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Review

From single agents to multi-enemy systems: a systematic review of mealybug (hemiptera: pseudococcidae) biological control research

Yolma Hendra^{1,2} Trizelia Zainuddin^{3*}, My Syahrawati³, Hasmiandy Hamid³

¹ Doctoral Program of Agricultural Sciences, Faculty of Agriculture, Universitas Andalas, Padang, Indonesia

² Agroteknologi, Faculty of Agriculture, Universitas Islam Riau, Pekanbaru, Indonesia

³ Plant Protection, Faculty of Agriculture, Universitas Andalas, Padang, Indonesia

*Corresponding address: trizelia@yahoo.com

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Abstract

Mealybugs (Hemiptera: Pseudococcidae) are major insect pests causing significant economic losses across diverse crops. This systematic review summarizes research on mealybugs, focusing on study types, species, host plants, and natural enemy groups in biological control, with emphasis on management-oriented literature to identify gaps in Integrated Pest Management (IPM). Literature searches in Scopus, PubMed, and Web of Science yielded 1,342 records, of which 56 peer-reviewed articles published between 2021 and 2025 met inclusion criteria through a PICOC-based screening. Research was geographically concentrated, with Brazil, Italy, the United States, and China as leading contributors. The 56 articles reported 35 mealybug species, highlighting a focus on biocontrol rather than global Pseudococcidae diversity. *Phenacoccus solenopsis* Tinsley, 1898 was the most studied species, and citrus and grapevine were the main host plants. Over half of the studies (53.6%) examined biological control, but research favored single-agent approaches: parasitoid-only studies (21.4%), predator-only and entomopathogen-only studies (10.7% each). Multi-agent systems were scarcely explored; six studies examined predator-parasitoid combinations, while only one investigated predator-entomopathogen interactions. Notably, no study examined three-agent systems. This gap is critical, as multi-agent outcomes are context-dependent, ranging from synergy to interference. The review identifies two key gaps: limited multi-agent experiments and absence of frameworks to manage their interactions. Addressing these gaps is essential to advance evidence-based, ecologically complex IPM strategies for mealybug management, emphasizing the need for research that evaluates multi-agent interactions and their practical implementation in pest management.

Keywords: biological control, mealybugs, natural enemies, integrated pest management, systematic review

Introduction

Mealybugs (Hemiptera: Pseudococcidae) rank among the world's most economically significant pest groups, distinguished by their extensive global distribution and remarkable ecological adaptability (Masten and Pellizzari 2016; Subramanian *et al.* 2021). With over 2,000 described species—more than 290 of which are recognized as crop pests—mealybugs possess the ability to infest a broad range of host plants, rapidly adapt to new environments, and develop resistance to conventional control methods (Subramanian *et al.* 2021; Sisodiya 2023; Si *et al.* 2025). Their damage is both direct and multifaceted indirect. Directly, their sap-feeding depletes nutrients, causing chlorosis, stunting, wilting, and reduced yields. Indirect damage is more complex: (1) they transmit harmful plant viruses (e.g., Grapevine leafroll-associated virus); (2) their honeydew promotes sooty mold growth, which blocks photosynthesis and degrades fruit quality; and (3) the honeydew also attracts protective ants, disrupting natural pest control (Subramanian *et al.* 2021). Globally, mealybugs cause billions of dollars in annual losses across horticultural, fruit, vegetable, and ornamental crops.

The distribution of mealybugs is influenced by a complex interplay of biogeographic factors, climate change, international trade, and the movement of plant materials (Li *et al.* 2025). Specifically, climate change is projected to expand the suitable climatic niches of key invasive mealybugs, potentially opening new geographic regions to colonization (Cui *et al.* 2024). Invasive species such as *Phenacoccus solenopsis* Tinsley, 1898 and *Paracoccus marginatus* Williams & Granara de Willink, 1992 have rapidly expanded their ranges in recent decades, establishing in

new regions including the Mediterranean, Middle East, and North Africa (Douglass *et al.* 2002; Cui *et al.* 2024; Diepenbrock and Ahmed 2021). Their polyphagous nature—some species attack over 200 plant species—facilitates their establishment and spread across diverse agroecosystems. Furthermore, mutualistic interactions with ants enhance mealybug population resilience by reducing pressure from natural enemies (Soler *et al.* 2021; Ricciardi *et al.* 2021; Puig *et al.* 2021). However, it should be emphasized that the evidence synthesized in this review is derived primarily from biological control and management-oriented literature; therefore, the resulting maps and patterns reflect the distribution of documented records and research attention within this domain rather than an exhaustive inventory of the natural global occurrence of mealybugs.

Mealybug control is increasingly reliant on biological control approaches within Integrated Pest Management (IPM) frameworks, driven by growing concerns over pesticide resistance and environmental impacts (Shoba *et al.* 2024). Biological agents such as parasitoids (*Anagyrus* spp. *Acerophagus papayae* Noyes & Schauff, 2003), predators (*Cryptolaemus montrouzieri* Mulsant, 1853), and entomopathogenic fungi (*Beauveria bassiana* (Bals.-Criv.) Vuill., 1912) have proven effective in suppressing mealybug populations (Soler *et al.* 2021)(Pacheco Da Silva *et al.* 2021)(Ricupero *et al.* 2025). However, the success of biological control is often hindered by taxonomic complexities, particularly in cryptic species complexes (e.g., *Planococcus ficus* Signoret, 1875), as well as incomplete surveys of natural enemies in many regions, especially in South America, Southeast Asia, and Africa. Despite the increasing adoption of biological control, most existing studies evaluate natural enemies in isolation, focusing on either parasitoids, predators, or entomopathogens as single control agents. Empirical evidence on the combined or interactive effects of multiple natural enemy guilds remains limited. This fragmented approach restricts our understanding of synergistic or antagonistic interactions that are critical for developing robust and sustainable Integrated Pest Management strategies.

Although numerous studies have documented the occurrence, diversity, and impacts of mealybugs worldwide, the available scientific literature remains highly fragmented, regionally biased, and methodologically heterogeneous. Most published studies consist of isolated case reports, taxon- or crop-specific surveys, or short-term ecological assessments, which limit to identify global patterns or draw broadly applicable conclusions. Accordingly, the “global patterns” discussed in this manuscript represent patterns emerging from the corpus of management and biological-control publications, and should not be interpreted as a complete ecological census of mealybug distributions across all scientific disciplines. Conventional narrative reviews are insufficient to address this complexity, as they lack standardized selection criteria, quantitative synthesis, and transparency in evidence integration. Consequently, critical questions regarding trends in management research, research intensity across regions, species–host associations in a biocontrol context, and gaps in integrated control approaches remain unresolved or inconsistently interpreted.

In this context, a systematic literature review (SLR) is essential to ensure a transparent, reproducible, and unbiased synthesis of the available evidence using predefined inclusion criteria and structured screening protocols. However, an SLR alone is not sufficient to capture the dynamics of scientific knowledge production. Therefore, integrating a bibliometric analysis is necessary to quantitatively map research trajectories, identify dominant themes, pinpoint geographic and institutional research hubs, characterize collaboration networks, and track temporal shifts in methodological focus. This combined approach enables the identification of not only management, but also of structural gaps in research investment, taxonomic coverage, and regional representation within the biological control and management literature.

By coupling systematic evidence synthesis with bibliometric mapping, this review provides a robust framework to bridge ecological understanding with research policy and practice. Such an approach is critically needed to support evidence-informed IPM planning and to help prioritize future research and development in biological control, guide future research agendas, and support the development of globally coordinated and evidence-based Integrated Pest Management strategies against invasive mealybugs.

Research Questions:

RQ1. What are the global patterns in research output and documented species records for mealybugs as reported in biological control and management-oriented literature?

RQ2. Which mealybug species and host plants are most frequently documented in management-focused studies, and which geographic regions emerge as primary research foci?

RQ3. What are the prevailing research themes in mealybug management, and where do the most critical knowledge gaps—particularly regarding the integration of multiple natural enemy guilds—exist?

Materials and Methods

Database sources

This study employs a systematic review approach to synthesize global evidence on mealybug species (Hemiptera: Pseudococcidae), their host plant associations, and their natural enemies within the framework of biological control. The review was conducted following the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) guidelines to ensure transparency, methodological rigor, and reproducibility. An initial comprehensive literature search was conducted on 20 November 2025 using Scopus and PubMed, selected for their broad coverage of agricultural sciences, entomology, invasion biology, and biological control research. Following reviewers' recommendations, the search strategy was expanded to include the Web of Science Core Collection (WOS) on 10 January 2026 to further enhance database coverage and reduce potential selection bias. All records retrieved from the three databases were exported into reference management software, and duplicate records were systematically identified and removed prior to screening.

Search term

Search terms were developed iteratively and adapted to the syntax of each database. Searches were conducted within titles, abstracts, and keywords using a combination of taxonomic and thematic terms related to mealybugs and biological control. Given the primary focus of this review on synthesizing evidence for biological control and integrated management, the core search string was designed to capture literature explicitly addressing natural enemies and control strategies. The core search string applied across databases was: (Hemiptera OR Sternorrhyncha) AND (Pseudococcidae OR “mealybug” OR “mealybugs”) AND (“biological control” OR “natural enemies” OR biocontrol). While this search strategy may not capture all mealybug literature (e.g., purely distributional studies without a biocontrol focus), it aligns with our objective to synthesize evidence specifically for biological control applications. The search was limited to peer-reviewed journal articles published between 2021 and 2025. Only articles written in English were

considered. Although the systematic search was restricted to peer-reviewed articles published during the period 2021–2025, relevant studies published prior to 2021 were also cited selectively to provide historical context, taxonomic background, and foundational concepts in mealybug biology and biological control. These earlier references were not included in the systematic screening process and were used solely to support the background and discussion sections.

Screening and eligibility criteria

Study selection was conducted through a structured and sequential screening process guided by the PICOC framework to ensure consistency, transparency, and reproducibility. Two reviewers (YH and T) independently screened titles/abstracts and full texts and performed data extraction. Discrepancies were resolved through discussion, with adjudication by the full author team when necessary. The population of interest comprised mealybug species belonging exclusively to the family Pseudococcidae, while the intervention included biological control agents and natural enemies such as parasitoids, predators, and entomopathogenic organisms. Where applicable, comparisons involved untreated controls, chemical control measures, or alternative biological control strategies, and the outcomes of interest encompassed parasitism and predation rates, insect mortality, population suppression, establishment or persistence of natural enemies, and ecological factors influencing biological control efficacy. The context of the review covered agricultural and horticultural production systems, including field crops, orchards, greenhouse cultivation, and ornamental plants across all geographic regions.

Articles were included if they met the following criteria: (1) they were peer-reviewed journal articles published between 2021 and 2025; (2) they were studies explicitly addressing mealybugs (Pseudococcidae) in relation to biological control, natural enemies, or management strategies; (3) they reported research conducted in agricultural or horticultural systems; and (4) they presented empirical data derived from laboratory, greenhouse, or field experiments, or provided new taxonomic or distributional records relevant to management. Articles were excluded if they met any of the following conditions: (1) they focused on insect pests outside the family Pseudococcidae; (2) they examined chemical control strategies without relevance to biological control; (3) they were conducted in non-agricultural or purely ecological systems without pest management implications; (4) they were non-journal publications such as conference proceedings, theses, dissertations, book chapters, or technical reports; or (5) they lacked sufficient methodological detail or biological/management control outcomes relevant to the objectives of this review.

Study selection process

The combined searches from Scopus, PubMed, and WOS initially yielded 1,342 records. After removing duplicate records across databases, 516 unique records remained for screening. All 516 records underwent a single title-and-abstract screening stage based on the eligibility criteria, followed by a separate full-text assessment. During this stage, 378 records were excluded because they were outside the publication period, were not journal articles, or were clearly irrelevant to mealybugs or management/biological control. The remaining 138 articles proceeded to full-text screening. After detailed assessment of the full texts, 82 articles were excluded due to insufficient relevance, for not meeting the PICOC criteria, or for lacking empirical/data components relevant to the synthesis. In total, 56 articles fulfilled all inclusion criteria and were included in the final

qualitative synthesis. The study selection process is summarized in the PRISMA flow diagram (Figure 1).

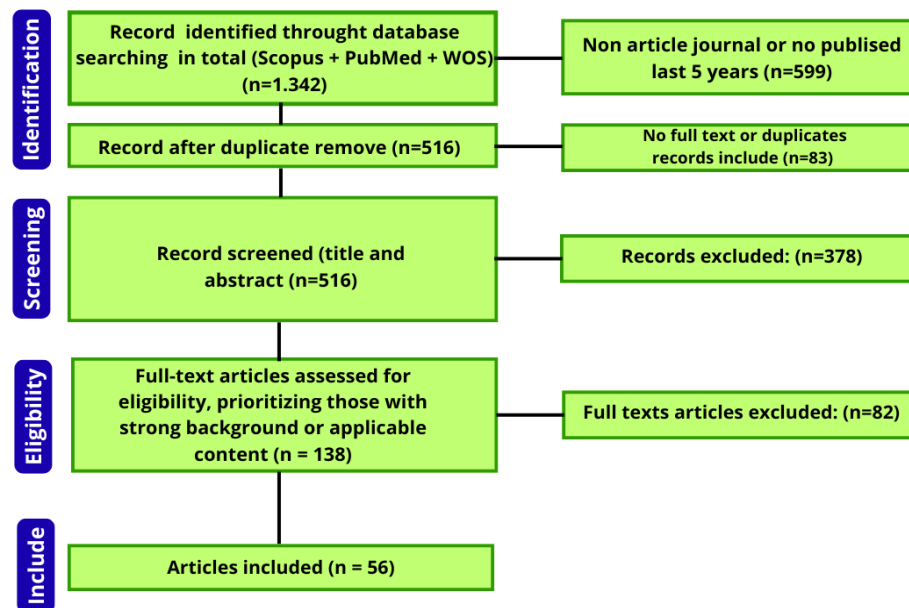


Figure 1. Preferred reporting items for systematic reviews and meta-analysis (PRISMA) diagram of the systematic quantitative literature review selection process

Data extraction and synthesis

Data extraction was conducted using a predefined extraction framework to ensure consistency and minimize bias. The framework was piloted on five randomly selected articles and refined before full application. Each included article was reviewed in full, and the following information was systematically recorded: mealybug species, host plant species, country or region of study, study setting (field, greenhouse, or laboratory), type of natural enemy (parasitoid, predator, or entomopathogen), reported biological control outcomes (e.g., parasitism rate, predation rate, mortality, or population suppression), and the study's primary focus category. For categorization, studies were classified as: (1) Single-agent biological control (parasitoid-only, predator-only, entomopathogen-only); (2) Multi-agent biological control (reporting on two or more enemy groups). This category was further divided into: (2a) Descriptive/Co-occurrence studies (reporting presence of multiple enemies without manipulative interaction tests); (2b) Experimental interaction studies (explicitly testing combined efficacy or interactions); (3) Foundational research informing biological control (taxonomic, ecological, distributional studies providing essential baseline data). Where available, additional ecological factors influencing biological control performance—such as ant–mealybug mutualisms or habitat characteristics—were also extracted.

Extracted data were synthesized descriptively to identify global patterns in documented mealybug records, host plant associations, and biological control strategies within the reviewed literature. Studies were further classified based on their primary focus as defined above and the relative proportion of each category was calculated to characterize research trends. The term “global patterns” in this review therefore refers to patterns of research activity and documented records within the biological control and management literature and not to an exhaustive ecological

census of worldwide mealybug occurrence. A quantitative meta-analysis was not conducted due to substantial heterogeneity in study designs, outcome metrics, and reporting standards.

Bibliometric analysis

A bibliometric analysis was conducted using VOSviewer software to map the conceptual structure and thematic evolution of the research field. The text data from the titles, abstracts, and keywords of the final 56 included articles served as the data source. A thesaurus file was used to merge synonymous terms (e.g., "biocontrol" and "biological control"). VOSviewer's text mining function was used to extract significant terms. The analysis was performed with the following parameters: counting method = full counting; minimum number of occurrences of a term = 3; relevance score for term selection = 60%. Standard VOSviewer stopwords lists were applied, and additional field-specific stopwords (e.g., "human", "male", "results") were removed. Network, overlay, and density visualizations were created to identify dominant themes, their temporal trends, and research intensity. The network normalization method chosen was association-strength normalization.

Result

Geographic distribution of biocontrol-oriented research output

The distribution of research output on mealybugs (Hemiptera: Pseudococcidae) conducted between 2021 and 2025 shows notable variation across countries. From the 56 articles included in this systematic review, most studies originated from regions with strong horticultural and plantation sectors, while others contributed fewer publications. One study did not report their country of origin and were therefore excluded from the visualization (Figure 2)

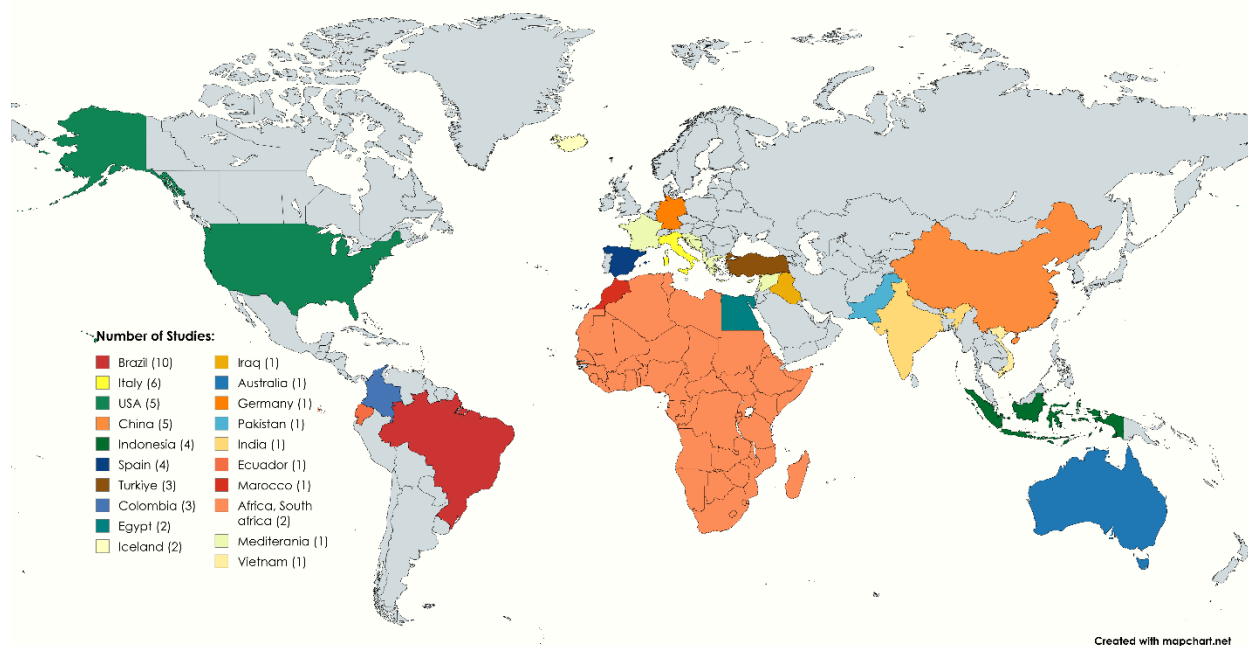


Figure 2. Geographic distribution of research output (number of studies) on mealybugs (Hemiptera: Pseudococcidae) published between 2021-2025.

The distribution indicates that Brazil contributed the highest number of studies (10), indicating the intensity of biocontrol-related research activity in plantation crops such as sugarcane, coffee, and various tropical fruits that are highly susceptible to Pseudococcidae infestations. Italy (6 studies) and USA (5 studies) show substantial attention to horticultural crops, particularly grapes and citrus. China (5 studies) and Indonesia (4 studies) also make notable contributions, primarily linked to their agricultural and plantation research activities. Other countries, including Turkey and Egypt, contributed 2–3 studies each, while several nations were represented by single publications, reflecting research effort rather than confirmed pest prevalence.

Documented mealybug species and host associations

Based on a synthesis of 56 scientific articles published between 2021 and 2025, research on mealybugs (Hemiptera: Pseudococcidae) has identified 35 distinct species that have been the focus of entomological studies worldwide. These figures represent species documented within the reviewed biocontrol-oriented publications and should not be interpreted as a comprehensive inventory of global mealybug diversity. This substantial number reflects both the diversity of this pest group and its global agricultural significance. The research reveals clear patterns in study focus, with particular attention given to certain key species. Most notably, *Phenacoccus solenopsis* Tinsley, 1898 emerges as the most extensively studied mealybug, with research documented across multiple continents including Asia, Africa, Europe, and South America. (Khudhair *et al.* 2025; Bakry and Abdel-Baky 2024; Ricupero *et al.* 2025). Other species receiving significant research attention include *Dysmicoccus brevipes*, studied by Kondo *et al.* (2022) and Moreno *et al.* (2021) in Colombia, and various *Planococcus* species affecting citrus and grape crops (Table 1).

Table 1. Mealybug species and their recorded host plants based on 56 articles published between 2021–2025

No.	Species of mealybug	Host plant(s)	Reference(s)
1	<i>Dysmicoccus brevipes</i> Cockerell, 1893	Pineapple	(Kondo <i>et al.</i> 2022; Moreno <i>et al.</i> 2021; Zart <i>et al.</i> 2021; Panti <i>et al.</i> 2024)
2	<i>Pseudococcus comstocki</i> Kuwana, 1902	Potato, grapevine, cocoa	(Ricciardi <i>et al.</i> 2021; Burgio <i>et al.</i> 2025; Puig <i>et al.</i> 2021)
3	<i>Phenacoccus solenopsis</i> Tinsley, 1898	Cotton, maize, coffee, okra, lantana, purslane	(Khudhair <i>et al.</i> 2025; Bakry and Abdel-Baky, 2024; Oliveira <i>et al.</i> 2023; Ricupero <i>et al.</i> 2025; Chen <i>et al.</i> 2021; Kahya <i>et al.</i> 2021; El-Aalaoui <i>et al.</i> 2024; Wang <i>et al.</i> 2023; Huang <i>et al.</i> 2022)
4	<i>Maconellicoccus multipori</i> Takahashi, 1951	Black pepper	(Mardiningsih <i>et al.</i> 2025)
5	<i>Hypogeococcus pungens</i> Granara de Willink, 1981	Cactus	(Ezeh <i>et al.</i> 2025)

6	<i>Ferrisia virgata</i> Cockerell, 1893	Mango, cocoa	(Asiri & Bakry, 2025; Puig <i>et al.</i> 2021)
7	<i>Paraputo raufi</i> Zarkani & Kaydan, sp. nov., 2025 <i>Paraputo martonoi</i> Zarkani & Kaydan, sp. nov., 2025	Forest trees	(Zarkani <i>et al.</i> 2025)
8	<i>Trionymus icelandensis</i> Gerö & Szita, sp. Nov., 2025	Tropical fruits, botanical garden	(Gerö <i>et al.</i> 2025)
9	<i>Pseudococcus longispinus</i> Targioni-Tozzetti, 1867	Not specified	(Vacas <i>et al.</i> 2024; Ballesteros <i>et al.</i> 2023; Caballero <i>et al.</i> 2024; Caballero <i>et al.</i> 2024)
10	<i>Peliococcus schmuttereri</i> Caballero & Kaydan sp. Nov., 2024	Japanese maple	(Caballero <i>et al.</i> 2024)
11	<i>Saccharicoccus sacchari</i> Cockerell, 1895	Sugarcane	(Monteiro <i>et al.</i> 2024; Oliveira <i>et al.</i> 2023; Monteiro <i>et al.</i> 2023)
12	<i>Delottococcus aberiae</i> De Lotto, 1961	Citrus	(Plata <i>et al.</i> 2024)
13	<i>Pseudococcus calceolariae</i> Maskell, 1879	Not specified	(Ballesteros <i>et al.</i> 2023)
14	<i>Planococcus citri</i> Risso, 1813	Citrus, rose	(Herrick and Cloyd 2023; de Paula <i>et al.</i> 2022; Laterza <i>et al.</i> 2024; Carvalho <i>et al.</i> 2023)
15	<i>Dysmicoccus boninsis</i> Kuwana, 1909	Coffee	(Oliveira <i>et al.</i> 2023)
16-17	<i>Dysmicoccus zeynepae</i> Zarkani & Kaydan sp. nov., 2023, <i>Dysmicoccus arachidis</i> Williams, 1978, <i>Dysmicoccus carens</i> Williams, 2004, <i>Pseudococcus leptotrichotus</i> Green, 1922	Wild and cultivated plants	(Zarkani <i>et al.</i> 2023)
18	<i>Pseudococcus viburni</i> Signoret, 1875	Citrus	(Soler <i>et al.</i> 2021; Pacheco <i>et al.</i> 2021)
19	<i>Nipaecoccus viridis</i> Newstead, 1894	Citrus, various fruits, vegetables, ornamental plants	(Olabiyyi <i>et al.</i> 2022); (Middleton <i>et al.</i> 2024); (Diepenbrock & Ahmed, 2021)
20	<i>Planococcus ficus</i> Signoret, 1875	Grapevine, grapes	(Ricciardi <i>et al.</i> 2022); (Muştu <i>et al.</i> 2022;

			Pacheco <i>et al.</i> 2021); (Correa <i>et al.</i> 2023)
21	<i>Drosicha mangiferae</i> Green, 1908	Citrus	(Rizwan <i>et al.</i> 2022)
22	<i>Paracoccus marginatus</i> Williams & Granara de Willink, 1992	Spicy jatropa	(Lin <i>et al.</i> 2025; Liang <i>et al.</i> 2021); Finch <i>et al.</i> 2024)
23	<i>Maconellicoccus hirsutus</i> Green, 1908	Various plants (>55 species), cocoa	(Dos Santos <i>et al.</i> 2022; Puig <i>et al.</i> 2021; de López <i>et al.</i> 2025)
24	<i>Pseudococcus sociabilis</i> Hambleton, 1941	Not specified	(Pacheco <i>et al.</i> 2021)
25	<i>Phenacoccus madeirensis</i> Green, 1923	Tomato, eggplant, pepper, pepino	(Bilgin <i>et al.</i> 2021)
26	<i>Phenacoccus manihoti</i> Matile-Ferrero, 1977	Cassava	(Gupta <i>et al.</i> 2021)
27	<i>Pseudococcus jackbeardsleyi</i> Gimpel & Miller, 1996	Cocoa, seed-rhizome ginger	(Puig <i>et al.</i> 2021; Rohimatun <i>et al.</i> 2024)
28	<i>Dysmicoccus neobrevipes</i> Beardsley, 1959	Sisal	(Li <i>et al.</i> 2025)
29	<i>Pseudococcus ficus</i> Signoret, 1875	Grapevine	(Ricciardi <i>et al.</i> 2021)
30	<i>Pseudococcus maritimus</i> Ehrhorn, 1900	Apple	(Moretti & Schmidt-Jeffris, 2025)
31	<i>Phenacoccus solani</i> Ferris, 1918	Cotton rose hibiscus	(Huang <i>et al.</i> 2022)
32	<i>Planococcus vitis</i> Niedielski, 1891	Grapes	(Correa <i>et al.</i> 2023)

In contrast, other species demonstrated marked host specificity. *Saccharicoccus sacchari* was consistently associated with sugarcane across multiple studies (Monteiro *et al.* 2023, 2024; Oliveira *et al.* 2023), while *Dysmicoccus boninsis* and *Phenacoccus manihoti* were predominantly linked to coffee and cassava, respectively (Oliveira *et al.* 2023; Gupta *et al.* 2021). Notably, a newly recorded host association was reported for *Pseudococcus jackbeardsleyi*, which was documented infesting ginger rhizomes, thereby expanding its known host range (Rohimatun *et al.* 2024).

Recent studies also contributed substantially to taxonomic knowledge and distribution records. Newly described species, including *Paraputo raufi* and *Paraputo martoni* (Zarkani *et al.* 2025) and *Dysmicoccus zeynepae* (Zarkani *et al.* 2023), along with new regional records such as *Trionymus icelandensis* (Gerö *et al.* 2025), highlight that mealybug diversity and host associations remain incompletely documented. Collectively, the results emphasize the ecological flexibility of several widely distributed mealybug species and underscore the need for continued surveillance and accurate host documentation.

Research themes and focus on natural enemies

A systematic analysis of 56 mealybug-related studies published between 2021 and 2025 reveals a markedly uneven distribution of research effort across thematic areas (Table 2; Figure 3). Research output is predominantly concentrated on applied biological control, which accounts for 53.6% (n = 30) of all publications. Within this category, a strong traditional bias toward single-guild approaches is evident. Parasitoid-only studies constitute the largest proportion of the literature (21.4% of total publications), reflecting the continued reliance on encyrtid wasps—such as *Anagyrus*, *Aenasius*, *Acerophagus*, and *Leptomastix*—as cornerstone biological control agents. In contrast, studies focusing exclusively on predators or entomopathogenic pathogens were less frequent, each representing 10.7% of the total literature.

Table 2. Categorization and distribution of research topics across 56 mealybug (*Pseudococcidae*) publications from 2021–2025

Sub-category	N	% of total	Representative studies (No.)	Key characteristics
Parasitoid-only	12	21.4 %	(Ricciardi <i>et al.</i> 2021; Khudhair <i>et al.</i> 2025; Soler <i>et al.</i> 2021; Chen <i>et al.</i> 2021; Kahya <i>et al.</i> 2021; Pacheco Da Silva <i>et al.</i> 2021; Muştu <i>et al.</i> 2022; Laterza <i>et al.</i> 2024; de López <i>et al.</i> 2025; Finch <i>et al.</i> 2024; Huang <i>et al.</i> 2022; Le <i>et al.</i> 2023)	Focus on Encyrtidae parasitoids (<i>Anagyrus</i> , <i>Aenasius</i> , <i>Acerophagus</i> , <i>Leptomastix</i>); laboratory and field parasitism assays
Predator-only	6	10.7 %	(de Paula <i>et al.</i> 2022; Lin <i>et al.</i> 2025; Dos Santos <i>et al.</i> 2022; Li <i>et al.</i> 2025; Carvalho <i>et al.</i> 2023; Moretti & Schmidt-Jeffris 2025)	Primarily Coccinellidae and Chrysopidae; evaluation of predation rates, functional responses, or population-level impacts
Entomopathogens-only	6	10.7 %	(Monteiro <i>et al.</i> 2024; Herrick & Cloyd 2023; Olabiyi <i>et al.</i> 2022; Panti <i>et al.</i> 2024; Zart <i>et al.</i> 2021; Mathulwe <i>et al.</i> 2023)	Entomopathogenic fungi and nematodes; virulence and mortality screening
Two-agent: predator + parasitoid (exploratory/descriptive)	5	8.9 %	(Kondo <i>et al.</i> 2022; Ricupero <i>et al.</i> 2025; Middleton <i>et al.</i> 2024; Gupta <i>et al.</i> 2021; Othim <i>et al.</i> 2024)	Studies reporting the co-occurrence or parallel use of two natural enemy guilds (predator–parasitoid); limited or no experimental testing of combined efficacy or interaction outcomes
Two-agent: predator + entomopathogen	1	1.8 %	El-Aalaoui <i>et al.</i> 2024	Studies reporting the co-occurrence or parallel use of two natural enemy guilds (predator–entomopathogens); (experimental interaction study)
Foundational research informing biological control	26	46.4 %	(Mardiningsih <i>et al.</i> 2025; Zarkani <i>et al.</i> 2025; Gerö <i>et al.</i> 2025; Caballero <i>et al.</i> 2024; Oliveira <i>et al.</i> 2023; Zarkani <i>et al.</i> 2023; Rohimatun <i>et al.</i> 2024; Correa <i>et al.</i> 2023; Ezech <i>et al.</i> 2025; Asiri & Bakry 2025; Bakry & Abdel-Baky 2024; Monteiro <i>et</i>	Taxonomy, ecology, chemical ecology, and invasion studies providing essential baseline data for biological control implementation

al. 2023; Rizwan *et al.* 2022;
Moreno *et al.* 2021; Bilgin *et al.*
2021; Vacas *et al.* 2024;
Ballesteros *et al.* 2023; Ricciardi
et al. 2022; Wang *et al.* 2023;
Liang *et al.* 2021; Plata *et al.*
2024; Burgio *et al.* 2025; Puig *et*
al. 2021; Diepenbrock & Ahmed
2021)

Despite a gradual increase in studies involving more than one natural enemy guild, research on integrated, multi-agent biological control remains severely limited. Only six studies (10.7%) were explicitly categorized as investigating multi-agent systems (Table 2). A deeper qualitative analysis of these studies (Table 6) revealed a critical methodological gap: only two of these six multi-agent studies were designed as controlled experiments to test interactive effects between natural enemy guilds (El-Aalaoui *et al.* 2024; Finch *et al.* 2024). The remaining four were descriptive or exploratory, reporting co-occurrence without manipulative tests of combined efficacy. Notably, no study assessed three-agent systems involving predators, parasitoids, and entomopathogens. Collectively, these findings indicate a profoundly compartmentalized research approach that remains misaligned with the holistic principles of Integrated Pest Management (IPM). This pattern indicates a compartmentalized research approach that remains misaligned with the holistic and integrative principles underpinning Integrated Pest Management (IPM).

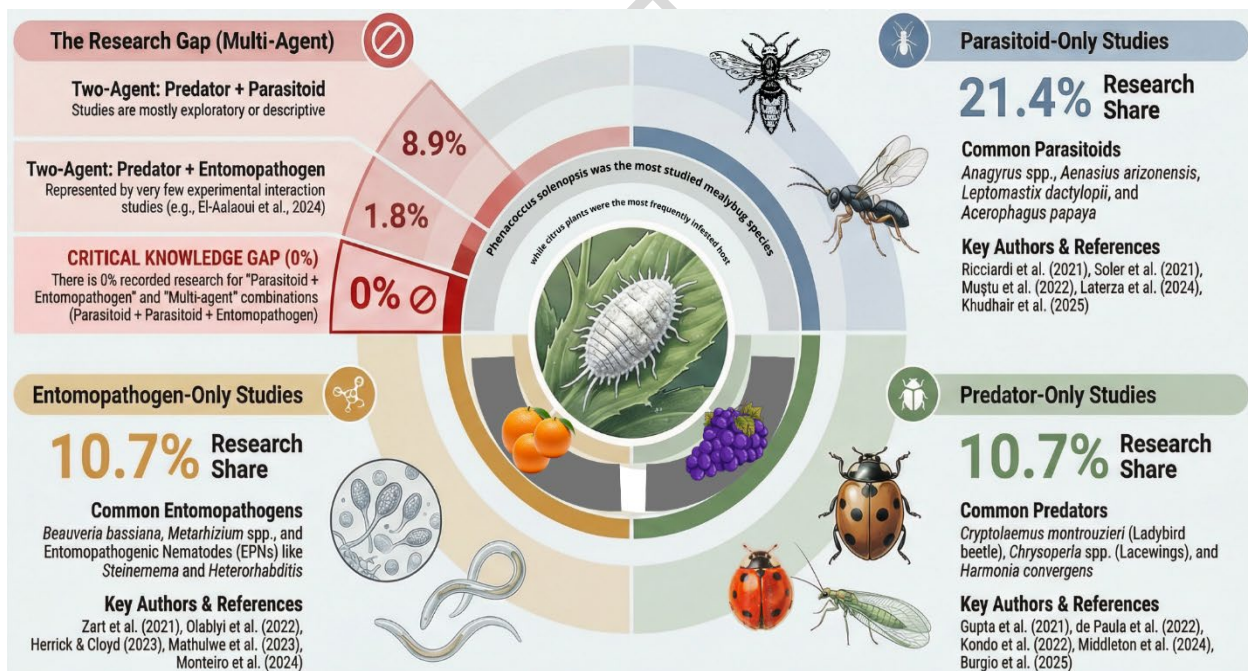


Figure 3. Conceptual synthesis of research intensity and knowledge gaps in mealybug biological control (2021–2025)

The remaining 44.6% ($n = 25$) of the literature comprised studies that did not evaluate natural enemies and were therefore characterized by greater thematic fragmentation. Foundational

research areas—namely taxonomy/systematics and ecology/population dynamics—each represented 14.3% of total publications, highlighting the continued challenges associated with accurate species with identification and the understanding of basic ecological processes. In contrast, mechanistic and forward-looking research domains critical for anticipating pest adaptation and invasion dynamics, including chemical ecology (5.4%), molecular physiology (3.6%), and explicit pest risk or invasion assessments (3.6%), were markedly underrepresented. This imbalance reveals a substantial knowledge gap that constrains our capacity to predict, prevent, and proactively manage mealybug invasions under accelerating global change pressures.

A. Predator

The management of mealybug populations in agricultural systems is significantly influenced by the activity of various predatory species. These natural enemies play a crucial role as biological control agents by directly reducing pest numbers through predation. The following analysis presents a synthesis of recent research documenting the interactions between specific mealybug species, their host plants, and their associated predators. This compilation serves to highlight the diversity of predatory species involved in the natural regulation of mealybugs across different cropping systems and geographical regions (Table 3).

Table 3. Predators associated with mealybug species based on 56 articles published between 2021–2025

Mealybug species	Host plant(s)	Predator	Reference
<i>Dysmicoccus brevipes</i> Cockerell, 1893	Pineapple	<i>Pseudiasata</i> sp.	(Kondo <i>et al.</i> 2022)
<i>Planococcus citri</i> Risso, 1813	Rose and pumpkin	<i>Chrysoperla externa</i> Hagen, 1861, <i>Cryptolaemus montrouzieri</i> Mulsant, 1853	(de Paula <i>et al.</i> 2022); (Carvalho <i>et al.</i> 2023)
<i>Nipaecoccus viridis</i> Newstead, 1894	Citrus	<i>Cryptolaemus montrouzieri</i> Mulsant, 1853, <i>Chrysoperla carnea</i> Stephens, 1836, <i>Euborellia annulipes</i> Lucas, 1847, <i>Ceraeochrysa</i> sp., <i>Fragosa</i> sp., dan <i>Anatrachyntis badia</i> Hodges, 1962.	(Middleton <i>et al.</i> 2024)
<i>Maconellicoccus hirsutus</i> Green, 1908	Fruits, vegetables, ornamentals	<i>Ceraeochrysa everes</i> Banks, 1910	(Dos Santos <i>et al.</i> 2022)
<i>Pseudococcus comstocki</i> Kuwana, 1902	Grapevine	<i>Cryptolaemus montrouzieri</i> Mulsant, 1853	(Burgio <i>et al.</i> 2025)

<i>Dysmicoccus neobrevipes</i> Beardsley, 1959	Sisal	<i>Plesiochrysa ramburi</i> Schneider, 1851, <i>Apertochrysa roseusfrontata</i> Freitas & Penny, 2001	(Li <i>et al.</i> 2025)
<i>Phenacoccus manihoti</i> Matile-Ferrero, 1977	Cassava	<i>Hyperaspis maindroni</i> Sicard, 1929, <i>Cheilomenes sexmaculata</i> Fabricius, 1781, <i>Mallada desjardinsi</i> Navás, 1911, <i>Pseudomallada astur</i> Banks, 1910, <i>Apertochrysa</i> sp., <i>Spalgis epius</i> Westwood, 1851, <i>Stathmopoda</i> sp., <i>Anarhopsyra</i> sp., <i>Nola</i> sp., <i>Thyenis imperialis</i> C. L. Koch, 1848, <i>Carrhotus viduus</i> C. L. Koch, 1846, <i>Thomismus pugilis</i> Stoliczka, 1869	(Gupta <i>et al.</i> 2021)
<i>Phenacoccus solenopsis</i> Tinsley, 1898	Purslane	<i>Harmonia convergens</i> Guérin-Méneville, 1842	(El-Aalaoui <i>et al.</i> 2024)
<i>Pseudococcidae</i> sp	Coffee	<i>Coccinellidae</i> sp	(Othim <i>et al.</i> 2024)
<i>Pseudococcus maritimus</i> Ehrhorn, 1900	Apple	<i>Cryptolaemus montrouzieri</i> Mulsant, 1853	(Moretti & Schmidt-Jeffris, 2025)

The compiled data reveals several important patterns in predator-mealybug interactions. *Cryptolaemus montrouzieri* Mulsant, 1853 emerges as a generalist predator with documented efficacy against multiple mealybug species, including *Planococcus citri* Risso, 1813 on rose crops and *Nipaecoccus viridis* Newstead, 1894 on citrus. This coccinellid beetle demonstrates considerable versatility in targeting different mealybug species across varied agricultural environments. The family Chrysopidae is well-represented among the identified predators, with multiple species showing effective predation capabilities. *Chrysoperla externa* Hagen, 1861, *Ceraeochrysa* sp, and *Apertochrysa* sp have all been reported as successful predators against various mealybug infestations, indicating the important role of lacewings in biological control programs.

Notably, the study by Gupta *et al.* (2021) documents an exceptionally diverse predator complex associated with *Phenacoccus manihoti* Matile-Ferrero, 1977 on cassava, encompassing species from Coleoptera, Neuroptera, Lepidoptera, and Araneae orders. This diversity suggests the potential for integrated predator communities in certain cropping systems, which may enhance biological control through complementary predation strategies. The data further indicates some degree of predator specialization, with certain species showing association with specific mealybug-host plant systems. For instance, *Pseudiasata* sp. was specifically reported preying on *Dysmicoccus brevipes* Cockerell, 1893 in pineapple, while *Harmonia convergens* Guérin-Méneville, 1842 was documented attacking *Phenacoccus solenopsis* Tinsley, 1898 on *Portulaca oleracea*.

B. Parasitoid

Beyond predation, parasitoids represent a highly specialized and effective group of natural enemies in the biological control of mealybugs. These organisms, primarily from the order Hymenoptera, employ a unique strategy of developing on or within a single host, ultimately leading to host death. The following analysis synthesizes recent research documenting the complex relationships between specific mealybug species and their associated parasitoids, highlighting the diversity and specificity of these interactions across different ecosystems and agricultural contexts. (Table 4).

Table 4. Parasitoids associated with mealybug species based on 56 articles published between 2021–2025

Mealybug species	Host plant(s)	Parasitoid	Reference
<i>Pseudococcus comstocki</i> Kuwana, 1902	Potato	<i>Anagyrus vladimiri</i> Triapitsyn, 2005	(Ricciardi <i>et al.</i> 2021)
<i>Phenacoccus solenopsis</i> Tinsley, 1898	Cotton	<i>Aenasius arizonensis</i> Girault, 1915, <i>Cheiloneurus nankingensis</i> Li & Xu, 1997, <i>Marietta pictus</i> André, 1878	(Khudhair <i>et al.</i> 2025)
<i>Pseudococcus viburni</i> Signoret, 1875	Citrus	<i>Anagyrus fusciventris</i> Girault, 1915, <i>Anagyrus borrianensis</i> Soler, 2021, <i>Anagyrus pseudococci</i> Girault, 1915, <i>Anagyrus vladimiri</i> Triapitsyn, 2005	(Soler <i>et al.</i> 2021)
<i>Phenacoccus solenopsis</i> Tinsley, 1898	<i>Lantana camara</i>	<i>Aenasius arizonensis</i> Girault, 1915, <i>Anagyrus matritensis</i> Alonso-Zarazaga, 2022	(Ricupero <i>et al.</i> 2025)
<i>Phenacoccus solenopsis</i> Tinsley, 1898	Various host plants	18 Hymenoptera species, including <i>Aenasius arizonensis</i> Girault, 1915, <i>Cheiloneurus nankingensis</i> Li & Xu, 1997	(Chen <i>et al.</i> 2021)
<i>Phenacoccus solenopsis</i> Tinsley, 1898	Not specified	<i>Aenasius arizonensis</i> Girault, 1915	(Kahya <i>et al.</i> 2021)
<i>Nipaecoccus viridis</i>	Citrus	<i>Anagyrus dactylopii</i> Howard, 1898, <i>Aprostocetus</i> sp.	(Middleton <i>et al.</i> 2024)
<i>Planococcus ficus</i> Signoret, 1875, <i>Pseudococcus sociabilis</i> Hambleton, 1941, <i>Pseudococcus viburni</i> Signoret, 1875	Not specified	<i>Acerophagus flavidulus</i> Brèthes, 1914, <i>Anagyrus calyxtoi</i> Zuparko, 2016, <i>Zaplatycerus</i> sp., <i>Chartocerus axillaris</i> Mercet, 1922	(Pacheco Da Silva <i>et al.</i> 2021)
<i>Planococcus ficus</i> Signoret, 1875	Grapevine, <i>Morus alba</i>	<i>Leptomastix dactylopii</i> Howard, 1885	(Muştu <i>et al.</i> 2022)
<i>Planococcus citri</i> Risso, 1813	Citrus	<i>Leptomastix dactylopii</i> Howard, 1885	(Laterza <i>et al.</i> 2024)
<i>Phenacoccus manihoti</i> Matile-Ferrero, 1977	Cassava	<i>Homolotypus turkmenicus</i> Myartseva, 1979, <i>Metateris concinnus</i> Walker,	(Gupta <i>et al.</i> 2021)

		1836, <i>Tetrastichus</i> sp., <i>Brachycyrtus</i> sp., <i>Anthrocephalus japonicus</i> Masi, 1933, <i>Apanteles</i> sp., <i>Brachymeria</i> sp., <i>Hockeria nikolskaye</i> Husain & Agarwal, 1982, <i>Eurytoma</i> sp.	
<i>Maconellicoccus hirsutus</i> Green, 1908	>55 plant species	<i>Anagyrus kamali</i> Moursi, 1948	(de López <i>et al.</i> 2025)
Pseudococcidae sp.	<i>Coffea</i> sp.	<i>Aenasius caeruleus</i> Ashmead, 1900, <i>A. bolowi</i> Girault, 1924, <i>A. tachigaliae</i> Kerrich, 1967, <i>Aenasius aff. mitchellae</i> , <i>Zarhopalus putophilus</i> Timberlake, 1924, <i>Hambletonia pseudococcina</i> Compere, 1936, <i>Hambletonia</i> sp., <i>Prochiloneurus aff. dactylopii</i> , <i>Leptomastix</i> sp., <i>Cicoencyrtus</i> sp. (Encyrtidae), <i>Cecidomyiidae</i> (Diptera)	(Othim <i>et al.</i> 2024)
<i>Paracoccus marginatus</i> Williams & Granara de Willink, 1992	Papaya and cassava	<i>Acerophagus papaya</i> Noyes & Schauuff, 2003	(Finch <i>et al.</i> 2024); (Le <i>et al.</i> 2023)
<i>Phenacoccus solenopsis</i> Tinsley, 1898, Ferris, 1918	Cotton rose hibiscus	<i>Aenasius arizonensis</i> Girault, 1915	(Huang <i>et al.</i> 2022)

The compiled data reveal several significant patterns in parasitoid-mealybug interactions. *Phenacoccus solenopsis* Tinsley, 1898 emerges as a species attacked by a particularly diverse parasitoid complex, with *Aenasius arizonensis* Girault, 1915 consistently identified as a dominant and widespread primary parasitoid across multiple studies and regions. Research by Chen *et al.* (2021) further underscores this by documenting a remarkable 18 Hymenoptera species associated with *P. solenopsis*, comprising both primary and hyperparasitoids, indicating a complex multi-trophic web. The genera *Anagyrus* and *Leptomastix* are prominently represented among the effective parasitoids. *Anagyrus* species demonstrate a broad host range, parasitizing various mealybugs including *Pseudococcus comstocki* Kuwana, 1902, *Pseudococcus viburni* Signoret, 1875, and *Maconellicoccus hirsutus*. Conversely, *Leptomastix dactylopii* Howard, 1885 shows a more specialized association with the *Planococcus* genus, effectively targeting both *Planococcus ficus* Signoret, 1875 on grapevines and *Planococcus citri* Risso, 1813 on citrus. The study by Gupta *et al.* (2021) reveals an exceptionally rich parasitoid fauna associated with *Phenacoccus manihoti* Matile-Ferrero, 1977 on cassava, encompassing multiple families within Hymenoptera. This diversity suggests the potential for robust natural biological control in certain cropping systems where these parasitoid communities are conserved.

Notably, the data indicate a degree of ecological adaptability, with some parasitoids like *Anagyrus vladimiri* Triapitsyn, 2005 successfully targeting different mealybug species (*Pseudococcus comstocki* Kuwana, 1902 and *Pseudococcus viburni* Signoret, 1875) on different host plants. This versatility enhances their value in integrated pest management programs across varied agricultural landscapes.

C. Entomopathogens

Entomopathogens represent a third crucial pillar in the natural regulation of mealybug populations, employing a microbial approach to control. These entomopathogenic organisms, including fungi, nematodes, and other microorganisms, infect and ultimately kill their hosts, providing a powerful biological control mechanism. The following analysis examines recent research on the entomopathogens associated with various mealybug species, highlighting the diversity of microbial agents and their potential applications in integrated pest management programs (Table 5).

Table 5. Entomopathogens associated with mealybug species and their host plants (2021–2025)

Mealybug species	Host plant(s)	Entomopathogens	Reference
<i>Saccharicoccus sacchari</i> Cockerell, 1895	Sugarcane	Entomopathogenic nematodes (<i>Steinernema rarum</i> Doucet, 1986, <i>Heterorhabditis bacteriophora</i> Poinar, 1976, <i>Steinernema carpocapsae</i> Weiser, 1955)	(Monteiro, Paulo, <i>et al.</i> 2024)
<i>Planococcus citri</i> Risso, 1813	Citrus	<i>Beauveria bassiana</i> (Bals.-Criv.) Vuill., 1912	(Herrick & Cloyd, 2023)
<i>Nipaecoccus viridis</i> Newstead, 1894	Citrus	<i>Beauveria bassiana</i> (Bals.-Criv.) Vuill., 1912	(Olabiya <i>et al.</i> 2022)
<i>Dysmicoccus brevipes</i> Cockerell, 1893	Pineapple	<i>Beauveria bassiana</i> (Bals.-Criv.) Vuill., 1912, <i>Metarhizium anisopliae</i> (Metschn.) Sorokin, 1883, <i>Paecilomyces fumosoroseus</i> (Wize) A.H.S. Br. & G. Sm., 1957	(Panti <i>et al.</i> 2024)
<i>Phenacoccus solenopsis</i> Tinsley, 1898	<i>Portulaca oleracea</i>	<i>Alternaria murispora</i> (J.J. Davis) E.G. Simmons, 2007	(El-Aalaoui <i>et al.</i> 2024)
<i>Dysmicoccus brevipes</i> Cockerell, 1893	Cassava	Entomopathogenic nematodes (<i>Heterorhabditis amazonensis</i> Andalo, Nguyen & Moino, 2006, <i>H. indica</i> Poinar, Karunakar & David, 1992)	(Zart <i>et al.</i> 2021)
<i>Pseudococcus viburni</i> Signoret, 1875	Not specified	<i>Metarhizium pinghaense</i> Q.T. Chen & H.L. Guo, 1986 & <i>Metarhizium robertsii</i> J.F. Bisch., Rehner & Humber, 2009	(Mathulwe <i>et al.</i> 2023)

The analysis of entomopathogens reveals distinct patterns in research focus and practical potential for mealybug management. The fungus *Beauveria bassiana* (Bals.-Criv.) Vuill., 1912 is the most extensively studied and versatile pathogen, documented effectively against multiple mealybug genera—including *Planococcus citri* Risso, 1813 on citrus (Herrick & Cloyd, 2023), *Nipaecoccus viridis* Newstead, 1894 on citrus (Olabiya *et al.* 2022), and *Dysmicoccus brevipes* Cockerell, 1893 on pineapple (Panti *et al.* 2024). Its broad-spectrum activity is further supported by comparative research by Panti *et al.* (2024), where *B. bassiana* outperformed other fungi like

Metarhizium anisopliae (Metschn.) Sorokin, 1883 and *Paecilomyces fumosoroseus* Wize) A.H.S. Br. & G. Sm., 1957 against *Dysmicoccus brevipes* Cockerell, 1893, causing up to 66% mortality.

Entomopathogenic nematodes demonstrate high, context-specific efficacy. Species such as *Heterorhabditis amazonensis* Andalo, Nguyen & Moino, 2006 achieved remarkable virulence (93.8% mortality) against *D. brevipes* on cassava (Zart *et al.* 2021), while others like *Steinernema carpocapsae* Weiser, 1955 were tested against *Saccharicoccus sacchari* on sugarcane (Monteiro *et al.* 2024). This suggests that nematodes may be particularly suitable for managing mealybugs in monocot-based or soil-influenced cropping systems, where environmental conditions favor their survival and host-seeking behavior.

Notably, research also identified non-conventional microbial agents with untapped potential. The pathogenicity of *Alternaria murispora* against *Phenacoccus solenopsis* (El-Aalaoui *et al.* 2024) represents a novel finding, highlighting opportunities for discovering and developing new biocontrol resources beyond established fungal and nematode taxa. Similarly, *Metarhizium pinghaense* and *M. robertsii* have shown activity against *Pseudococcus viburni* (Mathulwe *et al.* 2023), expanding the known spectrum of entomopathogenic fungi against mealybugs.

D. Synthesis of multi-agent interactions: evidence from case studies

To move beyond merely documenting the scarcity of multi-agent studies (Table 2) and provide deeper insight into their quality and outcomes, we conducted a qualitative analysis of six representative cases (Table 6). These cases illustrate the spectrum of methodological rigor in multi-agent research, from simple co-occurrence reports to experimentally managed synergistic systems.

Table 6. The spectrum of multi-agent study designs and outcomes in mealybug biological control: from descriptive co-occurrence to experimental synergy

No.	Mealybug species & location	Agent combination tested/found	Type of combination	Main outcome (effectiveness)	Evidence of interaction & dynamics	Level of evidence & study type
1	<i>Dysmicoccus brevipes</i> (Colombia)	<i>Hambletonia pseudococcina</i> (parasitoid) + <i>Pseudiaspata</i> sp. (predator)	Parasitoid + predator	Co-reported, combination efficacy not tested.	Found in the same host aggregation. Potential spatial synergy.	Initial exploration (survey). Observational evidence.
2	<i>Phenacoccus solenopsis</i> (Italy)	<i>Aenasius arizonensis</i> , <i>Anagrus matritensis</i> (Parasitoid) + <i>Cryptolaemus montrouzieri</i> , etc. (Predator)	Parasitoid + predator	Reported in natural community. Combination efficacy not tested.	Evidence of natural enemy diversity. Risk of intraguild predation noted.	Initial exploration (survey). Observational evidence.
3	<i>Nipaecoccus viridis</i> (Florida, USA)	A. Survey: 8+ species (parasitoid+predator). B. Augmentation experiment: C.	Survey: complex community. Experiment: single agent.	Single augmentation effective but not sustainable. Pest population	Highlights the need for sustainability potentially provided by a	Combination: exploration + partial experiment. Evidence that a

		<i>montrouzieri</i> (alone).		rebounded after predator died off.	multi-agent community.	single agent is insufficient.
4	<i>Phenacoccus manihoti</i> (India)	Complex community predator + hyperparasitoids). Primary parasitoids absent.	Predator + 4th trophic level agents (hyperparasitoids)	Unmanaged combination leads to failure. Hyperparasitoids weakened key predators (>63% parasitism).	Empirical example of destructive negative interference. High diversity is not a guarantee of success.	In-depth ecological analysis (food web). Strong evidence of risks.
5	<i>Paracoccus marginatus</i> (Kenya)	<i>Acerophagus papayae</i> (specialist parasitoid) + <i>Cryptolaemus montrouzieri</i> , etc. (generalist predators) via NEFR.	Parasitoid + predator + management technology (NEFR).	Managed combination highly effective. Reduced pests >62%, parasitism increased >116%, predator abundance rose.	NEFR simultaneously enhanced parasitoid and predator populations, creating managed synergy.	Field experiment (technology test). Direct experimental evidence of successful synergy.
6	<i>Phenacoccus solenopsis</i> (Morocco)	<i>Alternaria murispora</i> (entomopathogenic fungus) + <i>Harmonia convergens</i> (predator).	Entomopathogen + predator (different guilds).	Combination was the most effective. Lowest pest density (0.8/leaf), highest plant quality (9.9/10). Superior to single-agent treatments.	Proven functional synergy. Predator suspected to aid fungal conidia dispersal. A <i>trade-off</i> observed (lower predator population).	Controlled experiment (screenhouse). Strong experimental evidence of cross-guild synergy.

The case studies in Table 6 demonstrate a spectrum of outcomes that underscore the central finding of this review: simply documenting co-occurrence or releasing multiple agents (e.g., Cases 1, 2, and 3) is insufficient for sustainable control. Success depends critically on the type of interaction and active management. The failure in Case 4 (*P. manihoti*) illustrates the devastating impact of negative interference from a higher trophic level (hyperparasitoids), affirming that high natural enemy diversity does not guarantee pest suppression. Conversely, Cases 5 and 6 provide experimental proof that functional synergy is achievable. The success in Case 5 was driven by a management technology (NEFR) that simultaneously boosted both parasitoid and predator populations, while Case 6 demonstrated a cross-guild synergy between an entomopathogen and a predator. These cases, drawn from our systematic review, demonstrate that among the limited multi-agent studies (10.7% of the total), outcomes vary widely, serve as critical models for future research. They move beyond the predominant single-agent paradigm and show that the next frontier in mealybug biological control lies in intentionally designing and managing multi-agent systems based on an understanding of their ecology and interactions.

Vos viewer analysis

The bibliometric visualization represents conceptual structures within the included biocontrol-oriented corpus and does not depict ecological relationships of mealybugs in nature. The network map illustrates the co-occurrence structure of keywords extracted from 56 peer-reviewed articles on mealybugs (Pseudococcidae) published between 2021 and 2025. The analysis reveals "biological control" as the most prominent research theme, followed closely by "parasitoid" and taxonomic terms ("taxonomy," "Pseudococcidae," "Hemiptera"), underscoring the field's strong foundation in classical biocontrol and systematics. Specific natural enemies ("Aenasius arizonensis"), host plants ("citrus," "sugarcane"), and methodological terms ("life table," "identification key") feature noticeably, highlighting focal points within applied research. While modern tools like "DNA barcoding" and ecological concepts such as "invasive species" and "population dynamics" are present, their relative size indicates they remain secondary to the core taxonomic and parasitoid-based paradigm. This visual synthesis confirms that recent mealybug biocontrol research remains anchored in traditional entomological approaches (Figure 4).

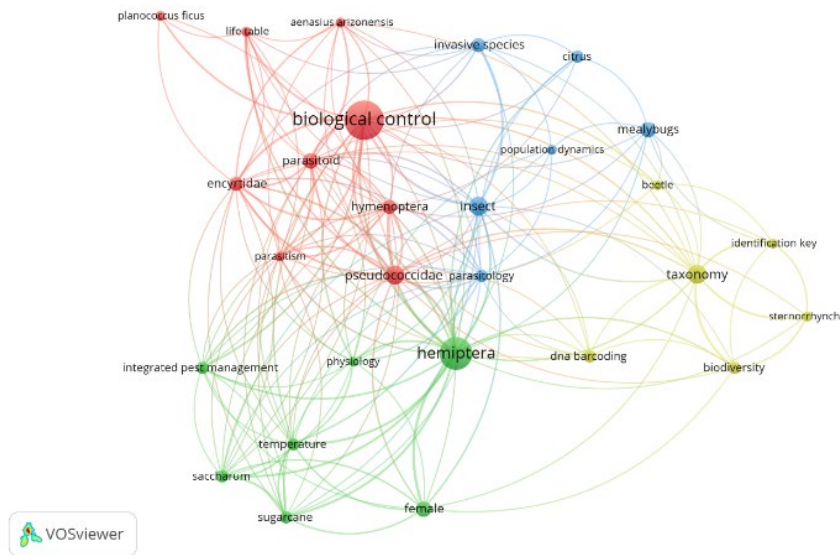


Figure 4. Network visualization of mealybug research themes in mealybug studies (2021–2025).

This overlay map depicts the temporal distribution of keyword usage, with node color indicating the average publication year. Earlier studies (blue tones) are predominantly associated with taxonomy, parasitoids, parasitism, and life-history traits, whereas more recent publications (green to yellow tones) increasingly emphasize integrated pest management, temperature-related factors, population dynamics, biodiversity, and molecular tools such as "DNA barcoding". The visualization suggests a gradual thematic shift toward more environmentally informed and systemic approaches, while core research themes like "biological control" and "parasitoid" remain persistently central over time (Figure 5).

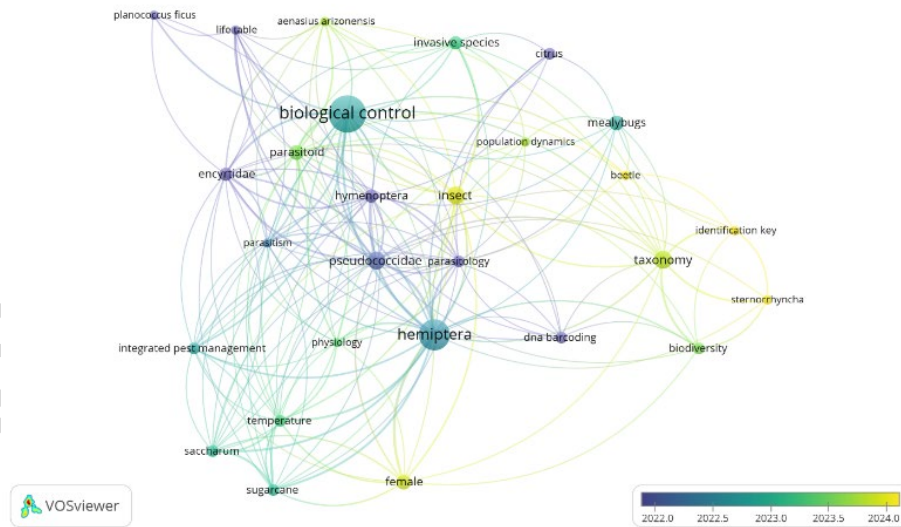


Figure 5. Overlay visualization showing temporal evolution of research themes in mealybug studies (2021–2025).

The density map highlights areas of high and low research intensity based on keyword frequency and co-occurrence density. High-density regions are concentrated around “biological control”, “parasitoids”, “taxonomy”, and Pseudococcidae, confirming these topics as the primary research foci during the study period. In contrast, low-density areas indicate limited attention to technology-based monitoring, automated detection systems, and precision pest management, underscoring significant research gaps and opportunities for future innovation.

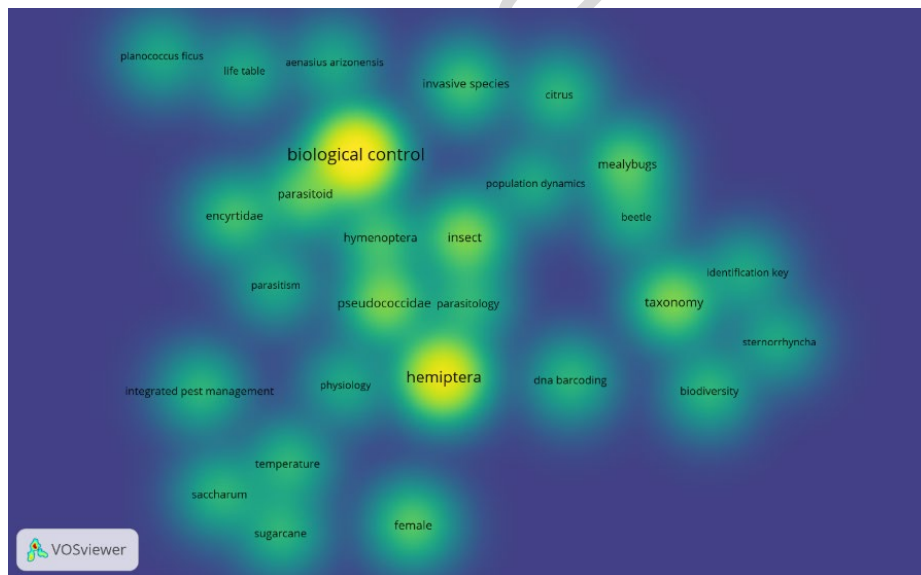


Figure 6. Density visualization of research focus in global mealybug literature (2021–2025)

The density map identifies the most active and concentrated areas of research. Regions in yellow indicate high research density and maturity, such as "biological control" and "taxonomy," whereas blue areas represent niche or emerging topics with less scientific attention. This

visualization effectively pinpoints well-established research fronts and underscores under-explored areas that present opportunities for future investigation.

Discussion

This systematic review synthesized published evidence within the biocontrol-oriented literature on documented mealybug occurrences, host plant associations, and natural enemies reported between 2021 and 2025. This review examines patterns in biocontrol-oriented literature on mealybugs, focusing on research geography, host associations, and documented natural enemies that have significant implications for pest management strategies worldwide.

Global distribution patterns and research focus

Research output was geographically concentrated in Brazil, Italy, the USA, and China, reflecting the origin of publications within the selected dataset rather than the actual distribution of the pest. Brazil contributed 10 studies, primarily addressing sugarcane, coffee, and tropical fruit systems, a pattern that directly correlates with agro-economic exposure. Brazil's research leadership (10 studies) is fundamentally driven by the need to safeguard its sugarcane, coffee, and tropical fruit industries from mealybug threats, as evidenced by focused studies on these systems (Oliveira *et al.* 2023; Monteiro *et al.* 2023). This pattern reinforces a commodity-driven research model, where scientific inquiry is disproportionately allocated to protect high-value capital in the global agri-food system. Such prioritization favors *ex-post* management of established pests in lucrative crops over *ex-ante* surveillance and the ecological study of potential invaders in economically marginal or non-agricultural systems. *Phenacoccus solenopsis* was the most frequently studied species, consistent with its status as a globally invasive and polyphagous pest. Its polyphagy and invasive success warrant attention, yet this very focus may divert resources from understanding the next emergent threat, potentially lurking among the many newly described and cryptic species (Zarkani *et al.* 2023, 2025; Gerő *et al.* 2025). The continued discovery of novel species and range expansions underscores that our biogeographic and taxonomic baselines are incomplete, representing a foundational weakness in global biosecurity frameworks.

Host plant associations and invasion ecology

The review delineates a continuum of host-use strategies that critically informs invasion risk. The contrast between specialists like *Saccharicoccus sacchari* (Monteiro *et al.* 2023, 2024) and extreme generalists like *Maconellicoccus hirsutus* (Dos Santos *et al.* 2022) is not merely ecological trivia but a predictor of invasion pathways and management complexity. The success of polyphagous species like *P. solenopsis* and *Nipaecoccus viridis* provides strong support for the "generalist genotype" hypothesis in invasion biology, whereby broad physiological tolerances and dietary plasticity pre-adapt species for colonizing disturbed, novel environments such as agroecosystems.

Crucially, our synthesis indicates that host ranges are dynamic rather than static traits. The report of *Pseudococcus jackbeardsleyi* on ginger rhizomes (Rohimatun *et al.* 2024) is a salient case of contemporary host-range expansion, likely facilitated by anthropogenic changes. This plasticity challenges the utility of historical host lists for long-term risk assessment and suggests that future invasions may arise from novel ecological fitting, not just the movement of known pest-

host combinations. The recurrent theme of mealybugs on perennial crops (citrus, grapes, coffee) highlights a specific agro-ecological vulnerability: these systems provide stable, resource-rich habitats that can favor mealybug population stability and undermine control tactics reliant on host removal or crop rotation.

Biological control potentials and implementation gaps

The finding that over half (55.4%) of the literature focuses on biological control (BC) underscores its theoretical centrality to mealybug IPM. However, a deeper analysis reveals a field constrained by historical path dependency. The overwhelming emphasis on parasitoid-only studies (21.4% of the total), particularly on encyrtid wasps such as *Anagyrus* and *Aenasius* species (Soler *et al.* 2021; Khudhair *et al.* 2025), reflects an enduring allegiance to a classical, single-species BC paradigm. This paradigm, rooted in the search for highly specific "natural enemy miracles," has yielded successes, but it has also limited conceptual diversification.

This gap is critically highlighted by the contrasting outcomes found within the reviewed literature itself. For instance, Finch *et al.* (2024) and El-Aalaoui *et al.* (2024) empirically demonstrated that managed multi-agent combinations can achieve powerful synergy, while unmanaged systems, as shown by Gupta *et al.* (2021) in India, can fail due to disruptive interference from higher trophic levels. These studies empirically demonstrate that managed multi-agent combinations can achieve powerful synergy, while unmanaged ones, as shown by Gupta *et al.* (2021) in India, can fail due to disruptive interference from higher trophic levels. These results indicate a gap between current research practice and multi-enemy IPM concepts that emphasize interactive effects among natural enemies, which emphasizes that diverse enemy assemblages enhance pest suppression through mechanisms like niche complementarity and spatial insurance. The research community continues to evaluate BC agents as isolated entities, despite the fact that they are deployed and persist within complex arthropod communities where factors like ant-mealybug mutualisms (Soler *et al.* 2021; Burgio *et al.* 2025) and cryptic pest diversity (Pacheco Da Silva *et al.* 2021) critically modulate outcomes.

Research evolution and future priorities

The bibliometric shift toward topics such as climate change, physiology, and molecular tools indicates an encouraging, albeit still nascent, transition toward a more mechanistic and predictive scientific framework. To build on this momentum and address the key gaps identified in the literature, future research must simultaneously advance along three interconnected trajectories.

First, the continued pace of morphological species descriptions (Zarkani *et al.* 2025; Caballero *et al.* 2024) needs to be integrated with molecular phylogenetics and population genomics within an explicitly integrative taxonomic framework, which is essential for resolving cryptic species complexes, accurately reconstructing invasion pathways, and enabling precise matching between invasive mealybugs and their co-evolved natural enemies—a fundamental prerequisite for effective classical biological control.

Second, research must progress from largely correlative ecological analyses toward mechanistic investigations that elucidate the physiological and genetic bases of invasion success, including explicit assessments of thermal tolerance limits (building on Ezeh *et al.* 2025), host-switching capacity under nutritional stress, and the genetic architecture of key adaptive traits;

incorporating these mechanisms into process-based models will enable a shift from reactive documentation toward proactive invasion risk forecasting.

Finally, biological control research must move beyond single-agent evaluations and embrace systems-level experimental designs that explicitly test interactions among predator communities (e.g., Gupta *et al.* 2021), parasitoid assemblages, and entomopathogens such as *Beauveria bassiana* (Herrick & Cloyd, 2023) across spatial and temporal scales, thereby reframing the objective from identifying the “best” individual agent to engineering resilient, multi-species biological control networks capable of withstanding agricultural disturbance and ant–mealybug mutualisms.

Limitations and future research directions

This systematic review has several limitations. First, restricting the search to English-language articles and three major databases (Scopus, PubMed, and Web of Science) may have excluded relevant studies published in other languages or in regional databases. Second, the focus on 2021–2025 literature captures recent trends but may not reflect longer-term ecological patterns or historical invasion pathways. Third, substantial heterogeneity in study designs, outcome metrics, and reporting standards precluded a quantitative meta-analysis, limiting our ability to statistically compare biological control efficacy across studies. Finally, while bibliometric analysis reveals research trends, it cannot assess the quality or practical impact of individual studies.

To mitigate these limitations in future research, we recommend the following actionable strategies. First, expanding database coverage to include specialized agricultural and entomological repositories, along with regional databases in South America, Africa, and Asia, would help reduce language and geographic bias. Second, applying standardized risk-of-bias and quality assessment tools such as SYREAF or ROBIS would improve the reliability and validity of evidence synthesis. Third, developing and adopting uniform reporting frameworks for biological control studies would enhance comparability and support future meta-analyses. Fourth, incorporating grey literature and publications in languages other than English—using translation tools or multilingual review teams when possible—would make systematic reviews more inclusive. Finally, integrating long-term monitoring data with experimental research would allow for a more robust assessment of natural enemy establishment, persistence, and ecological impact under field conditions.

Conclusion

This synthesis reveals a critical paradox in mealybug management science: while IPM principles advocate for a holistic approach, contemporary biological control research remains overwhelmingly compartmentalized, focusing on single agents—parasitoids, predators, or pathogens—in isolation. The stark contrast between the synergistic success of a *managed* parasitoid-predator combination (Finch *et al.* 2024) and the catastrophic failure of an *unmanaged* one due to hyperparasitoids (Gupta *et al.* 2021) provides a powerful object lesson. It demonstrates that the scarcity of robust multi-enemy experiments represents more than just a knowledge gap; it signifies a major operational risk for IPM programs that inadvertently assume that more natural enemies are always better. Geographically, the review reflects the distribution of published research activity rather than an exhaustive map of global mealybug occurrence, with studies concentrated in major agro-economic regions such as Brazil, Italy, and the USA. This bias is inherent to the biocontrol-oriented search strategy and should be considered when interpreting

patterns of distribution and research emphasis. Taxonomically, the literature is strongly focused on well-known invasive species such as *Phenacoccus solenopsis*, which may create blind spots regarding cryptic species and emerging invasions. To transform this trajectory, the research agenda must shift decisively from single-agent evaluations toward experimental studies of multi-enemy systems, strengthened by integrative molecular taxonomy and physiology-based predictive modelling. Convergence with digital technology—including AI-assisted diagnostics and decision-support systems—will pave the way for resilient precision biocontrol. Future studies must be designed to not only test multi-agent combinations but also to identify the management frameworks—be they technological, ecological, or spatial—that can reliably convert diverse natural enemy assemblages into stable, synergistic biological control networks. Only by overcoming this entrenched research fragmentation can we develop truly integrated, adaptive, and sustainable management strategies capable of mitigating the escalating global mealybug threat.

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Summary of the 56 studies on mealybugs (Hemiptera: Pseudococcidae) and their natural enemies included in the systematic review (2021–2025)

Ref. ID	Author (Year)	Country	Mealybug Species	Host Plant	Key Finding / Context
1	(Kondo <i>et al.</i> 2022)	Colombia	<i>Dysmicoccus brevipes</i> (Cockerell, 1893)	Pineapple (<i>Ananas comosus</i>)	First record of <i>Hambletonia pseudococcina</i> and the predatory fly <i>Pseudiastata</i> sp. in Colombia.
2	(Ricciardi <i>et al.</i> 2021)	Italy	<i>Pseudococcus comstocki</i> (Kuwana, 1902)	Potato	<i>Anagyrus vladimiri</i> effectively parasitized <i>P. comstocki</i> with parasitism rates of 51–67%.
3	(Khudhair <i>et al.</i> 2025)	Iraq	<i>Phenacoccus solenopsis</i> Tinsley, 1898	Cotton (nursery)	Recorded three parasitoids; <i>Cheiloneurus nankingensis</i> and <i>Marietta pictus</i> are new country records for Iraq.
4	(Mardiningsih <i>et al.</i> 2025)	Indonesia	<i>Maconellicoccus multipori</i> (Takahashi, 1951)	Black pepper (<i>Piper nigrum</i>)	First molecular confirmation (DNA barcoding) of <i>M. multipori</i> in Indonesia.
5	(Ezeh <i>et al.</i> 2025)	Australia	<i>Hypogeococcus pungens</i> Granara de Willink, 1981	Cactus (<i>Harrisia martinii</i>)	Optimal development at 25 °C; CLIMEX model suggests cold stress limits its biocontrol efficacy in southern Queensland.
6	(Asiri & Bakry, 2025)	Egypt	<i>Ferrisia virgata</i> (Cockerell, 1893)	Mango	Two annual population peaks driven by maximum temperature and solar radiation.
7	(Zarkani <i>et al.</i> 2025)	Indonesia	<i>Paraputo raufi</i> Zarkani & Kaydan, sp. nov., <i>P. martonoi</i> Zarkani & Kaydan, sp. nov.	Forest trees	Description of two new <i>Paraputo</i> species from Borneo, Indonesia.

8	(Gerő <i>et al.</i> 2025)	Iceland	<i>Trionymus icelandensis</i> Gerő & Szita, sp. nov.	Tropical fruits & Botanical Garden	New endemic mealybug species described from Iceland; expands scale insect records for the country.
9	(Vacas <i>et al.</i> 2024)	Spain	<i>Pseudococcus longispinus</i> (Targioni-Tozzetti, 1867)	Not specified	Identified a new sex pheromone attractive to males in field trials.
10	(Caballero <i>et al.</i> 2024)	Germany	<i>Peliococcus schmuttereri</i> Caballero & Kaydan, sp. n.	<i>Acer palmatum</i>	Redescription and validation of a previously invalid species, increasing <i>Peliococcus</i> count in Germany to two.
11	(Bakry & Abdel-Baky, 2024)	Egypt	<i>Phenacoccus solenopsis</i> Tinsley, 1898	Maize (<i>Zea mays</i>)	Infestation peaked three times per season; plant age and weather factors were key drivers.
12	(Monteiro <i>et al.</i> 2023)	Brazil	<i>Saccharicoccus sacchari</i> (Cockerell, 1895)	Sugarcane	More widespread and abundant than <i>Aclerda takahashii</i> ; highest infestation during vegetative and ripening phases.
13	(Plata <i>et al.</i> 2024)	Spain	<i>Delottococcus aberiae</i> De Lotto, 1961	Citrus	Native ant <i>Lasius grandis</i> forms a year-round mutualism, likely facilitating mealybug invasion success.
14	(Monteiro <i>et al.</i> 2024)	Brazil	<i>Saccharicoccus sacchari</i> (Cockerell, 1895)	Sugarcane	<i>Steinernema rarum</i> caused the highest mortality (79.25%) against the pink sugarcane mealybug.
15	(Ballesteros <i>et al.</i> 2023)	–	<i>Pseudococcus calceolariae</i> (Maskell, 1879), <i>P. longispinus</i> (Targioni-Tozzetti, 1867)	Not specified	Both species require mating; no asexual reproduction or hybridization, supporting pheromone-based management.
16	(Herrick & Cloyd, 2023)	USA	<i>Planococcus citri</i> (Risso, 1813)	Citrus	Commercial <i>Beauveria bassiana</i> and <i>Isaria fumosorosea</i> products caused <50% mortality in greenhouse trials.
17	(Oliveira <i>et al.</i> 2023)	Brazil	<i>Dysmicoccus boninsis</i> (Kuwana, 1909), <i>Saccharicoccus sacchari</i> (Cockerell, 1895), <i>Phenacoccus solenopsis</i> Tinsley, 1898	Coffee, Sugarcane, Okra	Molecular delimitation revealed misidentified COI sequences and ten mealybug species on Brazilian coffee.
18	(Zarkani <i>et al.</i> 2023)	Indonesia	<i>Dysmicoccus zeynepae</i> Zarkani & Kaydan, sp. n., <i>D. arachidis</i> Williams, 1978, <i>D. carens</i> Williams, 2004, <i>Pseudococcus leptotrichotus</i> (Green, 1922)	Wild and cultivated plants	Eighteen species recorded; one new species (<i>D. zeynepae</i>) and three new country records for Indonesia.
19	(Wang <i>et al.</i> 2023)	China	<i>Phenacoccus solenopsis</i> Tinsley, 1898	–	Gut bacterial communities differ significantly between sexes, possibly aiding polyphagy.
20	(Monteiro <i>et al.</i> 2023)	Brazil	<i>Saccharicoccus sacchari</i> (Cockerell, 1895)	Sugarcane	Asexual reproduction at tested temperatures; winged males suggest potential sexual reproduction.
21	(Soler <i>et al.</i> 2021)	Spain	<i>Pseudococcus viburni</i> (Signoret, 1875)	Citrus	Three <i>Anagyrus</i> species identified, including a new species (<i>A. borrianensis</i>) and a first Spanish record (<i>A. fusciventris</i>).

22	(Olabiya <i>et al.</i> 2022)	USA	<i>Nipaecoccus viridis</i> (Newstead, 1894)	Citrus	<i>Beauveria bassiana</i> -based products reduced mealybug survival comparably to chemical insecticides in mesh bags.
23	(Panti <i>et al.</i> 2024)	Mexico	<i>Dysmicoccus brevipes</i> (Cockerell, 1893)	Pineapple	<i>Beauveria bassiana</i> isolate BbCa caused 66% mortality; combined with neem oil achieved 100% mortality.
24	(Ricciardi <i>et al.</i> 2022)	Italy	<i>Planococcus ficus</i> (Signoret, 1875)	Grapevine	Demonstrated potential for pheromone-based mating disruption against vine mealybug.
25	(Rizwan <i>et al.</i> 2022)	Pakistan	<i>Drosicha mangiferae</i> (Green, 1908)	Citrus	Population peaks in April–May correlated positively with temperature, negatively with humidity.
26	(de Paula <i>et al.</i> 2022)	Brazil	<i>Planococcus citri</i> (Risso, 1813)	Rose	<i>Cryptolaemus montrouzieri</i> and <i>Chrysoperla externa</i> were compatible; combined release increased prey consumption by 11.8%.
27	(Lin <i>et al.</i> 2025)	China	<i>Paracoccus marginatus</i> Williams & Granara de Willink, 1992	<i>Jatropha integerrima</i>	<i>Diomus guilavogui</i> showed a type-II functional response, consuming up to 416 nymphs/day per female.
28	(Ricupero <i>et al.</i> 2025)	Italy	<i>Phenacoccus solenopsis</i> Tinsley, 1898	<i>Lantana camara</i>	Recorded <i>Aenasius arizonensis</i> (first in Europe) and <i>Anagyrus matritensis</i> plus three generalist predators.
29	(Chen <i>et al.</i> 2021)	China	<i>Phenacoccus solenopsis</i> Tinsley, 1898	Various hosts	Eighteen parasitoid species (8 primary, 10 hyperparasitoids) identified; <i>A. arizonensis</i> was dominant.
30	(Kahya <i>et al.</i> 2021)	Turkey	<i>Phenacoccus solenopsis</i> Tinsley, 1898	Cotton	<i>Aenasius arizonensis</i> achieved up to 80% parasitism in cotton fields, confirming high efficacy.
31	(Liang <i>et al.</i> 2021)	China	<i>Paracoccus marginatus</i> Williams & Granara de Willink, 1992	–	Two fatty acyl-CoA reductase genes were downregulated on resistant cassava, suggesting a role in host resistance.
32	(Middleton <i>et al.</i> 2024)	USA (Florida)	<i>Nipaecoccus viridis</i> (Newstead, 1894)	Citrus	<i>Cryptolaemus montrouzieri</i> and native predators/parasitoids were effective, but augmentative release gave only temporary control.
33	(Dos Santos <i>et al.</i> 2022)	Brazil	<i>Maconellicoccus hirsutus</i> (Green, 1908)	Fruits, Vegetables, Ornamentals	<i>Ceraeochrysa everes</i> successfully developed and reproduced on <i>M. hirsutus</i> , showing biocontrol potential.
34	(Pacheco Da Silva <i>et al.</i> 2021)	Brazil	<i>Planococcus ficus</i> (Signoret, 1875), <i>Pseudococcus sociabilis</i> Hambleton, 1941, <i>P. viburni</i> (Signoret, 1875)	Fruit-growing regions	Fifteen parasitoid species identified, including four new records for Brazil.
35	(Moreno <i>et al.</i> 2021)	Colombia	<i>Dysmicoccus brevipes</i> (Cockerell, 1893)	Pineapple (MD2)	Mealybugs associated with pineapple wilt found only in high-altitude zones (32% prevalence).
36	(Muştu <i>et al.</i> 2022)	Turkey	<i>Planococcus ficus</i> (Signoret, 1875)	Grapevine, <i>Morus alba</i>	<i>Leptomastix dactylopii</i> developed successfully on adult and 3rd-instar mealybugs, with higher fitness on adults.
37	(Burgio <i>et al.</i> 2025)	Italy	<i>Pseudococcus comstocki</i> (Kuwana, 1902)	Grapevine	Sugar dispensers (80/ha) plus predator releases reduced mealybug infestation by 22% and doubled <i>C. montrouzieri</i> density.
38	(Laterza <i>et al.</i> 2024)	Italy	<i>Planococcus citri</i> (Risso, 1813)	Citrus	Four of five biopesticides showed no lethal/sublethal effects on <i>Leptomastix dactylopii</i> , supporting compatibility in organic systems.

39	(Puig <i>et al.</i> 2021)	USA (Florida)	<i>Pseudococcus jackbeardsleyi</i> Gimpel & Miller, 1996, <i>Maconellicoccus hirsutus</i> (Green, 1908), <i>P. comstocki</i> , <i>Ferrisia virgata</i> (Cockerell, 1893)	Cocoa (<i>Theobroma cacao</i>)	First report of <i>P. jackbeardsleyi</i> and <i>M. hirsutus</i> as potential vectors of cacao mild mosaic virus.
40	(Li <i>et al.</i> 2025)	–	<i>Dysmicoccus neobrevipes</i> Beardsley, 1959	Sisal (<i>Agave sisalana</i>)	<i>Plesiochrysa ramburi</i> showed higher predation rate than <i>Apertochrysa roseusfrontata</i> ; both suppressed >80% in greenhouse releases.
41	(Diepenbrock & Ahmed, 2021)	USA (Florida)	<i>Nipaecoccus viridis</i> (Newstead, 1894)	Citrus	First report of <i>N. viridis</i> causing damage in Florida citrus, highlighting urgent need for management tools.
42	(Bilgin <i>et al.</i> 2021)	Turkey	<i>Phenacoccus madeirensis</i> Green, 1923	Tomato, Eggplant, Pepper, Pepino	Completed life cycle on all tested vegetables; highest reproduction and growth on eggplant.
43	(Gupta <i>et al.</i> 2021)	India	<i>Phenacoccus manihoti</i> Matile-Ferrero, 1977	Cassava	Native predators are heavily hyperparasitized, weakening natural control and underscoring need for specialist <i>Anagyrus lopezi</i> .
44	(de López <i>et al.</i> 2025)	Ecuador	<i>Maconellicoccus hirsutus</i> (Green, 1908)	>55 plant species	First record of <i>M. hirsutus</i> in Ecuador; its parasitoid <i>Anagyrus kamali</i> was also detected.
45	(El-Aalaoui <i>et al.</i> 2024)	Morocco	<i>Phenacoccus solenopsis</i> Tinsley, 1898	<i>Portulaca oleracea</i>	Combined treatment of <i>Alternaria murispora</i> and <i>Harmonia convergens</i> most effectively suppressed populations and preserved plant quality.
46	(Zart <i>et al.</i> 2021)	Brazil	<i>Dysmicoccus brevipes</i> (Cockerell, 1893)	Cassava	<i>Heterorhabditis amazonensis</i> (NEPET11) caused 93.8% mortality and dispersed effectively vertically/horizontally.
47	Rohimatun	Indonesia	<i>Pseudococcus jackbeardsleyi</i> Gimpel & Miller, 1996	<i>Curcuma aeruginosa</i> rhizomes (storage)	First documented report of <i>P. jackbeardsleyi</i> infesting stored rhizomes of <i>C. aeruginosa</i> .
48	(Othim <i>et al.</i> 2024)	Kenya	<i>Pseudococcidae</i> sp.	<i>Coffea</i> sp.	Natural Enemy Field Reservoirs (NEFRs) boosted parasitoid populations and reduced infestations by 62.8% when combined with prior releases.
49	(Carvalho <i>et al.</i> 2023)	Brazil	<i>Planococcus citri</i> (Risso, 1813)	<i>Cucurbita maxima</i>	Feeding only mealybug nymphs from 1st instar severely reduced <i>Chrysoperla externa</i> performance; moth-egg diet followed by mealybugs improved success.
50	(Moretti & Schmidt-Jeffris, 2025)	USA (Washington)	<i>Pseudococcus maritimus</i> (Ehrhorn, 1900)	Apple (<i>Malus domestica</i>)	Releases of <i>Cryptolaemus montrouzieri</i> showed limited efficacy in organic orchards due to rapid dispersal and host-density dependence.
51	(Finch <i>et al.</i> 2024)	Africa (regional)	<i>Paracoccus marginatus</i> Williams & Granara de Willink, 1992	Papaya	Climate suitability modeling indicated West Africa is highly suitable for <i>Acerophagus papayae</i> , while East/Central Africa have mismatched pest-parasitoid suitability.
52	(Huang <i>et al.</i> 2022)	China	<i>Phenacoccus solenopsis</i> Tinsley, 1898, <i>P. solani</i> Ferris, 1918	<i>Hibiscus mutabilis</i> , succulents	<i>Aenasius arizonensis</i> (specific to <i>P. solenopsis</i>) could parasitize the non-natural host <i>P. solani</i> , though offspring fitness was reduced.

53	(Correa <i>et al.</i> 2023)	Mediterranean	<i>Planococcus ficus</i> (Signoret, 1875) s.str., <i>P. vitis</i> (Niedzielski, 1891)	Grapevine (<i>Vitis vinifera</i>)	Molecular/morphological analyses confirmed <i>P. ficus</i> comprises two distinct species: <i>P. ficus</i> s.str. and the resurrected <i>P. vitis</i> .
54	(Plata <i>et al.</i> 2024)	Spain	<i>Delottococcus aberiae</i> De Lotto, 1961	Citrus (<i>Citrus</i> spp.)	Demonstrated that mutualism with the ant <i>Lasius grandis</i> accelerates invasion and increases pest populations.
55	(Le <i>et al.</i> 2023)	Vietnam	<i>Paracoccus marginatus</i> Williams & Granara de Willink, 1992	Cassava (<i>Manihot esculenta</i>)	<i>Acerophagus papayae</i> was the dominant parasitoid, lived ~16 days, laid ~60 eggs, and preferred 2nd-instar hosts.
56	(Mathulwe <i>et al.</i> 2023)	South Africa	<i>Pseudococcus viburni</i> (Signoret, 1875)	Not specified	Oil-based formulations maintained >95% viability and 60–90% pathogenicity of <i>Metarhizium</i> spp. for 8 weeks.

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