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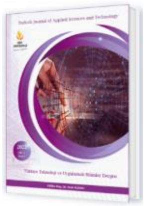

Interactions Between Parasitoids and Entomopathogenic Fungi: Approaches for Sustainable Agriculture

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Review Article

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Abstract

Fungi play an important role in agroecosystems by directly or indirectly influencing parasitoid-host dynamics and thereby contributing to biological control. Entomopathogenic fungi (EPFs), such as *Beauveria bassiana* and *Metarhizium anisopliae*, infect both insect hosts and different parasitoid species in Braconidae and Ichneumonidae, reducing parasitoid survival rates, developmental processes, and overall efficiency. EPFs can alter host physiology and the immune system, increasing or reducing the success of parasitoid infection. These processes are crucial factors in determining the effectiveness of pest control and maintaining ecological balance. Understanding the interactions between fungi, parasitoids, and hosts is essential for improving biological control programs and developing sustainable pest management strategies. This review highlights the role of some entomopathogenic fungal species associated with parasitoids in these diverse interactions and discusses their potential applications in integrated pest management.

Keywords: Entomopathogen, parasitoid, biological control, combinated effects

1. Introduction

Biological pest management, which utilizes organisms such as viruses, bacteria, fungi, and parasitoids, represents an environmentally sustainable alternative to synthetic pesticides. Although its effectiveness may vary, the integration of multiple biocontrol agents has been shown to enhance overall pest suppression efficacy (1). Intraguild predation (IGP) describes the interactions among insect pathogens, parasitoids, and predators that occur when two species either share the same host or prey, or interact directly through parasitism or predation (2). These of interactions have been shown to

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influence the population dynamics of both biological control agents and their target pests (1,2). Interactions among biological control agents are frequently observed, particularly between parasitoids and entomopathogenic fungi (EPFs) (3,4). Hochberg (5), emphasised the presence of two distinct interaction mechanisms between parasitoids and pathogens, which he referred to as 'intrahost interactions' and 'extrahost interactions'. The first aspect pertains to the developmental processes of natural enemies within a shared host, while the second involves interactions external to the host, in which parasitoids serve as vectors for the pathogen. Hochberg (6), further elucidated that intrahost interactions are characterised by asymmetry, determined by the temporal dynamics of parasitoid oviposition and fungal infection (7,8). In extrahost interactions, parasitoids can facilitate the spread of fungi to new host populations. Interactions between entomopathogens and other biological control agents are categorized as synergistic, neutral, or antagonistic, depending on factors such as the type of control agent, its concentration, timing of application and the host species involved (9). Synergistic interactions result in higher pest mortality than the sum of the mortality caused by individual agents. In neutral interactions, natural enemies do not influence each other, and total mortality simply reflects the sum of the individual effects of each agent. Antagonistic interactions, where the total mortality is lower than that caused by a single natural enemy alone, are also considered noteworthy (4,10) (Figure 1). The optimal outcome occurs when the selected natural enemies exhibit either synergistic or neutral interactions, as this typically results in higher pest mortality. Conversely, if an antagonistic interaction occur-possibly due to interference among the control organisms-the pest suppression may be less than expected, negatively affecting the effectiveness of biological control efforts (11).

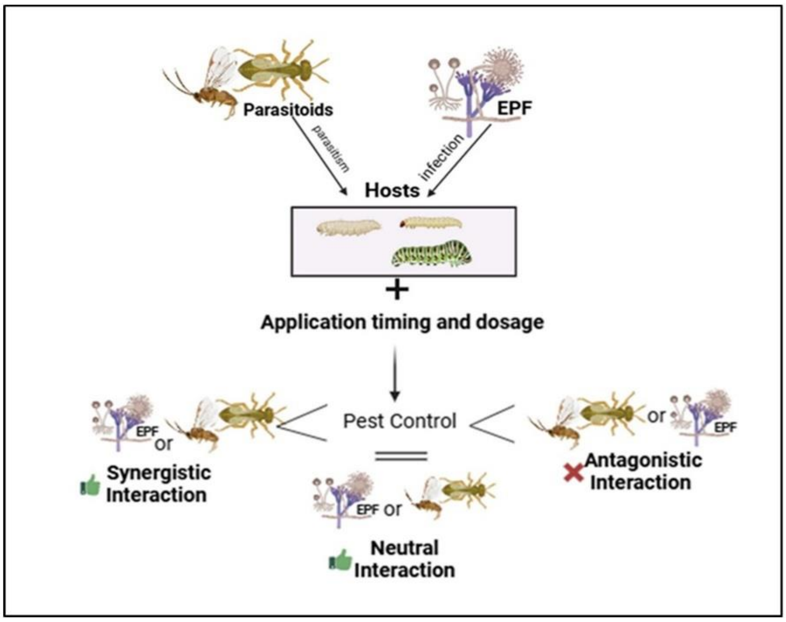

Figure 1: Interactions between entomopathogenic fungi and parasitoids

Research focusing on the interactions between EPFs and other natural enemies (parasitoids and predators) is an important area of research worldwide (12-15). In the field of biological control, the integration of EPFs with a parasiticide has been shown to increase the efficacy of pest control (16). Nevertheless, EPFs with broad host ranges can also infect non-target insects, such as parasitoids, potentially causing direct harm to these biological control agents (14). Consequently, it is imperative to undertake a comprehensive assessment of the potential lethal or non-lethal effects of entomopathogens on parasitoid behavioural and biological parameters of parasitoids (17-19).

2. Entomopathogenic Fungi (EPFs)

2.1. Classification of Entomopathogenic Fungi

Entomopathogenic fungi (EPFs) are organisms that establish parasitic or commensalistic relationships with insects and other arthropods (20,21). More than 1000 species of EPFs are known (22). A significant proportion of these orgamisms are classified within the divisions Ascomycota and Zygomycota, encompassing the orders Hypocreales, Zygomycote and Entomophthoralean. In the EPF grouping, the fungi Blastocladiomycota and Entomophthoromycotina and Kickxellomycotina, and Eurotiomycetes, Laboulbeniomycetes, Dothideomycetes, Sordariomycetes and Pucciniomycetes (12,23).

2.2. Infection Mechanism

The infection process of EPFs begins with the attachment of fungal conidia to the insect cuticle, facilitated by hydrophobic and electrostatic interactions between the conidia and the insect's exoskeleton (24). The fungal spores have the capacity to attach to any part of the insect cuticle, with the binding components varying between insect species and depending on the developmental stage of the insect (25). The second stage of infection is characterized by the germination of the spores that have adhered to the insect cuticle. Factors influencing spore germination include temperature, pH, humidity, oxygen levels, and the availability of nutrients. These factors can vary for different fungal species, although the optimal temperature for spore germination is generally between 20 and 30°C (26). It has been observed that fungi with a broad host range do not require specific carbon or nitrogen sources from the insect cuticle for germination, whereas fungi with a narrower host range rely on certain compounds present in the insect cuticle for spore germination (27). The third stage of infection involves penetration, which is facilitated by the formation of a structure known as the appressorium. This structure exerts mechanical pressure on the insect cuticle and, in conjunction with enzymes produced by the fungus that break down the cuticle, facilitates the process of fungal invasion into the host (27,28).

2.3. Enzymatic Actions and Host Physiology

The epicuticle of the host insect is composed of proteins, lipids, sterols, and fatty acids. The enzymes responsible for the degradation of the cuticle, such as lipase, protease, and chitinase, play a crucial role in facilitating fungal entry into the host insect (29). The lipase enzyme breaks down the lipids and lipoproteins in the epicuticle (30), thereby enhancing the hydrophobic interaction between the fungus and the host cuticle (31). Additionally, proteolytic enzymes produced by the fungus break down the proteins in the insect cuticle, exposing chitin fibrils, while chitinase facilitates the degradation of chitin, allowing the fungus to penetrate and proliferate within the insect cuticle (29). The fungus then traverses the insect’s hemolymph, where it proliferates and forms blastospores. This process disrupts the insect’s tissues and immune system. The fungus also utilizes trehalose, an essential disaccharide found in the insect’s hemolymph, as an energy source, by breaking it down using the enzyme acid trehalase. Finally, the fungus sporulates on the deceased insect, releasing spores that can potentially infect other hosts (32).

3. Parasitoids in Biological Control

Due to the increasing use of pesticides, the problem of resistance is also increasing (20,21). Biological control (biocontrol) is a safe and sustainable approach that utilizes natural enemies such as predators, parasitic insects, or pathogens to manage pests in agricultural ecosystems (21). Accordingly, parasitoids are applied in biological control by taking into account today's effective management strategies (33). Parasitoids, which are crucial contributors to biological pest control, represent a significant portion of the Hymenoptera and Diptera order (34,35). Parasitoids are groups that use various pest species in different periods, especially in order to complete their pre-adult developmental stages or to feed in the adult stage (36,37).

3.1. Types and Characteristics of Parasitoids

The characteristic features of parasitoids reflect their specialized role in biological control within insect populations. These organisms typically exhibit a strong preference for specific host species, with host selection predominantly performed by the female. Adult parasitoids are free-living and mobile, and in some cases may act as predators. One notable trait is that they are consistently smaller in size than their hosts. Their eggs are generally deposited near, on, or within the host body. As the immature stages develop, they feed on the internal tissues of the host, ultimately leading to the host's death. Additionally, different parasitoid species are often adapted to target distinct developmental stages of the host, such as the egg, larva, or pupa (38-40).

Parasitoids are classified as endoparasitoids when they oviposit within a host, which subsequently serves as a nutritional resource throughout the entire larval development. Conversely, when eggs are deposited externally and the host is exploited from the outside, they are termed ectoparasitoids (37). In the classification of parasitoids, two fundamental developmental strategies are recognized: idiobiont and koinobiont (41). Idiobiont parasitoids either immobilize their hosts by inducing paralysis, thereby halting their movement and feeding, or they target inactive developmental stages such as eggs or pupae. In contrast, koinobiont parasitoids develop within hosts that continue to grow, move, and feed during a substantial portion of the parasitoid's larval development. Typically, idiobionts are ectoparasitoids with a broader host range, whereas koinobionts are generally endoparasitoids and tend to exhibit a higher degree of host specificity (42).

Various types of parasitoids play a significant role in biological pest control by targeting different insect pests at various life stages. Braconid wasps (Braconidae) are among the most commonly utilized parasitoids in agriculture, attacking hosts such as caterpillars, aphids, and leafhoppers by depositing their eggs inside the host's body, where the larvae consume internal tissues and eventually cause death. Similarly, Ichneumonid wasps (Ichneumonidae) exhibit high diversity and parasitize a broad spectrum of insects including beetles, sawflies, and caterpillars, often laying eggs on or within the host. Chalcid wasps (Chalcidoidea), though minute in size, are efficient biological agents, frequently employed in horticultural and greenhouse environments to suppress pests like whiteflies, scale insects, and leaf miners. Equally vital are Trichogramma wasps (Trichogrammatidae), which specialize in parasitizing the eggs of moths and butterflies, effectively preventing pest emergence by consuming egg contents. Lastly, Tachinid flies (Tachinidae) are endoparasitoids that typically lay their eggs in proximity to or on the bodies of caterpillars, beetles, and true bugs, with their larvae feeding internally and eventually eliminating the host (40,43).

3.2. Factors Influencing Parasitism Success

In order to be successful during the use of parasitoids in biological control, it is necessary to have features such as mobility, the capacity to detect hosts, survival (longevity), parasitism ability and reproductive power (44,45). In parasitoids, the female's role is to locate a suitable host and oviposit her eggs on or within the host's body. Furthermore, the progeny of parasitoids that emerge post-oviposition do not kill their hosts until they reach adulthood, and although they are parasitic in the larval stage, they are able to live freely in the adult stage. Since they are very active in the adult stage, it is highly probable that they will locate their hosts and proceed to lay eggs (44-46). Additionally, factors such as the time it takes for a female parasitoid to mate, the speed and efficiency of host location and parasitism, the quality of the parasitized hosts, the number of eggs allocated, and the survival and successful development of offspring within the parasitized hosts are all crucial determinants of reproductive success (47).

4. Interactions between Entomopathogenic Fungi and Parasitoids

Parasitoids and predators are considered to be the most important biological control agents in the natural control of the agricultural pests affecting field crops, vegetables, orchards and ornamental plants. They play a vital role in Integrated Pest Management (IPM) programs, which encompass proper planting schedules, effective agricultural practices, the use of biological control agents either alone or in combination, and, when necessary, the application of selective chemical insecticides (48).
Research on IPM interactions and the compatibility of EPF with other biological control agents in pest management has tended to focus more on parasitoids than on predators (3,4,49). While most studies

have focused on fungi, the compatibility of viral and bacterial biocontrol agents with parasitoids has also been investigated. *Beauveria bassiana* (Bals.-Criv.) Vuill., 1912 (Hypocreales: Cordycipitaceae) was included in all of the most common combinations with *Trichogramma pretiosum* Riley, 1879 (Hymenoptera: Trichogrammatidae) (50), *Tamarixia triozae* (Burks, 1943) (Hymenoptera: Eulophidae) (51), *Encarsia formosa* Gahan, 1924 (Hymenoptera: Aphelinidae) and *Trichogramma atopovirilia* (Hymenoptera: Trichogrammatidae) (50). *T. pretiosum* (50) and *E. formosa* (51) were the most extensively studied parasitoids, followed by *Aphidius colemani* Viereck, 1912 (Hymenoptera: Braconidae) (52), *Cotestia flavipes* Cameron, 1891 (Hymenoptera: Braconidae) (53) and *Diaeretiella rapae* (M'Intosh, 1855) (Hymenoptera: Braconidae) (14).

In terms of microorganisms, *B. bassiana* (50,55,56) has been the subject of the most research, with *Metarhizium anisopliae* (Metschn.) Sorokin, 1883 (Hypocreales: Clavicipitaceae) (53,57) a close second. *Bacillus thuringiensis* Berliner 1915 (Bacillales; Bacillaceae) (58) is the most frequently used bacterium. Among the viruses, *Spodoptera exigua* (Hubner, 1808) (Lepidoptera: Noctuidae) multiple nucleopolyhedrovirus (SeMNPV) (59) and *Spodoptera frugiperda* Smith & Abbot, 1797 (Lepidoptera: Noctuidae) multiple nucleopolyhedrovirus (SfMNPV) (60) are among the most frequently tested with parasitoids.

4.1. Types of Interactions: Synergistic, Antagonistic, Neutral

Interactions among organisms both within and across trophic levels are key determinants shaping the dynamics of populations and the structure of ecological communities. When multiple biological control agents are involved, their combined effects may be synergistic, neutral, or even antagonistic in nature (61).

Synergistic interactions between parasitoids and entomopathogenic fungi have the potential to significantly enhance the efficacy of biological pest control. Such interactions may result in pest mortality levels that exceed the additive effects of each agent acting independently. In certain cases, fungal pathogens may compromise the host's physiological defenses, increasing its vulnerability to parasitism, or conversely, parasitism may predispose the host to fungal infection. These mutually reinforcing effects contribute to improved pest suppression, highlighting the value of integrated approaches in pest management programs (11).

Antagonistic interactions occur when one biological agent adversely affects the efficacy or survival of another, either directly or indirectly (11). EPFs may infect and kill the host insect before the parasitoid completes its development an effect particularly pronounced when fungal infection occurs shortly after parasitism. Moreover, fungal toxins can be harmful to immature parasitoid stages residing within or on the host (62). Fungal infection may also elicit host immune responses that lead to the encapsulation or destruction of parasitoid eggs or larvae. Additionally, infection-induced changes in host physiology or behavior can negatively impact the parasitoid’s ability to feed or successfully oviposit (63).

Neutral interactions are defined as scenarios in which parasitoids and EPFs coexist within the same ecological niche without exerting significant influence on each other’s efficacy. Such interactions typically occur when the agents target different developmental stages of the host or are active during temporally distinct periods (64).

4.2. Role of Timing, Dosage, and Host Specificity

The effectiveness of parasitoids in biological control programs is significantly influenced by factors such as timing, dosage, and host specificity. These elements are critical in ensuring successful parasitism and the overall suppression of pest populations.

Timing is a critical determinant in the effectiveness of parasitoid-based biological control strategies. The synchronization of parasitoid release with the susceptible stages of the pest’s life cycle significantly increases the likelihood of successful parasitism. Beyond release timing, the emergence schedule of parasitoids also plays an essential role in shaping population dynamics. Additionally, delayed emergence may expose parasitoids to intensified intra-host competition, potentially reducing individual fitness and altering long-term population stability. These complex, non-linear dynamics highlight the importance of precisely timing both the release and emergence of parasitoids to optimize their impact in pest management systems (65,66).

Dosage is a critical variable that directly influences both the efficacy of biological control applications and the dynamics between hosts and parasitoids. The quantity of parasitoids released into the environment must be sufficient to exert effective pressure on the target pest population. Suboptimal doses may hinder the parasitoids' ability to compete with pests, whereas excessive releases can lead to increased intraspecific competition, thereby reducing the overall productivity and efficiency of the parasitoid population (67). Moreover, high-density introductions may alter parasitoid behavior, such as reducing host-searching time, potentially impacting their ecological function. Beyond the direct effects on target hosts, the ecological consequences of dosage must also be considered. Overdosing can disrupt ecological balance by intensifying competition among natural enemies, potentially leading to reduced biodiversity. Therefore, within the scope of IPM, it is essential to apply parasitoid dosages in a controlled and strategically targeted manner to ensure both ecological sustainability and pest suppression efficacy (68).

Host specificity plays a pivotal role in shaping host-parasitoid population dynamics, as different host stages can significantly influence the development, reproductive success, and survival of the parasitoid. Since various host stages often coexist in natural environments, many parasitoid species display a marked preference for particular developmental stages or specific host species (69,70). In this context, host specificity emerges as a critical trait, particularly in the application of parasitoids for biological control. Parasitoids with narrow host ranges are advantageous, as they limit their activity to target pest species, thereby minimizing potential harm to non-target organisms. A thorough understanding of both host preference and host specificity is therefore essential for predicting parasitoid behavior in field conditions and for evaluating the ecological safety of biological control initiatives (66,71).

4.3. Effects on Parasitoid Biology

Several studies have demonstrated that EPF and parasitoids/predators can coexist and manage various pest species. However, EPFs have also been found to negatively affect the survival and other biological characteristics of certain parasitoids, in both adult and larval stages (72,73). Thus, understanding the potential lethal or sublethal impacts of entomopathogens on the behavioural and biological traits of parasitoids is crucial; numerous studies have documented these interactions (3,4,7,17,18,19,74,75). In their research on the interactions between EPF and other natural enemies, Roy & Pell (11) found that predators and parasitoids could aid in the spread of epizootics by transporting EPFs and facilitating increased movement of infected hosts. Quesada-Moraga et al. (76) evaluated the compatibility between EPF and parasitoids in their study and obtained mixed results. As a result of this study, it was determined that parasitoids carried the fungus and even showed synergistic interactions. In addition, it has been determined that EPF applications can affect the physiology of parasitoids, shortening their lifespan but increasing parasitism rates. In addition, it has been determined by Roy & Pell (11) that the combination is beneficial when the release times are adjusted appropriately, and the timing and order of application of the agents are critical.

5. Combined Applications and Species-Specific Interactions

Combining the application of parasitoids and fungal biological control agents provides more effective pest control. Ensuring the compatibility of the two distinct biological control agents is essential for achieving sustainable and successful pest management (77). Many studies have explored the combined use of potential natural enemies and eco-friendly pesticides as an effective biocontrol approach for various insect pests, reporting either compatible interactions or negligible effects on parasitoids (78-80). To observe the effect of combining two different biological control agents on the same host, the sensitivity of the parasitoid to the fungus can be assessed using direct and indirect infection approaches in interaction experiments. For this purpose, in different planned interaction scenarios, approaches such as dosing on the days following parasitism of the parasitoid on the larvae, parasitism after dosing on the larva or dosing on adult parasitoids reveal the effects of combination results (81,82).

5.1. Interactions Between *Beauveria bassiana* and Parasitoid

The combination of parasitoids and *Beauveria bassiana* is one of the most frequently used in biological control. *B. bassiana* has a broad host range (83), which renders the susceptibility of parasitoids to infection unsurprising. One factor contributing to an antagonistic interaction between an entomopathogenic fungus and a parasitoid is the level of virulence exhibited by the fungus (84), especially since *B. bassiana* is a generalist fungus capable of affecting non-target arthropods. Various studies have shown promising outcomes in pest management using entomopathogenic fungi alongside insect control agents, such as parasitoids or predators. The use of the parasitoid *E. formosa* in combination with the fungus *B. bassiana* has proven to be an effective method for controlling the greenhouse whitefly, *Trialeurodes vaporariorum* (West.) (Hemiptera: Aleyrodidae) (78) (Table 1). Similarly, results indicate that *B. bassiana* can be used in harmony with *Aphidius colemani* Viereck, 1912 (Hymenoptera: Braconidae) without any negative interactions between the two species (85). A study investigated the impact of *B. bassiana* on the biological characteristics of the peach aphid, *Myzus persicae* (Sulzer, 1776) (Hemiptera: Aphididae), and its parasitoid *Aphidius matricariae* Haliday, 1834 (Hymenoptera: Braconidae). In this study, aphids were infected with a concentration of $2×10^8$ conidia/mL and subsequently exposed to parasitoid females for durations of 1 and 4 days. The outcome of the interaction was influenced by the timing of exposure to the parasitoid relative to the aphid infection (4) (Table 1). In another study, the interactions between *B. bassiana* and the braconid aphid parasitoid *Diaeretiella rapae* (M'Intosh, 1855) (Hymenoptera: Braconidae) were investigated under two distinct scenarios. In the first, *M. persicae* nymphs were exposed to parasitoid females for 24 hours before *B. bassiana* (1×10^{10} conidia/mL) was applied at intervals of 0, 24, and 48 hours. In the second scenario, aphids were exposed to both *B. bassiana* and the parasitoid at 0, 24, and 48 hours after infection. The results demonstrated that the parasitism percentage exhibited a range from 13% to 66.5%, with a substantial decline observed between 0 and 24 hours in comparison to the control group in both treatments. The findings indicated that the timing of fungal application prior to parasitoid contact exerted a negative impact on the parasitoid emergence percentage (14) (Table 1).

In the present study, the parasitism rate of the eulophid ecto-nymphal parasitoid *Tamarixia* sp. was evaluated on *Bactericera cockerelli* (Sulk.) (Hemiptera: Triozidae). In the experiment, the nymphs were infected with a *B. bassiana* isolate, and the results indicated that the parasitism rates in the treated group did not show a significant difference compared to the untreated group (51) (Table 1).

A study by Tamayo-Mejia et al. (86) examined the effects of two *B. bassiana* isolates on the development of *Tamarixia* sp., a parasitoid of *B. cockerelli*. Three concentrations of the fungus (LC_{20}, LC_{50}, and LC_{90}) were applied to fourth instars parasitized by *Tamarixia* sp. 3, 5, 8, or 12 days prior to infection at 25 °C. The highest infection rate in parasitoid larvae occurred with LC_{90} when parasitism took place 3 or 5 days before infection, while the lowest infection rate was observed when parasitism occurred 8 or 12 days before infection. The highest parasitoid emergence was seen at the lowest *B. bassiana* concentration when applied 12 days prior to infection, and adult parasitoids from treated hosts showed increased longevity when parasitism occurred 12 days before infection (Table 1).

Studies on the negative effects of *B. bassiana* on adult parasitoids showed that applying *B. bassiana* at a concentration of 10^7 conidia/mL caused 48% mortality in *Cephalonomia stephanoderis* Betrem (Hymenoptera: Bethylidae), a parasitoid of the coffee berry borer, *Hypothenemus hampei* Ferrari (Coleoptera: Curculionidae) (87) (Table 1). In another study, exposure of adult parasitoids *B.*

hebetor and *Anagyrus lopezi* (De Santis) (Hymenoptera: Encyrtidae) to a *B. bassiana* isolate resulted in 100% mortality for both species (84).

A related study assessed the effects of direct application of *B. bassiana* (2×10^8 conidia/mL) on the longevity and fecundity of *Diadegma semiclausum* (Hymenoptera: Ichneumonidae). All treated wasps died within four days, and their cadavers showed typical mycosis. Additionally, fungus-treated females produced an average of 5.1 parasitoid pupae when exposed to healthy *Plutella xylostella* (Linnaeus, 1758) (Lepidoptera: Plutellidae) larvae, compared to up to 18 pupae produced by untreated females (88) (Table 1). In the applications of *B. bassiana* to adults of the larval parasitoid of *Delia radicum* (L.) (Diptera: Anthomyiidae), *Trybliographa rapae* Westwood (Hymenoptera: Figitidae), the LC_{50} values were determined as 1.83×10^7 conidia/mL (89).

B. bassiana transmission has been observed to be enhanced in the presence of the parasitoid *Aphidius ervi* (Hemiptera: Braconidae) of the pea aphid *Acyrthosiphon pisum* (Harris, 1776) (Hemiptera: Aphididae) (16) (Table 1). As Brobyn et al. (74) demonstrate, the females of the aphid parasitoid *Aphidius rhopalosiphi* (De Stephani-Perez, 1902) (Hemiptera: Braconidae) possess the ability to distinguish between hosts infected with *B. bassiana* and those that are uninfected. Furthermore, they lay a lesser number of eggs on hosts infected with *B. bassiana*. Similar results were obtained with the egg parasitoid, *Anagrus atomus* (Linnaeus, 1767) (Hymenoptera: Mymaridae) of the green leafhopper, *Empoasca decipiens* Paoli, 1930 (Hemiptera: Cicadellidae) treated with *B. bassiana* (90) (Table 1).

In another study, it was determined that adult females of the ecto-parasitoid *Cephalonomia tarsalis* (Ashmead, 1893) (Hymenoptera: Bethylidae) laid eggs on larvae of its host, *Oryzaephilus surinamensis* (Linnaeus, 1758) (Coleoptera: Silvanidae), infected with *B. bassiana*, up to one day after the host's death (91). In contrast, it was shown that *D. semiclausum* did not lay eggs on dead larvae by detecting *P. xylostella* larvae infected with *B. bassiana* (88).

5.2. Interactions with *Metarhizium anisopliae- Metarhizium brunneum*

Metarhizium species have been studied in various interguild predator-parasitoid (IGP) interactions. In research by Rannback et al. (89), the impact of the entomopathogenic fungus *Metarhizium brunneum* Petchy (Hypocreales: Cordycipitaceae) on the larvae of *Delia radicum* L. (Diptera: Anthomyiidae) and its parasitoid *Trybliographa rapae* Westwood (Hymenoptera: Figitidae) was assessed. The study indicated that *T. rapae* could differentiate between fungal-infected and healthy hosts of *M. brunneum*. Additionally, an investigation into the LC_{50} values for adult *T. rapae* larvae exposed to *M. brunneum* found the value to be 1.57×10^7 conidia/mL (89) (Table 1). Another study demonstrated that *M. brunneum* and *Aphidius colemani* Viereck, 1912 (Hymenoptera: Braconidae) could coexist without negative interactions, showing potential for their combined use (85).

A study was performed in which *Habrobracon hebetor* (Say, 1857) (Hemiptera: Braconidae) was reared using 3rd instar larvae of *Helicoverpa armigera* (Hubner, 1808) (Lepidoptera: Noctuidae). The study revealed that the parasitoid was subject to a detrimental effect from the fungal infection, depending on the time interval between infection and parasitism. The fungal infection was conducted using sublethal concentrations (LC_{30}) of *Metarhizium anisopliae* (Metschn.) Sorokin, 1883 (Hypocreales: Cordycipitaceae) at 0, 24, 48 and 72 hours (49) (Table 1). In another study on interaction applications, application of *M. anisopliae* at a concentration of *Cephalonomia stephanoderis* (Hymenoptera: Bethylidae), a parasitoid of the coffee berry borer, *Hypothenemus hampei* Ferrari (Coleoptera: Curculionidae) (87) (Table 1). The exposure of adult parasitoids *B. hebetor* and *A. lopezi* to the *M. anisopliae* isolate resulted in 100% mortality of both parasitoids, indicating an antagonistic interaction (84).

5.3. Interactions with *Lecanicillium muscarium- Verticillium lecanii*

Recent studies with *Lecanicillium* have shown that this group can be used effectively in combination with parasitoids. Mohamed and Hatcher (81) showed that the parasitoid *A. colemani* and *Lecanicillium muscarium* (Zimm.) Zare & W. Gams, 2001 (Hypocreales: Cordycipitaceae) can be used together to control *M. persicae* (Table 1). Another study investigated the interaction between the aphid parasitoid *Aphidius nigripes* (Ashmead) (Hymenoptera: Braconidae) and the fungus *Verticillium lecanii* (Zimm.) Viegas (Hypocreales: Cordycipitaceae). The findings showed that this interaction depends on the timing of parasitism and infection (75). In a study evaluating the effects of *V. lecanii* on the cereal aphids *Rhopalosiphum padi* (Linnaeus, 1758) (Hemiptera: Aphididae) and *Sitobion avenae* (Fabricius, 1775) (Hemiptera: Aphididae), the aphids were first treated with *V. lecanii* and then exposed to the parasitoid. The study concluded that the percentage of parasitism of *A. colemani* was not affected by the fungus in both insects (92,93) (Table 1).

5.4. Interactions with *Penicillium mallochii*

In the study on the interaction between *Penicillium mallochii* K.G. Rivera, M. Urb & Seifert, 2012 (Eurotiales: Aspergillaceae) and the parasitoid *Venturia canescens* Gravenhorst (Hymenoptera: Ichneumonidae) and the combined biological control of these two different control agents on *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae), different interaction scenarios were used. The effect of the fungus on the pre-adult developmental period of the parasitoid, the survival time of parasitoids hatched from dosed and dosed parasitized larvae, and the preference of the parasitoid over larvae treated with and untreated with ethanol extract and conidia of the fungus were evaluated. As a result of the dose applications after parasitism, it was observed that the number of adult emergence decreased as the dose concentration increased. In addition, it was determined that adult longevity was shortened at all doses and time intervals. In this case, the shortening of the life span of the parasitoid showed that there was an antagonistic interaction in the combined application of *P. mallochii* and *V. canescens* during the dose application stage after parasitism in biological control studies (46) (Table 1).

5.5. Interactions with *Nomuraea rileyi*

Furthermore, it was observed that *Heliothis zea* Boddie (Lepidoptera: Noctuidae) larvae infected with *Nomuraea rileyi* (Farl.) Samson, 1974 (Hypocreales; Clavicipitaceae) fungus one day after parasitism inhibited the development of the parasitoid *Microplitis croceipes* Cresson (Hymenoptera: Braconidae) (94) (Table 1).

The fungus *N. rileyi* has been shown to impede the development of the braconid parasitoid *M. croceipes* in *H. zea* larvae infected one day after parasitism (94). The fungus, *N. rileyi* did not affect the adults of the parasitoids, *Voria ruralis* (Fallen, 1810) (Diptera: Tachinidae), *Cotesia marginiventris* Cresson, 1865 (Hymenoptera: Braconidae) and *Campoletis sonorensis* (Cameron, 1886) (Hymenoptera: Ichneumonidaea) when exposed to high concentrations of conidia (25 times higher than used in field experiments) (95).

5.6. Interactions with *Pandora neoaphidis*

Although studies on this combination are scarce in the literature, the fungus *Pandora neoaphidis* (Entomophthorales: Entomophthoraceae) was found to inhibit the development of the parasitoid *A. rhopalosiphi* within four days of infection in aphids. It was also observed that *P. neoaphidis* required 8–9 days to cause mortality in adult *A. rhopalosiphi* parasitoids (7).

5.7. Interactions with *Isaria fumosorosea*

The interactions between *Tamarixia radiata* (Waterston) (Hymenoptera: Eulophidae) and the fungus *Isaria fumosorosea* (Hypocreales: Cordycipitaceae) on *Diaphorina citri* Kuwayama, 1908 (Hemiptera: Liviidae) (96) (Table 1). Topical application of a blastospore suspension (7×10^6 conidia/mL) to nymphs parasitized by second-instar parasitoid larvae (three days post-parasitization) resulted in a 50% reduction in host mummification and an 85% decrease in parasitoid emergence. In contrast, when the fungus was applied to mummies containing fourth-instar larvae (six days after parasitization), parasitoid emergence was unaffected. Similarly, fungal treatment of mummies containing pupae (nine days post-parasitization) covered with blastospores also did not inhibit parasitoid emergence.

5.8. Interactions with *Zoophthora radicans*

Adults of *Cotesia plutellae* (Kurdjumov) (Hymenoptera: Braconidae) were not susceptible to *Zoophthora radicans* (Zygomycetes: Entomophthorales) (97), yet treatment of *D. semiclausum* adults with the aforementioned fungus significantly reduced cocoon formation by *P. xylostella* larvae. Although direct application of *Z. radicans* resulted in 90% mortality of *D. semiclausum* adults, studies have demonstrated that the fungus did not transmit or infect *P. xylostella* populations (98) (Table 1).

5.9. Interactions with *Cordyceps javanica*

The biocontrol agents *Cordyceps javanica* (Frieder. & Bally) Kepler, B. Shrestha & Spatafora, 2017 (Hypocreales: Cordycipitaceae) and *Eretmocerus hayati* (Hymenoptera: Aphelinidae) are compatible when used jointly against *Bemisia tabaci* (Hemiptera: Aleyrodidae), resulting in more effective pest control compared to their individual applications (77) (Table 1).

Table 1: Species-specific interactions in combined applications

EPFs	PARASITOID	HOST INSECT	REFERENCES
B. bassiana	*E. formosa*	*T. vaporariorum*	(78)
B. bassiana	*A. matricariae*	*M. persicae*	(4)
B. bassiana	*D. rapae*	*M. persicae*	(14)
B. bassiana	*Tamarixia* sp.	*B. cockerelli*	(51,86)
B. bassiana	*C. stephanoderis*	*H. hampei*	(87)
B. bassiana	*D. semiclausum*	*P. xylostella*	(88)
B. bassiana	*A. ervi*	*A. pisum*	(16)
B. bassiana	*A. atomus*	*E. decipiens*	(90)
B. bassiana	*C. tarsalis*	*O. surinamensis*	(91)
M. brunneum	*T. rapae*	*D. radicum*	(89)
M. anisopliae	*H. hebetor*	*H. armigera*	(49)
M. anisopliae	*C. stephanoderis*	*H. hampei*	(87)
L. muscarium	*A. colemani*	*M. persicae*	(81)
V. lecanii	*A. colemani*	*R. padi*	(92)
V. lecanii	*A. colemani*	*S. avenae*	(93)
P. mallochii	*V. canescens*	*E. kuehniella*	(46)
N. rileyi	*M. croceipes*	*H. zea*	(94)
I. fumosorosea	*T. radiata*	*D. citri*	(96)
Z. radicans	*D. semiclausum*	*P. xylostella*	(97,98)
C. javanica	*E. hayati*	*B. tabaci*	(77)

6. Conclusion and Future Perspectives

The interplay between parasitoids and EPFs in pest management presents a multifaceted and context-dependent dynamic shaped by species-specific traits, application timing, environmental variables, and host physiology. These interactions may range from synergistic to antagonistic, underscoring the importance of strategic compatibility particularly in terms of host stage targeting and temporal alignment to enhance their combined biological control potential. Environmental conditions, especially humidity and temperature, critically influence the efficacy of EPFs, whereas parasitoids often display greater resilience. As such, careful microclimatic management can be instrumental in synchronizing their application. However, inappropriate fungal formulations may inadvertently harm parasitoids, highlighting the need for selective and targeted delivery systems. Additionally, host immune responses, pest population density, and parasitoid behavior such as the tendency to avoid infected hosts further complicate these interactions. Although theoretical frameworks support the integration of multiple biological control agents, practical success hinges on ecological optimization to mitigate competition and IGP. Realizing the full potential of EPF–parasitoid integration within IPM systems requires a holistic, interdisciplinary approach encompassing ecological modeling, environmental surveillance, and scenario-based field experimentation. When grounded in scientific evidence and adapted to field conditions, such integrated strategies offer a promising, sustainable alternative for long-term pest suppression.

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