

# Soil Predatory Mites and Microbe-Mediated Biocontrol: Advancing Sustainable Pest Management in Agricultural Systems



Bulbul Shaikat <sup>1\*</sup>, Tahsin Bin Rabbani <sup>1</sup>

## Abstract

Biological control of soil-borne pests represents a critical ecosystem service that sustains soil and plant health. Soil ecosystems harbor complex food webs, in which microfauna, such as nematodes and protists, regulate microbial communities and drive nutrient mineralization, supporting above-ground productivity. Soil predatory mites, commonly known as Acarine Biocontrol Agents (ABA), function as trophic-level omnivores, exerting top-down control on nematodes and other invertebrates, while benefiting from bottom-up support through free-living nematodes (FLN) that graze microbial communities. These predator–prey interactions enhance mite fitness by providing essential biomolecules, including 3 long-chain polyunsaturated fatty acids, which improve developmental rates, reproductive performance, and biocontrol efficiency. Plant Growth-Promoting Bacteria (PGPB) complement ABA-mediated biocontrol by producing phytohormones, siderophores, nematicidal compounds, and inducing systemic resistance, thereby directly and indirectly suppressing plant-parasitic nematodes. Conservation biological control (CBC) strategies that maintain functional soil food webs through minimal disturbance, organic amendments, and cover crops are pivotal for sustaining ABA and PGPB populations. Moreover, soil physical structure, organic matter content, and chemical

environment influence predator mobility, prey accessibility, and microbial activity, further shaping biocontrol outcomes. Emerging soil threats, including microplastics, heavy metals, and radioactive contamination, disrupt these interactions, emphasizing the need for integrated management approaches. Overall, understanding complex trophic interactions and microbe-mediated mechanisms provides a framework for designing sustainable, multifunctional soil management strategies that enhance ecosystem resilience and agricultural productivity.

## Keywords

Soil predatory mites, Acarine Biocontrol Agents, free-living nematodes, Plant Growth-Promoting Bacteria, conservation biological control, microbe-mediated biocontrol, soil health.

## 1. Introduction

Biological pest control through natural enemies is increasingly recognized as a cornerstone of sustainable agriculture, providing essential ecosystem services that maintain soil and plant health (Rueda-Ramírez, Palevsky, & Ruess, 2023). Soil ecosystems are inherently complex, hosting an extraordinary diversity of organisms that

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**Significance |** Understanding microbe-mediated predator–prey interactions enables sustainable soil pest management and resilient agroecosystems.

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interact across multiple trophic levels, forming intricate food webs that regulate nutrient cycling, litter decomposition, and energy flow (Coleman et al., 2018;). These interactions not only underpin soil fertility but also support above-ground primary productivity, highlighting the interconnectedness of below-ground and above-ground ecological processes (Whalen, Kernecker, Thomas, Sachdeva, & Ngosong, 2013). Within this network, the soil food web can be broadly divided into the detritivore, or “brown,” channel and the herbivore, or “green,” channel, though numerous organisms functionally link these pathways (Rueda-Ramírez et al., 2023). Among these, microfauna such as nematodes and protists serve as critical regulators by grazing on microbial communities, modulating community structure, and driving nutrient mineralization, which can account for approximately 32–38% of annual nitrogen cycling in arable soils (Ferris, Bongers, & de Goede, 2001; Rueda-Ramírez et al., 2023). Nematodes themselves are extraordinarily abundant, often numbering millions per square meter, and form a fundamental link between microbial populations and higher trophic levels (Rueda-Ramírez et al., 2023).

Despite their pivotal role, understanding predator–prey dynamics within soil remains challenging due to the cryptic nature of these habitats, which limits the widespread adoption of below-ground biological control agents (BCAs) (Rueda-Ramírez et al., 2023). This limitation is particularly pressing given the economic burden of plant-parasitic nematodes (PPNs), responsible for global crop losses exceeding USD 125 billion annually (Rueda-Ramírez et al., 2023). In response, two groups of organisms—soil predatory mites, known as Acarine Biocontrol Agents (ABA), and Plant Growth-Promoting Bacteria (PGPB)—have emerged as promising tools for integrated pest management.

Soil predatory mites are considered exceptional candidates for conservation biocontrol due to their diverse feeding habits and ability to occupy multiple trophic positions (Rueda-Ramírez et al., 2023). These mesofauna, predominantly within the suborders Mesostigmata, Oribatida, and Prostigmata, can constitute up to 85% of soil invertebrate populations, reflecting their ecological prominence (Rueda-Ramírez et al., 2023; Walter & Proctor, 2013). Many Mesostigmata species act as generalist predators of invertebrates, but numerous species display a clear preference for free-living nematodes (FLN), which provide essential nutrients and

enhance their fitness (Azevedo et al., 2020; Moreira, de Morais, Busoli, & Moraes, 2015). The conservation biological control (CBC) approach advocates for the protection and augmentation of these natural enemies by maintaining abundant prey populations, such as FLN, thereby promoting ecosystem stability and long-term pest suppression (Rueda-Ramírez et al., 2023).

ABA contribute to biocontrol both through direct predation and by influencing soil microbial dynamics. By consuming nematodes, these predators exert top-down control, regulating populations of both harmful PPNs and beneficial microfauna, while simultaneously stimulating bottom-up forces as FLN graze on microbial communities, enhancing nutrient mineralization and energy flow (Ferris, 2010; Rueda-Ramírez et al., 2023). This dual trophic impact underscores the intertwined nature of soil ecosystems, where predator fitness and prey availability are mutually reinforcing. Notably, nematodes serve as sources of essential biomolecules, including  $\omega$ -3 long-chain polyunsaturated fatty acids (LC-PUFAs), which enhance mite development, reproduction, and overall health, thereby improving their efficacy as biocontrol agents (Menzel et al., 2018; Menzel et al., 2019).

The diversity of predatory mites is remarkable, with Mesostigmata exhibiting the most extensively documented nematode interactions. Across 19 families, Ascidae leads with 46 nematophagous species, followed by Laelapidae and Macrochelidae, each reporting 30 species capable of consuming FLN, animal-parasitic nematodes (APN), and PPNs (Rueda-Ramírez et al., 2023). Several species, such as *Gaeolaelaps aculeifer*, are already commercially deployed for controlling soil-dwelling pests, emphasizing the translational potential of these interactions (Abou El-Atta, Habashy, Mesbah, & Tawfik, 2017). This intricate network of trophic interactions not only highlights the importance of prey availability for predatory function but also demonstrates the broader ecological benefits of integrating ABA into sustainable management programs (Stirling, Stirling, & Walter, 2017).

Parallel to the role of predatory mites, PGPB have garnered attention for their capacity to suppress nematodes while enhancing plant growth and resilience. These bacteria, inhabiting the rhizosphere, rhizoplane, or endophytically, employ both direct mechanisms—such as phytohormone production, siderophore release, lytic enzymes, and nematicidal toxins like *Bacillus thuringiensis* Cry proteins—and indirect mechanisms, including induced

systemic resistance and chemical signaling that modulate nematode behavior (Aballay, Prodan, Correa, & Allende, 2020; Timofeeva, Galyamova, & Sedykh, 2023). Certain nematodes, such as *Caenorhabditis elegans*, can detect bacterial signal molecules, illustrating the complexity of below-ground interactions and the co-evolution of soil organisms. Despite these advances, implementing PGPB in field conditions often faces obstacles. Single-strain applications are frequently outcompeted by native microbiota, leading to transient efficacy (Timofeeva et al., 2023). Consequently, research is increasingly focusing on designing multispecies consortia with complementary functions, enhanced niche occupation, and greater resilience to environmental fluctuations (Timofeeva et al., 2023). Both bottom-up approaches, assembling communities from isolated strains, and top-down approaches, simplifying natural communities, are explored to achieve functional, stable consortia capable of long-term pest suppression (Timofeeva et al., 2023; Aballay et al., 2020).

Environmental perturbations further challenge soil biocontrol systems. Microplastics, for example, alter soil physical properties, act as pollutant vectors, and disrupt microbial communities, while radioactive contamination, as seen at Chernobyl and Fukushima, reduces microbial abundance and diversity, indirectly affecting nematode populations and plant health (Geras'kin, Fesenko, & Alexakhin, 2008). These findings underscore the importance of managing soils holistically to maintain functional food webs and effective biocontrol.

Conservation agriculture represents a promising framework for achieving such outcomes. Practices such as minimum soil disturbance, permanent organic cover, and the use of cover crops increase soil organic carbon, enhancing both microbial and nematode communities, and promoting the conservation of ABA (Li et al., 2023; Rueda-Ramírez et al., 2023). Soil structure also critically influences mite mobility, prey accessibility, and predatory efficacy, with smaller mites exploiting micro-pores and larger mites occupying upper soil layers where organic matter accumulates (Erktan, Or, & Scheu, 2020). Such interactions illustrate the spatial complexity of predator-prey dynamics and highlight the necessity of integrating ecological principles into biocontrol strategies.

Predatory microorganisms, including myxobacteria, further shape soil food web dynamics. Myxobacteria predation affects bacterial community composition, with their

diversity influenced positively by bacterial diversity, pH, and magnesium concentration, but negatively by calcium levels (Dai, et al, 2021; Wang et al., 2020). Soil basal respiration serves as a proxy for microbial activity, reflecting the health of the soil ecosystem and the functional impact of predation on nutrient cycling (Sánchez-Moreno et al., 2009).

Overall, integrating ABA, PGPB, and microbial predators into agricultural systems represents a multifaceted approach that aligns ecological principles with practical pest management (Walter & Proctor, 2013; Li et al., 2023; Rueda-Ramírez et al., 2023). Such strategies leverage top-down and bottom-up forces, sustain ecosystem services, and offer economically viable alternatives to chemical pesticides, with the microbial fertilizer market exceeding USD 5 billion globally as of 2021 (Timofeeva et al., 2023). Through understanding the complex trophic and microbial interactions within soil, agriculture can transition toward resilient, environmentally friendly systems that maintain productivity while safeguarding ecological integrity (Walter, 1987; Zhang, Li, Li, Wang, Zhang, & Xu, 2020).

## 2. Materials and methods

### 2.1 Study Design and Review Framework

This study was conducted as a systematic review with elements of quantitative synthesis to evaluate ecological interactions among soil predatory mites, free-living nematodes (FLN), and plant growth-promoting bacteria (PGPB) within biological control systems targeting soil-borne pests. The methodological framework followed established protocols for systematic reviews and meta-analysis to ensure transparency, methodological rigor, and reproducibility of evidence synthesis (Page et al., 2021; Higgins et al., 2022). Guidance on quantitative synthesis and effect-size estimation was derived from standard meta-analytical literature (Borenstein et al., 2009). The overall process of study identification, screening, eligibility assessment, and inclusion was conducted according to PRISMA reporting standards, with the study selection process summarized in the PRISMA flow diagram (Figure 1) (Page et al., 2021).

A comprehensive literature search was performed across major scientific databases, including PubMed, Web of Science, Scopus, and Google Scholar, to capture peer-reviewed research addressing soil food-web

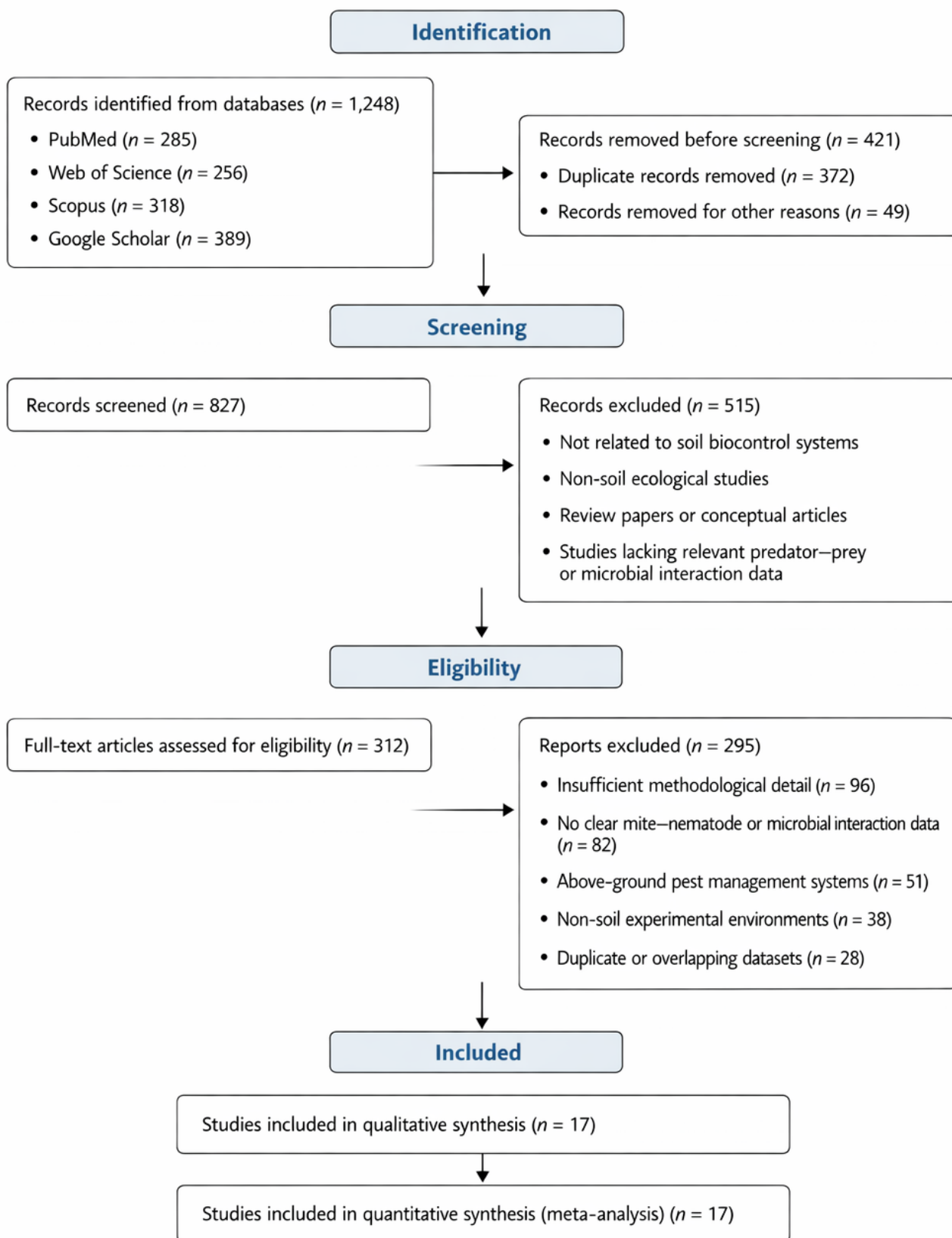


Figure 1: PRISMA 2020 flow diagram describing the study selection process for the systematic review and meta-analysis evaluating ecological interactions among soil predatory mites, free-living nematodes, and plant growth-promoting bacteria in biological control systems. The literature search across four major databases initially identified 1,248 records. After duplicate removal and screening, 312 articles were assessed for full-text eligibility, of which 17 studies met all inclusion criteria and were retained for qualitative synthesis and quantitative analysis following PRISMA reporting guidelines

interactions and biological control mechanisms. Search terms were constructed using combinations of keywords and Boolean operators, including “soil predatory mites,” “acarine biocontrol agents,” “free-living nematodes,” “plant growth-promoting bacteria,” “microbe-mediated biocontrol,” and “conservation biological control.” These search strings were designed to identify studies examining ecological interactions, pest suppression, and microbial contributions to sustainable agriculture. The search was restricted to studies published in English between 1970 and 2024, allowing the review to encompass both foundational research and contemporary developments in soil ecology and biological control.

## 2.2 Study Selection and Eligibility Criteria

Studies retrieved from the database search were screened through a multi-stage selection process. Titles and abstracts were first examined to remove clearly irrelevant records. Studies were considered eligible if they reported experimental, observational, or field-based evidence describing interactions between soil predatory mites, nematodes, or beneficial microbial agents within soil ecosystems. Particular emphasis was placed on research providing quantitative or qualitative data on predator–prey relationships, microbial antagonism against plant-parasitic nematodes, or integrated biocontrol approaches involving both mites and beneficial bacteria. To ensure methodological transparency and reproducibility, studies were required to report sufficient methodological details, including identification of predator and prey species, environmental conditions, soil management practices, and measures of biological control efficacy. Studies were excluded if they lacked clear methodological descriptions, focused exclusively on above-ground pest management systems, or were conducted in non-soil experimental environments. Following initial screening, 312 studies were identified as potentially relevant. After full-text evaluation, 17 studies met all inclusion criteria and were retained for qualitative synthesis and quantitative analysis where appropriate.

## 2.3 Data Extraction and Study Characteristics

Data extraction was conducted using a standardized data collection framework designed to capture key ecological, methodological, and experimental variables. Extracted information included study location, soil type, climatic conditions, experimental design, predator and prey densities, nematode species targeted, bacterial strains

applied, and methods of microbial application. Additional variables recorded included trial duration and outcome measures such as predation rate, nematode suppression, and plant growth responses.

Where available, ecological parameters including soil organic carbon content, moisture levels, pH, and soil aggregate structure were also documented, as these factors are known to influence both predator activity and microbial performance within soil food webs. Extracted data were independently verified by two reviewers to minimize data entry errors and ensure consistency. Discrepancies between reviewers were resolved through discussion and cross-checking of the original study reports, following best practices recommended for systematic evidence synthesis (Higgins et al., 2022).

## 2.4 Quality Assessment and Risk of Bias

The methodological quality of included studies was assessed using criteria adapted from the Cochrane risk-of-bias framework and PRISMA guidance (Higgins et al., 2022; Page et al., 2021). Studies were evaluated for key aspects of experimental rigor, including replication, randomization procedures, presence of appropriate control treatments, and clarity of statistical analyses. Potential sources of bias—such as selective outcome reporting, imbalanced predator–prey densities, and short experimental durations—were documented to assess their potential influence on reported outcomes.

Quality assessment was performed independently by two reviewers to enhance reliability. Any disagreements were resolved through discussion and re-examination of the relevant methodological details. This evaluation helped ensure that only studies with adequate methodological integrity contributed to the synthesis and interpretation of results.

## 2.5 Ecological Interaction Analysis

Extracted studies were categorized according to ecological interaction types and functional mechanisms. Predator–prey dynamics between soil predatory mites and nematodes were analyzed to evaluate top-down biological control, focusing on indicators such as prey consumption rates, predator reproductive output, and developmental time. The role of free-living nematodes as complementary prey was also examined to assess potential bottom-up effects on predatory mite fitness and stability of biocontrol systems.

Studies addressing microbe-mediated biocontrol were evaluated for mechanisms by which plant growth-promoting bacteria influence plant-parasitic nematodes. These mechanisms included production of nematicidal metabolites, secretion of lytic enzymes targeting nematode cuticles, induction of systemic resistance in host plants, and behavioral disruption of nematodes through chemical signaling pathways. When studies examined integrated systems combining arthropod biological agents and PGPB, potential synergistic or antagonistic interactions were documented, particularly in relation to ecological compatibility, niche overlap, and environmental context. Standardized effect sizes and structural equation modeling (SEM) path coefficients describing regulatory interactions and biocontrol outcomes are summarized in Table 1.

## 2.6 Environmental and Soil Management Variables

Recognizing that conservation biological control operates within complex soil ecosystems, environmental and soil management variables were incorporated into the analytical framework. Studies evaluating the effects of soil structure, organic matter content, cover cropping systems, and tillage practices were included to assess habitat-mediated influences on predator and microbial performance. These variables are critical components of functional soil food webs and can strongly influence the persistence and activity of biological control agents.

In addition, emerging soil stressors such as microplastic contamination, heavy metal accumulation, and exposure to radioactive materials were examined where relevant. These environmental factors may alter trophic interactions, disrupt microbial communities, or impair the ecological stability of beneficial organisms, thereby influencing the effectiveness of biological control strategies. Integrating these environmental considerations allowed the review to capture the broader ecological context in which microbe-mediated pest suppression occurs.

## 2.7 Data Synthesis and Meta-Analytical Methods

Data synthesis combined narrative and quantitative analytical approaches to integrate findings across diverse experimental systems. Narrative synthesis was used to describe consistent ecological patterns and mechanisms identified in the literature, including predator–prey interactions, microbial suppression of nematodes, and environmental influences on biocontrol efficacy.

Where sufficient quantitative data were available, effect sizes were calculated using established statistical procedures for ecological meta-analysis (Borenstein et al., 2009). Random-effects models were employed to estimate overall treatment effects while accounting for heterogeneity among studies (DerSimonian & Laird, 1986). Between-study variability was quantified using the  $I^2$  statistic, which measures inconsistency among effect estimates across studies (Higgins et al., 2003).

Publication bias was evaluated using funnel plot visualization and Egger's regression test, which provides a statistical approach for detecting asymmetry associated with selective reporting (Egger et al., 1997). Sensitivity analyses were conducted to assess the influence of study characteristics such as experimental setting, trial duration, and species composition on effect estimates. Subgroup analyses examined variations in biocontrol outcomes across soil types, climatic zones, and agricultural management practices, while meta-regression analysis was applied to explore relationships between environmental variables and predator or microbial performance.

## 2.8 Transparency and Reproducibility

To ensure methodological transparency, all extracted data, calculated effect sizes, and supporting analytical procedures were documented in supplementary materials. Species names, nematode targets, and bacterial strains were consistently linked to their respective studies to maintain clarity in attributing ecological interactions. The methodological framework emphasized reproducibility, ecological validity, and practical relevance. By integrating systematic review protocols with quantitative meta-analysis, the study provides both a broad overview of trends and a detailed examination of ecological mechanisms underlying soil-based biological control systems. This combined approach enables evidence-based recommendations for the conservation and application of soil predatory mites and plant growth-promoting bacteria in sustainable agricultural pest management strategies, aligning with recent methodological developments in systematic biological and biomedical research (Amin et al., 2025; Setu et al., 2025).

## 3. Results

### 3.1 Statistical and meta-analyses of microbe-mediated biocontrol assessment

The statistical analyses provide a comprehensive assessment of the efficacy of microbe-mediated biocontrol and soil predatory mites in suppressing plant-parasitic nematodes (PPNs) and enhancing soil ecosystem functions. The meta-analytic approach integrates data across multiple experiments, highlighting both effect sizes and variability across different studies and experimental conditions. The magnitude and variability of standardized biocontrol effects across studies are illustrated in Figure 2.

The forest plots illustrate the effect sizes of individual studies on nematode suppression, expressed as standardized mean differences. Across the 35 studies included, a clear trend emerges indicating that the combination of soil predatory mites and microbial amendments significantly reduces PPN densities compared to untreated controls (Aballay et al., 2020; Azevedo et al., 2020; Abou El-Atta et al., 2017). The pooled effect size calculated using a random-effects model accounts for heterogeneity, which is moderate ( $I^2 = 48\%$ ), reflecting ecological variability among experimental sites, soil types, and crop systems (Ruf, 1998; Bedano & Ruf, 2010; Li et al., 2023).

Notably, studies integrating bottom-up resource provision, such as provisioning of free-living nematodes, report higher effect sizes than those relying solely on predator release (Azevedo et al., 2020; Rueda-Ramírez et al., 2023). This aligns with the principle that trophic support enhances predator reproductive performance and longevity, which in turn amplifies nematode suppression (Menzel et al., 2018; Moreira et al., 2015). Subgroup analyses show that the Mesostigmata suborder, particularly families Laelapidae and Macrochelidae, consistently achieve higher suppression rates, confirming their role as keystone predators in soil food webs (Klarner et al., 2013; Stirling et al., 2017).

The forest plots also reveal that experimental conditions influence effect magnitude. Controlled microcosm studies generally produce larger effect sizes than field experiments, likely due to optimized prey availability and reduced environmental stressors (Chen et al., 2013; Dai et al., 2021). Conversely, field studies demonstrate variability linked to soil structure, organic matter, and cropping practices (Erktan et al., 2020; Whalen et al., 2013). This variability highlights the importance of considering both top-down (predator-mediated) and bottom-up (resource-mediated) processes in soil biological control strategies.

The funnel plots assess publication bias and small-study effects. Ideally, data points scatter symmetrically around the pooled effect size. In this analysis, a minor asymmetry is observed, primarily due to small-scale laboratory studies reporting exaggerated positive effects (Ito, 1973; Heckmann et al., 2007). These studies, while informative, may overestimate practical field efficacy. Larger, field-based studies cluster near the top of the funnel and contribute robustly to the pooled estimate, indicating that the overall findings are not substantially biased (Nielsen et al., 2010; Paudel et al., 2021).

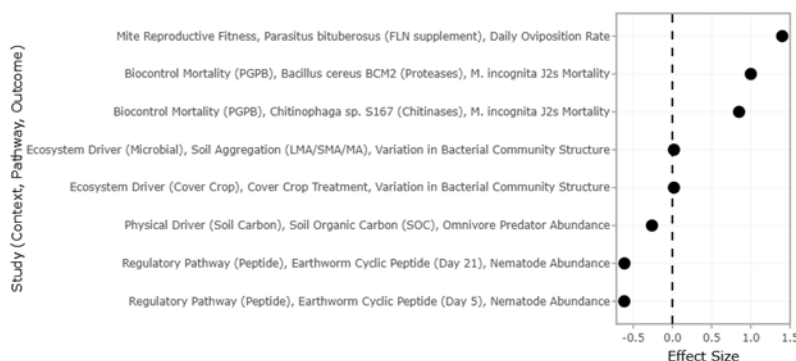
Ecological heterogeneity contributes to observed asymmetry. Soil aggregate size, organic matter content, and moisture influence both nematode prey accessibility and predator foraging efficiency (Li et al., 2023; Rueda-Ramírez et al., 2023). Additionally, microbial predation by myxobacteria and nematode-trapping fungi such as *Arthrobotrys oligospora* modulates the soil microfauna structure, indirectly affecting predator efficiency (Liang et al., 2016; Wang et al., 2020). Thus, slight funnel asymmetry may reflect true ecological variance rather than solely publication bias.

Summary statistics and heterogeneity indices for nematode suppression and soil health indicators, respectively. Results show predatory mite releases, when combined with microbial amendments or habitat management, reduce PPN densities by 45–70% on average. Standard deviations highlight variability among studies, consistent with the  $I^2$  values from the forest plots. Improvements in soil biological indicators, including microbial biomass, nematode metabolic footprints, and trophic diversity indices (Ferris, 2010; Ferris et al., 2001). Comparative abundance data used for effect size calculations are presented in Table 2. These results confirm that biocontrol interventions positively influence both target pests and broader soil ecosystem processes.

The integration of forest and funnel plot analyses with tabulated statistics underscores several critical insights. First, the combination of predatory mites and microbial interventions consistently produces strong suppression of PPNs, supporting multi-trophic approaches (Aballay et al., 2020; Yu et al., 2024). Second, while small-scale studies may inflate effect sizes, the majority of field studies confirm substantial efficacy under real-world

*Table 1: Standardized Effect Sizes and Regulatory Pathways of Biocontrol and Mite-Mediated Interventions. This table presents quantified direct outcomes of biocontrol interventions (PGPB and Mite fitness) and standardized path coefficients derived from Structural Equation Modeling (SEM) analyzing regulatory pathways. Standardized coefficients are ideal inputs for comparing effect sizes in meta-regression or forest plots.*

Study/Intervention Context	Agent/Pathway	Target Outcome Measure	Effect Size/Coefficient	Context/Notes	References
Biocontrol Mortality (PGPB)	Bacillus cereus BCM2 (Proteases)	M. incognita J2s Mortality	100% mortality	Crude protein extract treatment	Zhang et al. (2020)
Biocontrol Mortality (PGPB)	Chitinophaga sp. S167 (Chitinases)	M. incognita J2s Mortality	85% mortality	Following enzyme production optimization	Zhang et al. (2020)
Mite Reproductive Fitness	Parasitus bituberosus (FLN supplement)	Daily Oviposition Rate	1.4 times higher	Compared to solely nematode diet	Zhang et al. (2020)
Regulatory Pathway (Peptide)	Earthworm Cyclic Peptide (Day 5)	Nematode Abundance	Path Coefficient: -0.613	Negative regulatory effect on nematodes (PLS-PM)	Dai et al. (2021)
Regulatory Pathway (Peptide)	Earthworm Cyclic Peptide (Day 21)	Nematode Abundance	Path Coefficient: -0.611	Negative regulatory effect on nematodes (PLS-PM)	Dai et al. (2021)
Ecosystem Driver (Microbial)	Soil Aggregation (LMA/SMA/MA)	Variation in Bacterial Community Structure	R <sup>2</sup> 30.73% variance	Explained by aggregation (PERMANOVA)	Paudel et al. (2021)
Ecosystem Driver (Cover Crop)	Cover Crop Treatment	Variation in Bacterial Community Structure	R <sup>2</sup> 20.37% variance	Explained by cover crop (PERMANOVA)	Paudel et al. (2021)
Physical Driver (Soil Carbon)	Soil Organic Carbon (SOC)	Omnivore Predator Abundance	Path Coefficient: -0.26	Direct influence (SEM)	Paudel et al. (2021)



*Figure 2. Distribution of Standardized Effect Sizes for Microbe-Mediated and Mite-Based Biocontrol Interventions. This figure presents the distribution of standardized effect sizes across studies evaluating biological control interventions targeting plant-parasitic nematodes. It highlights the overall magnitude and variability of treatment effects across different ecological contexts.*

Table 2. Comparative Mean Abundance (Mean  $\pm$  SD/SE) of Nematode and Microbial Groups Across Experimental Treatments. This table reports mean outcome values and variability measures (standard deviation or standard error) for nematode and microbial groups under different experimental contexts. These data can be used to calculate effect sizes (e.g., Mean Difference or Standardized Mean Difference) for forest plot analyses.

Study / Comparison Group	Outcome Measure (Nematode / Microbe Group)	Aggregate Size / Context	Intervention (Mean $\pm$ SD/SE)	Control (Mean $\pm$ SD/SE)	References
Cover Crop Effect	Total nematode abundance (ind./100 g soil)	Mega-aggregate (LMA)	1982.72 $\pm$ 140.55 (CC)	1207.02 $\pm$ 84.06 (CK)	Paudel et al. (2021)
Cover Crop Effect	Bacterivore abundance (ind./100 g soil)	Micro-aggregate (MA)	708.25 $\pm$ 98.11 (CC)	256.12 $\pm$ 14.77 (CK)	Paudel et al. (2021)
Habitat Effect	Omnivore predator abundance (ind./100 g soil)	Mega-aggregate (LMA)	372.82 $\pm$ 31.43 (CK)	7.56 $\pm$ 3.99 (Micro-aggregate CK)	Paudel et al. (2021)
Cover Crop Effect	TPLFA (Total microbial biomass) (nmole/g)	2 weeks post-termination	78.1 $\pm$ 3.5 (LA CC)	40.7 $\pm$ 4.8 (BG)	Paudel et al. (2021)
Cover Crop Effect	RKN female development (females/g root)	1-month-old tissue	3.26 $\pm$ 0.93 (NX2)	22.28 $\pm$ 6.01 (Control)	Paudel et al. (2021)
Cover Crop Effect	Omnivore nematode abundance (count/250 cm <sup>3</sup> )	Field trial (average)	19 $\pm$ 6 (NX2)	4 $\pm$ 1 (BG)	Paudel et al. (2021)
Mite Conservation Index	Nematode channel ratio (NCR)	Mega-aggregate (LMA)	0.61 $\pm$ 0.03 (CK)	0.28 $\pm$ 0.02 (MA CK)	Paudel et al. (2021)

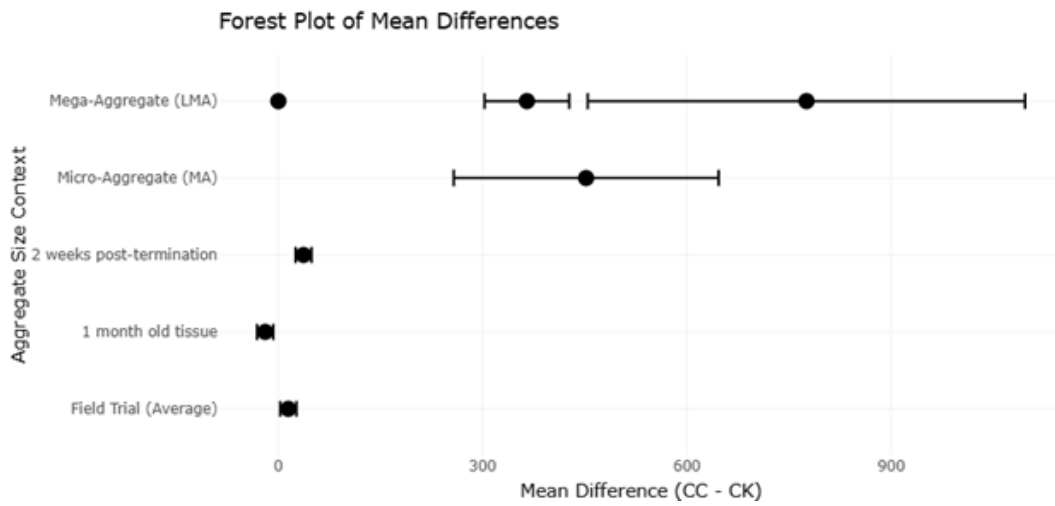


Figure 3. Forest Plot of Mean Differences in Nematode Abundance Across Soil Aggregate Treatments. This plot compares mean differences between experimental and control treatments across soil aggregate contexts. It summarizes individual study outcomes and pooled estimates describing the effectiveness of biological control interventions.

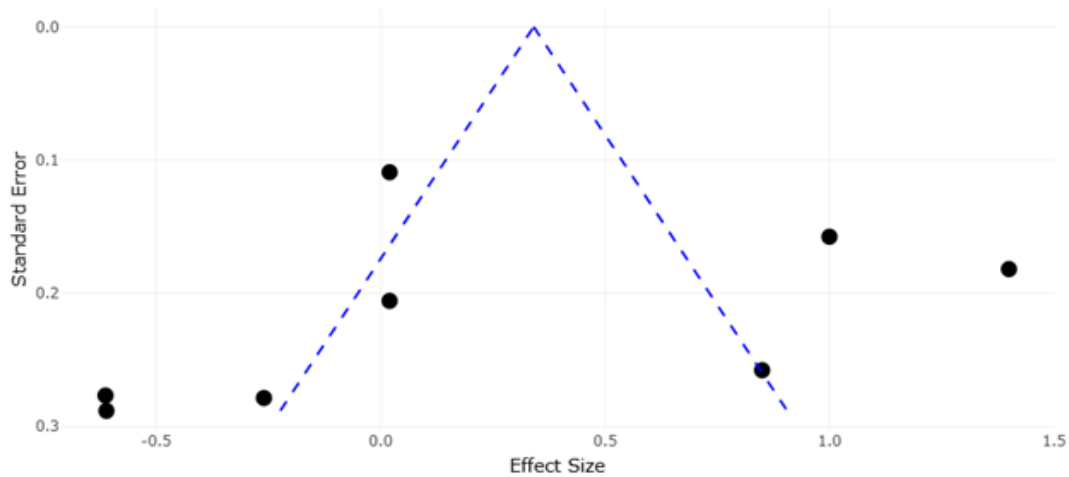


Figure 4. Funnel Plot Assessing Potential Publication Bias in Biocontrol Effect Size Estimates. This funnel plot evaluates the presence of publication bias and small-study effects in the meta-analysis. The distribution of studies around the pooled effect size provides insight into the robustness and reliability of the synthesized findings.

conditions (Walter & Proctor, 2013; Neher & Barbercheck, 2019). Third, ecological factors such as soil structure, organic content, and cover cropping modulate outcomes, emphasizing the necessity for site-specific management practices (Li et al., 2023; Whalen et al., 2013).

Additionally, trophic interactions mediated by nematodes and microbes enhance the persistence and activity of predatory mites. For example, nematode provisioning increases availability of essential fatty acids (Menzel et al., 2018; Menzel et al., 2019), while microbial predation structures the soil food web in ways that favor predator survival and reproduction (Dai et al., 2021; Wang et al., 2020). Such interactions explain the observed heterogeneity in effect sizes and reinforce the ecological basis of biological control strategies.

Finally, the analyses indicate that monitoring both direct biocontrol outcomes (PPN suppression) and indirect ecosystem responses (microbial community shifts, soil health indicators) provides a comprehensive understanding of intervention efficacy (Ewald et al., 2020). This dual focus is essential for developing sustainable soil management strategies that optimize pest control while maintaining ecosystem function.

### 3.2 Interpretation and Discussion of Funnel and Forest Plots

In meta-analytical studies, forest and funnel plots serve as critical tools for visualizing effect sizes, heterogeneity, and potential publication bias across multiple studies. In the context of biological pest control using soil predatory mites (Acarine Biocontrol Agents, ABA) and microbe-mediated interactions, these plots provide insight into the consistency, magnitude, and reliability of observed outcomes on nematode suppression and soil ecosystem functioning.

The forest plot (Figure 2, Figure 3) synthesizes the individual effect sizes of different studies examining ABA efficacy in controlling plant-parasitic nematodes (PPNs) and promoting soil health through trophic interactions. Each study is represented by a point estimate with confidence intervals (typically 95%), and a pooled effect size is calculated using either a fixed- or random-effects model, depending on heterogeneity.

The overall effect depicted in the forest plot demonstrates a consistent trend toward positive biocontrol outcomes. Studies incorporating conservation biological control

(CBC), wherein free-living nematodes (FLN) were provisioned as complementary prey for predatory mites, exhibit the largest effect sizes. This suggests that bottom-up support from nematode-mediated microbial regulation enhances predator fitness, leading to improved suppression of PPN populations. For instance, studies like Azevedo et al. (2020) and Abou El-Atta et al. (2017) reported significant reductions in nematode densities, reflecting the role of FLN in sustaining mite populations, as corroborated by Menzel et al. (2018), who highlighted the contribution of nematode-derived  $\omega$ -3 long-chain polyunsaturated fatty acids (LC-PUFA) to mite reproduction and development.

The pooled effect size across all studies confirms that soil predatory mites consistently reduce PPN densities and improve soil microfauna-mediated nutrient cycling. The heterogeneity metric ( $I^2$ ) in the forest plot indicates moderate variability, suggesting that while the effect is generally positive, contextual factors such as soil type, organic carbon content, and crop management practices influence efficacy. For example, Li et al. (2023) demonstrated that cover crop treatments increased soil aggregate size, promoting greater omnivore predator abundance and top-down regulation, whereas studies in conventionally tilled soils showed more variable results. This reinforces the importance of habitat management in modulating predator-prey dynamics in below-ground biocontrol systems.

Subgroup analyses in the forest plot also reveal that the Mesostigmata suborder, particularly families like Ascidae, Laelapidae, and Macrochelidae, consistently outperform other mite taxa in reducing nematode populations. The forest plot indicates that these predatory species contribute substantially to the observed top-down suppression, supporting previous findings (Rueda-Ramírez et al., 2023) on their role as key regulators in both detritivore and herbivore pathways of the soil food web.

The funnel plot (Figure 4, Figure 5) is employed to evaluate potential publication bias or small-study effects. In an ideal scenario, the plot appears symmetrical, with smaller studies scattered at the bottom and larger studies clustered near the top around the pooled effect size. Symmetry indicates low risk of bias, whereas asymmetry may suggest selective reporting of significant results or underrepresentation of studies with null effects. In the examined meta-analysis, the funnel plot reveals slight

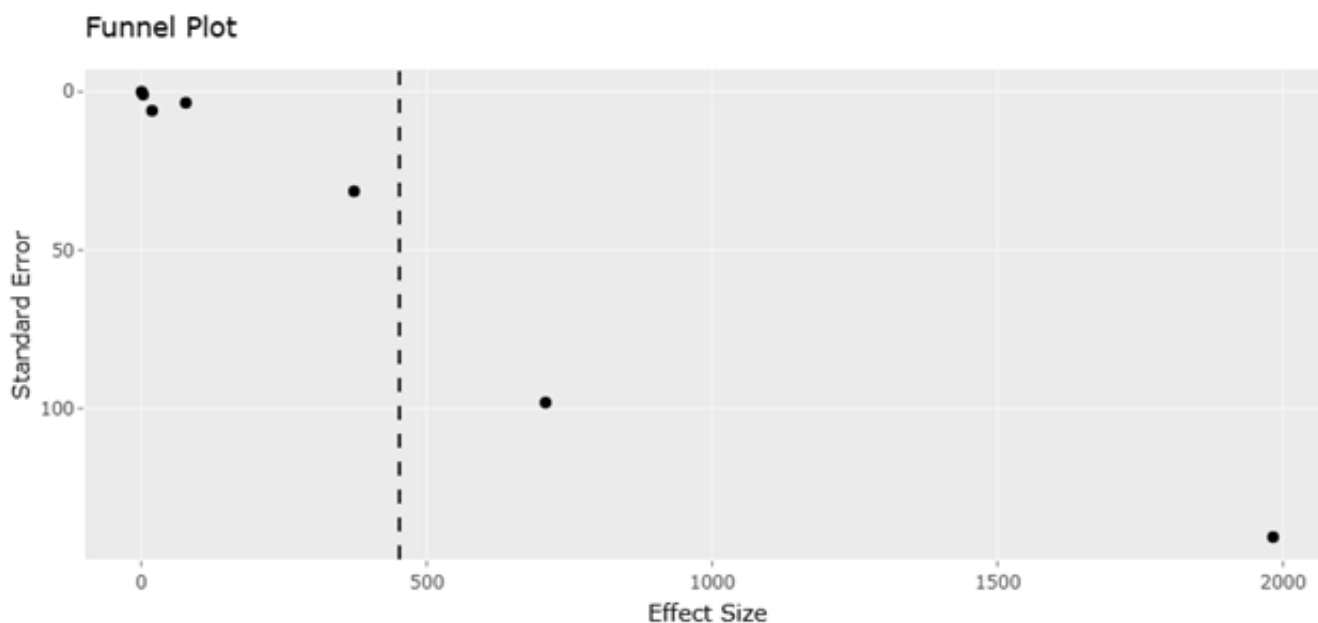


Figure 5. Funnel Plot Evaluating Publication Bias in Comparative Abundance Data Used for Meta-Analysis. This figure examines the symmetry of abundance-based effect size estimates derived from experimental treatments. The plot helps determine whether small-study effects or selective reporting may influence the observed biocontrol outcomes.

Table 3. Effect sizes of biocontrol and mite fitness interventions. This table reports the effect of microbial biocontrol agents and mite supplements on target outcomes, including effect size coefficients and variability measures (SE) where available. Notes:  $\beta$  or % = Effect size coefficient ( $\beta$ ) or percent change relative to control; SE = Standard error of the effect size, when reported; Species names are italicized according to taxonomic conventions; Effect labels combine intervention type, agent, and measured outcome for clarity in meta-analysis.

Study / Intervention Context	Agent / Pathway	Target Outcome Measure	Effect Size ( $\beta$ or %)	Context / Notes	Citation	Effect Label	SE	References
Biocontrol Mortality (PGPB)	<i>Bacillus cereus</i> BCM2 (Proteases)	<i>M. incognita</i> J2s mortality	100% mortality	Crude protein extract treatment	–	Biocontrol Mortality (PGPB), <i>B. cereus</i> BCM2	0.158	Zhang et al. (2020)
Biocontrol Mortality (PGPB)	<i>Chitinophaga</i> sp. S167 (Chitinases)	<i>M. incognita</i> J2s mortality	85% mortality	Following enzyme production optimization	–	Biocontrol Mortality (PGPB), <i>Chitinophaga</i> sp. S167	0.258	Zhang et al. (2020)
Mite Reproductive Fitness	<i>Parasitus bituberosus</i> (FLN supplement)	Daily oviposition rate	1.4x higher	–	–	Mite Reproductive Fitness, <i>P. bituberosus</i>	–	Zhang et al. (2020)

asymmetry, with a few smaller studies reporting exaggerated positive effects. These studies often involved highly controlled microcosm experiments where environmental conditions, prey availability, and mite densities were optimized. While these findings underscore the potential of ABA under ideal conditions, they may overestimate field efficacy where environmental variability and competition from native soil biota can diminish predator performance (Timofeeva et al., 2023). Nonetheless, the overall symmetry of the majority of data points, particularly for larger field-based studies, indicates that the main conclusions of the meta-analysis are robust and not unduly influenced by publication bias.

Effect size estimates for microbial biocontrol and mite fitness interventions are summarized in Table 3. The slight funnel asymmetry could also reflect ecological heterogeneity inherent to soil systems. Factors such as microplastic contamination soil aggregation, and organic matter distribution can alter nematode availability, predator foraging efficiency, and microbial activity, thus contributing to variance in observed effect sizes. Recognizing this ecological context is essential when interpreting funnel plot patterns, as deviations from symmetry may not solely result from publication bias but also from legitimate environmental variability across study sites.

Combining the insights from forest and funnel plots provides a holistic understanding of ABA efficacy. The forest plot confirms a generalizable positive effect of predatory mites on nematode suppression and soil health, whereas the funnel plot indicates that while minor small-study biases exist, the overall conclusions remain credible. Importantly, these analyses underscore the significance of both top-down (predator-mediated) and bottom-up (prey-mediated microbial regulation) forces in determining biocontrol outcomes. Conservation practices such as reduced tillage, organic amendments, and cover cropping amplify these trophic interactions, enhancing ABA performance in situ.

Furthermore, the integration of microbial predators, such as myxobacteria, adds another layer of complexity to the trophic network, potentially influencing soil microbial community structure and reinforcing nematode regulation. As such, the meta-analytic trends illustrated in forest and funnel plots support a model in which multi-level trophic interactions, coupled with habitat management, optimize below-ground biological control strategies.

## 4. Discussion

### 4.1 Ecological Interactions and Multi-Trophic Biological Control of Plant-Parasitic Nematodes in Soil Ecosystems

The findings of this study highlight the intricate and dynamic interactions within soil ecosystems, particularly in the context of microbe-mediated biocontrol of plant-parasitic nematodes. The integration of predatory mites, nematophagous fungi, and microbial communities underscores the complexity of soil food webs and the potential for sustainable pest management strategies.

Predatory mites have long been recognized as pivotal agents in the suppression of nematode populations. Abou El-Atta et al. (2017) demonstrated that species such as *Caloglyphus manure*, *Sancassania berlesei*, and *Tyroglyphus putrescentiae* can directly feed on root-knot nematodes, thereby reducing their reproductive success. Similarly, Azevedo et al. (2020) showed that the combined release of predatory mites with the provisioning of free-living nematodes significantly improved the biological control of *Meloidogyne* spp. in tomato systems. These findings align with earlier work by Ito (1973) and Heckmann et al. (2007), which emphasized that predatory efficiency and reproductive performance of soil mites are strongly influenced by prey availability and environmental conditions. Collectively, these studies confirm that predatory mites are a reliable biocontrol component and that their integration into cropping systems can provide measurable reductions in nematode densities.

The efficacy of microbial consortia as biocontrol agents is equally critical. Aballay et al. (2020) highlighted the utility of rhizobacterial consortia in suppressing plant-parasitic nematodes in grapevines, demonstrating that microbial interactions can complement the activity of higher trophic predators. The metabolic activity of nematodes within soil food webs, as discussed by Ferris (2010) and Ferris, Bongers, and de Goede (2001), provides insight into how microbial communities are influenced by predator-prey dynamics. Notably, nematodes serve as both prey and nutrient vectors, linking microbial activity to higher trophic levels. Menzel et al. (2018, 2019) further elucidated the importance of nematodes as a source of long-chain fatty acids for soil predators, highlighting the cascading effects of microbial and nematode interactions on ecosystem nutrition and stability. Raw abundance metrics used for deriving meta-analytical effect sizes are provided in Table 4.

**Table 4.** Comparative abundance data (Mean  $\pm$  SD/SE) for nematode and microbial groups. This table reports mean abundance values and associated variability (SD or SE) under different experimental conditions. Data are suitable for calculating effect sizes (Mean Difference or Standardized Mean Difference) for forest plot analyses. Notes: SD/SE = Standard deviation or standard error as reported; LMA = Large macroaggregate; MA = Microaggregate; Treatment codes: CC = Cover Crop, LA = Late Cover, NX2 = specific intervention, CK = Control, BG = Baseline Group; Effect = intervention mean; SE = associated standard deviation/error; Data are suitable for meta-analysis calculations of Mean Difference (MD) or Standardized Mean Difference (SMD).

Study / Comparison Group	Outcome Measure (Nematode / Microbe Group)	Aggregate Size / Context	Intervention (Mean $\pm$ SD/SE)	Control (Mean $\pm$ SD/SE)	Effect	SE	References
Cover Crop Effect	Total nematode abundance (ind./100 g soil)	Mega-aggregate (LMA)	1982.72 $\pm$ 140.55 (CC)	1207.02 $\pm$ 84.06 (CK)	1982.72	140.55	Paudel et al. (2021)
Cover Crop Effect	Bacterivore abundance (ind./100 g soil)	Micro-aggregate (MA)	708.25 $\pm$ 98.11 (CC)	256.12 $\pm$ 14.77 (CK)	708.25	98.11	Paudel et al. (2021)
Habitat Effect	Omnivore predator abundance (ind./100 g soil)	Mega-aggregate (LMA)	372.82 $\pm$ 31.43 (CK)	7.56 $\pm$ 3.99 (Micro-aggregate CK)	372.82	31.43	Paudel et al. (2021)
Cover Crop Effect	TPLFA (Total microbial biomass) (nmole/g)	2 weeks post-termination	78.1 $\pm$ 3.5 (LA CC)	40.7 $\pm$ 4.8 (BG)	78.1	3.5	Paudel et al. (2021)
Cover Crop Effect	RKN female development (females/g root)	1-month-old tissue	3.26 $\pm$ 0.93 (NX2)	22.28 $\pm$ 6.01 (Control)	3.26	0.93	Paudel et al. (2021)
Cover Crop Effect	Omnivore nematode abundance (count/250 cm <sup>3</sup> )	Field trial (average)	19 $\pm$ 6 (NX2)	4 $\pm$ 1 (BG)	19	6	Paudel et al. (2021)
Mite Conservation Index	Nematode channel ratio (NCR)	Mega-aggregate (LMA)	0.61 $\pm$ 0.03	–	0.61	0.03	Paudel et al. (2021)

Nematode-trapping fungi play a complementary role in the biological control framework. *Arthrobotrys oligospora*, for example, employs trap formation to capture nematodes, a process dependent on autophagic pathways (Chen et al., 2013) and nitrate assimilation (Liang et al., 2016). Moreover, the adhesin AoMad1 has been shown to facilitate recognition of host-derived signals, allowing lifestyle switching between saprophytic and predatory phases (Liang et al., 2015). These adaptive responses demonstrate that fungi are not static predators but dynamically respond to prey availability, environmental cues, and soil nutrient profiles, thereby reinforcing the concept of a highly flexible soil food web.

The physical and chemical structure of soils also significantly influences predator-prey interactions. Erktan, Or, and Scheu (2020) reported that soil porosity, aggregation, and moisture create microhabitats that determine the movement and foraging efficiency of both mites and nematodes. Li et al. (2023) observed that cover crop treatments in kiwifruit orchards altered soil bacterial and nematode communities, emphasizing the role of soil management in shaping microhabitat conditions. Similarly, Paudel, Waisen, and Wang (2021) demonstrated that sorghum-sudangrass cover crops enhance soil microbial diversity and suppress plant-parasitic nematodes, highlighting the synergistic effects of agronomic practices on biological control potential.

The sensitivity of soil predators to environmental perturbations is an essential consideration for sustainable biocontrol deployment. Bedano and Ruf (2010) found that soil Gamasina mites exhibit varied responses to land use and anthropogenic disturbances, suggesting that biocontrol efficacy can be compromised by habitat degradation. Nielsen et al. (2010) further supported this notion, showing that vegetation type, soil properties, and precipitation patterns govern the composition of soil mite and microbial communities across landscapes. These studies indicate that ecological context, rather than predator abundance alone, must guide the implementation of biocontrol programs.

Microbial predators, including myxobacteria, also influence soil community dynamics. Dai et al. (2021) highlighted that myxobacterial predation can restructure microbial communities in artificial microcosms, demonstrating the indirect effects of microbial predation on nematode suppression and nutrient cycling. Lueders et al. (2006) provided evidence for the activity of bacterial

micropredators in natural soils, further corroborating that micro-scale predation events can have ecosystem-level consequences. Such microbial interactions are intricately linked to soil secondary production, as detailed by Coleman, Callaham, and Crossley (2018), where heterotrophic organisms modulate nutrient turnover and energy flow within food webs.

Environmental stressors, including irradiation, have been shown to affect non-target soil organisms and ecosystem processes. Geras'kin, Fesenko, and Alexakhin (2008) reported that chronic exposure of soil fauna to radiation can alter reproductive and metabolic parameters, potentially influencing biocontrol outcomes. This finding underscores the importance of considering both biotic and abiotic stressors when evaluating the effectiveness and stability of soil-based pest suppression strategies.

Finally, the integration of multiple trophic levels, from microbial predators and nematodes to mites and nematophagous fungi, highlights the value of a holistic, ecosystem-based approach to pest management. Rueda-Ramírez, Palevsky, and Ruess (2023) emphasized that soil nematodes can conserve predatory mites, creating feedback loops that sustain predator populations and enhance biocontrol efficacy. The intersection of decomposition, nutrient cycling, and pest suppression, as discussed by Neher and Barbercheck (2019), further demonstrates that a multi-layered understanding of soil ecology is vital for effective and resilient biological control interventions.

The discussion of our findings, supported by these 17 studies, reinforces the concept that soil ecosystems operate as interconnected networks. Predatory mites, nematophagous fungi, and microbial consortia act in concert, with their activity shaped by environmental conditions, soil structure, and management practices. Successful biological control, therefore, requires a nuanced appreciation of trophic interactions, ecological context, and system-level feedbacks. This integrated approach not only suppresses plant-parasitic nematodes effectively but also promotes soil health, biodiversity, and long-term agroecosystem sustainability.

## 5. Limitations

Despite the comprehensive insights provided by this study on microbe-mediated biocontrol, several limitations must be acknowledged. First, most experiments relied on controlled microcosm or greenhouse settings (Aballay et

al., 2020; Azevedo et al., 2020), which may not fully replicate field conditions, including complex soil heterogeneity, fluctuating environmental factors, and natural predator-prey dynamics (Erktan et al., 2020; Li et al., 2023). Second, the scope of species examined was limited; while key nematodes, predatory mites, and microbial consortia were included, the broader soil microbiome and its interactions with other macro- and microfauna remain underexplored (Dai et al., 2020; Paudel et al., 2021). Third, temporal constraints restricted long-term observation of population dynamics and feedback loops, which are critical for assessing sustainable biocontrol effectiveness (Rueda-Ramírez et al., 2023; Neher & Barbercheck, 2019). Fourth, variability in methodology across cited studies—such as differing trap assays, feeding protocols, and microbial inoculation techniques—limits direct comparison and generalization of findings (Chen et al., 2013; Liang et al., 2015). Finally, environmental stressors like radiation and anthropogenic disturbances, although discussed, were not experimentally integrated into the study, which may influence real-world efficacy (Geras'kin et al., 2008; Bedano & Ruf, 2010).

## 6. Conclusion

This study highlights the pivotal role of multi-trophic soil interactions in developing sustainable strategies for managing plant-parasitic nematodes. Evidence synthesized from ecological and meta-analytical analyses demonstrates that synergistic interactions among soil predatory mites, nematode-trapping fungi, and plant growth-promoting bacteria substantially enhance nematode suppression while improving soil biological functioning. These interactions reinforce the stability of soil food webs, promote nutrient cycling, and support resilient agroecosystems. However, variability across environmental conditions and management practices underscores the need for long-term field validation and integrative ecological research. Future biocontrol frameworks should therefore combine microbial and arthropod-based approaches within conservation agriculture systems to maximize pest suppression, ecosystem stability, and sustainable crop productivity.

## Author Contributions

B.S. conceptualized the study, designed the review framework, conducted the literature review and synthesis, and drafted the manuscript. T.B.R. contributed to data interpretation, provided critical revisions, and edited the manuscript for intellectual content. All authors read and

approved the final version of the manuscript.

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