. thompsonii	*T. evansi*	Application of *H. thompsonii* on *P. longipes* eggs reduced its total fecundity to 12 eggs per female, while application to adult *P. longipes* reduced total fecundity to 9.40 ± 2.40 eggs per female.	Savi *et al*., 2024
B. bassiana	*A. limoniucus*	Sublethal concentrations of EPF (LC_{10} & LC_{30}) significantly reduced the fecundity of *A. limonicus,* and sublethal concentrations of EPF (LC_{30}) significantly shortened the oviposition period of *A. limonicus.*	Liu *et al*., 2019
B. bassiana	*A. japonicus*	Treatment of *B. bassiana* with concentrations 10^7, 10^8, and 10^9 significantly reduces the fecundity of *A. japonicus* to 70.00 ± 2.45, 69.33 ± 3.58, and 38.00 ± 1.21 eggs/female, respectively.	Li *et al*., 2024
M. brunneum	*H. didymator*	Treatment of *M. brunneum* on the reproductive potential of F1 generation of female parasitoids; 48.80% parasitized larvae compared with the control 65.90%	Miranda-Fuentes *et al*., 2019
M. brunneum	A. *aphidimyza*	Significantly more *Aphidoletes aphidimyza* eggs were found on untreated leaves (93.00%) than on fungus-treated leaves (65.00%)	De Azevedo *et al*., 2018

Longevity rate of natural enemies treated with Entomopathogenic Fungi

Ten interactions between EPF and natural enemies were identified, all resulting in reduced lifespan of the natural enemies (Table 4). Ideally, natural enemies should exhibit high fecundity and long longevity to optimize reproductive opportunities during their lifetime (Plouvier & Wajnberg, 2018). Exposure to fungal pathogens such as *M. brunneum, B. bassiana,* and *M. anisopliae* significantly shortened the longevity of various beneficial insects, including *A. aphidimyza* midges, *T. podisi* females, and *D. rapae* parasitoids (Martins *et al*., 2014; De Azevedo *et al*., 2018; Battisti *et al*., 2022). This shows that the negative impacts of EPF can also affect the longevity of natural enemies.

Table 4. Negative impact of entomopathogenic fungi on the longevity of natural enemies

Fungi Species	Natural Enemies	Effect on Longevity of Natural Enemies	References
M. brunneum	*Aphidoletes aphidimyza*	The longevity of *A. aphidimyza* midges exposed to *M. brunneum* was significantly reduced to 6.4 ± 0.3 days, which was 1.9 days shorter than untreated leaves.	De Azevedo *et al*., 2018
B. bassiana	*Telenomus podisi*	The longevity of adult *T. podisi* females exposed to *B. bassiana* was significantly reduced to 13.4 ± 0.35 days, which was 5.14 days shorter compared to the control group.	Battisti *et al*., 2022
M. anisopliae		The longevity of adult *T. podisi* females exposed to *M. anisoplia* was significantly reduced to 14.1 ± 0.35 days, a decrease of 4.49 days compared to the control.	
B. bassiana	*D. rapae*	The longevity of adult females *D. rapae* when aphids were first exposed to the parasitoid and then sprayed with *B. bassiana* was significantly reduced in all treatments (0, 24, 48 hr after parasitization) with 4.53 ± 0.17, 4.40 ± 0.19, and 2.20 ± 0.20 days, respectively. The longevity of adult females *D. rapae* when aphids were first sprayed with *B. bassiana* and then exposed to the parasitoid was significantly reduced in all treatments (0, 24, 48 hr after being sprayed with *B. bassiana*) with 1.50 ± 0.29, 3.00 ± 0.58, and 2.73 ± 0.15 days, respectively.	Martins *et al*., 2014
M. anisopliae	*Dolichogenidea gelechiidivoris*	Wasps had relatively longer longevity, with up to 8 days of median survival time.	Mama Sambo *et al*., 2022
H. thompsonii	*Phytoseiulus longipes*	The longevity of female *P. longipes* was reduced when applied to eggs (10.8 ± 2.44), female adults (6.0 ± 0.99), and male adults (5.3 ± 0.8).	Savi *et al*., 2024
B. bassiana	*A. limoniucus*	Sublethal effects of *B. bassiana* with LC_{10} and LC_{30} concentrations significantly reduced the longevity of F_0 *A. limoniucus* females to 9 and 7 days. LC_{30} concentration significantly reduced the longevity of F_1 *A. limoniucus* with males to 18.65 ± 1.92.	Liu *et al*., 2019
M. anisopliae Strain IBCB348	*Trichogramma atopovirilia*	The longevity of *T. atopovirilia* was reduced by the application of *M. anisopliae* IBCB348.	Araujo *et al*., 2020
B. bassiana Strain CG716		The longevity of *T. atopovirilia* was reduced by the application of *B. bassiana* CG716.	
L. longisporum	*D. rapae*	The longevity of F1 females *D. rapae* was reduced when aphids were first exposed to the parasitoid and then sprayed with *L. longisporum* at intervals of 0, 24, and 48 hr, resulting in lifespans of 6.07 ± 0.28, 4.06 ± 0.48, and 2.92 ± 0.45 days, respectively. The longevity of F1 females *D. rapae* was reduced when aphids were first exposed to the entomopathogen and then parasitized at intervals of 0, 24, and 48 hr, resulting in lifespans of 1.33 ± 0.33, 2.93 ± 0.30, and 2.67 ± 0.23 days, respectively.	José da Silva *et al*., 2017

Survival rate of natural enemies treated with Entomopathogenic Fungi

Survival rates of natural enemies decreased following treatment with EPF, with variation across species (Table 5). The survival rate of natural enemies can decrease by 22–93%, depending on the specific fungal species and the natural enemies treated (Table 5). The largest decrease in survival rate was reported in a previous study (Shrestha *et al*., 2017), where *B. bassiana* reduced the emergence of adult *A. abdominalis* by 10% and control treatment by 87%. This shows another negative impact of EPF on natural enemies.

Table 5. Negative impact of entomopathogenic fungi on the survival rate of natural enemies

Fungi Species	Natural Enemies	Effect on Survival Rate of Natural Enemies	References
B. bassiana GHA	*Chilocorus cacti*	*B. bassiana* GHA reduced the survival of adults *Chilocorus* spp. (57%) and larvae *Chilocorus* spp. (84%).	Matos Franco *et al*., 2022
B. bassiana GHA	*Hyperapis bigeminata*	*B. bassiana* GHA reduced the survival of adult *H. bigeminata* spp. (84%) and *H. bigeminata* larvae (93%).	
B. bassiana ANT-03	*C. cacti*	*B. bassiana* ANT-03 reduced the survival of adult *Chilocorus* spp. by 40%.	
I. fumosorosea	*H. bigeminata*	*I. fumosorosea* reduced the survival of *H. bigeminata* larvae by 69%.	
B. bassiana CEP 091	*Orius insidiosus*	Survival rate of *O. insidiosus* was reduced by approximately 50% in individuals treated with *B. bassiana* CEP 091 compared to the control.	Manfrino & Rocca, 2024
A. muscarius CEP 182		The survival rate of *O. insidiosus* was reduced by approximately 50% in individuals treated with *A. muscarius* CEP 182 compared to the control.	
C. fumosorosea CEP 315		The survival rate of *O. insidiosus* was reduced by approximately 50% in individuals treated with *C. fumosorosea* CEP 315 compared to the control.	
M. anisopliae	*D. gelechiidivoris*	Survival time of *D. gelechiidivoris* was significantly reduced, whereby 50% of wasps died by day three post-infection with dry *M. anisopliae*.	Mama Sambo *et al*., 2022
H. thompsonii	*T. evansi*	Survival rate of larvae and nymphs of *P. longipes* was reduced when *H. thompsonii* was applied to eggs with 74.4% ± 7.0 and 38.8% ± 6.9%.	Savi *et al*., 2024
B. bassiana	*Spalangia cameroni*	Survival of *S. cameroni* treated with *B. bassiana* strains shows survival times less than the control (in the range 5.63 - 6.13 days).	Pagac *et al*., 2023
B. bassiana	*Muscidifurax raptor*	Survival of *M. raptor* treated with *B. bassiana* strains shows survival times less than the control (in the range 5.20 – 5.36 days).	
B. bassiana	*Spalangia endius*	Survival of *S. endius*-treated *B. bassiana* strains shows survival times less than the control (6.04 ± 0.24 days).	
B. bassiana	*Amblydromalus limoniucus*	The survival rate of *A. limonicus* treated with *B. bassiana* LC30 was decreased by 90 ± 4.3% compared to the control.	Liu *et al*., 2019
L. longisporum	*Encarsia formosa*	Survival rate of *E. formosa* treated with *L. longisporum* LRC190 was decreased to 33–82% (larvae) and 45–66% (pupae). Survival rate of *E. formosa* treated with *L. longisporum* LRC216 was decreased to 22-57% (larvae) and 48-60% (pupae). The survival rate of *E. formosa* treated with *L. longisporum* LRC229 was decreased to 53% (larvae) and 63% (pupae).	Fazeli-Dinan *et al*., 2016
L. longisporum	*D. rapae*	Parasitoid emergence was affected in treatments consisting of spraying *L. longisporum* immediately (0 hr) after or before parasitism.	José da Silva *et al*., 2017
B. bassiana B2	*T. atopovirilia*	Reduced the percentage of emerged *T. atopovirilla* adults to 75.8% compared to the control 93.5%.	Araujo *et al*., 2020
B. bassiana	*D. rapae*	The mean emergence for the treatments with *B. bassiana* spraying after different periods ranged from 22.70 - 40.89%.	Martins *et al*., 2014
B. bassiana	*Aphelinus abdominalis*	High spore concentration of *B. bassiana* as measured by rates of adult emergence (10 ± 5.56%) compared to the control treatment adult emergence (87 ± 4.40%).	Shrestha *et al*., 2017
L. longisporum	*Encarsia formosa*	The emergence of parasitoid adults from treated pupae was observed in the control (85%), while LRC216 (48%) and LRC190 (45%) had the highest impact on immature *E. formosa.*	Fazeli-Dinan *et al*., 2016
M. brunneum	*Aphidoletes aphidimyza*	The proportion of midges that emerged from the soil was significantly higher in the control containers (71%) compared to those in the fungus-treated containers (53%).	De Azevedo *et al*., 2018
M. anisopliae	*Telenomus podisi*	A significant reduction in the percentage of emergence with *M. anisopliae* treatment (10.3%) compared to the control (45.3%).	Battisti *et al*., 2022
B. bassiana	*T. podisi*	A significant reduction in the percentage of emergence with *B. bassiana* treatment (10.2%) compared to the control (45.3%).	

Developmental time of natural enemies treated with Entomopathogenic Fungi

The negative impact of EPF on natural enemies was also observed in developmental time (Table 6). Fungal treatments significantly affected the developmental time and stages of various insects, with some fungi prolonging the egg, pre-adult, and mean generation times of *M. sexmaculatus*, *M. anisopliae,* and *M. rileyi*, reducing the duration of pre-pupae stages. The impact on developmental times varied by fungal species and application timing, influencing the periods between oviposition, mummification, and emergence of adults, particularly in *D. rapae* and *H. hebetor*. These results indicate that fungal pathogens can alter life cycle durations and developmental phases in insect populations.

The development period of natural enemies does not always indicate that their ability to control pests is decreasing. Rapid development can lead to a quicker increase in natural enemy populations, and a short parasitoid development time is often advantageous for biological control (Murdoch *et al*., 2003). Adult size is typically a primary trait in parasitoid selection, as fitness-related traits such as fecundity and longevity generally increase with larger size (Colinet *et al*., 2007). Both approaches require further observations on the ability of natural enemies to attack pests to determine whether the development time is beneficial or harmful.

Additionally, EPF treatment also affects the behavior of natural enemies, particularly in their consumption or parasitization of pests. Behavioral changes are evident through decreased consumption/parasitization of natural enemies against pests exposed to EPF (Table 6). This is likely due to the development of a fungal hyphal layer around the pests, which may deter natural enemies from consuming or parasitizing them. For example, lacewings often avoid fully consuming *S. littoralis* larvae infected by the fungus *M. brunneum*, possibly to avoid fungal-infected areas or because the fungal infection degrades the larvae's nutritional quality (Quesada-Moraga *et al*., 2022). Understanding these sublethal effects on natural enemies allows the development of effective integrated pest management programs.

Table 6. Negative impact of EPF on the developmental time of natural enemies

Fungi species	Natural Enemies	Effect on Developmental Time of Natural Enemies	References
M. anisopliae	*M. sexmaculatus*	The egg phase, preadult phase, and average generation time of EPF-treated *M. sexmaculatus* became longer compared to the control.	Atrchian *et al*., 2022
M. anisopliae	*C. externa*	The larvae treated with *M. anisopliae* had a lower average duration of the pre-pupae stage.	Dias *et al*., 2020
M. rileyi	*C. externa*	The larvae treated with *M. rileyi* had a lower average duration of the pre-pupae stage.	
L. longisporum	*D. rapae*	The developmental time from oviposition to mummification of the *D. rapae* F1 generation was negatively affected by the spraying of *L. longisporum* at 0 hr after parasitism; this treatment extended the mummification of *D. rapae* to 7.13 days. The developmental time from oviposition to emergence in the F1 generation of *D. rapae* treated with *L. longisporum* for both males and females was shorter than in the control.	José da Silva *et al*., 2017
M. brunneum	*H. didymator*	The fungal treatment significantly affected the pupal development time of the parasitoid, causing a slight yet significant reduction when *S. littoralis* larvae were inoculated with the fungus (6 days) compared to the non-inoculated control (6.73 days).	Miranda-Fuentes *et al*., 2019
M. anisopliae	*H. hebetor*	The treatment of *M. anisopliae* on *H. armigera* larvae with a sublethal concentration (LC_{30}), which is then parasitized by *H. hebetor* after 72 hr, can affect the development time of the *H. hebetor* life stage to be longer in each stadia (egg, larva, pupa, preadult), namely 1.86 ± 0.12; 3.27 ± 0.16; and 9.68 ± 0.15 days. Treatment of *M. anisopliae* on *H. armigera* larvae with sublethal concentration (LC_{30}) after 24, 48, and 72 hr can affect the total immature by 13.06 ± 0.19, 13.75 ± 0.23, and 14.82 ± 0.31, respectively.	Jarrahi & Safavi, 2016b
B. bassiana	*D. rapae*	Shortened developmental time from oviposition to mummification of *D. rapae* when aphids were first exposed to the parasitoid and then sprayed with *B. bassiana* (Dr+Bb) at 0h after the parasitism, with 6.03±0.03 days. Shorten developmental time from oviposition to emergence of *D. rapae* when aphids were first exposed to the parasitoid and then sprayed with *B. bassiana* (Dr+Bb) at 24 and 48 hr after the parasitism, with 9.68 ± 0.13 days for males and 9.67 ± 0.18 and 10.07 ± 0.13 for females, respectively. Shorten developmental time from oviposition to mummification of *D. rapae* when aphids were first exposed to the entomopathogen and then parasitized (Bb + Dr) at 0 and 24 hr after the inoculation with 6.05 ± 0.05 and 6.00 ± 0.05 days, respectively. Shorten developmental time from oviposition to emergence of *D. rapae* when aphids were first exposed to the entomopathogen and then parasitized (Bb + Dr) at 24 and 48 hr after the inoculation with 10.05 ± 0.05 and 10.17 ± 0.07 days for males. Shortened developmental time from oviposition to emergence of *D. rapae* when aphids were first exposed to the entomopathogen and then parasitized (Bb + Dr) at 24 hr after the inoculation, with 9.53 ± 0.16 days for females.	Martins *et al*., 2014

Table 6. Continued

M. anisopliae	*H. didymator*	*M. anisopliae* sprayed on leaves of melon increased pupal development time of *H. didymator* and preimaginal to 12.71 ± 0.30 and 19.46 ± 0.30, respectively. *M. anisopliae* unsprayed on leaves of melon increased the preimaginal stages of *H. didymator* to 13.44 ± 0.38 and 20.38 ± 0.44, respectively.	García-Espinoza *et al.*, 2024
B. bassiana	*H. didymator*	*B. bassiana* sprayed on leaf melon increased the pupal development time of *H. didymator* to 12.56 ± 0.29.	

Fungus application methods

The use of EPF requires appropriate application methods to optimize the infection process while minimizing impacts on natural enemies. Various studies have employed several application methods, including spraying on host targets, foliar spraying, soil inoculation, application on glass tubes, filter paper, rearing media, treatment tubes, direct spraying on natural enemies, immersion, seed coating, and soil drenching (Table 7).

The application of EPF as a biological control method has shown promising results in managing pests and the benefits associated with the host plant (Bamisile *et al*., 2021). However, its effects on non-target organisms, particularly natural enemies like predators and parasitoids, warrant careful evaluation. Different fungi species, when applied using various methods such as spraying, soil inoculation, or seed coating, have demonstrated significant impacts on the survival, reproduction, and overall fitness of these beneficial organisms (Jarrahi & Safavi, 2016; De Azevedo *et al*., 2018; García-Espinoza *et al*., 2024).

The most used methods in several studies are foliar spray and direct spraying on natural enemies (Table 7). The foliar spray method is widely employed for pest control due to its effectiveness (Heviefo *et al*., 2020). According to Butt *et al*. (2016), high insect mortality observed in foliar applications could be due to the large number of fungal conidia that come into direct contact with the insect cuticle. This direct contact allows the fungus to quickly germinate and invade the insect's hemocytes, thereby accelerating the onset of mycosis. This is likely to be the case as well when direct application to natural enemies is evaluated, as contact with conidia can produce similar effects to those observed with the foliar spray method. The lethal and sublethal effects of entomopathogenic fungi vary depending on several factors, including the fungal species tested, isolate, the organism being evaluated, application method (Table 7), concentration, and the time interval between the application of the entomopathogen and the release of natural enemies, among other abiotic factors (Battisti *et al*., 2022).

Table 7. Impact of different application methods on natural enemies

Application method	Species of Fungi	Optimum Concentration (cfu/ml)	Effects on Natural Enemies
Spraying on the host target	*M. anisopliae*	2×10^6	Reduced the development time, daily fecundity, net reproductive rate, and generation time of the adult parasitoid (*Habrobraon habator*)
	B. bassiana *M. anisopliae*	1×10^8	Caused mortality in the parasitoid (*Cleruchoides noackae*)
	B. bassiana	1×10^8	Increased time employed by lacewing predators to consume aphids
		1.5×10^5	Reduced percentage of emerged adults and longevity of parasitoid (*Tricogramma pretiosum*)
		1×10^9	Reduced the percentage of mummies, emergence, and longevity of *D. rapae* F1 generation
		1×10^9	Reduced the percentage of mummification, emergence of parasitoids (*Aphelinus abdominalis*)
	H. thompsonii	6×10^2	Reduced egg hatching, survival, total fecundity, and longevity of the predator (*Phytoseiulus longipes*) and caused larval mortality.
	L. longisporum	1×10^8	Reduced the percentage of mummification, adult emergence, longevity, and parasitization of parasitoids (*Diaeretiella rapae)* while increasing the developmental time from oviposition to emergence for both male and female *D. rapae*
	M. brunneum	1×10^8	Caused mortality in adult parasitoids (*Hyposoter didymator*) and reduced reproductive potential of the F1 generation of female parasitoids, and shortened pupal development time.
		1×10^8	Reduced feeding ability and weight gain of predators (*C. carnae*)
	M. anisopliae	1×10^8	Reduced survival time and longevity of parasitoid (*D. gelechiidivoris*)
	Lecanicillium longisporum	2.6×10^7	Reduced the percentage emergence and survival rate of adult parasitoids (*Encarsia formosa*)
Soil inoculation	*M. brunneum*	5×10^6	Reduced the percentage of emergence and caused mycosis symptoms in predators (*Aphidoletes aphidimyza*)

Table 7. Continued

Foliar spray	*M. brunneum*	5 × 10^6	Reduced predator longevity and egg numbers of predators (*A. aphidimyza*)
	A. sclerotigenum *B. bassiana* *P. variotii* *Simplicillium* sp. *L. muscarium*	1 × 10^8	Caused mortality in parasitoids (*D. rapae*)
	B. bassiana	11.5 × 10^7	Caused mortality in predators (*Macrolophus pygmaeus*)
		1 × 10^{10}	Caused the lowest mortality in parasitoid pupae (*Eretmocerus mundus*)
		1 × 10^8	Reduced population of predators (*C. carnea*, ant, and *Scymnus interruptus*)
	B. bassiana	1 × 10^8	Increased the pupal development time of the parasitoid (*H. didymato*r)
	M. brunneum	1 × 10^8	Increased pupal development time and preimaginal time stage of parasitoid (*H. didymator*)
Smearing on the inner surface of the glass tube	*M. ansiopliae*	1.38 × 10^8	Reduced longevity and percentage emergence of adult parasitoids (*Telenomus podisi*)
	B. bassiana	1 × 10^8	
Filter paper inoculation	*B. bassiana*	1.91×10^7	Reduced survival times of parasitoids (*Spalangia cameroni*, *Muscidifura*× *raptor*, *S. endius*)
Applied to the rearing media	*B. bassiana*	7 × 10^9	Inhibited reproduction of predators (*Amblyseius cucumeris*
Applied to the treatment tube	*B. bassiana*	1 × 10^9	Increased the mortality of predators (*Anastatus japonicus*) and reduced the total fecundity of *A. japonicus*
Direct spraying on natural enemies	*M. anisopliae*	2.6 × 10^7	Caused mortality in adult predators (*Menochilus sexmaculatus*) and increased egg developmental stage time, pupal developmental stage time, and pre-adult (male) time
	B. bassiana	4.31 × 10^7	Reduced the percentage survival of adult and larva predators (*Chilocorus* spp.) and reduced the percentage survival of adult and larva predators (*Hyperaspis bigeminata*)
	I. fumosorosea	9 × 10^6	Reduced the percentage survival of larvae (*H. bigeminata*)
	B. bassiana	1 × 10^7	Caused mortality in predators (*Orius insidiosus*)
	A. muscarius	1 × 10^7	
	C. fumosorosea	1 × 10^7	
	M. anisopliae	1 × 10^7	Caused mortality in *C. externa*.
	B. bassiana	1 × 10^7	Caused mortality in the predator (*C. externa*
	M. anisopliae	1 × 10^6	Reduced the average duration of *the C. externa* pre-pupae stage
	M. rileyi	1 × 10^9	Reduced the average duration of *the C. externa* pre-pupae stage
	M. anisopliae	1.15 × 10^7	Caused mortality and reduced the handling time of the parasitoid (*H. hebetor*)
Immersion	*B. bassiana*	2.5 × 10^9	Caused the mortality of parasitoids (*T. denrolim*i) and reduced the time spent in post-oviposition antennation.
		3.5 × 10^4	Caused mortality in female predators (*A. limonicus*) and reduced survival rate, the egg duration, preadult development, total pre-ovipositional, predation rates, fecundity, longevity, oviposition period, and predation rates of predators
Seed coating	*M. brunneum*	1 × 10^8	Reduced the percentage parasitization of parasitoid (*H. didymator*)
Soil drenching	*M. brunneum*	1 × 10^8	Reduced the percentage of parasitoid parasitization (*H. didymator*)

Limitations and recommendations

One of the primary challenges identified in these studies is the conditions under which the experiments were conducted. Many bioassays were performed in controlled laboratory or greenhouse environments, which do not fully replicate the complex and variable conditions of the field. This is because experiments conducted in laboratories and greenhouses are designed to evaluate the effects of a given treatment. Environmental conditions are optimised to increase the chance of these effects being elicited. This limitation raises concerns about the applicability of the findings to real-world agricultural settings, where factors such as temperature, humidity, and light can significantly influence the effectiveness of biological control agents and their interactions with pests. The effectiveness of these EPF, as well as their interactions over multiple generations of pests and natural enemies, remains insufficiently understood in field conditions. We anticipate that the application of EPF as a pest control method in the field may exert negative impacts on natural enemies. This possibility is supported by field studies reporting moderate harmful effects (Fergani *et al*., 2023). Moreover, although EPF applications do not directly target natural enemies, inoculum present on plant leaves and pests may serve as a source of EPF transmission to natural enemies (De Azevedo *et al*., 2018; Fazeli-Dinan *et al*., 2016).

To address these challenges, future research should be conducted under realistic field conditions to better account for environmental variability. In addition, research on parameters such as feeding behaviour by observing how long natural enemies take to obtain prey, as well as understanding the mechanism of spore transmission from EPF to natural enemies. This approach will provide a more realistic assessment of the effects on natural enemies and offer evidence for the simultaneous use of entomopathogens and natural enemies within an integrated pest management context. We also recommend monitoring the natural enemies present in the agricultural field beforehand. The results of this monitoring can be used to determine the EPF species to be applied. We found that certain EPF species do not cause high mortality to natural enemies, such as *M. anisopliae* sensu lato M14 against *H. hebetor*, which is classified as harmless based on the IOBC index (Table 2).

CONCLUSION

Entomopathogenic fungi offer a promising and environmentally friendly approach to pest control. However, there are still many questions about whether the use of EPF is safe for natural enemies. This review highlights the interactions between entomopathogenic fungi and natural enemies, showing lethal effects such as increased mortality, as well as sublethal effects on reproduction, longevity, survival rates, development time, and parasitism that significantly impact natural enemies. This finding could serve as an early warning to evaluate the use of EPF in pest control. At present, further field research is very necessary to explore these potential impacts at the field scale and to assess the broader ecological consequences of applying entomopathogenic fungi on natural enemies in their natural environment.

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ETHICAL STATEMENT

Not applicable

CONFLICT OF INTEREST

The authors declare no conflict of interest.

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