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# Revisão sistemática da comunicação química mediada por voláteis em plantas associadas a fungos entomopatogênicos–endofíticos: da herbivoria às interações com inimigos naturais

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## **A systematic review of chemical dialogues mediated by volatile compounds in plants associated with entomopathogenic–endophytic fungi: from herbivores to natural enemies**

**Revisão sistemática da comunicação química mediada por voláteis em plantas associadas a fungos entomopatogênicos–endofíticos: da herbivoria às interações com inimigos naturais**

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### **ABSTRACT**

*Rice production faces significant losses from *Spodoptera frugiperda*, with current control strategies relying heavily on chemical insecticides and *Bt* cultivars, leading to resistance development and environmental concerns. In search of alternative control methods this systematic review examined multitrophic interactions mediated by volatile organic compounds (VOCs) in *Oryza sativa* inoculated with the entomopathogenic fungus *Beauveria bassiana*, evaluating impacts on army worms *Spodoptera* spp. and parasitoids of the genus *Trichogramma*. Following PRISMA-ScR guidelines, 20 studies from 2000-2025 were analyzed. The results indicated that *B. bassiana* endophytic colonization modulates VOC profiles, including emission of green leaf volatiles, monoterpenes (e.g.,  $\alpha$ -pinene), and sesquiterpenes (e.g.,  $\beta$ -caryophyllene), enhancing parasitoid attraction and reducing pest oviposition and larval survival. The review also identified fungal VOCs, such as 3-methylbutanol, with direct behavioral effects on pests. Bibliometric analysis revealed increasing research interest but thematic fragmentation between applied entomopathogen studies and chemical ecology. Despite evidence supporting VOC-mediated indirect plant defenses, methodological limitations persist, including insufficient compound characterization and limited field validation. This synthesis underscored the potential of integrating endophytic entomopathogenic fungi to manipulate plant chemical signaling, offering a promising strategy for sustainable and ecologically based pest management in rice cultivation, particularly in tropical agroecosystems.*

**Key-words:** *Beauveria bassiana*, *Spodoptera* spp., *Trichogramma* spp., indirect plant defense, biological control.

## RESUMO

A produção de arroz enfrenta perdas significativas causadas por *Spodoptera frugiperda*, e as estratégias de controle atualmente disponíveis dependem fortemente do uso de inseticidas químicos e de cultivares *Bt*, o que tem levado ao desenvolvimento de resistência e a preocupações ambientais. Em buscas por controles alternativos, esta revisão sistemática analisou as interações multitróficas mediadas por compostos orgânicos voláteis (VOCs) em *Oryza sativa* inoculada com o fungo entomopatogênico *Beauveria bassiana*, avaliando os efeitos sobre lagartas do gênero *Spodoptera* e sobre parasitoides do gênero *Trichogramma*. Seguindo as diretrizes PRISMA-ScR, foram analisados 20 estudos publicados entre 2000 e 2025. Os resultados indicaram que a colonização endofítica por *B. bassiana* modula os perfis de VOCs, incluindo a emissão de voláteis de folhas verdes, monoterpenos (como  $\alpha$ -pineno) e sesquiterpenos (como  $\beta$ -cariofileno), aumentando a atratividade dos parasitoides e reduzindo a oviposição e a sobrevivência larval das pragas. A revisão também identificou VOCs fúngicos, como o 3-metilbutanol, com efeitos comportamentais diretos sobre os insetos-praga. A análise bibliométrica revelou um crescente interesse científico pelo tema, mas também uma fragmentação entre os estudos de entomopatógenos aplicados e os de ecologia química. Apesar das evidências que sustentam as defesas indiretas das plantas mediadas por VOCs, ainda persistem limitações metodológicas, como a caracterização insuficiente dos compostos e a escassez de validações em campo. Esta síntese destaca o potencial de integração dos fungos entomopatogênicos endofíticos na manipulação do sinal químico das plantas, configurando uma estratégia promissora para o manejo de pragas de forma sustentável e ecologicamente fundamentada na cultura do arroz, especialmente em agroecossistemas tropicais.

**Palavras-chave:** *Beauveria bassiana*, *Spodoptera* spp., *Trichogramma* spp., defesa indireta induzida, controle biológico.

## INTRODUCTION

Rice (*Oryza sativa* L.) is one of the most widely cultivated and consumed cereals worldwide, serving as a staple food for over half of the global population. In Brazil, it is a dietary mainstay for approximately 84% of the population, highlighting its social, economic, and nutritional significance (FUKAGAWA & ZISKA, 2019; IBGE, 2020). Among different cultivation systems, upland rice plays a particularly important role, especially in the Brazilian Cerrado, which hosts the largest non-irrigated rice-growing area in Latin America (HEINEMANN et al. 2019).

The productivity of rice crops is frequently threatened by pests, particularly the fall armyworm (*Spodoptera frugiperda*), a highly adaptable and polyphagous species capable of causing severe damage, from seedling emergence to panicle formation (MONTEZANO et al. 2018; JIANG et al. 2014). Conventional control of this pest relies heavily on chemical insecticides and *Bt* cultivars, leading to the selection of resistant populations (BERNARDI, D et al. 2016; BERNARDI, O et al. 2016; SILVA et al. 2021), in addition to posing environmental and human health risks (BARRIGOSSI & MARTINS, 2015). These challenges underscore the urgent need for more-sustainable and ecologically sound pest-control strategies.

Among such strategies, the use of biological control agents — particularly egg parasitoids of the genus *Trichogramma* and entomopathogenic fungi such as *Beauveria bassiana* and *Metarhizium anisopliae* — has received increasing attention (BARRIGOSI & MARTINS, 2015). In addition to their pathogenic effects on insects, these fungi can also act as endophytes, colonizing plant tissues without causing visible damage and providing systemic protection to the host plant (RODRIGUEZ et al. 2009). The plant–endophytic fungus association can modulate plant physiology and activate defense mechanisms, including those involved in the emission of volatile organic compounds (VOCs), which have the potential to influence the behavior of other organisms (DICKE & BALDWIN, 2010).

These VOCs, particularly herbivore-induced plant volatiles (HIPVs), play a crucial role in mediating multitrophic interactions. When attacked by herbivores, plants emit complex blends of volatile compounds that can serve as alarm signals, attracting the natural enemies of herbivores such as predators and parasitoids (HOWE & JANDER, 2008). These signals can be highly specific, depending on the plant species, the herbivore involved, and the associated microbial community (TURLINGS & ERB, 2018). Consequently, plant indirect defense becomes a functional pathway in the natural suppression of pest populations.

Research has shown that endophytic entomopathogenic fungi can induce or modulate VOCs emission in different crops, even in the absence of herbivory. For instance, GONZÁLEZ-MAS et al. (2021) reported that *B. bassiana* colonization significantly altered the volatile profile in melon, promoting the release of compounds that are potentially attractive to parasitoids. These effects may vary depending on the plant species, inoculation method, colonization duration, and environmental conditions.

Endophytic fungi also function as agents of associative ecological resistance, promoting bottom-up effects, i.e., from plants to higher trophic levels (BARON & RIGOBELLO, 2021). These interactions can reduce plant attractiveness to herbivores such as *S. frugiperda* while enhancing their appeal to natural enemies such as *Trichogramma* spp., by modulating parasitoid host-searching and oviposition behavior through chemical signaling.

Chemical communication among plants, herbivores, and parasitoids is therefore a promising avenue for innovation in integrated pest management (IPM). Intentional manipulation of this communication by promoting multitrophic interactions may enhance the efficacy of biological control agents, reduce reliance on external inputs, and contribute to the resilience of agricultural systems. Nonetheless, the outcomes of such interactions are often complex and context-dependent, reinforcing the need for systematic reviews that consolidate existing knowledge.

Despite growing evidence of the effects of endophytic entomopathogenic fungi on VOCs emissions and insect behavior, studies integrating *O. sativa*, *B. bassiana*, *S. frugiperda*, and *Trichogramma* within complete tritrophic systems remain few. A deeper understanding of these ecological and chemical interaction networks is essential for the development of sustainable pest-management strategies, particularly for rice grown in tropical environments. This systematic review aimed to consolidate existing knowledge on the effects of inoculation of endophytic entomopathogenic fungi on VOCs emission by *O. sativa*, and to explore how these volatiles influence interactions with *Spodoptera* spp. and egg parasitoids of the genus *Trichogramma*.

## MATERIAL AND METHODS

This scoping review was carried out in accordance with the guidelines outlined in the Preferred Reporting Items for Systematic Reviews and Meta-Analyses extension for Scoping Reviews (PRISMA-ScR), which provides a structured framework to ensure consistency and transparency in the reporting of such reviews (TRICCO et al. 2018; PAGE et al. 2021). As a method to synthesize knowledge, scoping reviews aim to systematically map the breadth of existing research on a given topic, highlighting core concepts, theoretical frameworks, sources of evidence, and areas where knowledge remains limited (TRICCO et al. 2018). To guide both the construction and documentation of this review, the 20-item PRISMA-ScR checklist was utilized (Table S1).

These terms were selected for their relevance to the thematic areas addressed in this study: chemical communication, herbivore-induced indirect defenses, and tritrophic interactions. An initial search on the databases: ScienceDirect, Web of Science and PubMed were conducted with the 14 search terms combination (Table 1). The PubMed platform yielded few results using these same 14 combinations. To improve data retrieval on this platform, an additional seven tailored keyword combinations were developed and employed (Table 2), considering the specific indexing and terminology structure of PubMed. Article selection within each database was conducted by screening titles and abstracts to determine eligibility for full-text retrieval. When titles and abstracts lacked sufficient clarity, the full text was consulted to minimize the risk of excluding relevant studies (SAMPAIO & MANCINI, 2007). Additional relevant articles were included manually.

The articles identified through the initial search strategy were evaluated by two researchers independently. During this process, each researcher assessed the title and abstract of each article and recorded whether they agreed with its inclusion. All articles selected during this screening phase were subsequently assessed for eligibility through full-text reading. Final eligibility decisions were made jointly by the two researchers, and any disagreements were resolved through discussion, with each researcher providing a reasoned justification for either including or excluding the study (STOLL et al. 2019).

In total, 1,076 articles were excluded: 231 were duplicate entries across the databases, and 845 were removed after the titles and abstracts were screened (Fig. 1). The inclusion criteria for this study were: articles written in English, Portuguese, or Spanish; published from January 2000 through June 2025; peer-reviewed scientific articles presenting complete research results; studies addressing fungi with endophytic activity and their role in indirect plant defense; and articles available in the selected databases up to June 2025.

The exclusion criteria included theses, dissertations, and conference abstracts; technical reports; duplicate publications; articles in a language other than English, Portuguese, or Spanish; articles published before the year 2000; studies unrelated to the topic; and review articles.

A total of 44 studies were analyzed after the articles were read and evaluated in full, and 24 were excluded for not meeting the inclusion criteria. Nineteen articles were selected in the databases. One relevant study cited in this review was added manually. In total, 20 articles were selected for the systematic review (Fig. 1).

Data were extracted from the eligible articles by collecting the following information and characteristics of the studies: 1. Reference; 2. Organisms studied; 3. Type of interaction; 4. Identified volatile compounds; 5. Observed effects; 6. Methodology.

The bibliometric analysis was conducted using only the Web of Science database. The search was performed on 3 July 2025, employing the same 14 search-term combinations that were used for the systematic review (Table 1). The search strategy was designed to capture studies focusing on multitrophic interactions among plants, entomopathogenic fungi, insect pests, and their natural enemies.

Initially, 742 records were retrieved. To ensure scientific relevance, a filter was applied to include only original research articles, excluding reviews, proceedings, and other document types. Use of the publication time frame from January 2000 through June 2025 reduced the dataset to 645 articles. Duplicate records were then removed based on their Digital Object Identifier (DOI), eliminating 55 redundant entries. After this curation process, the final dataset comprised 590 valid articles. The data were exported in [.bib] format, compatible with the Bibliometrix package in RStudio (ARIA & CUCCURULLO, 2017), for subsequent quantitative analysis of scientific production.

## RESULTS

### The bibliometric analysis:

This analysis aimed to outline the scientific-production landscape focused on tritrophic interactions involving rice plants (*Oryza sativa*), the pest insect *Spodoptera frugiperda*, the entomopathogenic fungus *Beauveria bassiana*, and egg parasitoids such as *Trichogramma* spp., with an emphasis on chemical communication dynamics mediated by herbivore-induced volatile compounds. This interdisciplinary approach integrated concepts from chemical ecology, biological control, and plant physiology, allowing the identification of research trends, potential knowledge gaps, and leading scientific production centers in this research area.

The analysis of annual scientific output revealed a clear upward trend in publications between 2000 and 2021 (Fig. 2). The number of studies increased progressively over the decades, with a more pronounced acceleration after 2010, reaching a peak in 2021 with over 60 published articles. This pattern can be attributed to the growing recognition of the importance of biological control in sustainable pest management, especially in light of the limitations of synthetic pesticides, such as pest resistance, side effects on natural enemies, and environmental contamination (DESNEUX et al. 2007).

From 2022 onward, annual publication rates declined markedly. This drop may be partially explained by the lingering impacts of the COVID-19 pandemic on funding cycles, field-experiment execution, and the publication of research findings (ELSE, 2020). Delays in the indexing of more recent articles in scientific databases may also have contributed to this apparent decrease, particularly for the current year (2025).

The thematic trend analysis presents the keyword co-occurrence network, revealing two major thematic clusters (Fig. 3). The blue cluster represented the more traditional approach in the field, centered on entomopathogenic fungi as biological-control agents. Keywords such as "*Beauveria bassiana*," "*Metarhizium anisopliae*," "biological control," "virulence,"

"infection," and "efficacy" dominated this core, reflecting a focus on technical and applied aspects of pathogenicity, formulation, and field performance of these microorganisms. In contrast, the red cluster reflected a more ecological and integrative approach, involving tritrophic interactions, plant responses, volatile emission, identification of semiochemical compounds, and the attraction of natural enemies such as parasitoids. Terms such as "resistance," "plant volatiles," "behavioral responses," "herbivore," and "semiochemicals" indicated significant advancements in the field toward understanding herbivore-induced, plant-mediated chemical communication (HEIL, 2008; TURLINGS & ERB, 2018).

The articulation between the two clusters remained weak, as evidenced by the limited number of connecting nodes between groups. This suggests a thematic fragmentation, where studies on entomopathogens and those focused on chemical ecology are still largely conducted independently, despite growing efforts toward integration.

The word cloud generated from the bibliometric analysis highlighted the main research foci within the field of multitrophic interactions involving biological control and reinforced the thematic duality observed (Fig. 4). The most frequent terms included "*Beauveria bassiana*," "*Metarhizium anisopliae*," "biological control," "resistance," "identification," and "virulence," reflecting the predominance of applied studies in biological control. However, terms such as "plant volatiles," "semiochemicals," "behavioral responses," "*Lepidoptera*," and "herbivore" also stood out, underscoring the growing body of research exploring multitrophic interactions and plant indirect-defense mechanisms.

The survey of leading authors, affiliations, and publication sources (Three-field plot) revealed that authors such as Wakil Waqas, Yong-Jun Zhang, Ted CJ Turlings, Jiali Wang and Kevin David Hyde stood out, associated particularly with China, the United States, India, and Brazil (Fig. 5). For instance, Turlings TCJ was a key reference in chemical ecology and tritrophic interactions (TURLINGS & ERB, 2018), while Zhang YJ and Wang J represented the strong Asian output focused on entomopathogens and large-scale applications.

Among the most important journals are *Pest Management Science*, *Journal of Chemical Ecology*, *Biological Control*, *Insects*, and *Egyptian Journal of Biological Pest Control*. This set reflects a balance between journals specialized in applied entomology and those focused on ecology, reinforcing the interdisciplinary nature of the field.

### **The systematic review**

This systematic review compiled data from 20 scientific studies published from 2000 through 2025, focusing on multitrophic interactions mediated by volatile organic compounds (VOCs) in agricultural systems. Most studies investigated interactions involving cultivated plants, primarily *Oryza sativa*, *Zea mays*, and *Cucumis melo*; entomopathogenic fungi such as *Beauveria bassiana* and *Metarhizium anisopliae*; herbivorous insects of the genus *Spodoptera*; and egg parasitoids, particularly of the genus *Trichogramma* (Table 3).

Regarding the types of interaction, plant–endophyte–herbivore associations were the most frequently reported, accounting for approximately 45% of the studies. About 25% of the studies focused on tritrophic systems involving a plant, herbivore, and parasitoid, while direct interactions between fungi and either insects or plants comprised roughly 20%. More-complex networks, including pollinators and natural enemies, were also observed (GONZÁLEZ-MAS et al. 2023).

The volatile compounds identified had widely diverse structures, with a predominance of compounds derived from the lipoxygenase pathway, such as green leaf volatiles (GLVs), as well as monoterpenes (e.g.,  $\alpha$ -pinene, D-limonene), sesquiterpenes (e.g.,  $\beta$ -caryophyllene), fungal alcohols (e.g., 1-octen-3-ol, 3-methylbutanol), and volatile phenolics (e.g., methyl salicylate). Studies addressing plant–herbivore–parasitoid interactions recurrently reported the involvement of volatiles such as indole,  $\alpha$ -copaene, and (Z)-3-hexenyl acetate in parasitoid attraction (ZHUANG et al. 2012; ROQUE-ROMERO et al. 2020).

The reported effects were highly diverse. For herbivorous insects, VOCs acted as repellents or attractants, modifying oviposition patterns, reducing foliar consumption, and affecting larval survival rates (ZHU et al. 2023; RAMÍREZ-ORDORICA et al. 2024). In parasitoids, VOCs released by plants colonized by fungi or induced by herbivory were consistently attractive, suggesting that endophytic fungi may enhance indirect plant defenses (PEÑAFLORES et al. 2011; PEC et al. 2024).

Methodologically, most studies employed gas chromatography–mass spectrometry (GC–MS) to characterize volatile profiles, often combined with behavioral bioassays using Y-tube olfactometers, oviposition trials, and larval-mortality assessments. In some cases, PCR was used to confirm endophytic colonization (KHASHABA, 2021), and targeted metabolite quantification or gene expression analyses were applied to investigate plant defense pathways (RASOOL et al. 2021; ZHAO et al. 2010).

In summary, the dataset highlighted an expanding research field with diverse biological models and chemical mediators. There is high potential for practical application in integrated pest-management strategies through the manipulation of plant volatile emissions and the strategic use of microorganisms to prime indirect defense.

## DISCUSSION

The bibliometric analysis revealed a fully mature research field, progressively shifting from unidimensional approaches toward more complex and integrative frameworks. Research on entomopathogenic fungi remained dominant; however, studies of chemical ecology, plant–insect communication, and behavioral resistance of pests have grown substantially in response to the need for finer, more selective, and ecologically tailored solutions for insect management.

A significant gap persists between applied microbiology and tritrophic ecology, opening opportunities for new projects integrating the use of entomopathogenic fungi as endophytes that induce volatiles attractive to parasitoids, as suggested by recent advances (VIDAL & JABER, 2015).

The integrated analysis of the studies revealed significant advances in the understanding of multitrophic interactions mediated by volatile organic compounds (VOCs), particularly in systems involving cultivated plants, herbivorous insects, endophytic microorganisms, and egg parasitoids. In *Oryza sativa*, inoculation with *Beauveria bassiana* has proven capable of significantly altering the host plant's VOC profile, with substantial effects on the attraction of natural enemies and deterrence of pests. While some studies did not specify the compounds involved (KHASHABA, 2021), others identified marked changes in the emission of

compounds such as  $\beta$ -caryophyllene, naphthalene, and  $\alpha$ -pinene, which influence the oviposition behavior and offspring survival of *Spodoptera frugiperda* (ZHU et al. 2023).

VOCs produced directly by entomopathogenic fungi also emerged as ecologically important factors. Compounds such as 1-octen-3-ol, benzyl alcohol, and 3-methylbutanol, commonly emitted by *B. bassiana* and *Metarhizium anisopliae*, directly affect larval feeding behavior, oviposition-site selection, and survival of lepidopteran pests (RAMÍREZ-ORDORICA et al. 2024). These volatiles may also function as semiochemicals, interfering with chemical communication across trophic levels. For instance, RAMÍREZ-ORDORICA et al. (2022) demonstrated that VOCs produced by different strains of *B. bassiana* modulate *S. frugiperda* oviposition, with strain-specific effects that could either promote or suppress egg-laying behavior.

In plant–herbivore–parasitoid interactions, compounds such as (Z)-3-hexenyl acetate and indole play key roles in attracting egg parasitoids such as *Trichogramma chilonis* and *Chelonus insularis* (PEÑAFLORES et al. 2011; ZHUANG et al. 2012; ROQUE-ROMERO et al. 2020). These compounds are typically induced by herbivory and reflect the activation of plant defense pathways that may be further modulated by endophytic microorganisms. Thus, the colonization of host plants by *B. bassiana* may not only act directly against insect pests but also enhance plant indirect defenses by increasing parasitoid recruitment (GONZÁLEZ-MAS et al. 2021).

Microbial modulation of secondary metabolism in host plants may also provide ecological advantages under abiotic stress. For instance, CHATTERJEE et al. (2018) showed that inoculation of *Brevibacterium linens* into salt-stressed rice plants suppressed the emission of stress-induced volatiles while enhancing photosynthesis-related VOCs from the lipoxygenase pathway. These findings support a multifunctional role for endophytic microorganisms, simultaneously enhancing tolerance to abiotic stress and strengthening plant-insect communication.

However, not all studies identified the specific VOCs involved. While this did not undermine the ecological outcomes observed, the lack of chemical characterization limited mechanistic insights and hampered the reproducibility of results. For example, in the study by GONZÁLEZ-MAS et al. (2019), natural enemies were more successful on endophyte-colonized plants, but no specific compounds were linked to this effect. This type of methodological gap was recurrent and highlights the need for integrated chemical and ecological approaches.

The predominant methods included GC–MS analysis of volatile profiles, Y-tube olfactometer bioassays, oviposition tests, and larval mortality assays. Fewer studies employed molecular or transcriptomic tools, which could provide a deeper understanding of VOCs biosynthesis pathways and plant–microbe–insect signaling networks. One example is the report by WANG et al. (2023), which used RNA interference to study the molecular basis of insect response to specific VOCs. Nevertheless, most experiments remained restricted to laboratory or semi-controlled conditions, emphasizing the need for validation under real agricultural environments.

Taken together, these findings indicated that integration of entomopathogenic and endophytic fungi, especially *B. bassiana*, can profoundly influence plant chemical ecology.

The resulting effects extend beyond pest mortality and include the priming of indirect defenses through VOCs and the enhancement of ecosystem services such as pollination (GONZÁLEZ-MAS et al. 2023). However, challenges remain in elucidating the specific biochemical pathways involved, understanding multi-species interactions among natural enemies, and applying this knowledge to develop sustainable and multifunctional cropping systems.

## CONCLUSION

This systematic review and bibliometric analysis revealed that multitrophic interactions mediated by volatile organic compounds (VOCs) in rice systems have evolved from fragmented approaches toward a more integrated framework that connects chemical ecology, biological control, and plant physiology. The inoculation of *Beauveria bassiana* as an endophyte in *Oryza sativa* demonstrated its ability to modulate the plant's volatile profile—particularly through compounds such as  $\beta$ -caryophyllene,  $\alpha$ -pinene, and indole—enhancing the attraction of *Trichogramma* parasitoids while reducing *Spodoptera frugiperda* oviposition and larval performance. Moreover, fungal VOCs such as 1-octen-3-ol and 3-methylbutanol exhibited direct behavioral effects on pests, broadening the ecological role of these microorganisms.

The results highlight the potential of endophytic entomopathogenic fungi as strategic tools for sustainable pest management, acting simultaneously as biological control agents, modulators of chemical signaling, and inducers of plant indirect defenses. However, methodological gaps persist, particularly regarding VOC characterization, integration of molecular approaches, and field validation. Progress in these areas is essential to consolidate the application of these microorganisms in ecological intensification and to reduce the reliance on synthetic insecticides in rice production systems.

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## AUTHORS' CONTRIBUTIONS

**Tiago Tavares Ferreira:** Conceptualization, Writing – original draft, Methodology, Investigation, Data curation, Formal analysis. **Kamila Emmanuella Xavier de Azevedo:** Investigation, Data curation, Formal analysis, Writing – review & editing. **Maxdouglass Santos:** Investigation, Formal analysis, Writing – review & editing.

## DECLARATION OF CONFLICTS OF INTEREST:

We have no conflict of interest to declare.

## DECLARAÇÃO DE DISPONIBILIDADE DE DADOS DA PESQUISA

Todo o conjunto de dados de apoio aos resultados deste estudo foi publicado no próprio artigo.

## DATA AVAILABILITY STATEMENT

All data supporting the findings of this study are included within the article itself.

## BIOETHICS AND BIOSSECURITY COMMITTEE APPROVAL

Not applicable.

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Table 1 - Search terms used for article selection in ScienceDirect and Web of Science databases.

Search terms <sup>1</sup>	
1	" <i>Oryza sativa</i> " AND " <i>Beauveria bassiana</i> " AND " <i>Trichogramma</i> "
2	" <i>Oryza sativa</i> " AND " <i>Beauveria bassiana</i> " AND "volatile organic compounds"
3	" <i>Oryza sativa</i> " AND "entomopathogenic fungi" AND " <i>Trichogramma</i> "
4	" <i>Oryza sativa</i> " AND "endophytic fungi" AND "volatile organic compounds"
5	" <i>Beauveria bassiana</i> " AND " <i>Spodoptera</i> " AND "volatile organic compounds"
6	" <i>Beauveria bassiana</i> " AND " <i>Trichogramma</i> " AND "herbivore-induced plant volatiles"
7	" <i>Spodoptera</i> " AND " <i>Trichogramma</i> " AND "volatile organic compounds"
8	" <i>Spodoptera</i> " AND " <i>Trichogramma</i> " AND "kairomone"
9	" <i>Oryza sativa</i> " AND " <i>Spodoptera</i> " AND "volatile organic compounds"
10	" <i>Oryza sativa</i> " AND " <i>Trichogramma</i> " AND "herbivore-induced plant volatiles"
11	"Entomopathogenic fungi" AND " <i>Spodoptera</i> " AND "olfactory response"
12	"Endophytic fungi" AND " <i>Trichogramma</i> " AND "kairomone"
13	" <i>Beauveria bassiana</i> " AND "herbivore-induced plant volatiles" AND " <i>Trichogramma</i> "
14	" <i>Oryza sativa</i> " AND "endophytic fungi" AND " <i>Spodoptera</i> "

<sup>1</sup>The search terms were designed based on their relevance to the PECO research question and the following inclusion criteria: (i) presence of the host plant (*Oryza sativa*) and/or the entomopathogenic/endophytic fungus (*Beauveria bassiana*); (ii) inclusion of at least one target organism (*Spodoptera* spp. or *Trichogramma* spp.); and (iii) incorporation of chemical

communication terms such as volatile organic compounds (VOCs), herbivore-induced plant volatiles (HIPVs), or kairomone.

Table 2 - Adjusted search terms for selection of articles in the PubMed database

Search terms <sup>1</sup>	
1	" <i>Oryza sativa</i> " AND " <i>Beauveria bassiana</i> " AND " <i>Trichogramma</i> "
2	" <i>Oryza sativa</i> " AND " <i>Beauveria bassiana</i> " AND "volatile organic compounds"
3	" <i>Oryza sativa</i> " AND "entomopathogenic fungi" AND " <i>Trichogramma</i> "
4	" <i>Oryza sativa</i> " AND "endophytic fungi" AND "volatile organic compounds"
5	" <i>Beauveria bassiana</i> " AND " <i>Spodoptera</i> " AND "volatile organic compounds"
6	" <i>Beauveria bassiana</i> " AND " <i>Trichogramma</i> " AND "herbivore-induced plant volatiles"
7	" <i>Spodoptera</i> " AND " <i>Trichogramma</i> " AND "volatile organic compounds"

<sup>1</sup>The search terms

listed in Table 2 were adjusted and simplified for the PubMed database, due to the limited number of results returned from the three-term combinations used for the ScienceDirect and Web of Science databases. The revised queries were still aligned with the PECO framework

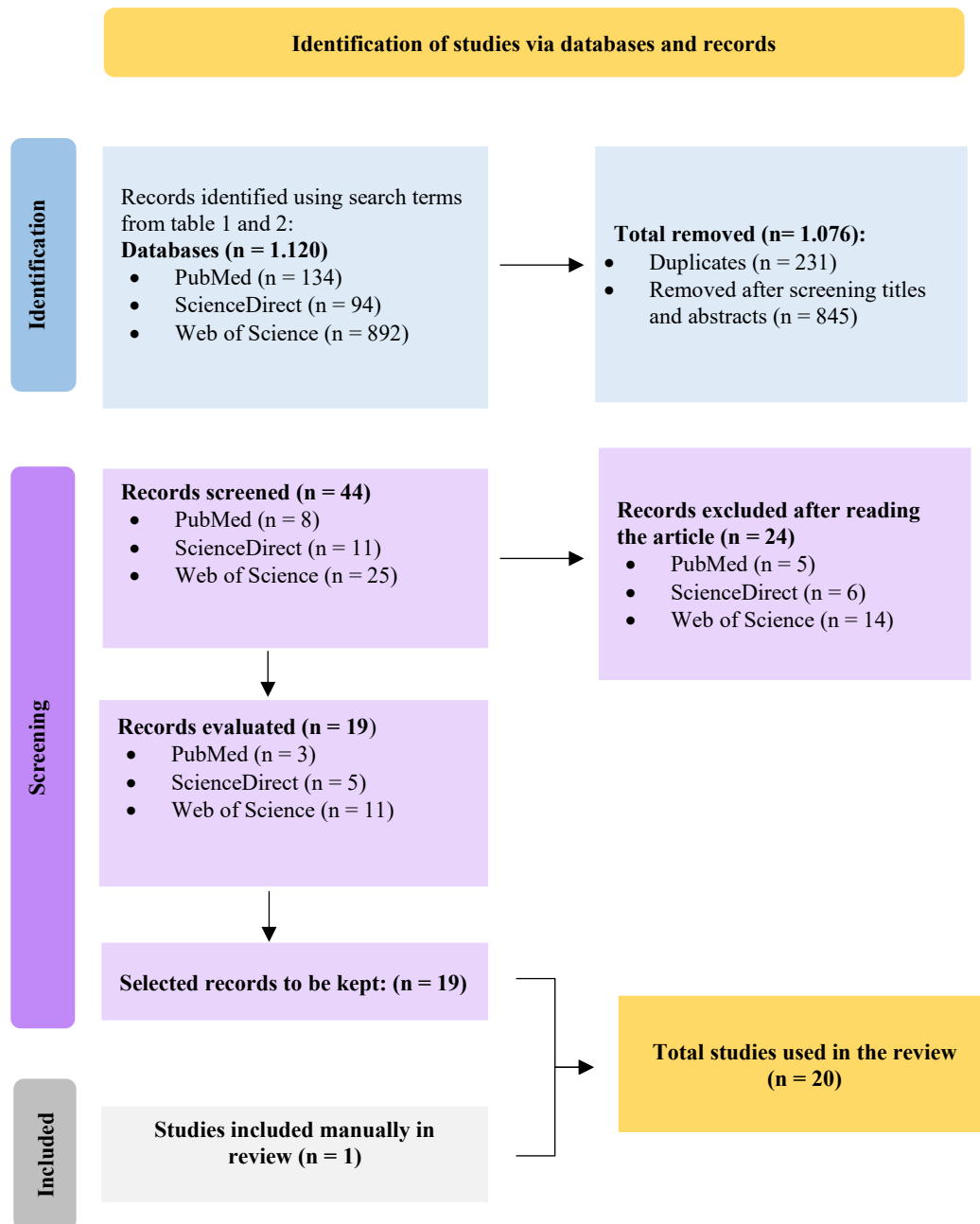


Figure 1 - PRISMA 2020 flowchart representing the article selection process in the systematic review

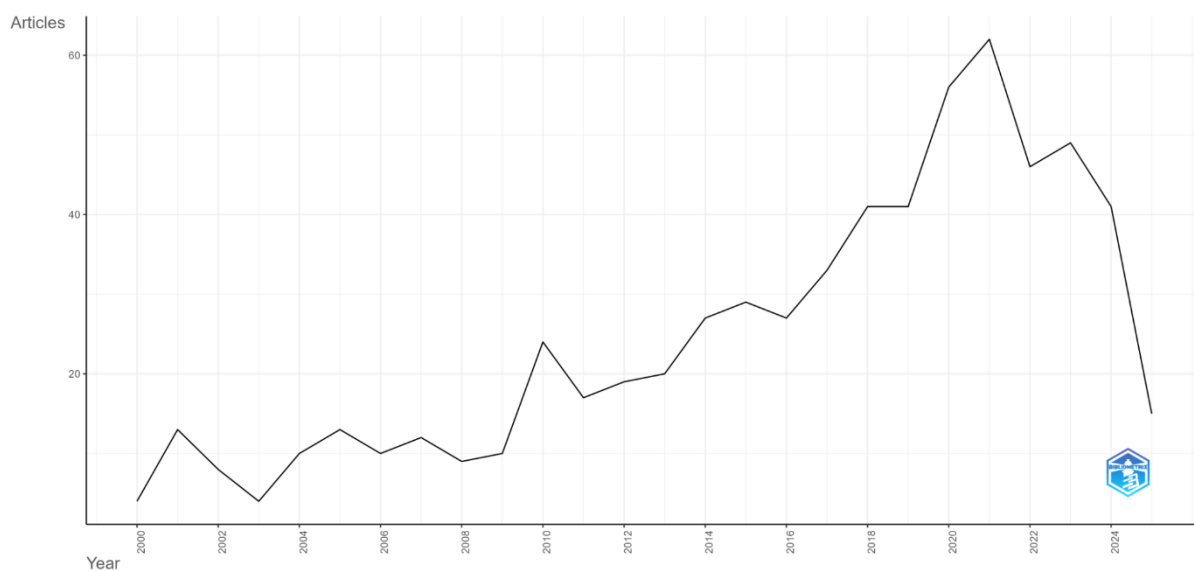


Figure 2 - Temporal distribution of scientific publications related to chemical communication dynamics mediated by herbivore-induced volatile compounds from January 2000 through June 2025





Figure 4 - Word cloud highlighting research focus areas in herbivore-induced plant volatiles and multitrophic interactions in entomopathogenic fungus-inoculated plants

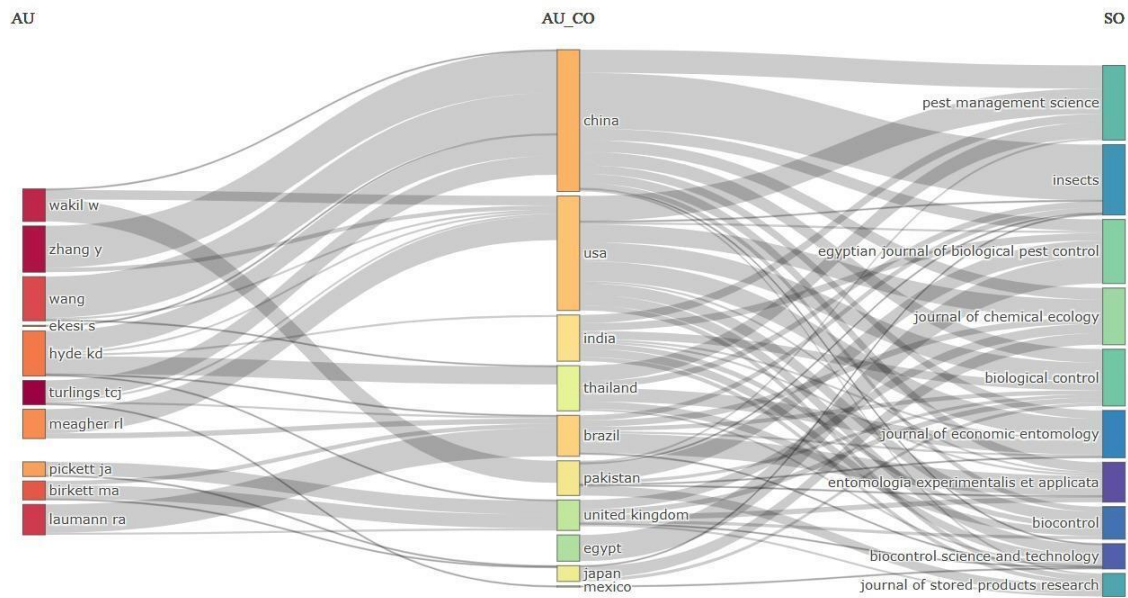


Figure 5 - Three-field plot illustrating the relationships among authors (au), their countries of origin (au\_co), and publication journals (so). The thickness of the lines indicates the intensity of collaboration or frequency of publications

Table 3 - Summary of multitrophic interactions mediated by volatile organic compounds among cultivated plants, entomopathogenic fungi, herbivorous insects, and natural enemies, including the organisms studied, compounds identified, effects observed, and methods employed

Reference	Organism studied	Type of Interaction	Identified Volatile Compounds	Observed Effects	Methods	DOI
Alamgir et al. (2016)	<i>Oryza sativa</i> , <i>Spodoptera mauritia</i> , <i>Nilaparvata lugens</i>	Herbivory-induced defense	p-coumaroylputrescine, feruloylputrescine	Toxic to BPH; increased mortality	Metabolomics + feeding assays	<a href="https://doi.org/10.1111/1/pce.12640">10.1111/1/pce.12640</a>
Chatterjee et al. (2018)	<i>Brevibacterium linens</i> RS16, <i>Oryza sativa</i>	Bacterial inoculation in plant	Lipoxygenase pathway volatiles, aldehydes, benzenoids, terpenes	Reduced stress-induced VOC emissions; improved photosynthesis under salinity	Inoculation + salinity treatments; GC-MS	<a href="https://doi.org/10.1016/j.scitotenv.2018.07.187">10.1016/j.scitotenv.2018.07.187</a>
Chebet et al. (2021)	<i>Hypocrea lixii</i> , <i>Beauveria bassiana</i> , <i>Phaseolus vulgaris</i> , pests	Endophytic fungi as biopesticides	$\beta$ -phellandrene	Reduced pest survival; altered volatile profiles	Seed inoculation, GC-MS, bioassays	<a href="https://doi.org/10.3390/molecules26185694">10.3390/molecules26185694</a>
González-Mas et al. (2019)	Melon ( <i>Cucumis melo</i> ), <i>Aphis gossypii</i> , natural enemies, <i>Beauveria bassiana</i>	Endophytic fungus-plant-aphid-natural enemy	Not specified	Predators/parasitoids successful on colonized plants	Endophyte inoculation, bioassays	<a href="https://doi.org/10.1007/s10340-019-01098-5">10.1007/s10340-019-01098-5</a>
González-Mas et al. (2021)	Melon, cotton, <i>Beauveria bassiana</i> , S. <i>frugiperda</i> ,	Endophyte-induced plant VOCs	Altered VOC blends (herbivore-typical, antimicrobial)	Different blends under herbivory; potential enemy attraction	VOC profiling under insect damage	<a href="https://doi.org/10.3389/fpls.2021.660460">10.3389/fpls.2021.660460</a>

	<i>Aphis gossypii</i>					
González-Mas et al. (2023)	Melon, <i>Apis mellifera</i> , <i>Bombus terrestris</i> , <i>Beauveria bassiana</i>	Endophyte–plant–pollinator	D-limonene, benzeneacetaldehyde	Earlier flowering; more pollen; altered bee preference	Foliar spray inoculation; VOC analysis	<a href="#">10.1127/ento.mologia/2023/1991</a>
Hountondji et al. (2005)	Cassava, <i>Neozygites tanaoae</i> , green mite	Plant volatiles–fungal sporulation	GLVs	Herbivore-damaged plant volatiles promote fungal sporulation	Fungal culture with volatile exposure	<a href="#">10.1007/s10886-005-4244-2</a>
Khashaba (2021)	<i>Beauveria bassiana</i> , rice ( <i>Oryza sativa</i> )	Endophytic colonization	Not specified	Successful colonization via seed immersion	Seed immersion inoculation, PCR	<a href="#">10.1186/s41938-021-00434-1</a>
Pec et al. (2024)	<i>Metarhizium robertsii</i> , <i>Diatraea saccharalis</i> , <i>Cotesia flavipes</i>	Endophyte–plant–Herbivory–natural enemy	Linalool, methyl salicylate, $\beta$ -myrcene, $\beta$ -elemene, $\alpha$ -humulene, $\alpha$ -pinene, (E)- $\beta$ -farnesene, indole	Enhance direct and indirect defense against <i>D. saccharalis</i> , modulating the JA and SA pathways and volatile emissions	(GC–MS); (GC–FID, GC–MS); Y-tube olfactometer bioassays; oviposition preference tests	<a href="#">10.1016/j.cropro.2024.106872</a>
Peñaflor et al. (2011)	Maize, egg parasitoids	Herbivore-induced plant volatiles	GLVs, aromatic compounds, mono-, sesquiterpenes	Attraction of parasitoids to damaged plants	Y-tube olfactometer assays	<a href="#">10.1007/s10886-0047-9</a>
Raghava et al. (2010)	<i>Solanum lycopersicum</i> , <i>Spodoptera litura</i> , <i>Trichogramma chilonis</i>	Herbivory/mechanical injury VOCs	Monoterpenes (65%), sesquiterpenes (15%), aldehydes (10%)	Attracted parasitoids	GC profiling, behavioral assays	<a href="#">10.1016/j.plantsci.2010.07.020</a>
Ramírez-Ordorica	<i>Beauveria bassiana</i> ,	Fungal VOCs	3-methylbutanol,	Induced oviposition	VOC profiling,	<a href="#">10.1093/fems</a>

et al. (2022)	<i>Spodoptera frugiperda</i>	influencing oviposition	short-chain fatty acids		oviposition assays	<a href="#">ec/fiac14</a>
Ramírez-Ordorica et al. (2024)	<i>Beauveria bassiana</i> , <i>Spodoptera frugiperda</i>	Fungal VOCs affecting larval feeding	3-methylbutanol, 4-coumaric acid	Reduced feeding; strain-specific	Dual-choice olfactometer, UPLC-MS	<a href="#">10.3390/jof10060438</a>
Rasool et al. (2021)	Wheat, bean, <i>Beauveria</i> , <i>Metarhizium</i> , aphids	Seed-inoculated fungi-plant-aphid	Benzoxazinoids, flavonoids (altered)	Reduced or increased aphid populations	Seed inoculation, metabolite quantification	<a href="#">10.1111/nph.16979</a>
Roque-Romero et al. (2020)	Maize, <i>Spodoptera frugiperda</i> , <i>Chelonus insularis</i>	Parasitoid attraction to plant/host volatiles	$\alpha$ -pinene, $\alpha$ -copaene	Parasitoid attraction	Y-olfactometer assays	<a href="#">10.1016/j.biocontrol.2019.104100</a>
Staffa et al. (2020)	<i>Tulbaghia violacea</i> , <i>Beauveria bassiana</i> , ticks	Endophyte-plant-arthropod	4 altered volatiles (unspecified)	Growth promotion; dose-dependent tick repellency	Inoculation, GC-MS, repellency assays	<a href="#">10.14202/vetworld.2020.1159-1166</a>
Wang J et al. (2023)	Maize, rice, <i>Spodoptera frugiperda</i>	Plant-insect (oviposition preference)	(Z)-3-hexenyl acetate	Attracted FAW females to maize	GC-EAD, RNAi of odorant receptors	<a href="#">10.1186/s12915-023-01642-x</a>
Zhao et al. (2010)	Rice ( <i>Oryza sativa</i> )	Herbivory-induced defense	Methyl salicylate, methyl benzoate	Indirect defense	Gene expression, enzyme assays	<a href="#">10.1016/j.plaphy.2010.01.023</a>
Zhu et al. (2023)	<i>Beauveria bassiana</i> , maize, <i>Ostrinia furnacalis</i>	Endophyte-herbivore-plant	2-ethyl-1-hexanol, 3-hexen-1-ol, $\beta$ -caryophyllene, naphthalene, $\alpha$ -pinene	Altered oviposition preference; reduced offspring survival	Inoculation, oviposition assays, volatile analysis	<a href="#">10.1007/s10340-022-01527-y</a>
Zhuang et al. (2012)	Rice ( <i>Oryza sativa</i> )	Herbivory-induced defense	Indole	Parasitoid attraction	Gene expression,	<a href="#">10.1016/j.phytochem.</a>

enzyme [2011.0](#)  
assays [8.029](#)

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