



REVIEW ARTICLE

Beyond synergy: Integration of entomopathogenic fungi and botanicals as eco-friendly solutions for sustainable pest management

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Abstract

The widespread use of synthetic pesticides in contemporary pest management has been a double-edged sword, while they initially providing effective control of pest populations, their extensive use has ultimately contributed to the emergence of pesticide-resistant pests, accelerating biodiversity loss and environmental polluting by hazardous chemicals. As a result, the development of sustainable alternatives for pest control, including entomopathogenic fungi (EPF) and botanical-derived insecticidal agents, is emerging. Despite their potential, critical limitations inherent to EPF include a slow rate of action and acute sensitivity to abiotic factors, which necessitate synergistic integration with rapid-action botanicals. This paper aims to review combinatorial strategies, that leverage independent yet complementary modes of action, not only preventing the evolution of resistance but also increasing mortality, yielding significantly lower median lethal concentration (LC₅₀) and median lethal time (LT₅₀) values than those obtained with single agent treatments. The reduced doses required for both components improve their suitability for organic agriculture and integrated pest management (IPM) programmes, where minimising pesticide residues is a priority. This review synthesises the current literature and incorporates meta-analysis to discuss how botanicals enhance EPF performance by interfering with insect cuticular defences, altering cuticular permeability, modulating host behaviour and providing protection against ultraviolet radiation and temperature stress. We identified the key issues and areas for improvement in these integration strategies and proposed future directions focusing on compatibility optimisation, advanced formulations and predictive models for sustainable pest management.

Keywords: botanical insecticide; entomopathogenic fungi; integrated pest management; synergism; virulence

Introduction

Pest infestation is one of the major threats to agricultural productivity worldwide, causing substantial economic losses and threatening global food security. This loss in agriculture production may be attributed to both biotic and abiotic factors, of which insect pests alone account for about 38 % of the loss. Arthropod pests are known to destroy 18–20 % of the world's crop yield (estimated at over US \$470 billion/annum) (1). Conventional insect pest management have relied heavily on synthetic insecticides. However, their indiscriminate use has resulted in environmental contamination, non-target toxicity, bioaccumulation and increasing regulatory concerns, thereby threatening human health and agricultural sustainability (2). Therefore, the demand for alternative pest management strategies that are both effective and environmentally sustainable is exponentially increasing. Alternative pest management using different biological control agents, including botanical insecticides, entomopathogens, predators and

parasitoids, has gained significant attention (3). Botanical insecticides are attractive components of biological control programs because they are biodegradable, relatively inexpensive and generally compatible with beneficial organisms. Variations in the phytochemical composition of plant species underlie their distinct mechanisms of action against insect pests (4). These biopesticides primarily target insects' fundamental physiological mechanisms and disrupt their nervous, metabolic and endocrine systems (4). For instance, recent studies on botanical insecticides have shown that certain compounds are effective against a range of agricultural and human health pests, such as bufadienolides of *Drimys panchratium*, which were reported to have high efficacy against the two-spotted spider mite (*Tetranychus urticae*). Additionally, *Thymus* spp. and citrus oils were found to be effective against stored-product beetle *Rhyzopertha dominica* and stable fly (*Stomoxys calcitrans*), exhibiting strong contact and fumigant toxicity respectively (5). However, they are not as effective as synthetic pesticides (6). The large-scale adoption of botanical insecticides is

constrained by the high quantities of active ingredients required, which increases application costs. Furthermore, many botanicals exhibit delayed or stage-limited action, making them less effective under intense pest pressure. Many botanicals also have short persistence due to rapid decomposition in the environment or vaporisation. Entomopathogenic fungi represent another potent class of biocontrol agent. Several entomopathogenic fungi (EPF) genera, including *Beauveria*, *Metarhizium*, *Akanthomyces*, *Hirsutella* and *Entomophthora*, are widely incorporated into integrated pest management (IPM) programmes (7). Entomopathogenic fungi provide better management than many other commonly used conventional control options (8). *Beauveria bassiana* has a broad host range, infecting over 700 insect species, demonstrating its effectiveness in insect control. Unlike synthetic chemical pesticides, EPF operates by penetrating the cuticle, inducing enzyme production and depriving nutrients, thereby inducing mortality in the target pest, but with a relatively long mortality period. The EPF have several limitations that restrict their utility. Environmental factors, including high temperature, low humidity, ultra-violet (UV) radiation and unfavourable pH, hinder spore germination, virulence and persistence. Formulation difficulties have rendered in a very short shelf life under specific storage conditions.

Potential impacts on non-target organisms, particularly beneficial arthropods, also require careful evaluation before large-scale deployment (9). Constant innovation is needed to address the rising harm caused by insect pests. *Metarhizium anisopliae* achieved more rapid mortality against rice planthoppers when combined with compatible insecticides, shortening median lethal time (LT_{50}) compared with the fungus alone and improving field suppression of planthopper populations (10). Compatible co-formulations also accelerate EPF-driven mortality by shielding conidia from abiotic degradation, enhancing cuticular adhesion and lowering the effective lethal dose required for host kill. Across sucking and stored-product pests, combinations of *M. anisopliae* or *B. bassiana* with botanical carriers (sesame, sunflower and mineral oil) or plant extracts (neem and eucalyptus) consistently shortened LT_{50} and increased corrected mortality compared with fungus-only treatments (11–16). This study established an important methodological framework for assessing compatibility, synergism and performance enhancement in combined treatments.

Building on such approaches, increasing emphasis is now being placed on EPF–botanical combinations as a more ecologically aligned alternative to EPF–chemical integrations. These methods have been reported to induce both synergistic and antagonistic effects. These contrasting findings indicate that the outcome of botanical–EPF integration is highly dependent on compatibility between the fungal strain, botanical source, formulation, concentration and application strategy. Several synergistic studies indicate that it could not only combat potential mechanisms of resistance development through multiple modes of action but also provide systemic plant protection and eco-friendly pest control (11–13). The botanicals act as carriers, particularly oils, which enhance the adhesion of conidia, their distribution on hydrophobic cuticles and their survival (14). Sunflower oil formulations of entomopathogenic fungus exhibit high viability and superior pest mortality, supporting their use as oil-based carriers for performance and handling (15). Some formulations contain botanicals as UV protectors, which perform better under UV stress than water-only formulations (16). Corn oil suspensions have been used as low-cost thermal protectants to preserve conidial viability at high temperatures during

long-term storage, with improvements in heat tolerance and shelf life (17).

Despite the increasing number of studies on botanical–EPF combinations, the available evidence remains fragmented and often inconsistent because these studies differ considerably in botanical species, fungal isolates, formulations, concentrations, compatibility assessments and experimental conditions. Existing reviews have largely focused on botanicals or EPF independently or have summarised their combined efficacy without critically evaluating the important factors like their combined mode of action, practical implementation, molecular and formulation aspects. Consequently, a comprehensive synthesis that integrates all these aspects is still lacking.

This review critically examines the integration of EPF and botanical insecticides as complementary tools for sustainable pest management. Particular emphasis is placed on their mechanisms of interaction, effects on pest mortality, formulation strategies and compatibility under field conditions. The review also identifies current research gaps and proposes future directions for developing effective, residue-free pest management approaches suitable for organic agriculture and IPM systems.

Botanical insecticides: Evolution and role in contemporary pest management

Botanical insecticides have been used for pest control for several millennia. Historical records indicate that nicotine extracted from tobacco was used against insect pests during the seventeenth century, whereas rotenone derived from Derris roots became widely adopted during the 19th century. Plant-based pest management practices may date back more than 3000 years (18, 19). Modern research highlights a vast diversity of plant sources, with the most studied families being Meliaceae, Lamiaceae, Asteraceae, Myrtaceae and Rutaceae, which collectively dominate the literature on botanical insecticide research. The insecticidal activity of botanicals is largely attributed to phytochemicals such as terpenoids, alkaloids, phenolics and related secondary metabolites (20). Among these, azadirachtin, a triterpene isolated from *Azadirachta indica*, has been reported to exhibit broad insecticidal activity. The majority of botanically derived insecticides have been evaluated for the control of coleopterans (mainly storage pests), lepidopterans and dipterans, which together account for about 88 % of the species examined (20). Botanical insecticides from these families and their phytochemical classes are likely to remain universal alternatives to synthetic pesticides, especially in ecologically fragile environment. The interaction among various botanical pesticides and target insect orders, based on a literature survey of 5679 papers on botanical insecticides (Fig. 1). The thickness of bars and connecting lines below each taxon or group indicates the relative number of papers focused on specific taxa or insect orders.

Eco-selective pest control using entomopathogenic fungi

Entomopathogenic fungi are important biological control agents that contribute to sustainable agriculture through their natural ability to infect and suppress insect pests. This results in enhanced soil health and diversity of microbes in the environment. Such benefits help maintain environmental balance and minimise chemical use (21). They exhibit a highly selective and environmentally friendly mode of action; however, their effectiveness in the field may vary depending on the external conditions or vulnerability to insects (21). They have been universally recognised for their high diversity in terms of species

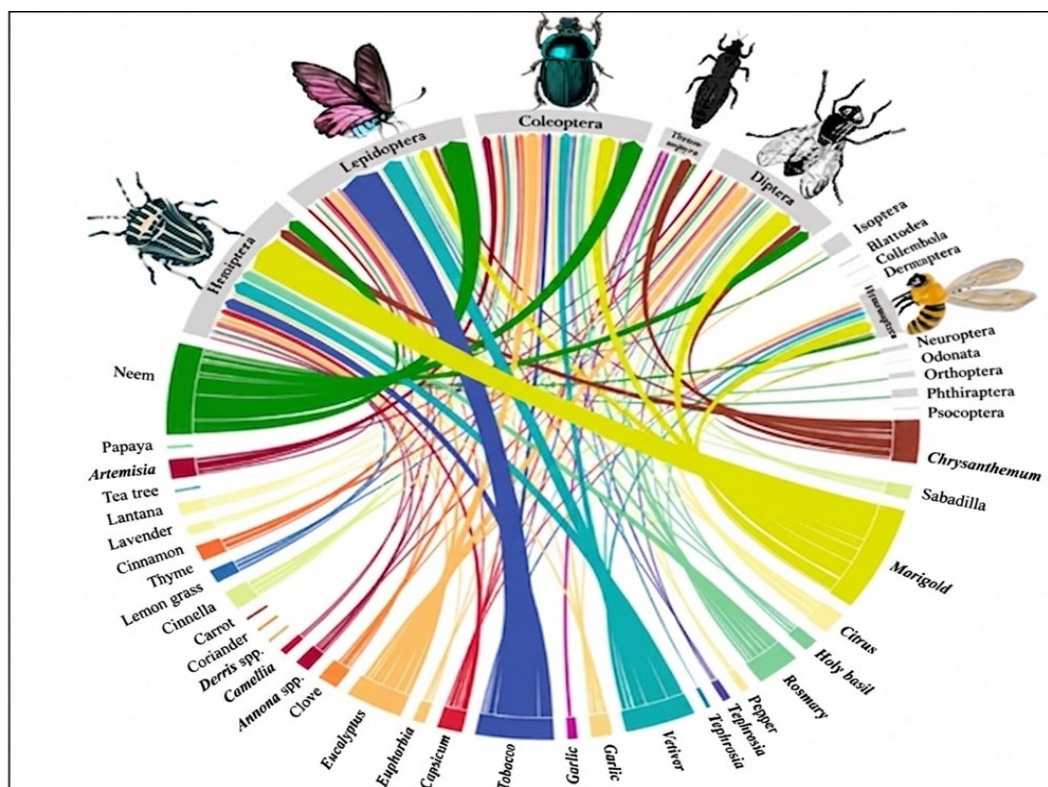


Fig. 1. Schematic representation of the chord chart based on a literature survey of papers on botanical insecticides ($n = 5679$).

and strains (8). *Beauveria*, a cosmopolitan genus of arthropod pathogens within Cordycipitaceae, is a monophyletic genus with multilocus phylogenies defining numerous well-supported species (22). *Beauveria bassiana* and *Beauveria brongniartii* both exhibited cryptic species complexes with many well-supported lineages, highlighting the dependence of strain selection in ensuring successful performance (22). Globally, the most common EPF used as mycoinsecticide products is *B. bassiana* (33.9 % of 171 products) and *M. anisopliae* (33.9 % of products), both of which have broad adoption in IPM programmes with approximately 75 % of these products registered or commercially available (23). The EPF are found to infect the most important insect orders, such as Hemiptera, Coleoptera, Thysanoptera and Orthoptera. However, their efficacy and specificity may vary among insect species, requiring field trials and optimised cost-effective formulations in relation to pest and environmental conditions (21, 23). The interaction among various EPF and target insect orders, based on a literature survey of EPF-related papers ($n = 4575$), has been schematically represented in Fig. 2. The bars and line thickness below each taxon/group or connecting them represent the relative number of papers focused on specific taxa or insect orders.

Dual-action biocontrol: Integrating entomopathogenic fungi and botanicals for enhanced pest management (EPF + B)

Biocontrol agents include EPF and botanicals, which, when applied individually, exhibit different insecticidal mechanisms and eco-compatibility. There is growing evidence indicating that these bioagents can be used together to produce additive or even synergistic effects on target pests (24). The combination of EPF and botanicals combats pest in an integrative manner by providing multiple complementary modes of action. Botanical-induced stress conditions significantly increase host susceptibility to fungal infection, often accelerating mortality rates (25, 26). Certain plant extracts and oils have been reported to enhance fungal germination, sporulation, conidial adhesion and environmental persistence upon

achieving optimal botanical composition and concentration (15, 16, 27, 28). This integrated application not only increases insect mortality but also addresses issues associated with individual applications and provides an alternative to synthetic insecticides (29).

Meta-analysis of pest mortality responses to entomopathogenic fungi–botanical combinations

The combined effects of botanicals and EPF are mostly reported to cause higher insect mortality than when either of the agents is applied alone and the majority of studies have reported synergistic or additive effects, with a few antagonistic outcomes (30, 31). Beyond mortality, such combinations also influence reproductive performance. For instance, treated populations produced an average of 7 nymphs per female, compared with 29 under individual treatments. This highlights that synergistic effects also extend to reproductive inhibition (11).

To quantitatively evaluate the effectiveness of EPF–botanical combinations, we performed a meta-analysis using a random-effects model. This included 25 independent comparisons from peer-reviewed studies (Fig. 3). The analysis was conducted using Stata and R (metafor v4.5.1) and quantified the overall impact of this integrated approach on insect mortality.

Literature search strategy

A comprehensive literature search was conducted using the Scopus database to identify relevant studies on the compatibility of EPF and botanical pesticides in sustainable pest management. The search was restricted to the subject areas of Agriculture and Biological Sciences and limited to publications in the English language. The keywords used for the search included "compatibility", "fungi", "fungus", "biological control", "entomopathogenic fungi", "biocompatibility", "plants", "integrated pest management", "self-incompatibility", "incompatibility", "germination", "biocontrol agents" and "biological pest control". Retrieved records were screened sequentially based on subject area, language, relevance of

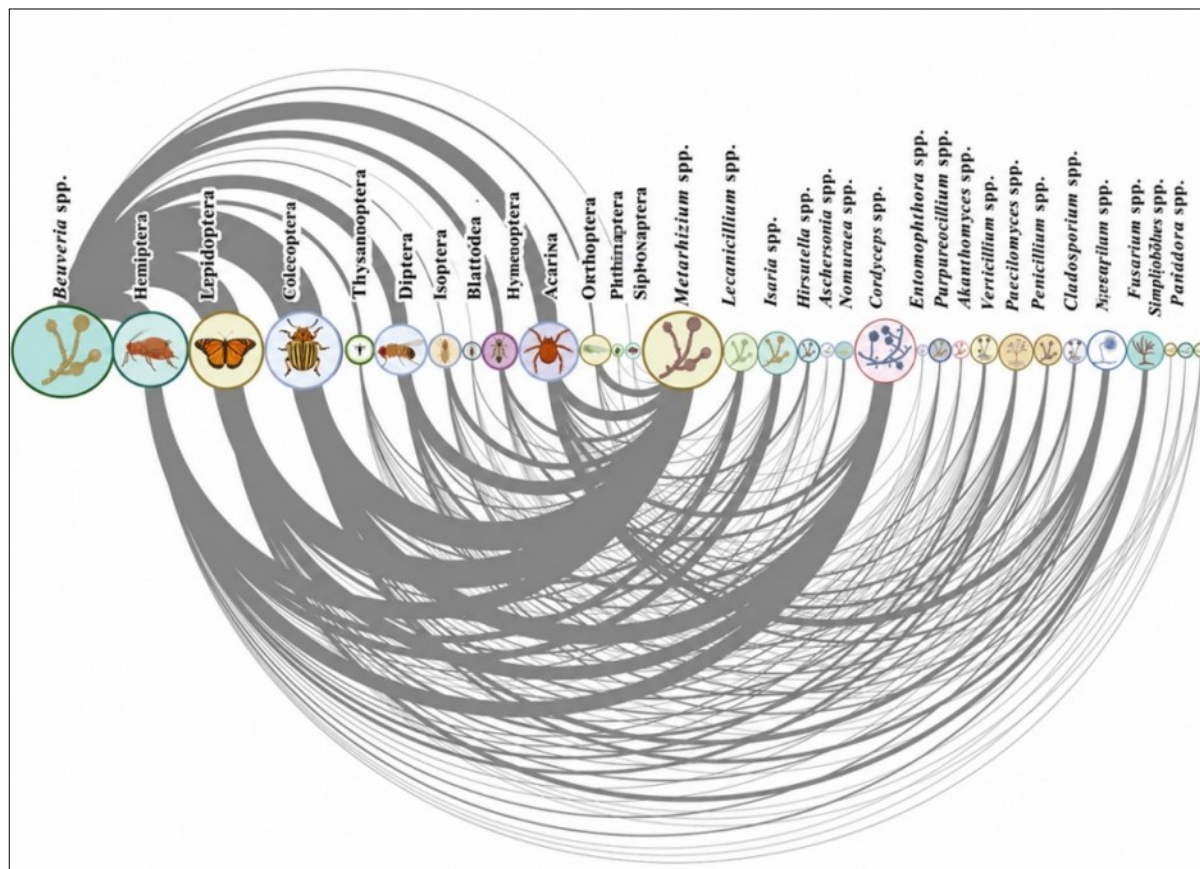


Fig. 2. Schematic representation of an arc chart based on a literature survey of papers on entomopathogenic fungi ($n = 4575$).

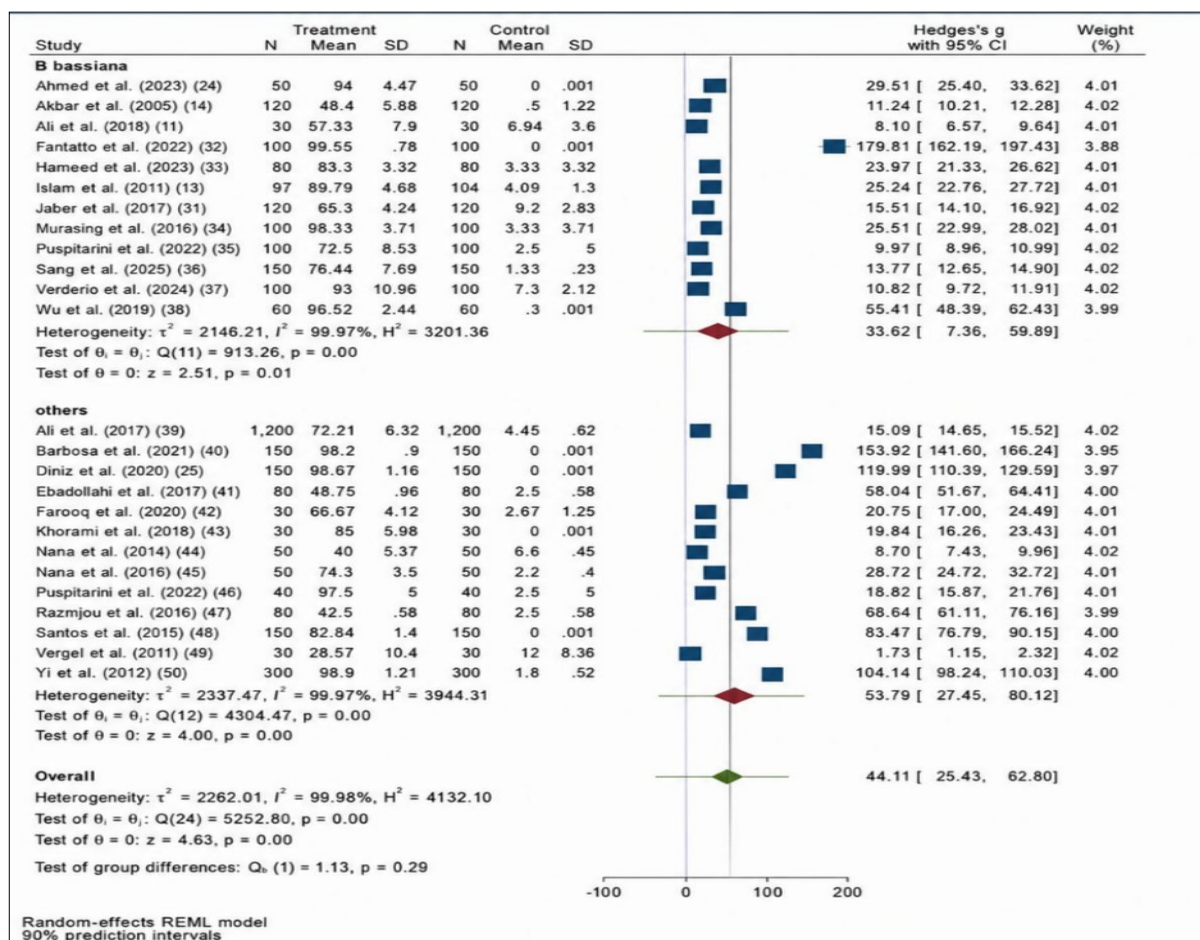


Fig. 3. This meta-analysis summarises effect size estimates (Hedges' g) from 25 peer-reviewed studies evaluating the combined effects of entomopathogenic fungi (EPF) and botanical extracts on insect responses. Individual studies are represented by squares proportional to their weight, with 95 % confidence intervals shown as horizontal lines, and the overall effect as a diamond. Included taxa comprise *Beauveria bassiana*, *Metarhizium* spp., *Lecanicillium* spp. and *Fusarium* spp. A random-effects model was applied to account for between-study variability, with analyses performed using the Stata and the metafor package in R (v4.5.1).

titles, abstracts and removal of duplicate records. Studies relevant to the compatibility and integration of EPF and botanical pesticides were selected for inclusion in the review. The literature identification, screening, eligibility assessment and study selection process are illustrated in Fig. 4.

Results

The analysis confirmed a significant overall effect of EPF–botanical treatments (Hedges' $g = 44.11$; 95 % CI: 25.43–62.80; $p < 0.001$), indicating enhanced efficacy compared to controls. Subgroup analysis showed that *B. bassiana*-based treatments had a positive effect ($g = 33.62$; 95 % CI: 7.36–59.89), while other EPFs' combination treatments exhibited a higher effect size ($g = 53.79$; 95 % CI: 27.45–80.12), suggesting stronger synergistic interactions.

A high degree of heterogeneity was observed ($I^2 \approx 99.98\%$), indicating substantial variability among studies. The extremely high heterogeneity suggests substantial variation among fungal strains, botanical compounds, target pest species, formulations, application methods and experimental conditions. Therefore, pooled effect estimates should be interpreted with caution. This variability was further explored through meta-regression analysis, which demonstrated that moderator variables collectively explained a large proportion of the heterogeneity ($R^2 = 81.64\%$, $p < 0.0001$). Among the moderators, insect developmental stage (larval stage; $p = 0.0013$), fungal species (notably *Fusarium*; $p = 0.0104$) and time after treatment (1 day; $p = 0.0296$) significantly influenced the observed outcomes.

Despite this heterogeneity, the test for subgroup differences was not statistically significant ($p = 0.29$), indicating that the overall efficacy remained comparable across groups. This finding suggests that the overall efficacy of EPF–botanical combinations remain broadly consistent despite variation in biological and experimental factors. Importantly, the direction of effects was consistently positive across studies, reinforcing the robustness of EPF-based IPM strategies and supporting their reliability across varying biological and experimental conditions.

These findings indicate that the use of botanical combinations with EPF at optimal, often reduced concentrations leads to higher insect mortality, due to synergistic or additive effects. Nevertheless, antagonistic effects may occur when elevated levels of fungitoxic botanicals inhibit fungal colonisation.

Botanical oils and extracts as ultra-violet and thermal protectants for entomopathogenic fungi

The application of botanical extracts as natural protectants has also been recognised, with the potential to augment EPF's UV tolerance. For instance, the spore germination percentage of *M. anisopliae* suspended in sesame oil was 79.5 %, whereas it is only 43.3 % in aqueous suspensions upon exposure to UV light (16), implying that botanicals can be used as ecological alternatives to synthetic additives, which are widely used in the production of insecticides (51). The application of plant extracts and oils, such as *A. indica* (neem), *Camellia sinensis* (tea), *Sesamum indicum* (sesame), *Helianthus annuus* (sunflower) and *Zea mays* (corn), has been reported to provide protective effects on EPF spores against UV radiation under both laboratory and field conditions (51, 52). The UV-protective action of botanicals involves the use of oil-based botanicals as UV-absorbing shields for spores; high-polyphenol

and antioxidant-rich extracts create protective layers on conidia, thereby reducing UV penetration (16, 52). Furthermore, the bio-efficacy of *M. anisopliae* (MET-GRA4) oil in glycerol emulsion against *Rhynchophorus ferrugineus* was evaluated and it was reported that this formulation stabilises conidia, enhances shelf life and minimises damage induced by UV and heat stress (53).

Botanicals, particularly plant oils containing unsaturated fatty acids, have demonstrated substantial efficacy in improving the thermal tolerance of EPF and thus help overcome one of the major bottlenecks in the storage and field application of biopesticides. Plant oils, including corn oil, sunflower oil and cottonseed oil, have been observed to have a dual-purpose protective role as substrate amendments and coating agents, thereby significantly increasing conidial thermotolerance during fungal production. Conidia development in corn oil-amended *B. bassiana* (ARSEF-7060) showed significantly higher wet-heat tolerance at 45 °C for 90 min. The LT_{50} value was 45.7 min longer with oil than without, at 25.7 min (54). Additionally, coating with corn oil also provided improved dry-heat protection for 8 hr at 50 °C compared with the non-coated one, which lasted 2.13 hr. This protective mechanism is attributed to the presence of unsaturated fatty acids. Corn oil contains about 87 % unsaturated fatty acids (28 % monounsaturated and 59 % polyunsaturated), followed by sunflower oil (84 %) and cottonseed oil (70 %), respectively, reporting improved thermotolerance results (54). Likewise, conidia of *Isaria fumosorosea* (SFP-198) in a corn oil mixture resulted in only a 7 % reduction in germination after 2 hr at 50 °C compared with a 67 % reduction in the absence of oil. Linoleic and oleic acid showed a dose-dependent increase in conidial thermotolerance (55). Long-term storage studies also showed a dramatic increase of fungal persistence using corn oil-based suspensions, where powdered formulations reported a decrease in viability by 34.0 % within 3 months, whereas corn oil suspensions showed only a 38.0 % reduction at 4 °C over 24 months (17). Beyond field protection, oil-based formulations substantially improve storage stability, which is an essential factor for commercial production, transport and shelf-life extension of fungal biopesticides.

Although many botanical oils improve environmental stability and fungal performance, compatibility varies among fungal strains and botanical products. Therefore, compatibility assessments are essential before incorporating botanicals into EPF-based pest management programs (Table 1). Although antagonistic interactions are less frequently reported than synergistic effects, they represent an important limitation of botanical–EPF integration. Available evidence indicates that antagonism primarily occurs when botanicals possessing intrinsic antifungal activity or applied at non-optimal concentrations inhibit conidial germination, fungal growth, sporulation or infectivity, thereby reducing EPF efficacy (14, 58, 59). Based on current evidence, compatibility can be predicted by four key factors: botanical concentration, phytochemical composition, fungal strain tolerance and formulation strategy. Therefore, concentration optimisation and compatibility screening should precede field application. However, the molecular mechanisms governing these antagonistic interactions remain largely unexplored, warranting future transcriptomic, proteomic and metabolomic studies to elucidate how phytochemicals influence fungal physiology and pathogenicity.

Table 1. Summary of positive and negative interaction dynamics between botanical extracts and entomopathogenic fungi against insect pests

Sl. No.	Insect	Treatment	Interaction	Effective concentration	Mode of action	References
Positive interactions						
Hemiptera						
1	<i>Bemisia tabaci</i>	<i>Beauveria bassiana</i> + neem	Synergism	1 % + 1×10^8 conidia per mL	The systemic action of soil-drenched neem weakens pests and enhances foliar EPF cuticle invasion	(13, 56)
2	<i>Dactylopius opuntiae</i>	<i>Fusarium caatingaense</i> + <i>Nicotiana tabacum</i>	Additive	10 % + 1×10^7 conidia per mL	The botanical insecticide weakens insects, changes their behaviour, and makes them more vulnerable to fungal infection and death	(25)
3	<i>Bemisia tabaci</i>	<i>Beauveria bassiana</i> + <i>Calotropis procera</i>	Additive	30 % + 1×10^7 conidia per mL	Endophytic fungi produce toxic metabolites in plants, and the extract's activity targets pests through a dual mode of action	(31)
4	<i>Bemisia tabaci</i>	<i>Citrullus colocynthis</i> seed part + <i>Beauveria bassiana</i>	Synergism	1 % + 1×10^7 conidia per mL	Insecticidal crude proteins from plants and fungi break down tissues and suppress the immune system	(33)
5	<i>Bemisia tabaci</i>	<i>Lecanicillium muscarium</i> + Matrine	Synergism	0.75 % + 0.8×10^8 conidia per mL	Suppression of detoxification enzymes (CarE, GSTs and CHI) and antioxidant systems	(39)
6	<i>Aleurocanthus woglumi</i>	<i>Ricinus communis</i> + <i>Fusarium proliferatum</i>	Additive	5 % + 1×10^7 conidia per mL	Botanical affects the nervous system; fungi penetrate the cuticle and secrete toxins/enzymes	(40)
7	<i>Aphis gossypii</i>	<i>Mentha piperata</i> + <i>Lecanicillium muscarium</i>	Additive	0.001213 % + 1×10^4 conidia per mL	EO acts as a neurotoxin, possibly targeting the nervous system, and conidia that infect through the cuticle act independently	(41)
8	<i>Aphis gossypii</i>	<i>Lecanicillium muscarium</i> + <i>Capsicum capiticum</i>	Additive	0.001325 % + 1×10^4 conidia per mL	EO acts as a neurotoxin, while the fungus infects the host through the cuticle	(47)
9	<i>Dactylopius opuntiae</i>	<i>Fusarium incarnatum</i> + <i>Quercus agrifolia</i> + <i>Ricinus communis</i>	Potentiated	5 % + 1×10^7 conidia per mL	Botanical stressor alters behaviour and enhances susceptibility to a lethal fungal infection	(48)
10	<i>Aphis gossypii</i>	Destruxin + Matrine	Synergism	0.000018 % + 0.000042 %	Destruxins target the insect immune system and hemocytes. Matrine is an alkaloid known to act on insect acetylcholine receptors. Their synergistic mechanism relies on these distinct actions	(50)
Coleoptera						
11	<i>Sitobion avenae</i>	<i>Metarhizium anisopliae</i> + neem extracts	Synergism	10 % + 1×10^6 conidia per mL	Botanical causes neuro, digestive, and reproductive stress; fungus causes lethal invasion of the cuticle	(11)
12	<i>Callosobruchus chinensis</i>	<i>Beauveria bassiana</i> + <i>Phlogocanthus thysiflorus</i>	Synergism	5 % + 8.13×10^7 conidia per mL	The extract weakens the host; the fungus causes a lethal disease through spore germination and penetration	(34)
Acarina						
13	<i>Rhipicephalus microplus</i>	<i>Achyrocline satureioides</i> + <i>Beauveria bassiana</i>	Synergism	20 % + 1×10^6 conidia per mL	The combination results in a "hormesis effect", where lower doses increase mortality. The fungus boosts the plant extract's acaricidal effect	(32)
14	<i>Panonychys citri</i>	<i>Jatropha curcas</i> + <i>Akanthomyces lecanii</i>	Synergism	7.5 % + 1×10^8 conidia per mL	The plant extract disrupts the mite's nervous system, causing abnormalities and making it more vulnerable to the fungus	(35)
15	<i>Rhipicephalus appendiculatus</i>	<i>Metarhizium anisopliae</i> + <i>Calpurina aurea</i>	Additive	10 % + 4.1×10^5 conidia per mL	Entomopathogenic effect through cuticle infection with <i>C. aurea</i> extract's attractive properties to draw ticks to the inoculum (attract-and-infect strategy)	(44)
16	<i>Rhipicephalus pulchellus</i>	<i>Metarhizium anisopliae</i> + <i>Calpurina aurea</i>	Additive	1.25 % + 1×10^9 conidia per mL	The botanical acts as a stressor, weakening the tick; the combined effect increases the likelihood of a lethal fungal infection	(45)
17	<i>polyphagotarson emus latus</i>	<i>Mimosa pudica</i> + <i>Beauveria bassiana</i>	Synergism	3 % + 1×10^6 conidia per mL	Phytochemicals, such as flavonoids in the plant extract, can disrupt the pest's reproductive system, further increasing the pathogenic stress caused by the fungus	(46)

Sl. No.	Insect	Treatment	Interaction	Effective concentration	Mode of action	References
Lepidoptera						
18	<i>Spodoptera frugiperda</i>	<i>Withania somnifera</i> + <i>Metarhizium anisopliae</i>	Synergism	20 % + 6.50×10^7 conidia per mL	Botanical stressor: increases fungal virulence by raising susceptibility	(24)
19	<i>Spodoptera litura</i>	<i>Beauveria bassiana</i> + Matrine	Synergism	0.1 % + 1×10^8 conidia/mL	Both agents target acetylcholine receptors (Ach), increasing neurotoxicity and they also affect detoxification processes (cytochrome P450) and endocrine pathways	(36)
20	<i>Gyropsylla spegazziniana</i>	Azamax + <i>Beauveria bassiana</i>	Additive	0.0066 % + 1×10^9 conidia per mL	Azadirachtin (Azamax) functions as an IGR and phagostimulant disruptor, thereby enhancing EPF penetration of cuticle	(37)
21	<i>Spodoptera litura</i>	Matrine + <i>Beauveria brongniartii</i>	Synergism	0.0001 % + 1×10^9 conidia per mL	Matrine targets acetylcholine receptors; fungi may produce secondary metabolites that affect the same neurological systems as matrine	(38)
22	<i>Pectinophora gossypiella</i>	<i>Metarhizium anisopliae</i> + <i>Azadirachta indica</i>	Synergism	10 % + 1×10^8 conidia per mL	The fungus produces enzymes to break down the insect cuticle, while <i>A. indica</i> (neem) disrupts the pest's hormonal system, raising mortality	(42)
23	<i>Pieris brassicae</i>	<i>Metarhizium anisopliae</i> + Savory	Synergism	0.004349 % + 1.3×10^3 conidia/mL	The plant extract stresses insect, lowering their defences and making them more susceptible to infection by <i>M. anisopliae</i>	(43)
Negative interactions						
Coleoptera						
24	<i>Tribolium castaneum</i>	<i>Beauveria bassiana</i> + Neemix 4.5	Antagonism	4.5 % + 9.5×10^{10} conidia/g	EPF at nonoptimal doses with Neemix 4.5, resulted in mortality reduction	(14)
25	<i>Tenebrio molitor</i>	1-Chlorooctadecane + <i>Metarhizium anisopliae</i>	Antagonism	0.048 % + 9.6 mg/mL spores	Certain metabolite ratios were toxic to conidia and delayed infection process	(57)

CarE: carboxylesterase; GSTs: glutathione-S-transferases; EPF: entomopathogenic fungi; IGR: insect growth regulator; CHI: chitinase; EO: essential oil.

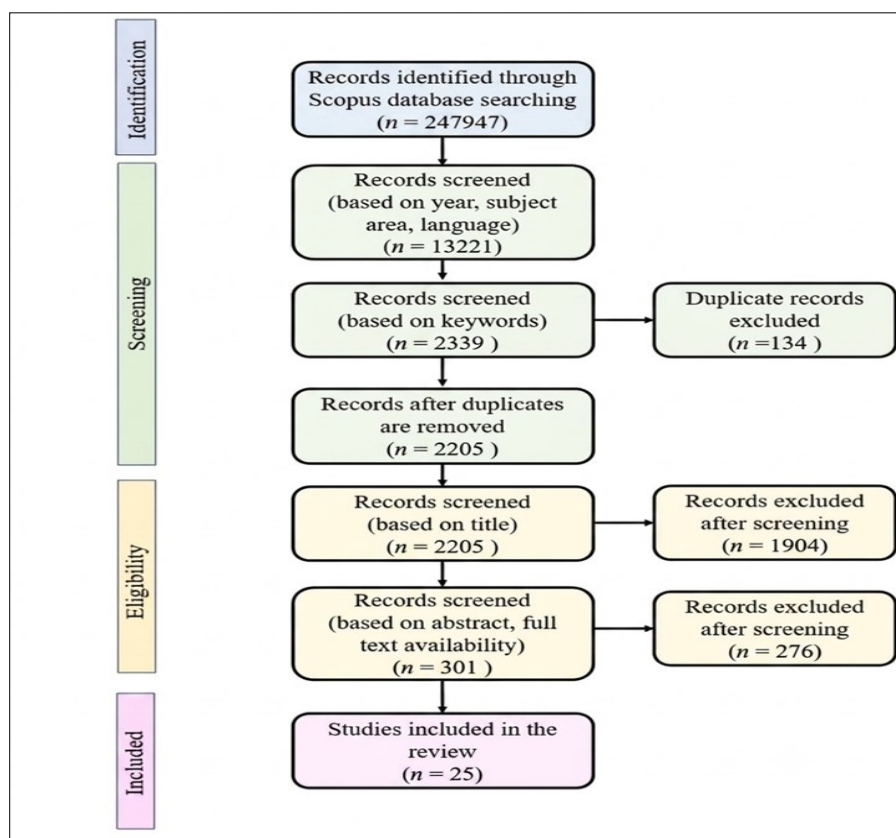


Fig. 4. Flowchart depicting the literature search, screening, and selection process of studies included in meta-analysis.

Botanical modulation of hydrophobin-mediated adhesion in entomopathogenic fungi

Hydrophobins form the rodlet layer essential for conferring conidial hydrophobicity. They also mediate adhesion and surface interactions that are vital for infection. Botanicals can remodel this interface in ways that either enhance or inhibit hydrophobin function. Botanical oils act as an effective carrier that increase

conidial adhesion and deposition on the lipophilic insect cuticle by disrupting cuticular waxes and reducing surface tension, thereby increases hydrophobins-mediated contact and wetting (14, 58, 60, 61). Enhanced adhesion increases the probability of successful germination, appressorium formation and cuticle penetration, thereby improving overall infection efficiency. On the other hand, the plant extract *Thymus vulgaris* can modify the hydrophobicity of fungal cells. In this instance, ethyl acetate fractions augment hydrophobicity, whereas methanolic fractions diminish it through

changes in the protein-to-carbohydrate ratios and the electron-donor-acceptor characteristics, which could affect hydrophobin assembly and exposure on the spore surface (62). These observations highlight that the biological effects of botanicals depend not only on plant species but also on extraction solvent, phytochemical composition and concentration. Essential oils have also been reported to modify surface energy parameters, including Lifshitz-van der Waals, electron acceptor and electron donor components (γ_{LW} , γ^+ , γ^-), shifting the surface from hydrophobic to hydrophilic. These essential oils impair hydrophobin-mediated attachment, resulting in a severe decrease in spore adhesiveness from 56.22 % in controls to 21.84 % with β -ionone and 9.34 % with 1,8-cineole (63).

These contradictory effects of botanicals are largely attributed to differences in their chemical composition, polarity and interactions with both the fungal surface and the insect cuticle. Despite these insights, the available literature is disproportionately focused on the inhibitory effects of botanicals, with relatively few studies systematically investigating conditions under which hydrophobin-mediated adhesion is enhanced. Future studies should investigate how specific classes of botanical compounds influence hydrophobin expression, rodlet-layer organisation and conidial surface chemistry to identify formulations that consistently enhance fungal attachment.

Botanicals as facilitators of infection: Making insects vulnerable to fungal infection

The primary disruptive effect of cuticle-active botanicals is to interfere with the insect's exoskeleton, including its epicuticular waxes and chitinous layers, resulting in softened cuticles, improved penetration and compromised structural integrity. The protective role of the epicuticular wax layer has been demonstrated through dewaxing and rewaxing experiments, where removal of surface waxes increased insect susceptibility, whereas restoration of wax layers enhanced resistance to external agents (60). For instance, triterpenoids (tea saponins) extracted from *Camellia oleifera* penetrate this wax layer, enter the cuticle to form pores and cause larval dehydration, while also depleting chitin content in the outer epidermis and midgut lining, ultimately resulting in mortality. Such structural alterations likely facilitate fungal germ tube penetration and accelerate the establishment of infection. Physico-chemically, this saponins lower interfacial tension and increase viscosity, enabling droplets to spread, adsorb and penetrate the hydrophobic cuticle more effectively, thereby producing a mechanical softening effect. Reduction in chitin content may weaken one of the structural defences that insects use to limit pathogen penetration, although direct evidence for this interaction remains limited (60, 64). The terpenoids of essential oil mixtures alter the cuticle to facilitate penetration. For instance, 1,8-cineole in rosemary oil reduces surface tension and enhances the affinity of camphor to the lipid wax layer, resulting in better cuticular penetration of both molecules when applied together (61). Non-target activity and toxicity, however, vary with the extent of chemical composition and the mode of delivery (65). In addition, limonene, a monoterpene, exhibits fumigant and repellent activity due to its ability to act in the vapour phase and penetrate the insect cuticle (66). Botanicals increase the susceptibility of hosts; these cuticular activities aid fungal penetration and internal colonisation, resulting in accelerated

hyphal emergence, causing desiccation and respiratory stress in insects in cases where EPF is combined with rapid-action botanicals (67, 68).

Beyond cuticle disruption, EPF-botanical combinations influence insect susceptibility through four major physiological pathways: behavioural modification, endocrine disruption, gut impairment and neural dysfunction.

Mechanism I: Behavioural response, where spores and botanicals cause repulsion, avoidance or attraction, which control the locomotion of insects and influence spore germination upon exposure to UV and temperature following cuticle and epidermal damage by lipases, proteases and chitinases (52, 69, 70).

Mechanism II: Endocrine disruption, manifested as interference with corpora allata, which suppresses the juvenile hormone binding proteins, damages the epidermis and fat bodies, deprives nutrients, terminates production of vitellogenin and forms malformed oocytes, underdeveloped ovaries and decreased fecundity (36, 37, 42). Disruption of juvenile hormone signalling and vitellogenin production contributes to reduced reproductive fitness and population growth.

Mechanism III: Gut disruption, transition of the healthy midgut with an intact peritrophic membrane and epithelial cells to a compromised state after 24–48 hr following treatment is characterised by rupture of the membrane, flattening of epithelial cells and total fungal invasion of the hemocoel (71).

Mechanism IV: The neural disruption describes using two processes: opening of sodium channels through pyrethrum, leading to paralysis and behavioural stress and interfering with synaptic function. The fungal metabolite bassianolide blocks acetylcholinesterase (AChE) (increasing acetylcholine levels), while the botanical matrine blocks acetylcholine receptors, accelerating spore penetration, mortality and mycosis (38, 39, 67). A summary of these mechanisms is presented in Fig. 5.

Effects of botanical influences compounds on sporulation and conidial germination of entomopathogenic fungi

The combination effect of plant extracts on EPF shows complex interactions that induce both synergistic and antagonistic effects on fungal sporulation and conidial germination. Overall, the available evidence suggests that compatibility cannot be generalised across all botanical-fungal combinations, as responses are strongly influenced by botanical composition, fungal species or strain, extraction method, formulation and application concentration. Notably, the synergistic effect is primarily exhibited at optimal concentration and with botanicals exhibiting compatibility, as documented in the earlier studies (26, 72, 73).

At lower dosage, plant extracts usually have negligible or minimal effects on growth parameters of EPF, for instance, the biological index (BI) values of various plant extracts like *Syndrella nodiflora*, *Premna tomentosa*, *Vitex negundo*, *Pteridium aquilinum* and *Annona squamosa* at lower doses on EPF isolates varied from 78.58 to 99.01, demonstrating high growth and conidiation without altering the compatibility and viability of the fungus (73, 74). However, these findings are predominantly based on controlled laboratory studies and therefore their applicability under variable field conditions remains uncertain.

Several botanical extracts, including neem seed, tobacco powder and catigua leaf extracts, maintained conidial viability

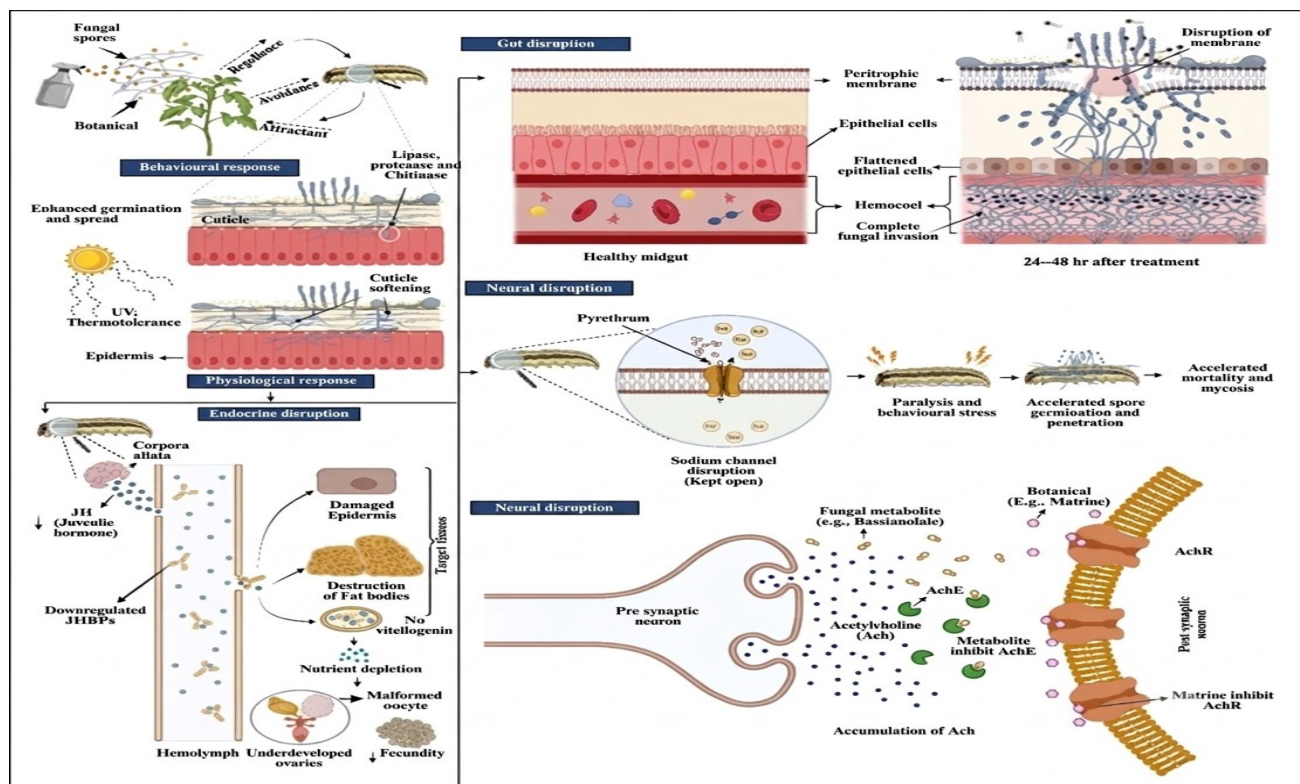


Fig. 5. Diagrammatic representation of the mechanism of action in which entomopathogenic fungi spores and botanical agents interfere with insect physiology.

above 90 %, suggesting minimal adverse effects on fungal infectivity. Conversely, certain botanical extracts at higher concentrations have adverse effects; extracts of tobacco powder at 10 % inhibited mycelial growth and conidia formation, but not germination potential or conidial viability, compared to lower concentrations, emphasising the significance of concentration-dependent trade-offs (75). These contrasting observations indicate that compatibility is largely governed by concentration thresholds rather than the botanical source alone. Nevertheless, direct comparisons among studies are difficult because of considerable variation in extraction procedures, solvent systems, fungal isolates, incubation periods and compatibility assessment methods.

However, some strains of *Akanthomyces lecanii* were identified to be widely tolerant to a range of plant extracts and commercial botanical pesticides, resulting in high mycelial growth and sporulation, which necessitated the proper selection of a strain (35). Some plant extracts (e.g., *Phlogocanthus thyriflorus* and *Ocimum sanctum*) are not only compatible with the fungus strains used but also have a stimulatory effect for specific fungal isolates, which, upon combination, reported increased sporulation (35, 76), highlighting the presence of growth-promoting compounds in phytochemicals. Low concentrations of compatible phytochemicals may function as physiological elicitors that activate stress-response pathways, enhance metabolic activity and promote reproductive development without causing cellular damage.

The beneficial effects of combined applications on sporulation can be explained by a few mechanisms: some plant extracts were identified to contain biocompatible metabolites that trigger fungal physiological mechanisms to endure mild botanical stress (77). Furthermore, the use of plant extracts at sublethal doses caused slight osmotic stress to the fungus, which may serve as a survival mechanism, resulting in an increased viability of propagules; consequently, elevated conidia production and

germination rates compared to control treatments (78). Despite these proposed mechanisms, most studies infer physiological responses from phenotypic observations, while direct molecular evidence remains scarce. Future investigations integrating transcriptomic, proteomic and metabolomic approaches, together with standardised compatibility protocols and long-term field validation, are needed to elucidate the mechanisms underlying botanical-mediated enhancement of fungal sporulation and to improve the reproducibility and practical applicability of EPF–botanical formulations.

Biochemical mechanisms underlying synergy between entomopathogenic fungi and botanical insecticides

The enzymes secreted by EPF interact with plant metabolites in several distinct ways. First, they participate in the detoxification of insect-sequestered plant-toxic compounds. For example, glutathione S-transferases in *B. bassiana* (ARSEF 2860) are involved in the conjugation of harmful isothiocyanates, which cabbage aphids sequester from their Brassicales host plants, with glutathione; this conjugate is then processed via the mercapturic acid pathway to produce cysteine and N-acetylcysteine conjugates. This mechanism allows the fungus to mitigate the toxicity of insect-sequestered plant toxins, making it easier to infect its host. Additionally, these enzymes coordinate with botanical extracts to bypass insect defence systems and enhance the efficacy of infection (79). *Beauveria bassiana* (ARSEF 8465), synergised with (+)- α -pinene, was found not to suppress the growth of fungi directly but did retain enzyme activity that caused oxidative and neurological stress in insects, leading to elevated mortality rates (59). Nevertheless, these synergistic impacts are mostly based on laboratory bioassays and the stability of terpene-induced enzymatic stress in the field, where volatility and fast degradation are probable, has not been thoroughly addressed. When combined at specific proportions, Destruxins, a fungal

secondary metabolite, exhibit synergistic or additive effects when combined with plant-derived insecticides such as rotenone, azadirachtin, paeonol and saponins. Their combined action involves multiple biochemical mechanisms: destruxins suppress insect immune cells; rotenone inhibits mitochondrial respiration; azadirachtin disrupts hormonal regulation and growth; and saponins interfere with insect antioxidant enzyme systems. Simultaneous disruption of multiple physiological pathways reduces the likelihood that insects can compensate through metabolic adaptation or detoxification responses. Together, these plant metabolites and fungal toxins simultaneously target diverse enzymatic pathways in insects, resulting in enhanced insecticidal efficacy (50, 80). *Beauveria bassiana* mycotoxin, beauvericin, when formulated as a nano-gel with essential oils containing monoterpenes, gives very low LC₅₀ values and strong repellency towards *Sitophilus oryzae* and *Sitophilus granarius*. Nanoformulation technologies may improve stability, controlled release and target-site delivery of fungal and botanical metabolites, thereby enhance efficacy while reducing application rates. In this case, the ionophoric properties of this fungal toxin likely complement the insecticidal action of essential oils constituents that are known to inhibit insect AChE and destabilise membranes, delivering an enzymatic and membrane-based toxicity (81). The pesticidal plant extract, when conjugated to a nanosilica chitinase (SiNpChs), exhibits high stability, controlled release and exceptionally high mortality of *Spodoptera litura* larvae. Upon contact, chitinase breaks down the cuticular chitin and the co-delivered phytochemicals induce their own toxic effects, resulting in an increased cumulative mortality (82). Collectively, these integrations influence the insect's immune defence system to deactivate the insect's detoxification system and neuromuscular activity, thereby allowing multi-target biochemical stress to enhance pest control.

Biochemical disruption of insect defence systems following integrated entomopathogenic fungi–botanical applications

In combination with botanical insecticides, EPF interfere with insect enzyme systems, resulting in significantly stronger and longer-lasting effects than when used as either agent alone. In whitefly *Bemisia tabaci*, applications of matrine or the fungus *Lecanicillium muscarium* (V1–1) initially increase detoxifying enzymes such as carboxylesterase (CarE) and glutathione-S-transferases (GSTs). However, when both agents are used together, CarE and GST activities drop significantly throughout the infection, indicating the insect's detoxification systems are overwhelmed and cannot mount an adaptive response (39). This combination led to an accelerated reduction in AChE activity, an indicator of the action of matrine on nicotinic acetylcholine receptors and to the further disruption of cholinergic signalling by fungal metabolites such as bassianolide (39). Simultaneous interference with acetylcholine synthesis, receptor function and degradation may contribute to rapid paralysis and mortality. The requirement of chitinase (CHI) to facilitate normal moulting is abnormally elevated in fungus alone treatments, yet in matrine-fungus combinations, CHI activity increases initially and then decreases, suggesting impaired cuticle turnover and ecdysis (Fig. 5) (39). Such interference with chitin metabolism may further facilitate fungal penetration while impairing insect development. Nevertheless, enzyme activity alone may not fully capture downstream effects on cuticle integrity and moulting success,

highlighting the need for complementary physiological and histological assessments. On the other hand, antioxidant enzymes show a characteristic pattern: in insects or mites treated with sublethal doses of insecticidal plant toxins such as 1-chlorooctadecane, as well as *M. anisopliae* (V245) there is initially greater expression of superoxide dismutase (SOD) and catalase (CAT) in response to oxidative stress, but these levels subsequently decline as reactive oxygen species (ROS) accumulate, leading to oxidative damage (57). Once antioxidant capacity is exceeded, reactive oxygen species accumulate, resulting in oxidative damage to cellular proteins, lipids and nucleic acids.

These patterns across insect and mite systems supports oxidative stress as a central mechanism of synergy, even though the precise timing and thresholds of antioxidant failure may differ among taxa. Similarly, in mosquitoes, the corresponding synergistic combinations between them inhibit a vast number of key detoxification and immune enzymes (esterases, proteases, phenoloxidase, acid phosphatase, GSTs), destabilising xenobiotic metabolism and cellular defences, promoting a faster proliferation of the fungus. Taken together, EPF and botanical blends exceed insects' capacity to detoxify and suppress their developmental enzymatic pathways that are responsible for the survival of insects'. The simultaneous disruption of these interconnected pathways creates a physiological state from which recovery is unlikely, leading to accelerated mortality and reduced fitness.

Molecular mechanisms underlying entomopathogenic fungi –botanical synergy: A transcriptomic perspective

The combined action of EPF and botanical insecticides is mediated by a sophisticated molecular mechanism that impairs immune and metabolic pathways in insects, causing profound homeostatic disruption that hampers recovery (36, 38, 83). Only 51 differentially expressed genes (DEGs) (35 upregulated and 16 downregulated) were found in *B. tabaci* treated with *Akanthomyces attenuatus* (SB010) and matrine, compared with EPF and matrine individually, which represented 71 and 1194 DEGs, respectively. This markedly reduced DEG response provides strong evidence for a distinct and more focused molecular outcome, indicating substantial suppression of overall gene activity. Although 65 genes were common to both treatments, only two genes, a LEA1 protein isoform (Bta00818) and a cathepsin F-like protease (Bta05911), were observed to be shared by all three treatments, signifying that the combination exerts a unique molecular action. It is interesting to note that the combination treatment abolished all immunity-related transcripts that could be detected (zero DEGs), reflecting a complete immune suppression. Reduced expression of metabolic and cuticle-associated genes indicates a broad collapse of physiological maintenance processes that are essential for survival and defence. In contrast, individual treatments induced more extensive metabolic reprogramming, with 19 DEGs in EPF and 359 DEGs in matrine, along with significant upregulation of cuticle proteins, indicating the general suppression of physiological functions when one is exposed to combined stress. Furthermore, in integrated treatments, pathway analyses revealed enrichment of apoptosis (programmed cell death) and NOD-like receptor signalling pathways, suggesting a shift from immune defence to systemic cellular apoptosis (38). Accordingly, another example of synergetic action is observed with *S. litura* treated with *B. bassiana* (BbR2) and matrine, which, on this occasion, experiences a more specific action in multiple stages. The combined treatment triggers a more focused reaction and fewer

DEGs are found with the integrated treatment in comparison with fungus or matrine application individually: 1500, 2400 and 2326 at day one, respectively (36), which later stimulated longevity-related and protein-processing responses without raising a general alarm response (36). This results in malregulation of core gene families, which were involved in development, immunity and reproduction, including erratic expression of cuticle genes, zinc-finger genes and ecdysone-inducible genes. Such disruptions result in impaired moulting processes and biphasic expression of vitellogenin genes, ultimately compromising reproductive capacity and fecundity (36).

Building on these molecular disruptions, integrated treatments further impair insect immune recognition and defence signalling pathways. Where the genes encoding peptidoglycan recognition proteins (PGRPs) and other recognition molecules that were not induced, including those in the Toll and immune deficiency (IMD) signalling pathways, thereby leading to the downstream production of antimicrobial peptides (AMPs). Furthermore, it blocks the Nod-like receptor pathway, causing “No cytosolic danger sensing” which suppresses phagocytosis, inhibiting hemocyte activation and preventing phagosome formation (36, 38). These interconnected mechanisms are illustrated in Fig. 6.

Relative safety of entomopathogenic fungi–botanical combinations to non-target and beneficial organisms

The combination of EPF and botanicals has a lower, inconsistent, non-target effect compared to broader-spectrum synthetic pesticides. Regarding natural enemies, individual application of various strains of *Beauveria* and *Metarhizium* can infect or impact beneficial insects like predators, parasitoids, honeybees, bumblebees and silkworms, etc., resulting in higher mortality or lower reproduction, making it necessary to assess the safe use of mycoinsecticides within IPM programs explicitly (9). This recognition of risk provides an important baseline against which

the relative safety of EPF and botanical combinations can be evaluated. EPF–botanical combinations have been reported to show compatibility benefits for important natural enemies, such as predatory mites. For instance, in laboratory and greenhouse experiments with roses, a combination of *B. bassiana* (DSM 15126) or *Purpureocillium fimosorosense* (DSM 12256) with garlic-pepper extract did not cause significant mortality in the predatory mites *Phytoseiulus persimilis* and *Neoseiulus californicus* and exceeded the safety margins compared to the highly toxic synthetic controls (49). Likewise, under field conditions, EPF strain applied at a 1:1 ratio with neem seed oil was minimally disruptive, preserving populations of predatory coccinellids and arachnids at levels comparable to the neem-based standards and imidacloprid, which were toxic (12). At a higher trophic level, in a single laboratory experiment, *M. anisopliae* (F52) by itself was reported to repel the aphid parasitoid *Aphidius colemani*. Conversely, a mix of pyrethrum, *M. anisopliae* did not affect parasitoid foraging, implying that a suitable botanical associate can mitigate the adverse effect of EPF (67). In soil ecosystems, botanical pesticides have dual effects as they either enhance or retard the growth of microorganisms. They have a low-to-non-toxic impact on earthworms but show an unpredictable impact on other arthropods; however, the effects on other soil arthropods remain insufficiently characterised (84). Soil ecosystems represent a critical but understudied component of non-target risk assessment. Botanical compounds and EPF may influence microbial communities, nutrient cycling processes and soil arthropod populations, although current evidence remains limited and often inconsistent. In general, the existing literature indicates that properly chosen EPF and botanical mixtures can be potentially compatible with a broad range of beneficial organisms. However, their efficacy is generally product, dose and species-specific.

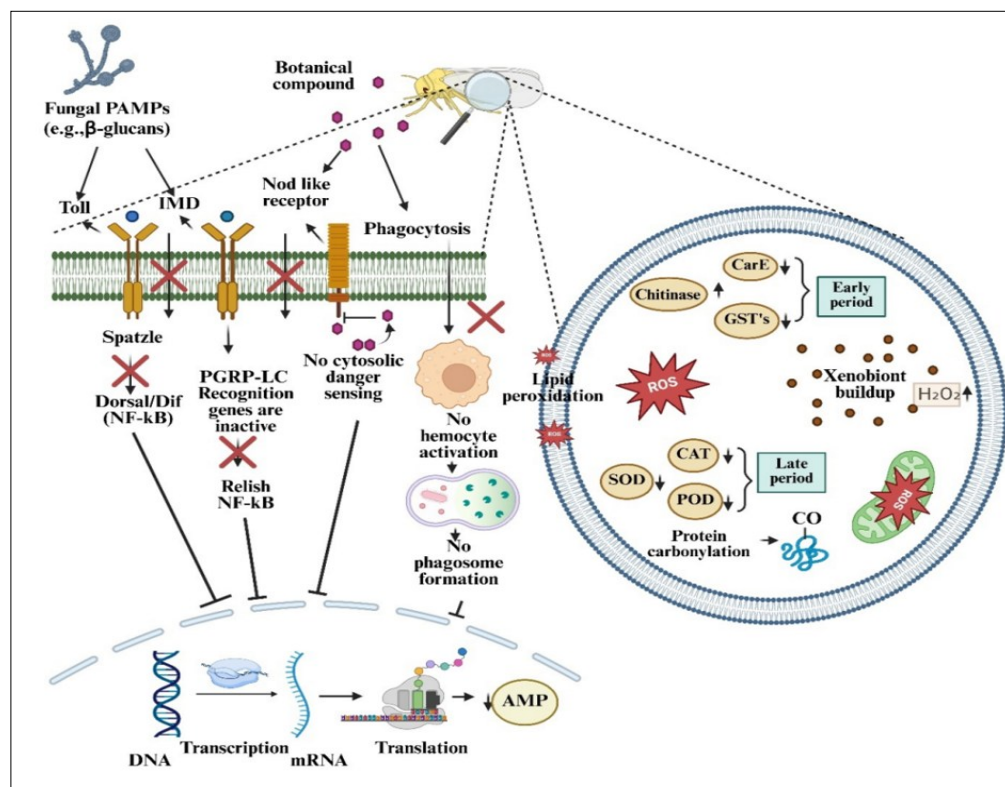


Fig. 6. Diagrammatic representation of how the integration of botanical compounds with entomopathogenic fungi disrupts the insect's immune defence system.

Formulation and stability of entomopathogenic fungi–botanical combinations for sustainable pest management

In lab-based bioassays, where conditions are tightly controlled, efficacy can be assessed rapidly. However, the consistency of such a combination does not perform significantly well outside the lab under natural conditions, due to environmental extremes that reduce their survival and infection rates (69). Therefore, bioassay outcomes must be integrated with field data and rigorously evaluated to mitigate bias and error, thereby ensuring reliable efficacy estimates for strategic decision-making (85). Consequently, each strain must undergo in vitro screening over a range of botanical doses before field deployment (27). In order to make it more stable, *Metarhizium* or *Beauveria* conidia are suspended in neem, sesame, sunflower, corn, or groundnut oils and subsequently, the emulsion is made with a surfactant in water to form an oil-in-water emulsion. These formulations enhance dispersion, adhesion and tolerance to UV and thermal stress and when the oil possesses inherent insecticidal activity, they further increase overall toxicity. For instance, the emulsions of sesame and sunflower oil promoted the germination and virulence of *M. anisopliae* (MIITAC 11.3.4, MET-GRA4) and *B. bassiana* (BIITAC 6.2.2) against *Bactrocera zonata*, *Aedes aegypti* and *S. litura*, respectively and increased the half-life of the fungi (15, 16, 53). Incorporating chitin into a bioformulation of *B. bassiana* (B2) and *Pseudomonas fluorescens* (Pf1) enhanced pest suppression in groundnut under both glasshouse and field conditions, suggesting that adding biotic carriers can improve fungal persistence and efficacy in realistic cropping systems (86). More advanced types of combination formats include nano formulations, encapsulation techniques, such as loading conidia in combination with botanicals into biopolymers: loaded sodium alginate beads with *M. anisopliae* (OL375172) and freeze-dried, vested long shelf-life (± 10 months), which resulted in high efficacy against white grubs (28, 87). Despite promising advances, information on optimal formulation ratios, long-term stability, large-scale production and performance across diverse agroecosystems remains limited. Accordingly, filling this gap should be based on a systematic exploitation of promising botanical and entomopathogenic fungal combinations to increase efficiency, reduce application dose and delay insect resistance, as pests are exposed simultaneously to multiple, very different modes of action (29, 88, 89).

Limitations

These combination studies indicate that various factors together constrain the commercialisation of EPF–botanical mixtures: compatibility is highly strain, extract, formulation and dose-specific, which means that each new pair should be screened and optimised separately (90, 74). For a multi-active biopesticide registration, separate data are required for each compound, with their interaction studies and long-term non-target or ecological effects (89). This led to an increased cost of production and logistics, products requiring accurate preparation, application and storage are less appealing to farmers who are used to simple synthetic insecticides with a fast onset of action; companies therefore often tend not to fully commercialise or test in field conditions and collect data for their portfolio (91, 92).

Future prospects

Combinations of EPF with botanicals could become key tools in sustainable pest management, often yielding additive or synergistic control, which is ideal for resistance management and organic systems (11, 21, 29, 67). It should develop in the future with emphasis on (i) rational strain-botanical matching, using high-throughput bioassay and omics to identify the EPF isolates which are most virulent, physiologically compatible with certain standardised botanicals or by making use of modern technologies to improve strain properties and environmental competence to guarantee field persistence under local temperature, humidity and UV conditions (9, 69); (ii) Development of advanced dual-active formulations, such as oil-based and nano-encapsulated systems, which can stabilise and protect conidia while enabling the controlled release of botanical compounds. Such approaches hold promise for enhancing formulation stability and delivery efficiency without compromising environmental safety (16, 93, 94); (iii) Ensuring consistent botanical quality through dedicated cultivation of pesticidal plants, chemical fingerprinting and batch standardisation, with the support of supply-chain alliances and public-private collaborations and (iv) Regulatory barriers arise from the absence of standardised registration frameworks, whereas high formulation costs and variable botanical quality remain key economic constraints. These barriers can be addressed by working with regulators to create streamlined pathways for a few “reference” EPF–botanical pairs with strong safety records, supported by robust non-target, residue and field-performance data, so registration costs are proportionate to risk and companies have an incentive to invest. Several important research questions also remain unresolved. Future studies should determine the optimal concentration thresholds that maximise synergism while minimising antagonism, elucidate the molecular mechanisms governing compatibility between fungal isolates and phytochemicals, investigate the influence of environmental variables on long-term field performance and evaluate the persistence, non-target safety and resistance management potential of repeated EPF–botanical applications under diverse agroecosystems. Addressing these questions will facilitate the development of predictive compatibility models for selecting effective botanical–EPF combinations. These, combined with farmer training and IPM packages, have the potential to overcome the existing bottlenecks of strain-specificity, formulation instability, raw material inconsistency and regulatory burden and make EPF–botanical combinations step forward as scalable, reliable pillars of climate-resilient, pesticide-free crop protection.

Conclusion

The integration of entomopathogenic fungi (EPF) with other biopesticides represents a promising approach for sustainable pest management, yet current recommendations derived from standalone applications do not always translate effectively to combined systems. These integrations offer clear advantages, including enhanced insect mortality, reduced fecundity and lower application rates through additive or synergistic interactions, along with improved persistence under environmental stress. However, compatibility remains highly context-dependent, as factors such as botanical composition, concentration and fungal strain can influence conidial viability and performance. Further research is needed to optimise formulation strategies, application timing and

delivery methods under field conditions and to assess potential risks to non-target organisms and the stability of these interactions across different agroecosystems. In addition, precise calibration of application timing, dosage and delivery methods will be critical to fully harness the potential of these combinations for sustainable and resilient pest management.

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Authors' contributions

DM carried out the literature survey, conceptualisation, investigation, visualisation, writing of the original draft and writing - review & editing. PK participated in conceptualisation, supervision, investigation and writing - review & editing. RT participated in conceptualisation, supervision and writing - review & editing. JS participated in conceptualisation, validation and writing - review & editing. HS participated in the review and editing of the manuscript. UD participated in the review and editing of the manuscript. All authors have read and approved the final manuscript.

Compliance with ethical standards

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