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Potential negative effects of introduced or augmented entomopathogens on non-target predators and parasitoids

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Abstract:	This review examines the complex interactions between introduced or augmented entomopathogens (viruses, bacteria, fungi, and nematodes) and naturally occurring arthropod natural enemies (predators and parasitoids) within Integrated Pest Management programs. Entomopathogens are increasingly recognized as sustainable alternatives to chemical pesticides, which have detrimental effects on ecosystems and human health and are frequently banned before viable biocontrol alternatives are readily available. Consequently, biological control, a fundamental aspect of pest management, must expand to bridge this gap and safeguard adequate food production. This expansion necessitates a thorough understanding of potential negative impacts associated with biocontrol methods, even though such effects are generally anticipated to be less severe than those stemming from chemical control. The review synthesizes current knowledge on how entomopathogenic infections influence predator and parasitoid populations, focusing on infection, repellency, and attractancy effects across different pathogen groups, particularly concerning those feeding on or developing within infected hosts. Studies show varied impacts on predators, from tolerance to potential harm, with some predators even contributing to viral dispersal of entomopathogens, potential negative impacts warrant consideration. Combined applications of natural enemies can enhance pest control, but precise timing, concentration and formulations are crucial to maximize benefits and minimize harm to beneficial organisms. While entomopathogens can affect certain beneficial insects, the benefits outweigh the non-target impacts. A common thread across all groups is the need for further research, particularly long-term field studies under realistic conditions, to fully understand their interactions within complex ecosystems. By understanding these interactions, we can develop optimized pest control strategies that promote biodiversity and enhance the sustainability of agriculture, habitat management, and conservation.
Opposed Reviewers:	
Response to Reviewers:	

Highlights

-Entomopathogens are vital natural enemies and sustainable alternative to chemical pesticides.

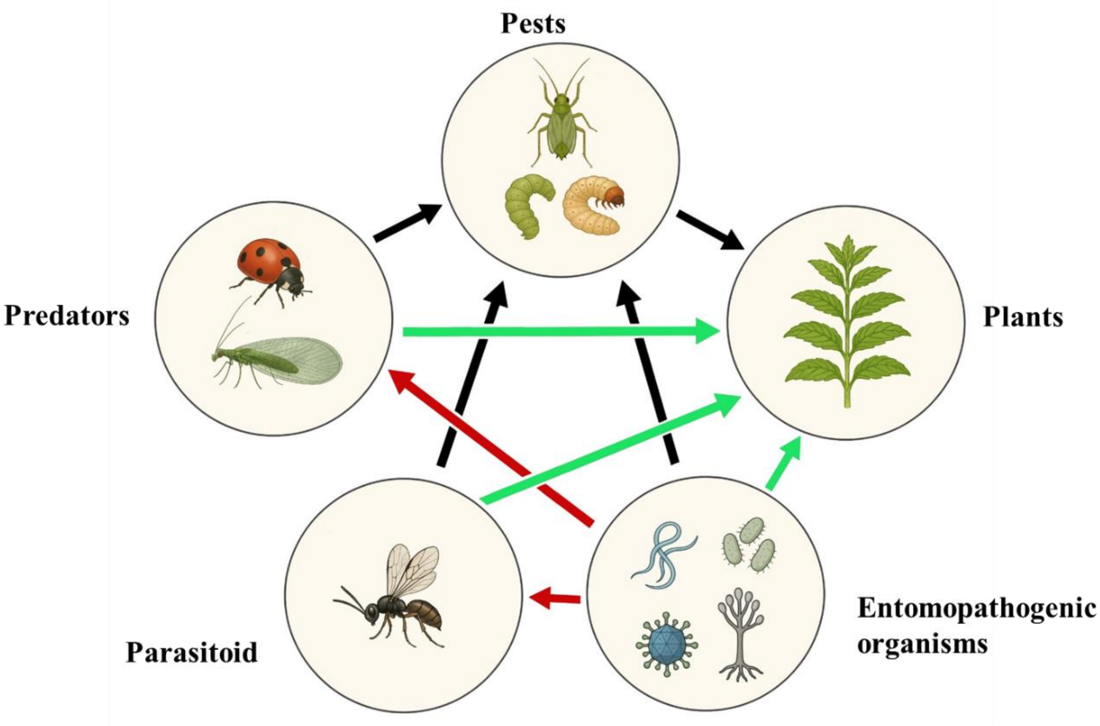
-Impacts on predators and parasitoids vary, often disrupting host biology & mortality.

-Some predators tolerate certain entomopathogens, aiding in their effective dispersal.

-Endoparasitoids are highly susceptible to negative effects when developing in infected hosts.

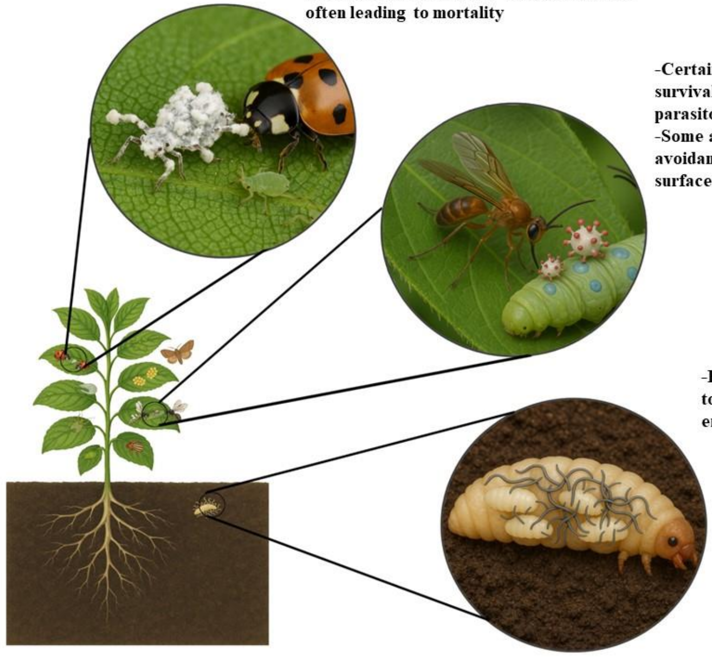
- Parasitoids and predators can sometimes avoid direct contact with entomopathogens.

Graphical Abstract



Entomopathogens offer a diverse approach to pest control across various habitats. These microbial agents can interact with other natural enemies (parasitoids and predators) within applied ecosystem. Black arrows show direct effects on pests; red arrows show non-target effects on non-target arthropods by entomopathogens in these ecosystems and green arrows indicate positive effects on plants.

Figure 1 Entomopathogenic organisms offer a diverse approach to pest control across various habitats. The provided figure effectively illustrates how these microbial agents can interact with beneficial arthropods within a terrestrial ecosystem, highlighting potential impacts on other natural enemies



-Impacts on predators and parasitoids vary, with infection disrupting host biology and often leading to mortality

-Certain entomopathogen species/strains can affect the survival, longevity or fecundity of predatory and parasitoid insects.
-Some arthropods can show tolerance and can exhibit avoidance behavior on entomopathogen-treated leaf surfaces

-Endoparasitoids are particularly susceptible to negative effects when developing within entomopathogen-infected hosts.

Plants offer refuge and sustenance for numerous organisms. All are enmeshed in complex interactions that have important effects on the health and function of both natural and planted ecosystems

Table 1. Ecological Roles of Natural Enemies

Natural Enemy Group	**Examples**	**Attributes**	**Potential Benefits**
Predators	Insects - Ladybugs (Coccinellidae) - Lacewings (Chrysopidae) - Assassin bugs (Reduviidae) - Praying mantises (Mantodea) - Hoverflies (Syrphidae)	- Actively hunt and kill prey - Generalist or specialist feeders - May consume multiple pest stages (eggs, larvae, adults)	- Reduce pest populations directly - Can provide long-term pest suppression
	Predatory mites - *Phytoseiulus persimilis* - *Amblyseius cucumeris* - *Galendromus occidentalis* - *Neoseiulus californicus* - *Typhlodromus athiasae* - *Macrocheles robustulus* - *Transeius montdorensis*	- Feed on soft-bodied insects like aphids and thrips - Highly mobile and prolific reproducers - Often used in greenhouses and other controlled environments	- Provide effective control of specific soft-bodied pests like thrips, spider mites, white flies, fungus gnats. - Can establish long-term populations in suitable habitats

Parasitoids	-Wasps (Hymenoptera: Braconidae, Ichneumonidae) - Flies (Diptera: Tachinidae)	- typically, smaller than their host. -Lay eggs inside or on pest host - Developing parasitoid larvae feed on and kill the host -Allow the host to survive (initially) until the developing parasitoid young are mature - Often specific to a single pest species	- Can provide excellent control of specific pests such as greenfly, cabbage caterpillars, whitefly, and scale insects - May regulate pest populations at low levels
Pathogens	- Baculovirus -Entomopathogenic fungi (e.g., *Beauveria bassiana, Metarhizium anisopliae*) - Entomopathogenic bacteria (e.g., *Bacillus thuringiensis*) - Entomopathogenic nematodes (e.g., *Steinernema and Heterorhabditis spp.*)	- Infect and kill insects through virulence factors such as spores, enzymes or toxins. - Can be persistent in the environment - May affect a broad range of pest species - Can be found in diverse habitats like soil, foliage, flowers, etc	- Offer long-term pest suppression - Can be used in a variety of application methods

Table 2. Interactions between Entomopathogenic organisms and Natural Enemies (Predators and Parasitoids)

Entomopathogen group	**Species**	**Assessed Natural Enemy**	**Natural Enemy group**	**Interaction Type**	**Observed Effect and notes**	**References**
Entomopathogenic virus	Alphabaculovirus (AgNPV)	*Podisus maculiventris* *Podisus maculiventris*, *Nabis capsiformis*, *Geocoris punctipes*, *Calleida decora*, *Chrysoperla carnea*, *Orius albidipenni*, *Labidura riparia*	Predators	Tolerance	No replication, but viral persistence. Tissue assays confirmed absence of replication.	(Abbas, 1988; Abbas and Boucias, 1984; Black, 2017; Gupta et al., 2013; Smith et al., 2000; Treacy et al., 1997).
	AgNPV	*Chrysoperla carnea*	Predator	Tolerance	Unaffected. No viral replication.	(Castillejos et al., 2001).
	AgNPV	*Coccinella septempunctata*	Predator	Dispersal	Viable PIBs excreted in feces. Potential for viral dissemination.	(Groner, 1990)
	AgNPV	*Bracon brevicornis*	Parasitoid	Impacted Development	Reduced adult emergence if parasitism occurs after viral infection. Time lag between infection and parasitism is critical.	(Abbas, 1988)
	AgNPV	*Trichogramma evanescens*	Parasitoid	Tolerance	No effect on parasitism or development. No discrimination between infected and uninfected eggs.	(Irabagon and Brooks, 1974)
ntomopathogenic bacteria	Btk (HD1 strain)	*Muscidifurax raptor*	Parasitoid	Tolerance	No effect on survival or reproduction. Spores added to sugary solutions; direct exposure.	(De Bortoli et al., 2017)
	Btk (4D22 strain)	*Trichogramma chilonis*	Parasitoid	Dose-dependent toxicity	Spores with Cry toxins: acute toxic effects; spores without Cry toxins: no effect. Highlights the importance of Cry toxins in toxicity.	(Amichot et al., 2016)
	Cry1Ab (from Bt maize)	*Chrysoperla carnea*	Predator	Ingestion/Tolerance	Toxin ingested, but no impact on pupation or adult emergence. Indirect exposure via Bt maize-reared prey (*T. urticae*, aphids, S. *littoralis* larvae).	(Hilbeck et al., 1998)
	Bti	*Eylais* sp.	Predator	Tolerance	High tolerance; no mortality or changes in feeding behavior. Aquatic environment; even at recommended dosages, non-target effects are minimal.	(Mansouri et al., 2013)

	Bt cotton (Cry toxins)	*Haptoncus luteolus*	Predator	Ingestion/Tolerance	Trace amounts of toxins detected, but no significant toxic effects. Exposure via feeding on leaves and pollen of Bt cotton varieties.	(Head et al., 2001)
	Btk	Non-target Lepidoptera larvae	General	Negative impact	Temporary reductions in non-target insect abundance and species richness. Early season applications pose the most risk.	(Konecka et al., 2014)
Entomopathogenic nematodes	*Steinernema feltiae, Heterorhabditis bacteriophora*	*Aphidoletes aphidimyza*	Predator	Reduced Impact (Field vs. Lab)	Significantly less effect in greenhouse vs. lab. Highlights differences between lab and field conditions.	(Powell and Webster, 2004).
	Heterorhabditis bacteriophora, Steinernema carpocapsae	Lady Beetle Species	Predators	Reduced Susceptibility	Lower susceptibility compared to target pest. Field conditions and natural enemy behavior play a role.	(El-Mandarawy et al., 2018; Harvey et al., 2016; Rojht et al., 2009; Shannag and Capinera, 2000).
	Steinernema carpocapsae	*Cardiochiles diaphaniae*, *Mastrus ridibundus* and *Liotryphon caudatus*	Parasitoid	Susceptibility	Developing larvae of parasitoids vulnerable to EPN infection in insect hosts. Parasitoids to avoid nematode-infected larvae	(Lacey et al., 2003; Shannag and Capinera, 2000).
	Steinernema carpocapsae	*Diglyphus begini*	Parasitoid	Repellency	Avoidance of oviposition in infected hosts	(Sher et al., 2000).
	Heterorhabditis amazonensis	*Calosoma granulatum*	Predator	Resistance	Adult and later-stage larvae are resistant	(Mertz et al., 2015).
Entomopathogenic bacteria	*Beauveria bassiana*	*Amblyseius swirskii*	Predator	Susceptibility	High susceptibility to some isolates especially when cnidia applied directly to mites.	(Seiedy et al., 2015).
	Beauveria bassiana/Metarhizium anisopliae	*Podisus nigrispinus*	Predator	Variable Susceptibility	High mortality with direct commercial product application, but not with residual contact. Application method is significant.	(Araujo et al., 2020)
	Beauveria bassiana	*Hippodamia convergens, Coleomegilla maculata, Harmonia axyridis and Cryptolaemus montrouzieri*	Predator	Variable Susceptibility	*B. bassiana* only significantly reduced the survival of *C. montrouzieri*. Combined use was effective.	(Smith and Krischik, 2000)

	Metarhizium brunneum	*Aphidoletes aphidimyza*	Predator	Tolerance/Synergism	No effect on emergence, enhanced aphid suppression. Combined use was effective.	(de Azevedo et al., 2017).
	Beauveria bassiana/ Lecanicillium lecanii/ Metarhizium brunneum	*Phytoseiulus persimilis, Neoseiulus californicus*	Predator	Susceptibility	Fungi can infect 60-90% predatory mites. No impact on mite oviposition	(Dogan et al., 2017)
	Beauveria bassiana	*Anthocoris nemorum*	Predator	Avoidance	Predators can detect and avoid fungi-treated surfaces.	(Meyling and Pell, 2006).
	Lecanicillium lecanii	*Aphidius colemani*	Parasitoid	Timing Dependent Effect	Negative effect if applied around the time of parasitization. Timing is critical for parasitoid impact.	(Potrich et al., 2009).
	Beauveria bassiana/ Metarhizium brunneum	Trichogrammatid parasitoids	Parasitoid	Susceptibility and Impacted Development	Fungi can decrease adult emergence and can kill developing stages. Minimal adverse effects observed.	(Kim et al., 2005; Polanczyk et al., 2010; Potrich et al., 2009).
	Beauveria bassiana	*Mischocyttarus metathoracicus* (Social Wasp)	Predator	Horizontal transmission	Horizontal transmission between colony members. Minimal harm observed, potential concern for wipeout scenarios needs futher research.	(de Souza et al., 2023).

Table 3. Microbial natural enemies offer a diverse approach to pest control across various habitats. These microbial agents can interact with other natural enemies within a terrestrial ecosystem. Here are potential ecological impacts and implications of entomopathogens on beneficial arthropods

Beneficial Arthropod	**Entomopathogen**	**Exposure Route**	**Ecological Impact on Natural Enemy**	**Ecological Implications**
Non-target Predators	Baculovirus	Indirect (consuming infected prey)	- Potential for altered prey availability (reduction). - Possible behavioral changes: prey avoidance.	- Potential for temporary decline in predator populations due to reduced food resources. - Shifts in predator foraging behavior.
	Entomopathogenic bacteria	Indirect (consuming infected prey)	- Generally minimal direct impact. - Rapid prey mortality can lead to temporary food limitation.	- Potential for short-term fluctuations in predator populations. - Influence on predator-prey dynamics through rapid pest reduction.
	Entomopathogenic fungus	Direct (contact with fungus spores on treated surfaces or consuming prey infected with the fungus).	- Potential for direct infection (species-specific). - Possible prey avoidance behavior. - Altered prey quality.	- Potential for direct mortality or reduced fitness in some predator species. - Shifts in predator foraging and habitat use. - Potential for altered trophic cascades.
Non-target Parasitoid	Baculovirus	Indirect (Parasitoids developing within insect hosts infected with baculoviruses). Direct encounter and infection by baculovirus particles in the environment	- Potential for parasitoid mortality or impaired development (host-dependent). - Possible oviposition avoidance in infected hosts.	- Potential for reduced parasitoid populations and biocontrol efficacy. - Influence on parasitoid host selection and population

				dynamics.
	Entomopathogenic bacteria	Indirect (consuming infected prey)	- Generally minimal direct impact. - Potential for indirect effects due to early host mortality.	- Potential for reduced parasitoid emergence due to rapid host death. - Influence on parasitoid life cycle synchrony with host availability.
	Entomopathogenic nematodes	Indirect (developing infected prey)	- Potential for parasitoid mortality or impaired development (species-specific). - Possible oviposition avoidance in infected hosts.	- Potential for reduced parasitoid populations and biocontrol efficacy. - Influence on parasitoid host selection and population dynamics.
	Entomopathogenic fungus	Indirect (developing infected prey)	- Potential for minimal direct impact. - Possible oviposition avoidance in infected hosts. - Potential for reduced emergence if infection occurs close to parasitism.	- Potential for reduced parasitoid emergence depending on timing of infection. - Influence on parasitoid host selection.

Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Potential negative effects of introduced or augmented entomopathogens on non-target predators and parasitoids

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Abstract

This review examines the complex interactions between introduced or augmented entomopathogens (viruses, bacteria, fungi, and nematodes) and naturally occurring arthropod natural enemies (predators and parasitoids) within Integrated Pest Management programs. Entomopathogens are increasingly recognized as sustainable alternatives to chemical pesticides, which have detrimental effects on ecosystems and human health and are frequently banned before viable biocontrol alternatives are readily available. Consequently, biological control, a fundamental aspect of pest management, must expand to bridge this gap and safeguard adequate food production. This expansion necessitates a thorough understanding of potential negative impacts associated with biocontrol methods, even though such effects are generally anticipated to be less severe than those stemming from chemical control. The review synthesizes current knowledge on how entomopathogenic infections influence predator and parasitoid populations, focusing on infection, repellency, and attractancy effects across different pathogen groups, particularly concerning those feeding on or developing within infected hosts. Studies show varied impacts on predators, from tolerance to potential harm, with some predators even contributing to viral dispersal of entomopathogens, potential negative impacts warrant consideration. Combined applications of natural enemies can enhance pest control, but precise timing, concentration and formulations are crucial to maximize benefits and minimize harm to beneficial organisms. While entomopathogens can affect certain beneficial insects, the benefits outweigh the non-target impacts. A common thread across all groups is the need for further research, particularly long-term field studies under realistic conditions, to fully understand their interactions within complex ecosystems. By understanding these interactions, we can develop optimized pest control strategies that promote biodiversity and enhance the sustainability of agriculture, habitat management, and conservation.

Keywords: Biological control, Entomopathogenic organisms, safety, natural enemies, risks, intraguild interaction

Introduction

Nature is filled with diverse groups of organisms from a broad range of taxa that live in close association. They maintain relationships that are often either one-sided (commensal), or interdependent (mutualistic) in terms of the numerous benefits they provide each other such as nutrients, protection, or transportation. In some cases, there is no benefit for either organism (Moran, 2006). In parasitic interactions, one organism exploits the other, typically at the expense of its health, fitness, or survival (Leung and Poulin, 2008).

While plants offer refuge and sustenance for numerous organisms (Philippot et al., 2013), some herbivorous insects, mites and other invertebrates inflict damage on plant crops and trees in many ways. They obtain their food from various above and below ground plant parts and cause physical damage, which significantly affects plant development, or transmit or provide entry points for pathogens which cause infectious plant diseases. Agricultural pests cause substantial losses (up to 40% of global production) and financial losses estimated at billions of dollars (Culliney, 2014; IPPC Secretariat, 2021; Savary et al., 2019). Additionally, arthropods like mosquitoes, midges, sandflies, ticks, blackflies serve as critical transmitters of infectious pathogens of human and animal diseases. The global impact of these diseases is severe with over 700.000 human deaths reported annually, developing countries bear the heaviest burden, affecting individuals, communities, and economies (Bursali and Touray, 2024; Socha et al., 2022). These pests are mainly controlled using synthetic pesticides which are known to have undesirable toxic effects on the environment and on human health (Bernays, 2009; Diaz-Montano et al., 2011; Kumar, 2020; Savary et al., 2019).

Natural enemies are organisms that feed, infect, or impact the fecundity of other organisms generally considered to be pests. Natural enemies are grouped into three categories: predators, parasitoids and pathogens (van Lenteren et al., 2018) (Table 1). Invertebrate predators e.g. dragonflies, predatory mites, mantids, lady beetles, lacewings, actively hunt or ambush, kill and consume other organisms (prey) (Walton et al., 2012). Parasitoids lay their eggs in or on the host insects and the larvae emerged from the eggs develop by feeding on the host's tissue (van Lenteren et al., 2018). Pathogens are natural enemies including viruses, bacteria, protista, fungi, and nematodes that infect and cause disease in their target host. Infection by these organisms can reduce the host's biological activities such as feeding, development and reproduction rates as well as often causing mortality (Ravensberg, 2010; Walton et al., 2012).

Entomopathogenic organisms can be found naturally in most regions of the world and are important in terms of their role in maintaining pest populations to suitable/manageable levels. Their use has been increasing in both fields and greenhouses applications as well as vector control (Deans and Krischik, 2023; Parrella and Lewis, 2017). In most cases, these organisms need to be introduced in large numbers as biological control agents into agroecosystems. In other areas where the microbial agents are already found their natural population often do not occur in sufficient numbers to effectively control insect pests, hence natural populations are augmented with lab-reared and commercial products (Hazir et al., 2022; van Lenteren et al., 2018). However, it is inevitable that there will be a close interaction between these entomopathogens (viruses, bacteria, fungi, and nematodes) introduced into the environment to control insect pests and the natural enemies naturally found in that environment.

This review focuses specifically on the interactions between introduced or augmented entomopathogens and naturally occurring arthropod natural enemies, namely predators and parasitoids, within Integrated Pest Management (IPM) programs. Such programs offer a more sustainable approach, emphasizing a combination of tactics, including biological control, to minimize pest populations while preserving beneficial organisms (Barzman et al., 2015). This review explored the current knowledge regarding the impact of entomopathogen groups of biological control agents, focusing on repellency, attractancy and infection effects on arthropod natural enemies. It is structured by entomopathogen group (viruses, bacteria, fungi, and nematodes) with each section beginning with a brief overview of the basic biology and ecology of the respective pathogen group, providing essential context for the subsequent discussion of their interactions. Protista were excluded from this review due to their limited success in practical biocontrol applications. By synthesizing the literature across different entomopathogen groups, we aim to identify commonalities and differences in their interactions with predators and parasitoids. This comparative approach allowed us to draw broader conclusions about the potential for enhancing biocontrol efficacy and developing more predictive models for successful IPM implementation. Furthermore, we highlighted critical research gaps and outlined future research directions needed to improve our understanding of these complex ecological relationships. Studies focusing solely on the mechanisms of action of entomopathogens, combined application of groups or those that did not include data on non-target effects related to predators or parasitoids, were excluded. Therefore, this review prioritizes key examples that represent the diversity of observed interactions, rather than attempting a comprehensive compilation of all available literature.

Overview of plant-invertebrate pest-natural enemy interaction

Plants, invertebrate herbivores, and natural enemies are enmeshed in complex interactions that have important effects on the health and function of both natural and planted ecosystems. This interconnectedness helps in regulating flora and fauna populations, preserving biodiversity, and providing essential ecosystem services such as pollination, pest control, and nutrient cycling (Murray and Kinsman, 2000).

In natural ecosystems such as forests and grasslands, diverse insects contribute to ecological balance through pollination, decomposition, and nutrient cycling (Eckerter et al., 2021; Guo et al., 2023). Natural enemies help control herbivorous insects and other invertebrate populations (Balla et al., 2021). They contribute to the stability of ecosystems by reducing damage and disease in crops/trees , hereby maintaining the health and productivity of forest and grassland ecosystems (Bozdoğan, 2020; Klapwijk et al., 2016; Nyffeler and Birkhofer, 2017). The biodiversity of plants and invertebrates supports ecosystem stability and function (Dix et al., 1995; Landmann et al., 2023; Staab and Schuldt, 2020). Like natural ecosystems, these interactions provide natural pest control and thereby promote crop health and yield while reducing reliance on environmentally and economically detrimental pesticides in various agricultural systems (Islam et al., 2021; Rajput et al., 2023). Besides the reduction of herbivore abundance, natural enemies are also known to indirectly influence or alter plant trait evolution (e.g. rewards, production of chemical cues when attacked by herbivores and attraction of other natural enemies), population dynamics, and community structure (Abdala-Roberts et al., 2019).

The interactions between different natural enemies can be complex and can vary depending on the specific species involved and can be either synergistic, additive, or antagonistic (Shapiro-Ilan et al., 2012). Different groups or species with complementary traits and synergistic and additive interactions can be combined for overall improved pest control (Spescha et al., 2023). A concern with using multiple biological control agents is that there is a possibility of intraguild predation or infection. Entomopathogens can indirectly affect non-target organisms that occupy the same habitats as targeted pests (Figure 1). Therefore, compatible species/strains need to be carefully selected and applied at the right time and in the right way to minimize the impact on non-target organisms and maximize the effectiveness of biological control (Ansari et al., 2008, 2006; DeBach and Rosen, 1991; Raymond et al., 2000; Snyder and Ives, 2008). Also, in intraguild interactions, non-target organisms can accidentally ingest host pathogens during consumption. This could result in a trophic transmission of parasites with non-target organisms serving as a non-target host if susceptible. If not susceptible, then the pathogens do not affect the new host and may be inadvertently removed from an ecological community (Cirtwill and Stouffer, 2015; Flick et al., 2020; Johnson et al., 2010; Lafferty et al., 2006).

Sustainable agricultural practices emphasize the importance of maintaining biodiversity within fields to promote natural pest control. This can be achieved through various strategies. For instance, providing essential resources like food, water, and shelter within crop fields creates a more hospitable environment for natural enemies (predators and parasitoids) and pollinators. This encourages them to establish resident populations within the fields, where they can readily feed and reproduce. Hedges serve a multifaceted role in supporting biodiversity within agricultural landscapes providing vital habitat for a diverse assemblage of species, encompassing invertebrates, flora, and broader wildlife communities (Garratt et al., 2017; Ponisio et al., 2016; Sardiñas and Kremen, 2015). This biodiversity enrichment extends beyond mere species presence, fostering a natural ecosystem service – biological pest control. Hedgerows and flower strips serve as reservoirs for beneficial predators and parasitoids that prey upon crop pests (Garratt et al., 2017; Jachowicz and Sigsgaard, 2025; Lecq et al., 2017; Morandin et al., 2016, 2014). These natural enemies readily disperse from hedgerows into adjacent fields, inherently regulating pest populations. Interestingly, hedgerows may even surpass the value of cultivated crops themselves as a food source for pollinators. Furthermore, hedgerows function as essential corridors, facilitating pollinator movement between fields (Hanley and Wilkins, 2015; Sardiñas and Kremen, 2015). This connectivity significantly enhances crop pollination rates within agricultural landscapes.

Impact of entomopathogenic viruses

Viruses in the Baculoviridae and Ascoviridae families, are two out of 12 families that stand out for their exceptional host specificity and environmental safety. Among these, only baculoviruses (BV) are commercially available as viral biopesticides against several lepidopteran, hymenopteran, and dipteran insect pests (Reid et al., 2023).

Natural hosts get infected after ingestion of occlusion-bodies (OB), which are protein crystals containing the viral particles encased in protein crystals which pass into gut wall cells, fat body, and hemolymph. Upon reaching the insect's highly alkaline midgut (pH >9.5), these OBs swiftly dissolve, releasing virions. These virions then initiate the infection process by binding to receptors and penetrating the epithelial cells lining the insect gut OBs swiftly dissolve within the highly alkaline midgut environment (pH >9.5), releasing virions that initiate the infection process between cells (Rohrmann, 2019). Subsequent viral replication leads to systemic infection, spreading from the midgut to other tissues like the fat body and hemolymph. Thesse orally infectious OBs can be horizontally transmitted between insects and can be remain stable outside the host for long extended periods (Erler et al., 2022; Harish et al., 2021; Raj et al., 2022). Baculoviruses (BV), can be grouped into Alphabaculovirus (formerly Nucleopolyhedrovirus, NPV), Betabaculovirus (Granulovirusm GV), Deltabacuulovirus, and Gammabaculovirus based on occlusion body morphology (Zhang et al., 2005).

BVs are renowned for their insect-specific infection and OB formation and harbor accessory genes which can manipulate cellular processes like the cell cycle, apoptosis, and even host physiology and behavior (Clem and Passarelli, 2013; McWilliam, 2007). Around 60 baculovirus-based insecticides are commercially available and registered worldwide for the control of diverse insect pests (Reid et al., 2023). While the mode of action and replication differ across virus families, ingestion remains the nearly universal route for entomopathogenic virus infection (Gelaye and Negash, 2023). Mortality due to entomopathogenic virus infection varies by host larval age, with younger individuals succumbing within 2 days and older ones within 4-9 days (Afolami and Oladunmoye, 2017).

There are numerous studies examining the effects of entomopathogenic viruses on non-target biological control organisms (Table 2). Some predators exhibit tolerance or even benefit from alphabaculoviruses, while others face potential harm (Black, 2017; Gupta et al., 2013; Smith et al., 2000; Treacy et al., 1997). Various predatory insect species, including *Podisus maculiventris* (Hemiptera: Pentatomidae), *Nabis capsiformis* (Hemiptera: Nabidae), *Geocoris punctipes* (Hemiptera: Geocoridae), *Calleida decora* (Coleoptera: Carabidae), *Chrysoperla carnea* (Neuroptera: Chrysopidae), *Orius albidipennis* (Hemiptera: Anthocoridae) and *Labidura riparia* (Dermaptera: Labiduridae), were unaffected after feeding on larvae infected with nucleopolyhedroviruses two days post-application. Tissue assays confirmed the absence of viral replication within these predators (Abbas, 1988; Abbas and Boucias, 1984). In a field trial, treatment of soybean plots with AgNPV for the biocontrol of lepidopteran pest, *Anticarsia gemmatalis* (2.3×10^{11} PIBs/ha) had no significant impact on predator abundance compared to controls (Boucias et al., 1987). Bioassays revealed AgNPV presence in 41% of predators, suggesting potential non-lethal viral persistence among predators regardless of treatment. Certain predator adults and larvae can harbor the viruses after feeding on infected-prey but their role in viral dissemination seems to be limited (Young and Yearian, 1990). They are capable of dispersing viruses in their feces, and susceptible insects that consume these viruses when feeding on leaves can get infected (Abbas, 2020; Groner, 1990; Olofsson, 1989). *Coccinella septempunctata* (Coleoptera: Coccinellidae) larvae excreted viable polyhedral inclusion bodies (PIBs) after feeding on infected *Neodiprion sertifer* (Hymoneptera: Diprionidae) larvae and *C. undecimpunctata* larvae and adults with *Spodoptera littoralis*. This ability was attributed to the predators' resilient digestive systems, possibly due to higher acidity, allowing them to handle infected prey with minimal harm (Groner, 1990).

Predators do not discriminate between non-infected and alphabaculoviruses-infected prey. Three predatory insects from Carabidae family *Pterostichus melanarius*, *Harpalus rufipes* and *Agonum dorsale* were indifferent to healthy and infected *Mamestra brassicae* (Lepidoptera: Noctuidae) larvae and transmitted infective alphabaculoviruses through the soil for 15 days after consuming virus-infected prey, albeit at relatively low rates (Vasconcelos et al., 1996). Similarly, *Chrysoperla rufilabris* (Neuroptera: Chrysopidae) larvae targeted both healthy and infected *S. frugiperda* larvae equally; but interestingly, *Doru taeniatum* (Dermaptera: Forficulidae) adults exhibited a preference for NPV-infected prey (Castillejos et al., 2001). No initial detrimental effects were observed on predator survival and reproduction when *Podisus nigrispinus* (Hemiptera: Pentatomidae) was fed for three generations on AgNPV-infected *A. gemmatalis* larvae (De Nardo et al., 2001). However, subsequent generations suffered adverse impacts potentially associated with inert components in the commercial formulation used. Similarly, *Eocanthecona furcellata*'s development, survival, sex ratio, and egg incubation remained unaffected by dietary components of healthy and NPV-infected *S. litura* larvae. At higher levels, significant reductions in predator body weight, fecundity, longevity, and egg hatchability were observed. In soybean fields, *Lygus lineolaris*, *Geocoris* spp., and various predators have been observed to transmit NPV among *H. armigera* larvae through feeding and contact with liquefied remains (Black, 2017).

Parasitoids can encounter alphabaculoviruses through various routes, including the ovipositor, body surface, and gut (Irabagon and Brooks, 1974). *Compsilura concinnata*, *Campoletis sonorensis*, *Hyposoter exiguae,* and *Cotesia marginiventris* parasitoids have been found to readily pupate in NPV infected *Mythimna* (formerly *Pseudaletia*) *unipuncta* and GV-infected *S. exigua* larvae, but *Chelonus insularis* died alongside its host in both infection types, and *Glyptapanteles militaris* succumbed only to NPV (Hotchkin and Kaya, 1983). *Trichogramma evanescens* did not discriminate between NPV-covered and control *S. littoralis* eggs, successfully parasitizing both and showing normal development in parasitized progeny (Abbas, 1987). Similarly, NPV had no effect on *Chelonus insularis* parasitism of *S. frugiperda* eggs (Escribano et al., 2000). Successful parasitism of alphabaculovirus-treated *H. armigera* larvae by *Bracon brevicornis*, was observed with offspring development being inversely proportional to the time lag between larval NPV infection and parasitism (Abbas, 1988). Only 24.6% of the parasitoid progeny reached adulthood when parasitism occurred 48 h after larval infection, and none survived beyond that (Abbas, 1988). Looking at the interaction between baculoviruses and parasitoids, while parasitoids can lessen the harm caused by viruses in hosts in laboratory trials, field trials did not reveal a decrease in overall death rates from applied baculovirus (Cossentine, 2009). Interestingly, parasitoids may even promote the spread of the virus within hosts, potentially enhancing their effectiveness in real-world situations. However, baculovirus infections can reduce parasitoid populations as parasitoid development inside the host is affected especially if the virus infection is advanced (Cossentine, 2009). Endoparasitoids (developing within the host) are generally more susceptible to alphabaculoviruses compared to ectoparasitoids (developing externally) due to longer exposure times (Gonthier et al., 2023; Jervis et al., 2008).

The combined application/presence of viruses and predator/parasitoids in field settings might be advantageous for pest control. Optimization of application time is important during simultaneous use. Successful development of the larval parasitoids like *Cotesia kazak*, *Meteorus demoliter* and *Hyposoter didymator* on *Heliothis armigera* larvae required a 3-day interval between parasitism and host treatment with NPV (Murray et al., 1995). Likewise, PuGV negatively impacted *Cotesia kariyai* development in *Mythimna* (formerly *Pseudaletia*) *separata*, with no emergence when parasitism followed late-stage larval infection, and complete failure in simultaneously infected and parasitized hosts (Kunimi et al., 1999). The larval parasitoid *Meteorus gyrator* displayed a preference for healthy *Lacanobia oleracea* (Lepidoptera: Noctuidae) larvae, laying fewer eggs in virus-infected individuals (Matthews et al., 2004). Parasitoid females that previously developed in virus-infected larvae subsequently oviposit in new hosts perpetuating the viral infection. *Microplitis pallidipes* females carrying SeNPV achieved a significantly higher reduction (82.3–89.7%) in the *S. exigua* population compared to virus-free females (59.5–62.4%) in a greenhouse trial (Jiang et al., 2011). These studies showcase the potential of parasitoids carrying NPVs for enhanced pest control, while highlighting the risk of negative impacts on their progeny through vertical transmission (Arai et al., 2018; Guo et al., 2013). In contrast, *Meteorus pulchricornis* parasitoids developed normally in NPV-infected *S. litura* larvae, showing no ill effects or viral transmission (Nguyen et al., 2005). Strategically timed baculovirus-based biopesticides may have minimal impact on beneficial host-parasitoid relationships. However, the potential economic benefits of combined application remain unclear due to the increased costs associated with implementing such a combination strategy (Koller et al., 2023).

Impact of entomopathogenic bacteria

Entomopathogenic bacteria and their toxins are the most commercially successful microbial insecticides. The most widely studied bacterial entomopathogens are the Gram-positive sporulating bacteria belonging to the Bacillaceae family. These bacteria are found in soil habitats. They are virulent by producing endospores with parasporal crystals (δ-endotoxins), Cyt (cytotoxic) toxins, and toxic insect proteins that upon ingestion, bind and perforate insect midgut causing insect death. These spores remain dormant outside the host and are only activated by larva's gut pH and enzymes (Mampallil et al., 2017; Sharma et al., 2020). Not all entomopathogenic bacteria produce spores. Species in the families Pseudomonadaceae, Yersiniaceae and Enterobacteriaceae are also highly virulent but are rarely used commercially due to theirto their short shelf life (Glare et al., 2017; Irsad et al., 2023)**.**

Bacillus thuringiensis (Bt) has been used successfully for insect control and accounts for approximately 2% of the total insecticide market and 95% of microbial biopesticides (Bravo et al., 2011). *Bacillus thuringiensis* products are deemed safe for pest control in agriculture, forestry, and horticulture. *Bacillus thuringiensis* encompasses various subspecies, such as *Bt. kurstaki* (Btk), *Bt. israelensis* (Bti) and *Bt. aizawai* (Bta). These varieties, also known as serovars, are distinguished by their flagellar antigens, in addition to the toxins and crystals they produce. Additionally, the target insects susceptible to these toxins differ significantly due to the varying mechanisms by which the toxins act (Drummond and Pinnock, 1994; Ibrahim et al., 2010). Multiple factors contribute to the target selectivity of Bt insecticidal proteins throughout the intoxication process (Vachon et al., 2012). At the initial encounter stage, the protein's physical form can limit its accessibility. Cry toxins, existing as crystals, might pose a barrier to ingestion by certain insects with specialized feeding habits, such as sap-feeders. Additionally, limited environmental colonization by Bt restricts exposure for insects residing in those specific habitats (Argôlo-Filho and Loguercio, 2013). Btk produces primarily Cry1Aa, Cry1Ab, Cry1Ac, and Cry2A proteins and Btk products are extensively used against various foliar feeding Lepidoptera whereas, *Lysinibacillus sphaericus* and Bti are more target-specific biocides that have been used in mosquito, blackfly and fungus gnat larvae control programs for decades (Brühl et al., 2020). Bti produces *Cry4Aa, Cry4Ba, Cry10Aa, Cry11Aa* and two *Cyt toxins, Cyt1Aa, and Cyt2Ba* that work synergistically against mosquito larvae (Ben-Dov, 2014).

While crystals offer stability, their dissolution is essential for Cry protein activity. Specific digestive tract pH levels within the host insect are crucial for solubilization. Hence Cry proteins primarily affect insects possessing a compatible digestive environment (acidity). Upon release from the crystal structure, the Cry protoxin becomes vulnerable to digestive enzyme breakdown (Pardo-López et al., 2013; Vachon et al., 2012). The extent of this degradation varies between Cry toxin families, impacting their size and potentially their insecticidal activity. Furthermore, some insects possess enzymes like elastases and chymotrypsin specifically designed to target and degrade Cry proteins, further diminishing their effectiveness (Jurat-Fuentes and Crickmore, 2017). Even after processing, Cry toxins need to maintain their activity within the gut lumen. The insect midgut possesses a protective barrier, the peritrophic matrix, that Cry proteins can generally traverse. However, this matrix also contains sugars that can bind to specific Cry toxins, potentially reducing their availability for interaction with target sites (Mitsuhashi and Miyamoto, 2020). Binding to specific midgut receptors, such as the aminopeptidase N (APN) receptors and the cadherin-like receptors, is essential for Cry toxin activity (Pigott and Ellar, 2007). Furthermore, mere binding does not guarantee toxicity. The observed lack of a direct correlation between binding and efficacy suggests that additional post-binding processes contribute to target specificity.

The persistence and toxicity of Bt product formulations can vary based on different abiotic conditions such as humidity and sunlight. Usually, 50% of insecticidal activity is lost in 1-3 days on foliage (Joung and Jean-Charles, 2000). Btk HD-1 strain used in the Foray biopesticide persisted for a relatively long time (up to 1 year) in the soil of a 195-hectare oak forest on the Krotoszyn Plateau, Poland. Persistence on leaf surfaces is shorter, lasting up to 6 months (Konecka et al., 2014). Concerns exist regarding potential ecological impacts on non-target insects, particularly Lepidoptera and other invertebrate groups. These non-target organisms may be exposed to *Bacillus* spores either directly e.g. by eating leaves or indirectly, by consuming infected prey (Table 2). Btk can cause immediate but temporary reductions in non-target insect abundance and species richness. A study in Virginia indicated that early season treatment of Btk for gypsy moth (*Lymantria dispar dispar*) control can potentially affect some of the more common non-target lepidopteran larvae present during treatment application period (Rastall et al., 2003). The study highlights the importance of using appropriate controls and considering natural fluctuations in insect populations when evaluating pesticide impacts. Btk had negligible short-term effects on non-target diurnal lepidopterans when assessing the effect of (Btk) on the survival of *Cydalima perspectalis* (Box-tree moth) under field and controlled conditions in Italian valleys in the Piedmont region for three years (Barbero et al., 2023).

Bt toxins do not affect the development of predator or parasitoid in Bt-sensitive prey and hosts but can involuntarily impact parasitoid populations as these are affected by premature death of the host (Lacey and Siegel, 2000). Btk spores (HD1strain) added to sugary solutions and offered to *Muscidifurax raptor,* a parasitoid of *Musca domestica*, had no effect on survival and reproduction parameters of this parasitoid (Ruiu et al., 2007). Spores of Btk 4D22 strain without Cry toxins presented no acute toxicity on *Trichogramma chilonis* females when added to diet at all the doses tested, but spores with the Cry toxins had acute toxic effects against wasp females (LC_{50}=84.2 µg/µL) (Amichot et al., 2016). Eight *Drosophila* fly species exposed to varying doses of commercial Btk and Bti formulations were only affected by doses that were 1000 times higher than recommended field rates, in which case emergence of adult flies was completely suppressed (Babin et al., 2020). De Bortoli et al. (2017) investigated the compatibility of Bt-bioinsecticides with parasitoids, suggesting their combined use could enhance crop protection and yields. However, research on the effects of Bt on beneficial arthropods remains ongoing, particularly regarding the untested Cry toxins. A crucial aspect of this research is understanding the indirect effects of Bt products on parasitoid behavior and physiology.

Non target herbivores and even beneficial predators can consume insects that have ingested Cry toxins from plant material or non-targets might also be exposed through accidental plant consumption (Abbas, 2018; Head et al., 2001; Obrist et al., 2006; Peterson et al., 2020). For example, *Chrysoperla carnea* larvae ingests the Cry1Ab toxin, when feeding on Bt maize-reared *T. urticae,* aphids and *S. littoralis* larvae (Hilbeck et al., 1998; Moussa et al., 2018; Obrist et al., 2006); however, pupation or adult emergence was not impacted (Moussa et al., 2018). Likewise, trace amounts of toxins were detected in adult insects of *Adelphocoris suturalis* (Hemiptera: Miridae), a current pest, and the pollinating beetle *Haptoncus luteolus* (Coleoptera: Nitidulidae) feeding on leaves and pollen of two Bt cotton varieties, ZMSJ and ZMKCKC, which express different toxin combinations for a week. Neither Bt cotton variety caused any significant increase in insect mortality, there was no binding of the toxins to the insects, suggesting no toxic effects.

Bti and *L. sphaericus,* applied to mosquito and blackfly breeding sites, are easily biodegraded in such aquatic habitats but non-target organisms especially in natural wetlands can encounter Bti spores (Mulla, 1990). Most of these non-target organisms coexist with mosquitoes in aquatic habitats and play a critical role in regulating the aquatic stages of mosquitoes through competition and predation. Although it might be difficult to predict non-target effects under different application conditions in the field, there are reports that these microbial larvicides are harmless to nearly all non-target organisms when applied at recommended dosages (Lacey, 2007; Lacey and Siegel, 2000). Adult *Eylais hamata* (water mites) were not affected by Bti after 12 days of oral treatment with an LC_{50} rate (0.08µg/ml) used against *Culex pipiens* mosquitoes; however, the freshwater snail *Physa marmorata* was sensitive to this Bti dose (Mansouri et al., 2013). In contrast, studies on the environmental impacts of Bti used in wetland mosquito control in countries including France, Sweden, and the US have indicated considerable reductions of aquatic chironomid species (Boisvert, 2007; Fillinger, 1998; Land and Miljand, 2014; Theissinger et al., 2018). Similarly, Allgeier et al. (2019) investigated the impact of Bti on chironomid populations and insect emergence in seasonal freshwater wetlands. Using both artificial enclosures and natural field conditions, their semi-field study found that Bti, at typical mosquito control rates, significantly reduced chironomid emergence by 50% in treated pond mesocosms, making them the most affected invertebrate group. However, it was stated that Bti is safe for 100 different non-target invertebrates found in mosquito breeding habitats (Garcia et al., 1980; Lagadic et al., 2013).

Impact of entomopathogenic nematodes

Steinernema and *Heterorhabditis* (Rhabditidae) are genera containing insect-parasitic nematodes with a global distribution (found on all continents except Antarctica). These organisms occur naturally in soil and are used as bio-agents in lieu of or with chemical pesticides to manage insect pests that dwell in soil environments or those ensconced in cryptic sites such as under bark, rhizomes (Abate et al., 2017; Gumus et al., 2015; Lacey and Georgis, 2012) (Table 2 and 3). They can also be applied against foliar pests after formulation in special UV- and desiccation-protective materials or in under controlled-environments such as greenhouses (Mazurkiewicz et al., 2021; Ramakrishnan et al., 2022; Shapiro-Ilan and Goolsby, 2021). The nematodes enter the insect through natural orifices or the cuticle. Once inside the insect, collectively, these nematodes with their respective enteric bacterial symbionts, *Xenorhabdus* spp. and *Photorhabdus* spp. kill susceptible insect hosts using virulence factors they release in host hemocoel. Entomopathogenic nematodes (EPNs) do not just succeed in killing insects. They develop and emerge in numbers ranging from hundreds to tens of thousands (depending on host size) from killed insect in thousands from killed host (but in very small hosts can be hundreds) and can thrive in applied areas if environments are favorable (Hazir et al., 2022; Koppenhöfer et al., 2020).

EPNs effectively target soil-dwelling pests like grubs, fungus gnats, Colorado potato beetle and turfgrass pests, leading to increased plant growth and yield (Guo et al., 2017; Li et al., 2023). EPNs can also impact the densities of non-target organisms, especially those that occupy similar habitats. Insects that spend at least some time or complete a developmental period in soil can be susceptible to nematode infection (Somasekhar et al., 2002). Virulence observed mainly in laboratory studies against predatory insects such as ladybirds and lacewings suggest these effects might be caused by reduced food availability (El-Mandarawy et al., 2018; Harvey et al., 2016; Rojht et al., 2009; Shannag and Capinera, 2000). Resistance of some carabids to the EPN infection has been demonstrated (Georgis et al., 1991; Půža and Mráček, 2010a, 2010b). Both living carabid beetles, specifically *Poecilus cupreus*, and elaterid larvae (Coleoptera) showed resistance to the *S. affine* and *S. kraussei* infection (Půža and Mráček, 2010b). Likewise, adult and later-stage larvae of *Calosoma granulatum* (Coleoptera: Carabidae) an important predator of agricultural pests are resistant to *H. amazonensis* infective juveniles (IJs) in laboratory (Mertz et al., 2015). *Steinernema feltiae*, *S. carpocapsae*, and *H. bacteriophora* presented significantly less effects on the larvae of *Aphidoletes aphidimyza* (Cecidomyiidae), an aphid predator that pupates in soil, in greenhouse studies compared to a laboratory assay (Powell and Webster, 2004). Similarly, lady beetle species (*Coleomegilla maculata* and *Olla v-nigrum*, *Harmonia axyridis* and *Coccinella septempunctata*) exhibited a lower susceptibility to the *H. bacteriophora* and *S. carpocapsae*, compared to the designated lepidopteran pest, *Agrotis ipsilon* (Shapiro-Ilan and Cottrell, 2005). A recent study (Glover et al., 2025) revealed that ten EPN strains exhibited significant virulence (>50%) against the key pest, *Lygus lineolaris*. Importantly, these EPN strains were less effective against the generalist predator, *Nabis roseipennis* (Hemiptera: Nabidae). Furthermore, the predatory insects demonstrated clear behavioral avoidance of EPN-infected prey.

Although EPNs can cause mortality of beneficial insects like ladybirds and lacewings in laboratory assays, field studies report mixed results (El-Mandarawy et al., 2018). This inconsistency highlights the need to critically evaluate laboratory findings within the context of real-world conditions. Several factors might contribute to these discrepancies. In controlled laboratory settings, prey escape options are limited, which increases the chances of encountering and being infected by EPNs. Meanwhile, field environments offer diverse habitats and escape routes, potentially reducing non-target effects. Additionally, natural enemy behavior, such as avoidance of infected prey or reduced susceptibility during specific life stages, might influence field outcomes. Also, while a significant portion of arthropod natural enemies inhabit the soil during some stage of their life cycle (Gillott, 2005), certain species lack this soil-dwelling phase altogether. Alternatively, even for species with a soil stage, infrequent ground contact can significantly reduce their exposure to nematodes applied as a soil drench. This limited interaction with the soil environment minimizes their potential encounters with EPNs within this habitat. However, the increasing adoption of foliar EPN applications (Mazurkiewicz et al., 2021; Ramakrishnan et al., 2022) raises concerns about potential non-target effects on these beneficial organisms, especially those that do not typically spend time in the soil. For example, developing larvae of parasitoids such as *Cardiochiles diaphaniae* (Braconidae), *Mastrus ridibundus* and *Liotryphon caudatus* (Ichneumonidae) are vulnerable to EPN infection in insect hosts (Lacey et al., 2003; Shannag and Capinera, 2000). *Diglyphus begini* (Eulophidae) parasitoids avoid ovipositing in *Liriomyza trifolii* (Diptera: Agromyzidae) larvae infected with *S. carpocapsae* (Sher et al., 2000). This necessitates further research to assess their vulnerability and develop mitigation strategies.

Impact of Entomopathogenic Fungi

Entomopathogenic fungi (EPF) are another compelling group of biocontrol agents. They are arthropod killing organisms found in soil or as endophytes in plants. Over 800 EPF species have been identified, yet very few species are being commercially produced as biopesticides to control a range of significant pests including noctuids, scarabs, mosquitoes, curculionids, greenhouse pests such as thrips and white flies, and ticks (Um et al., 2018) (Table 2 and 3).

These organisms are geographically widespread. They attack and infect arthropod hosts by contact of microscopic spores on host cuticles. Major groups of EPF belong to the phyla *Ascomycota* and *Entomophthoromycotina*. Within the *Ascomycota*, many important EPF belong to the order Hypocreales, including genera such as *Metarhizium*, *Beauveria*, *Lecanicillium*, *Verticillium*, *Hirsutella*, and *Paecilomyces*. The order Entomophthorales within *Entomophthoromycotina* also contains important EPF species. (Alonso-Díaz and Fernández-Salas, 2021; Butt et al., 2016; Gielen et al., 2024).

Entomopathogenic fungi serve a variety of functions in the environments they inhabit such as they can killing insects, ticks, and affecting their behavior, acting as plant growth stimulants, suppressing various plant pathogens, inducing the production of plant hormones, and increasing plant tolerance to abiotic factors (Fernández-Salas et al., 2019; Hummadi et al., 2021; Khoja et al., 2021; Lacey et al., 2015; Meyling and Eilenberg, 2007). Based on these important roles, these fungi can be used in the control of important insect pests such as aphids, whiteflies, caterpillars, mosquitoes, and other similar pests. Over 800 EPF species have been identified, yet, very few species are being commercially produced as biopesticides to control a range of significant pests including locusts, termites, grasshoppers, cockroaches, noctuids, scarabs, mosquitoes, curculionids, greenhouse pests such as thrips and white flies, and ticks (Um et al., 2018) (Table 2 and 3).

Although the role of EPF in pest management is well-established, the use of EPF in pest management strategies may inadvertently affect beneficial natural enemies, especially when these enemies share the same host or interact within the food chain (Oreste et al., 2016; Roy et al., 2008; Zimmermann, 2007a, 2007b). Due to their mode of infection, the effects of EPF on non-target organisms like predatory insects, and other biocontrol agents have gained increased attention over the years. EPF can infect predators through both prey consumption and direct contact with treated surfaces. The ecological implications of such infections are multifaceted, as they may disrupt natural predator-prey dynamics, potentially leading to shifts in insect populations and community structures (Oreste et al., 2016; Roy et al., 2008; Zimmermann, 2007a, 2007b). Factors influencing the effects of EPF on predators/parasitoids include (i) fungal dosage, (ii) the timing of fungal infection relative to parasitism, and (iii) the specific type of fungus used (iv) the type of predator/parasitoid present (Roy and Pell, 2000).

Certain EPF species/strains such as *B. bassiana, M. anisopliae* and *Lecanicillium lecanii*, used to control spider mites, can affect survival, longevity or fecundity of predatory mites, lacewings and predatory bugs and coccinellids that feed on the spider mites, thrips and aphids. For instance, Smith and Krischik, (2000) assessed the effects of *B. bassiana* against the adults of four different species of coccinellids (*Hippodamia convergens*, *Coleomegilla maculata*, *Harmonia axyridis* and *Cryptolaemus montrouzieri*) and found that *B. bassiana* significantly reduced the survival of *C. montrouzieri*. In another laboratory study, predatory mite *Amblyseius swirskii* adults were found to be highly susceptible to some isolates of *B. bassiana* when conidia were applied directly to the mites (Seiedy et al., 2015). Similarly, *L. lecanii, M. brunneum* V275 and 4556, *B. bassiana* that demonstrated 60-90% virulence to *T. urticae* were found to kill predatory mites *Phytoseiulus persimilis* and *Neoseiulus californicus* (Acari: Phytoseiidae) adult females with mortality ranging between 51 and 90%. However, fungal infection did not affect the oviposition of predatory mites until death (Dogan et al., 2017). Araujo et al. (2020) assessed the susceptibility of two predator insects, *Podisus nigrispinus* (Hemiptera: Pentatomidae) and *H. axyridis* (Coleoptera: Coccinellidae) to different isolates of *B. bassiana* and two commercial products of *B. bassiana* and *M. anisopliae* (Bovemax® and Methamax®) under laboratory conditions. Different isolates of *B. bassiana* did not affect the number of preys consumed by *P. nigrispinus* and *H. axyridis*. The direct application of commercial products caused a high mortality of *P. nigrispinus* adults, whereas no differences among treatments were observed when EPF were applied via residual contact. Conversely, *H. axyridis* was not affected by any EPF treatment or different types of application. This study suggested that combining these two predators with EPF can be possible if they are released with a certain delay after applying the EPF. The possible effects of combining fungal pathogen *M. brunneum* and aphidophagous gall midge *Aphidoletes aphidimyza* were assessed under greenhouse conditions. The presence of *M. brunneum* did not affect *A. aphidimyza* emergence and when both biocontrol agents were combined, the aphid population was suppressed the most (de Azevedo et al., 2017). In Kenya, *M. anisopliae* (strain ICIPE 30) did not present direct toxicity on two common ant species, *Crematogaster mimosae* and *Camponotus spp.*, (Hymenoptera: Formicidae) found in association with *Odontotermes* termite mounds in laboratory assays (Abonyo et al., 2016). These ants are known predators of termites and can disrupt their resource exploitation. Additionally, field monitoring tracked ant diversity changes over 18 months at *M. anisopliae*-treated termite mounds located near the Mpala Research Centre in Kenya. Similarly, field monitoring at treated mounds did not show any statistically significant difference in ant species diversity compared to untreated control mounds (Abonyo et al., 2016). The invasive lady beetle, *Harmonia axyridis*, newly established in North America and Southern Canada, exhibits resistance to the *B. bassiana*, which infects and kills the native lady beetle, *Olla v-nigrum*. This difference in susceptibility gives *H. axyridis* an advantage over *O. v-nigrum*, potentially allowing it to outcompete the native species (Cottrell and Shapiro-Ilan, 2003). Under semi field conditions in citrus plantations, *B. bassiana* and *M. anisopliae* used to kill *Diaphorina citri* (Hemiptera: Liviidae), presented no significant effects on syrphids, lacewings and coccinellids (Corallo et al., 2021). However, *B. bassiana* (B1–B6) application affected *Amblyseius cucumeris* (Acari: Phytoseiidae) and *Anastatus japonicus* (Hymenoptera: Eupelmidae), natural enemies of *Bactrocera dorsalis*. This fungal isolate exhibited dose-depended effects, reducing the number of *A. cucumeris* and killing *A.*

japonicus adults (Li et al., 2024). Similarly, the mosquito predator *Toxorhynchites brevipalpis* (Diptera: Culicidae) appears to be more tolerant of *Metarhizium* spores compared to the target mosquito pests (Alkhaibari et al., 2018). The impact of EPF on *T. brevipalpis* depended on the fungal concentration. Higher inoculum is required than what is required to kill target larvae (Alkhaibari et al., 2018; Garrido-Jurado et al., 2016).

The formulation and application method of EPF significantly influence the exposure risk for beneficial predators. For instance, direct spraying, regardless of whether the formulation is conidia in oil or water-dispersible granules, dramatically increases the likelihood of infection compared to soil drenching. Furthermore, predator susceptibility to EPFs varies considerably by species with immature stages generally more susceptible to infection than adults (Cottrell and Shapiro-Ilan, 2003; de Azevedo et al., 2017; Garrido-Jurado et al., 2011; Li et al., 2024).

Certain EPF formulations appear to be safe for beneficial predators. Studies have shown that three formulations of *B. brongniartii* (Melocont-Pilzgerste, Melocont-WP, and Melocont-WG) used to control European cockchafer larvae (*Melolontha melolontha*) had no negative impacts on the survival of *Poecilus versicolor*, a natural predator of these cockchafer larvae. Even when these predator larvae encountered *B. brongniartii*-infected cockchafer carcasses, they showed no detrimental effects (Traugott et al., 2005). Similar findings were observed with *M. anisopliae* in olive groves (Garrido-Jurado et al., 2011). This research demonstrated that the soil environment promoted the persistence of a native *M. anisopliae* isolate at sufficient levels (10^5 CFU/g of soil) for long-term control of olive fly puparia (*Bactrocera oleae*). Importantly, field monitoring using pitfall traps did not detect any fungal infections in soil arthropods after EPF treatment. Notably, ants, which are often beneficial predators, were the most abundant group captured. Additionally, laboratory assays revealed no significant differences in mortality rates between fungal treatments and the control group for these non-target organisms. While a slight reduction in average lifespan was observed in the treated groups compared to the control, there were no significant changes in overall ant activity before and after fungal application (Garrido-Jurado et al., 2011). *Beauveria bassiana* strain ATCC 74040 had negligible effects on the survival, immature development, adult emergence, or fecundity of both laboratory-reared and wild *Chrysoperla lucasina* larvae (Morda et al., 2024). These findings suggest that the impact of EPF formulations on beneficial predators is species- and formulation-specific, requiring careful consideration for integrated pest management strategies.

Predators can avoid contact with EPF. For instance, adults of the generalist predator *Anthocoris nemorum* detected and avoided contact with *B. bassiana* conidia inoculated leaf surfaces, and females were very reluctant when they were forced to enter EPF-treated leaf surfaces (Meyling and Pell, 2006). In another study, starved and non-starved *Cheilomenes lunata* adults, a predatory coccinellid, were able to differentiate between *M. anisopliae*-infected and non-infected aphid cadavers and showed feeding avoidance behavior towards EPF-infected cadavers (Bayissa et al., 2016). Similarly, a research conducted by Avery et al. (2022) demonstrated that the predator *Podisus maculiventris* can discriminate between infected and healthy *S. frugiperda* larvae, significantly preferring the latter in choice experiments. Interestingly some arthropods can transport EPF spores from infected cadavers to other healthy arthropods. This phoretic interaction (i.e. conidial dissemination) observed between other arthropods and fungi has been shown to have minimal harm to host (Dromph, 2003; Lin et al., 2017; Zhang et al., 2015). Transmission of a *B. bassiana*-based biopesticide in treated populations of predatory social wasp *Mischocyttarus metathoracicus* has been reported. The treated and released wasps were not discriminated against by colony mates leading to horizontal transmission of fungi in colonies (de Souza et al., 2023). There is limited evidence for such transmission of fungal pathogens to cause "wipeout" scenarios with social insects like wasps that benefit plants (de Souza et al., 2023; Mayorga-Ch et al., 2021), but it is a potential concern that requires further field research.

The impact of EPF on parasitoids can be mixed. Kim et al. (2005) showed that the parasitoid *Aphidius colemani* developed normally when offered its host *Aphis gossypii* that has been infected with *Lecaniciliium lecanii* for 5-7 days, however, applying the fungus 1 day before to 3 days after parasitization reduced parasitoid emergence. Evidently, albeit *M. anisopliae* can decrease adult emergence and can kill *Trichogramma pretiosum* parasitoids, which are important and easily mass-produced bioagents used against a lepidopteran pest, however, this fungus has no effect on the number of parasitized *Ephestia kuehniella* eggs (Potrich et al., 2009). Also, no negative effects of *B. bassiana* and *M. anisopliae* were found against the parasitoid *T. atopovirilia* (Polanczyk et al., 2010). Trichogrammatid parasitoids seem to not be affected by *B. bassiana* strains. Observations showed only minimal adverse effects on *T. pretiosum* and *T. atopovirilia*, suggesting the tested *B. bassiana* strains and products are largely harmless to these parasitoids (Araujo et al., 2020). Parasitism of *Myzus persicae* aphids and adult emergence of a parasitoid *Diaeretiella rapae* was significantly affected in the presence of *B. bassiana* (Martins et al., 2014). Female parasitoids significantly preferred to infect aphids in the control (without *B. bassiana*) compared to aphids treated with the EPF (Martins et al., 2014). While it is well established that prior fungal infection can negatively impact parasitoid fitness, reducing lifespan, but potentially increasing egg-laying rates, overall, most research suggests a potential benefit when release times are carefully coordinated; thus, the critical importance of timing and order of application for these biological control agents is highlighted (Quesada-Moraga et al., 2022).

EPFs can colonize various plant tissues including leaves, branches, stems, fruits, flowers, and roots (Bamisile et al., 2018; Ghafari et al., 2025; Vega, 2008). Notably, naturally occurring and asymptomatic endophytes provide various benefits such as improvement of plant's physiological parameters (Canassa et al., 2019; Qing et al., 2023), herbivore protection, disease defense, and resistance to nematodes (Martinuz et al., 2012; Russo et al., 2015; Wilberts et al., 2024, 2023, 2022). To reduce herbivore damage, endophytic fungi employ diverse strategies, including the manipulation of plant chemistry through the production of insect-repellent or toxic compounds (Luo et al., 2023; Samal et al., 2023; Vega, 2018, 2008). While the precise mechanisms remain elusive, these fungi also release a diverse array of biomolecules that trigger a cascade of hormonal and metabolic changes within the plant upon recognition. This multifaceted response ultimately serves to deter or harm herbivores, bolstering plant defense (Fonseca et al., 2018). Furthermore, some insects feeding on endophyte-colonized plants may exhibit decreased survival and egg-laying, further limiting herbivore populations (Klieber and Reineke, 2015; Shaalan et al., 2021). Plant colonization of endophytes might influence predator and parasitoid behavior by altering their attraction to both host plants and prey or can have potential drawbacks such as diminished growth, fecundity, and survival in natural enemies that prey on herbivores. These effects have been thoroughly covered in recent reviews and references therein (Quesada-Moraga et al., 2024, 2022).

Challenges in risk assessment of biocontrol agents

In the previous sections we outlined the direct and indirect risks posed by entomopathogenic organisms to non-target species (Table 2 and 3). While these biological control agents are generally considered safe, some species can pose risks. It is crucial to distinguish between introducing entirely new (exotic) species and augmenting existing populations. *Bacillus thuringiensis,* for example, is widespread, yet its effectiveness as a biopesticide typically relies on inundative applications. Similarly, many entomopathogen applications involve augmenting existing populations of organisms like EPF and EPN already present in agricultural systems (e.g., pecan and peach orchards) but at insufficient levels for effective pest control. While augmentative releases might seem less risky, they can still impact native biodiversity through spillover effects on resident species, such as competition for resources, food web disruption, or even the introduction of new diseases. The absence of natural enemies capable of regulating these augmented populations can further exacerbate these risks.

Also, many commercial biopesticide products are non-native to their application sites (even if the species is native to the region), the potential for unintended ecological consequences remains a critical, yet understudied, aspect of biological control. While significant, widespread negative impacts from biocontrol introductions are rare (Hajek et al., 2007), the possibility of less obvious effects warrants ongoing research.

Registration for commercial use of entomopathogens in many countries in Europe, Asia, and America is relatively easy after rigorous testing and research (Ehlers, 2005; Montesinos, 2003; Ortiz and Sansinenea, 2023). However, there has been a longer authorization time for some biocontrol agents in Europe than in comparable jurisdictions, because of inconsistent application of biocontrol expertise in safety assessments, necessitating more robust and standardized protocols (Sundh and Eilenberg, 2021).Tthere are significant challenges that can hinder thorough risk assessment and subsequent mitigation strategies (Table 3). Firstly, there is the impossibility of comprehensive testing. The vast number of potential non-targets within a test area makes it impractical to evaluate the impact of exotic organisms on all potentially susceptible species. Also, although controlled environments provide beneficial research opportunities, replicating natural conditions within laboratory and semi-field settings remains challenging. Consequently, findings from such studies may not serve as definitive evidence of side effects. Field investigations yield the most valuable and conclusive data regarding the impacts of pathogens on non-target organisms. Secondly, entomopathogens can disperse beyond their release site, potentially exposing unforeseen non-target species that are further afield. Therefore, even with existing discussions acknowledging potential risks, a precautionary approach remains essential. Knowledge gaps regarding exotic organism behavior in novel environments and the potential effects of genetic modifications necessitate continued research and careful consideration before widespread field applications.

Conclusion

The use of chemical pesticides in urban and protected ecosystems has been increasingly reduced or banned, and use of biocontrol agents seems to be the only sustainable management solution. These bioagents have increasingly been introduced into new areas. Also there has been an increased interest in developing effective entomopathogenic organism-based attractant baits. Potential benefits from the use of these organisms include reduced reliance on chemical pesticides and long-term pest suppression.

Even though their effectiveness against pests is well-documented and overall entomopathogens are considered safe, it should be noted that some of these organisms can have potential and unpredictable negative impacts on non-target organisms including other natural enemies. For example, secondary viral infections, particularly when advanced, can negatively impact populations of parasitoids and predators. *Bacillus thuringiensis* toxins, while exhibiting targeted oral toxicity and generally low environmental impact, can indirectly affect parasitoid populations through premature host death. Direct effects on predators and parasitoids have been observed, but typically only at *Bt* doses far exceeding recommended field rates. EPNs, primarily soil-dwelling, typically have limited contact with beneficial insects. However, the increasing exploration of foliar EPN applications necessitates field research to fully understand their interactions with beneficial insects and pests under real-world conditions. Certain EPF species/strains can negatively affect the survival, longevity, or fecundity of predators and parasitoids that prey on targeted pests. Consequently, these natural enemies may avoid contact with EPF-infected hosts or treated surfaces, mitigating some of this risk. The impact of EPF on aquatic invertebrates is concentration-dependent, with higher inoculum levels required to impact these organisms compared to mosquito larvae.

Laboratory studies may suggest negative effects of entomopathogens on non-target organisms. However, these findings may not always reflect the actual ecological consequences observed in field settings. Field studies are therefore crucial for a more comprehensive understanding of potential environmental impacts. Existing research largely indicates minimal field-level influence of entomopathogens on non-target natural enemies. While all these groups require additional research along similar lines (e.g., long-term field studies, non-target effects, etc.), they differ in their potential to impact non-targets. For example, EPNs, due to their primarily soil-dwelling nature, have a lower likelihood of impacting above-ground insects. Future research should prioritize long-term field studies assessing these impacts, particularly of soil and foliar EPN applications, on a broader range of non-target organisms and further investigate the effects of entomopathogenic fungi, especially concerning endophytic colonization.

Furthermore, it is essential to recognize that the impact of entomopathogens on non-targets is generally expected to be considerably lower than the detrimental effects associated with broad-spectrum chemical insecticides. Understanding the long-term ecological impacts of biocontrol application is crucial for ensuring their sustainability and responsible integration into pest management strategies. Research should continuously assess the impact on predator-prey dynamics and non-target effects of these organisms. Also, we should develop strategies to mitigate potential risks by adopting IPM approaches with diverse bioagent groups as well as optimizing application timing, dosage, and formulations.

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