

BEYOND THE RHIZOSPHERE: BACTERIAL ENDOPHYTES AS SUSTAINABLE BIONEMATICIDES FOR PLANTATION CROPS

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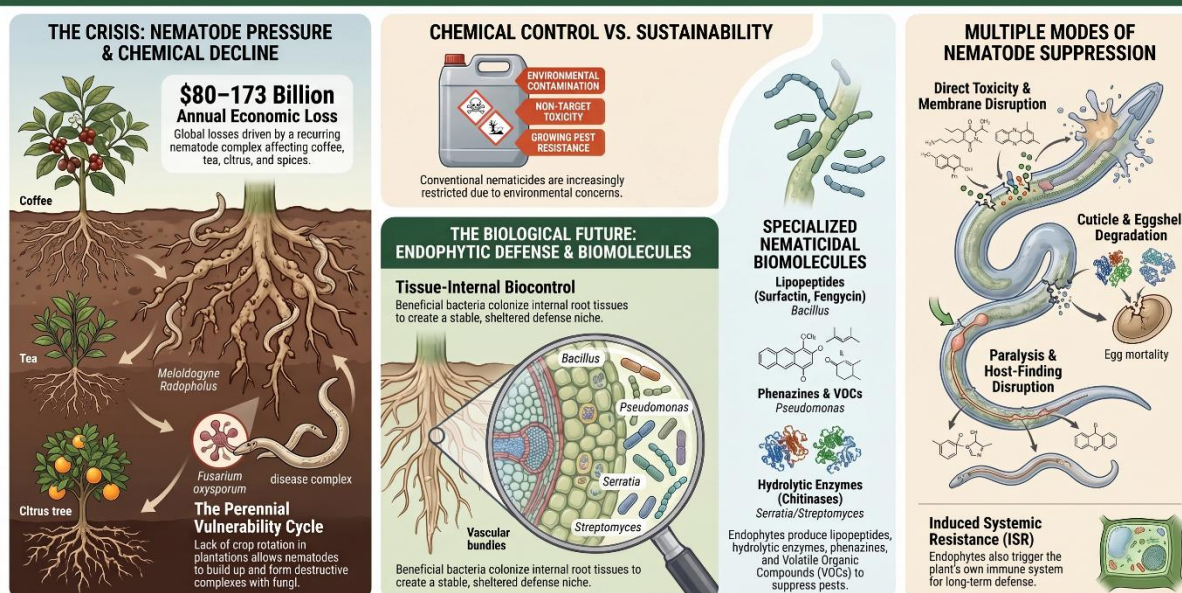
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GRAPHICAL ABSTRACT

Beyond Chemical Control: Bacterial Endophytes for Sustainable Nematode Management



ABSTRACT

Plant-parasitic nematodes (PPNs) impose annual global losses estimated between US\$80 billion and US\$173 billion, with root-knot nematodes (*Meloidogyne* spp.), the burrowing nematode (*Radopholus similis*), lesion nematodes (*Pratylenchus* spp.), and the reniform nematode (*Rotylenchulus reniformis*) forming a recurring damage complex across coffee, black pepper, cardamom, coconut, tea, citrus, and other long-lived plantation crops. Because these perennial systems cannot be rotated out of production, nematode populations accumulate over decades, interact synergistically with fungal pathogens such as *Fusarium oxysporum*, and progressively erode yield and plantation lifespan in ways that annual-crop management strategies are poorly suited to address. Chemical nematicides, long the default control measure, are increasingly constrained by environmental contamination, non-target toxicity, and regulatory phase-outs of key active ingredients, creating an urgent demand for sustainable alternatives. This review synthesises current evidence on bacterial endophytes principally *Bacillus*, *Pseudomonas*, *Serratia*, and *Streptomyces* as a biologically grounded, tissue-internal alternative to rhizosphere-confined biocontrol agents. We examine the nematode complexes and disease biology specific to each major plantation crop; catalogue the taxonomic diversity of endophytic bacteria recovered from black pepper, coffee, coconut, cardamom, tea, and citrus; and detail the mechanistic basis of nematode suppression, spanning direct antagonism (lipopeptides, phenazines, hydrolytic enzymes, volatile organic compounds), induced systemic resistance, nutrient- and phytohormone-mediated indirect effects, and competitive niche exclusion. Crop-wise case studies including genome-guided *Bacillus velezensis* strains deployed across coffee and black pepper field trials illustrate both the promise and the persistent gap between laboratory efficacy and field-scale reproducibility. We further identify critical research gaps, including underexplored crops (cardamom, coconut), smallholder accessibility barriers, fragmented regulatory pathways for microbial biopesticides, and strain performance variability across agro-climatic zones. Finally, we outline future directions genome- and multi-omics-guided biomolecule discovery,

nano-formulation for perennial-crop delivery, bacterial–fungal consortia, integration with rootstock resistance breeding, and region-specific biopesticide development that together chart a pathway toward field-durable, endophyte-based nematode management for sustainable plantation agriculture.

KEYWORD: Bacterial endophytes, Plant-parasitic nematodes, Plantation crop, Sustainable nematode management

1. INTRODUCTION

Plantation crops coffee, black pepper, cardamom, coconut, tea, and rubber form the backbone of agricultural economies across South and Southeast Asia, Africa, and Latin America. Unlike annual field crops, these are long-lived perennials that often remain productive for decades, sometimes even approaching a century of continuous cultivation. This fundamentally reshapes the economics of pest management: a single planting decision locks in land, capital, and labour for the crop's entire lifespan, and any belowground pest that gains a foothold early on can quietly suppress yields for years before its presence is detected (Abd-Elgawad, 2016; Pires et al., 2022).

Plant-parasitic nematodes (PPNs) rank among the most damaging biotic constraints in agriculture worldwide. Annual global losses are estimated at anywhere from US\$80 billion to US\$173 billion, depending on the methodology and crop coverage used in the analysis (Abd-Elgawad, 2016). While more than 4,100 species of plant-parasitic nematodes have been documented, only a relatively small fraction is responsible for severe economic damage (Abd-Elgawad, 2016; Pires et al., 2022). Root-knot nematodes (*Meloidogyne* spp.) bear a disproportionate share of these losses due to their extraordinarily wide host range; *Meloidogyne incognita* alone is known to parasitize over 3,000 plant species (Conceição et al., 2025). Across plantation crops, a recurring nematode complex comprising *Meloidogyne* spp., *Radopholus similis*, *Pratylenchus* spp., and *Rotylenchulus reniformis* affects coffee, black pepper, banana, citrus, and cardamom. This pattern suggests that management approaches developed for one perennial crop may well translate effectively to others (Pires et al., 2022; Saikai et al., 2023).

Perennial cropping systems face a unique vulnerability: without the natural breaks provided by crop rotation or fallow periods, nematode populations are free to build up year after year (Sikora et al., 2023). Once these pests take hold, they are nearly impossible to eliminate entirely. The damage extends well beyond reduced annual yields infections can cut short the productive life of a plantation and drive up replanting costs, which are far steeper than those seen in annual cropping systems (Pires et al., 2022). While using certified clean planting material and resistant cultivars remains the gold standard for nematode management, putting these practices into widespread use is often hindered by scarce availability, steep prices, and a lack of awareness, especially among smallholder farmers in developing regions (Abd-Elgawad, 2016; Pires et al., 2022).

For decades, chemical nematicides have served as the primary weapon against nematodes. But their prolonged use has come under increasing fire due to environmental contamination, harm to non-target organisms, risks to human health, and tightening regulatory frameworks (Sikora et al., 2023; Westerdahl, 2021). The phase-out or restricted application of several key active ingredients including methyl bromide, aldicarb, and phenamiphos has only accelerated the push for greener alternatives (Westerdahl, 2021). Compounding the problem, chemical treatments tend to offer only short-lived relief in perennial systems. Nematodes can persist in soil and root tissue for extended periods, which means growers must reapply chemicals repeatedly driving up costs and amplifying environmental concerns (Pires et al., 2022).

Among the emerging biological approaches, bacterial endophytes stand out as especially promising. These microorganisms take up residence inside plant tissues without triggering disease, forging close, enduring partnerships with their hosts (Kumar & Dara, 2021). Unlike microbes confined to the rhizosphere, endophytes occupy sheltered internal spaces where they steadily churn out bioactive compounds, trigger systemic resistance in the plant, and promote growth all while sidestepping the fierce competition that plays out at the root surface (Hardoim et al., 2015; Kumar & Dara, 2021). A wide range of endophytic bacteria including species from *Bacillus*, *Pseudomonas*, *Streptomyces*, *Paenibacillus*, and *Serratia* have shown potent nematicidal effects by producing lipopeptides, volatile organic compounds, hydrolytic enzymes, siderophores, and other secondary metabolites (Li & Zhang, 2023; Seong et al., 2021). Still, translating this potential into reliable field results remains a hurdle. Inconsistent performance under real-world conditions, difficulties in formulation, and limited commercial pathways continue to hold back broader agricultural adoption (Kumar & Dara, 2021; Seong et al., 2024) (Kumar & Dara, 2021; Seong et al., 2021).

Therefore, this review aims to (i) synthesize current knowledge on bacterial endophyte diversity associated with major plantation crops, (ii) summarize nematicidal biomolecules and their mechanisms of action, (iii) compare evidence across plantation cropping systems to identify transferable management strategies, and (iv) discuss current limitations and future opportunities for developing effective endophyte-based technologies for sustainable management of plant-parasitic nematodes.

1.1 METHODOLOGY

This study followed the PRISMA framework to systematically identify and screen literature indexed in Scopus. The search using “Bacterial endophytes AND NOT nematode AND NOT plantation crops” initially retrieved 6,644

records. Sequential filters based on publication year (2021–2026), subject area, document type, language, keywords, country/territory, and source type reduced the dataset to 220 articles. No records were excluded based on publication stage or open-access status. The overall literature identification and screening process is presented in Figure 1. The final records were exported in CSV format and analysed using Bibliometrix/Biblioshiny and VOSviewer to assess publication trends, keyword co-occurrence, bibliographic networks, citation patterns, and emerging research themes. The selected literature was further examined to identify major research trends, knowledge gaps, and future research directions.

Figure 1. PRISMA flow diagram of the literature search and screening process.

2. Nematode Complex in Major Plantation Crops: Biology and Damage

Tropical plantation crops are long-lived perennials, often intercropped, which allows nematode populations to build steadily year after year. The damage is compounded when nematodes team up with soil-borne fungi to form disease complexes more destructive than either agent alone. Sustainable management therefore demands a systems-level view of nematode biology, host range, associated pathogens, and the wider cropping environment (Nisha, 2024).

2.1 Black pepper: *Radopholus similis* and slow decline disease

The burrowing nematode *Radopholus similis* is the principal driver of black pepper slow decline (Aravind et al., 2010; Ramana & Eapen, 1999). As a migratory endoparasite, it tunnels through the root cortex, destroying feeder roots and triggering progressive vine deterioration. Because black pepper is a perennial, infected roots remain in the ground and suffer repeated assault.

Slow decline is not a single-pathogen problem. (Anandaraj et al., 1996) showed that *R. similis*, *Meloidogyne incognita*, and *Phytophthora capsici* act synergistically sequential inoculation accelerated wilting and root rot far beyond what any pathogen caused alone. Controlling *R. similis* is difficult because it operates deep inside root tissues, which is why endophytic bacteria capable of antibiosis, enzyme production, and competition have drawn attention as internal defenders (Siddiqui & Mahmood, 1999). (Aravind et al., 2010) demonstrated that black-pepper endophytes can suppress *R. similis* experimentally, but translating that into stable field performance across heterogeneous plantations remains the critical hurdle.

2.2 Coffee: Root-knot nematodes and *Fusarium*-associated disease complexes

Coffee suffers from several nematodes, but root-knot nematodes (*Meloidogyne* spp.) dominate. They remodel root architecture and can intensify damage by interacting with soil-borne fungi. A stark example is corky-root disease in Costa Rica, where *Meloidogyne arabica* and *Fusarium oxysporum* together inflict serious harm on *Coffea arabica* (Bertrand et al., 2002). (Bertrand et al., 2002) also found clear genetic variation in resistance among *C. arabica* and *C. canephora* lines, underscoring the value of host resistance within an integrated package.

In perennial coffee systems, root injury accumulates across cycles, gradually opening doors to secondary pathogens. Shaded plantations add complexity: shade trees, weeds, and intercrops can act as alternative hosts, so managing nematodes on coffee roots alone is insufficient. The entire agroecosystem must be considered.

2.3 Comparative nematode profiles of coconut, cardamom, tea and citrus

Coconut (*Cocos nucifera*): Red ring disease, caused by *Bursaphelenchus cocophilus* and vectored by the palm weevil *Rhynchophorus palmarum*, is the most distinctive threat. Infected palms display internal reddish discoloration, canopy decline, and eventual death. In mixed cropping systems, multiple nematode species persist across the host mosaic, requiring system level rather than palm-specific management.

Cardamom (*Elettaria cardamomum*): Root-knot nematodes (*Meloidogyne* spp.), lesion nematodes (*Pratylenchus* spp.), and other migratory endoparasites attack the fine root system, causing galls and cortical lesions. Unlike black pepper and coffee, cardamom has seen little strain-level endophyte screening or field validation, making it a priority target for future bioprospecting.

Tea (*Camellia sinensis*): *Pratylenchus loosi* is the major threat, migrating through roots and producing progressive lesions. (Amarasena et al., 2019) confirmed significant pathogenicity across six Sri Lankan isolates and noted population-level differences in aggressiveness. Further work revealed intraspecific variation and strong environmental modulation rainfall, soil temperature, and moisture all shape population dynamics. Sustainable tea management must therefore account for both nematode population identity and local abiotic conditions.

Citrus (*Citrus* spp.): The citrus nematode *Tylenchulus semipenetrans* drives slow decline syndrome. Because orchards persist for decades, so do nematode populations. Recent research has explored resistant rootstocks and endophytic bacteria as complementary pillars of sustainable control, offering a model for integrating genetics and beneficial microbes.

2.4 Citrus as a Perennial-Crop Comparator: Integrating Rootstock Resistance and Biological Management

Citrus provides a practical template for merging host resistance and biological control into a single integrated strategy. *Tylenchulus semipenetrans* is the most economically important citrus nematode globally, causing slow-decline syndrome. Because no single tactic suffices, experts have long advocated combined approaches resistant material, clean nursery stock, cultural practices, and post-plant management (Verdejo-Lucas & McKenry, 2004). Resistant rootstocks are especially valuable in perennial orchards. Early screening of 52 hybrids identified several *Poncirus trifoliata*-derived selections that blocked or severely limited *T. semipenetrans* reproduction (Verdejo-Lucas et al., 2000). More recently, (Hamid et al., 2025) confirmed differential responses among Huanglongbing-tolerant *P. trifoliata* hybrids, reinforcing that rootstock choice is central to integrated

management. Still, resistance alone is not enough. *T. semipenetrans* persists in perennial systems, and host suitability varies, so durable control needs complementary tactics. (Verdejo-Lucas & McKenry, 2004) emphasized blending pre-plant and post-plant measures rather than relying on any single intervention. Bacterial endophytes fit neatly into this framework. (Banihashemian et al., 2026) evaluated five rootstocks alongside endophytic bacterial strains against *T. semipenetrans*. Rootstock susceptibility varied, and bacterial endophytes suppressed nematode populations while improving plant growth, lending experimental support to biological approaches (Banihashemian et al., 2026). Notably, rootstocks and bacteria were tested separately, so their combined performance remains a key gap for future work. Citrus thus provides a conceptual blueprint for other long-lived plantation crops black pepper, coffee, cardamom, tea, and coconut. Sustainable management in these systems will not rest on one silver bullet. Instead, the path forward lies in integrating host resistance, crop-adapted bacterial endophytes, nematicidal biomolecules, improved formulations, and crop-specific delivery. This sets the stage for the sections that follow on endophyte diversity, suppression mechanisms, and nematicidal biomolecules.

3. Endophytic Bacterial Diversity in Plantation Crops

3.1 General Diversity

Endophytic bacteria inhabit internal plant tissues without causing apparent disease and constitute an important component of the plant microbiome. Their diversity and abundance are influenced by host genotype, tissue type, developmental stage, environmental conditions, geographical location, and cultivation practices. Despite this variability, several bacterial genera including *Bacillus*, *Pseudomonas*, *Enterobacter*, *Serratia*, *Burkholderia*, and *Streptomyces* are recurrently reported from the endosphere of diverse plant species (Kandel et al., 2017).

The functional importance of these endophytes extends beyond simple colonization. Endophytic bacteria can enhance plant performance through nutrient acquisition, nitrogen fixation, phytohormone production, and modulation of host responses to biotic and abiotic stresses (Kandel et al., 2017). They may also improve tolerance to drought, salinity, temperature stress, and pathogen pressure through direct and indirect mechanisms, including the production of bioactive metabolites and modulation of plant physiological responses (Watts et al., 2023).

Within this broad diversity, *Bacillus* and *Pseudomonas* are particularly relevant to biological control because members of these genera possess multiple traits favourable for plant colonization and pathogen suppression. Their widespread occurrence as endophytes and demonstrated plant-growth-promoting and antagonistic activities have made them promising microbial biocontrol agents. However, the composition of endophytic communities remains strongly host and environment dependent, and the dominance of individual genera should not be generalized across different plant species or geographical regions (Kandel et al., 2017).

3.2 Black Pepper Endophyte Screening Studies

Black pepper (*Piper nigrum* L.) represents one of the most systematically investigated plantation crops for bacterial endophytes with biocontrol potential. In a foundational culture-based survey, (Aravind et al., 2009) recovered 74 bacterial endophytes from internal root and stem tissues of black pepper. The collection comprised *Pseudomonas* (20 isolates), *Bacillus* (22), *Arthrobacter* (15), *Micrococcus* (7), *Serratia* (1), *Curtobacterium* (1), and eight unidentified isolates. Three isolates identified as *Pseudomonas aeruginosa*, *P. putida*, and *Bacillus megaterium* provided more than 70% suppression of *Phytophthora capsici* under greenhouse conditions (Aravind et al., 2009). This bacterial collection was subsequently investigated for suppression of the burrowing nematode *Radopholus similis*, an important component of the slow-decline syndrome of black pepper. (Aravind et al., 2010) evaluated endophytic isolates using in vitro and in vivo approaches and demonstrated that selected bacterial endophytes could suppress *R. similis*. Importantly, laboratory responses did not always correspond directly with performance in planta, illustrating a recurring limitation of relying exclusively on in vitro screening for selection of nematode biocontrol agents.

One of the promising black-pepper endophytes, *Bacillus megaterium* BP17, was subsequently characterized for its antimicrobial metabolite profile. (Munjal et al., 2016) demonstrated broad-spectrum antimicrobial activity mediated by volatile compounds, with pyrazine-group chemicals implicated in the antagonistic activity of BP17 against several plant pathogens. This finding illustrates the potential of plantation-crop endophytes not only as living microbial inoculants but also as reservoirs of biologically active metabolites (Munjal et al., 2016).

Collectively, these studies establish black pepper as an important model for the progressive selection of endophytes from isolation and diversity characterization → pathogen/nematode screening → identification of promising strains → characterization of their bioactive metabolites.

3.3 Coffee Leaf and Root Endophytes

Coffee (*Coffea arabica* L.) harbours a taxonomically diverse endophytic bacterial community across vegetative and reproductive tissues. In an early multi-country survey, (Vega et al., 2005) recovered 87 culturable bacterial endophytes belonging to 19 genera from coffee plants collected in Colombia, Hawaii, and Mexico. Approximately 68% of the isolates were Gram-negative. Endophytes were recovered from adult leaves, different berry tissues, and leaves, stems, and roots of seedlings, demonstrating extensive colonization of the coffee plant. The seed contained the greatest diversity among the examined berry tissues, with genera including *Bacillus*, *Burkholderia*, *Pantoea*, *Pseudomonas*, and *Serratia* (Vega et al., 2005).

Subsequent research expanded the functional characterization of coffee endophytes. (Silva et al., 2012) recovered 217 bacterial and 17 fungal endophytes from healthy coffee tissues and evaluated their potential as plant-growth promoters and biological control agents against coffee leaf rust. These findings demonstrated that the coffee

endosphere contains microorganisms with functions extending beyond microbial diversity to plant-growth promotion and disease suppression.

More recently, endophytic *Bacillus* spp. has continued to receive attention in coffee. More recently, endophytic *Bacillus* spp. isolated from *Coffea arabica* leaves were characterized for their biocontrol potential against phytopathogenic fungi and lepidopteran larvae. The study identified *Bacillus mycoides*, *B. thuringiensis*, and *B. velezensis*, highlighting the functional diversity of coffee-associated *Bacillus* endophytes (de Castro et al., 2025). Although not all of these coffee endophyte studies specifically targeted plant-parasitic nematodes, they demonstrate that coffee tissues harbour a substantial reservoir of bacterial taxa with antagonistic, growth-promoting, and metabolite-producing capabilities. Such diversity provides a valuable foundation for targeted screening against economically important coffee nematodes.

3.4 *Bacillus velezensis* in Coffee and Black Pepper: From Strain Selection to Field Validation

Among plantation-associated bacterial taxa, *Bacillus velezensis* has emerged as one of the most promising species for translating microbial biocontrol from laboratory screening to field application (Rabbee et al., 2019). This progression was demonstrated particularly clearly by (Thanh Tam et al., 2023), who characterized plant-associated *B. velezensis* strains using genome analysis and metabolite profiling before evaluating selected candidates in greenhouse and large-scale field trials.

Two strains, *B. velezensis* TL7 and S1, were selected for further development based on their combined biocontrol and plant-growth-promoting characteristics. TL7 represented an endophytic strain, whereas S1 was soil-associated. Genome-level comparisons placed the strains close to the well-characterized *B. velezensis* FZB42 lineage, while metabolite analyses supported their capacity to produce compounds associated with biological control (Thanh Tam et al., 2023).

Their activity was subsequently evaluated against disease complexes involving *Meloidogyne* spp. and *Fusarium oxysporum*. Greenhouse experiments demonstrated suppression of root-knot development, while subsequent field-scale application to coffee and black pepper provided evidence that the selected strains could maintain biological activity under agronomically realistic conditions. Importantly, the study reported improved harvest performance in treated coffee and black pepper plantations overall, providing one of the more instructive examples of translating *B. velezensis* based biocontrol from genomic and metabolomic characterization toward field deployment in plantation crops instructive precisely because the two strains did not perform equally: the soil-associated S1 reached the trial's $\geq 60\%$ disease-suppression benchmark, while the endophytic TL7 did not. This strain-specific divergence, and its likely ecological explanation, is examined in detail in Section 6.3 (Tam et al., 2023).

Evidence from non-plantation systems further demonstrates the broader nematocidal potential of *B. velezensis*. For example, strain Bv-25 has shown strong activity against *Meloidogyne incognita* in cucumber, including effects on egg hatching, juvenile mortality, root colonization, plant defence responses, and root-knot development (Tian et al., 2022). However, Bv-25 originated from cucumber rhizosphere soil rather than from an endophytic plantation-crop niche. It should therefore be regarded as a mechanistic comparator supporting the broader nematocidal potential of *B. velezensis*, rather than as direct evidence of plantation-crop endophyte diversity (Thanh Tam et al., 2023).

The field performance reported by (Thanh Tam et al., 2023) is particularly significant for plantation agriculture because perennial systems impose challenges that are difficult to reproduce in short-duration pot experiments, including heterogeneous soils, established microbial communities, variable climatic conditions, and long crop cycles.

3.5 Endophytes in Citrus, Kiwifruit, and Other Woody Perennials

Evidence from other perennial crops further supports the widespread occurrence and biocontrol potential of bacterial endophytes. In citrus, endophytic bacteria were isolated from six healthy *Citrus* species and evaluated for their antagonistic activity against *Xanthomonas citri* subsp. *citri*, the causal agent of citrus canker. Among the recovered isolates, *Bacillus amyloliquefaciens* LE109, *B. subtilis* LE24, and *B. tequilensis* PO80 exhibited promising antagonistic activity. Application of these isolates significantly reduced citrus canker development in lime plants, demonstrating the effectiveness of citrus-derived endophytes as biological control agents (Daungfu et al., 2019).

Although the (Daungfu et al., 2019) study addressed a bacterial pathogen rather than a plant-parasitic nematode, it provides relevant evidence that woody perennial crops harbour endophytes capable of establishing within host tissues and expressing biologically significant antagonistic activity. More direct evidence for nematode suppression has been reported in kiwifruit, where endophytic bacteria isolated from root and leaf tissues were characterized and evaluated against the root-knot nematode *Meloidogyne incognita*. The study identified a taxonomically diverse endophytic bacterial community and demonstrated the nematode-suppressive potential of selected isolates in a perennial fruit crop (Banihashemian et al., 2022).

Among the evaluated isolates, *Pantoea ananatis* and *Pseudomonas chlororaphis* showed promising activity by reducing nematode infection and reproductive parameters while improving plant-growth characteristics under greenhouse conditions (Banihashemian et al., 2022). This study is particularly relevant as a perennial-crop comparator because it directly links endophyte isolation, taxonomic identification, nematode suppression, and plant-growth responses within a woody/vine crop system.

Taken together, studies in black pepper, coffee, citrus, and kiwifruit reveal considerable taxonomic and functional diversity among bacterial endophytes. *Bacillus* and *Pseudomonas* recur prominently across these systems, but their abundance and functional importance should not be interpreted as universal dominance across all perennial crops. Instead, the available evidence indicates that plantation and other perennial crops harbour host- and tissue-specific endophytic communities from which strains with nematicidal, antimicrobial, growth-promoting, or stress-mitigating traits can be selected. The current evidence, major nematode targets, reported bacterial endophytes, and research status across selected plantation crops are summarized in Table 1. The successful progression of selected strains from isolation to greenhouse and, in some cases, field validation provides a strong rationale for expanding similar endophyte-discovery programmes to comparatively understudied plantation crops such as cardamom, coconut, and tea.

Table 1. Current evidence and research gaps in the application of bacterial endophytes for the management of plant-parasitic nematodes in plantation crops

Crop	Major nematode(s)	Bacterial endophyte(s)	Key findings	Research status	Reference(s)
Black pepper (<i>Piper nigrum</i>)	<i>Radopholus similis</i>	<i>Bacillus megaterium</i> BP17, <i>Curtobacterium luteum</i> TC10	BP17 and TC10 consistently suppressed <i>R. similis</i> following greenhouse screening of 74 endophytic isolates.	Strong greenhouse evidence; field validation limited.	(Aravind et al., 2010; Munjal et al., 2016)
Coffee (<i>Coffea</i> spp.)	<i>Pratylenchus coffeae</i> , <i>Meloidogyne</i> spp.	Coffee-derived bacterial endophytes (K6)	Isolate K6 produced 65.8% mortality of <i>P. coffeae</i> and showed the highest nematicidal activity.	Direct crop-specific evidence available.	(Munif & Giyanto, 2015)
Coffee / Black pepper	<i>Meloidogyne</i> spp.; <i>Fusarium oxysporum</i>	<i>Bacillus velezensis</i> TL7, S1	Genome-guided strain selection followed by greenhouse and field validation (>60% disease suppression; increased yield).	Strong field-scale validation; strain-dependent performance (see Section 6.3).	(Thanh Tam et al., 2023))
Cardamom (<i>Elettaria cardamomum</i>)	<i>Meloidogyne incognita</i> , <i>R. similis</i> , <i>Pratylenchus coffeae</i> , <i>Rotylenchulus reniformis</i>	No validated bacterial endophytes reported	No published bacterial endophyte nematode bioassays.	Major research gap.	(Kumar & Dara, 2021; Nisha, 2024)
Coconut (<i>Cocos nucifera</i>)	<i>Bursaphelenchus cocophilus</i> ; <i>Radopholus similis</i>	<i>Bacillus subtilis</i> , <i>Pantoea dispersa</i>	Endophytes isolated from coconut tissues, but nematicidal activity has not been evaluated.	Endophyte isolation only; no nematode studies.	(Kumar & Dara, 2021; Salo & Novero, 2020)

4. Mechanisms of Nematode Suppression

4.1 Direct Antagonism Antibiosis and Enzymatic Degradation

Endophytic bacteria attack nematodes directly via two main categories of bioactive compounds: toxic secondary metabolites and lytic enzymes. Biocontrol mechanisms include direct antagonism (antibiosis, enzymatic degradation) and indirect interactions with the host plant (competition for nutrients, niche exclusion, and siderophore-mediated suppression) (Meel & Saharan, 2025). Among enzymatic tools, cuticle- and eggshell-degrading enzymes are particularly important, since the nematode cuticle represents the first physical barrier a

biocontrol agent must overcome. Collagenases, chitinases, and serine proteases released by endophytic bacteria serve as virulence factors that break down the chemical components of the nematode cuticle (Kumar & Dara, 2021). This mechanism was demonstrated experimentally using the endophyte *Bacillus cereus* BCM2: its crude extracellular proteins killed 100% of *Meloidogyne incognita* second-stage juveniles within 72 hours, and scanning electron microscopy revealed progressive damage to the cuticle and eggshell prior to destruction of internal structures (Kumar & Dara, 2021).

In addition to enzymes, several endophyte-associated bacteria generate diffusible toxins that act directly against nematodes. The symbiotic bacteria carried by entomopathogenic nematodes exemplify this potency cell-free culture filtrates of *Xenorhabdus indica* caused mortality rates reaching 95.3% in *M. incognita* within 72 hours, while associated biogenic silver nanoparticles produced comparable or even greater lethality (Ghareeb et al., 2025). Soilborne isolates outside the traditional biocontrol genera display similar activity; for instance, a *Brevundimonas bullata* isolate exhibited nematocidal and suppressive effects against both *M. incognita* and the model nematode *Caenorhabditis elegans*, with a toxic metabolite identified from its culture supernatant (Li et al., 2022).

4.2 Induced Systemic Resistance (ISR)

Rather than attacking the nematode directly, endophytic colonization often works by waking up the plant's own immune machinery. Because these bacterial endophytes are woven into intricate root microbiome networks, they are perfectly positioned to strengthen the host's defenses against parasitic infection promoting growth and pushing back through phytohormones, antibiotics, hydrolytic enzymes, and volatile organic compounds. Various *Bacillus* species including *B. velezensis*, *B. pumilus*, *B. megaterium*, *B. subtilis*, *B. firmus*, *B. thuringiensis*, and *B. amyloliquefaciens* have been shown to activate both systemic acquired resistance and induced systemic resistance against root-knot nematodes (Kamalanathan et al., 2023).

The ability of these bacteria to successfully colonize root tissues appears to be the fundamental driver of this priming effect. In *Panax notoginseng*, for example, rhizosphere strains *Bacillus velezensis* GJ-7 and *Bacillus cereus* NS-2 colonized roots quickly and stably, and this presence switched on defense-responsive genes in the host, ultimately trimming down root-gall numbers across multiple control experiments (Wu et al., 2022). Importantly, this immune activation isn't trapped underground: studies with the olive endophyte *Pseudomonas fluorescens* PICF7 demonstrated that root colonization by this biocontrol agent can trigger systemic defense responses in distant aerial tissues, ramping up genes for lipoxygenase, catalase, ACC oxidase, and phenylalanine ammonia-lyase while also boosting defense-related transcription factors (Gómez-Lama Cabanás et al., 2014).

Mechanistically, endophytes trigger systemic resistance by upregulating plant genes involved in phytohormone signaling, phytoalexin biosynthesis, and pathogenesis-related protein production, while also releasing bacterial volatile organic compounds (VOCs) that contribute to defense, and by igniting salicylic acid, jasmonic acid, and ethylene signaling pathways. Documented cases include *Bacillus sphaericus* B43 inducing resistance to *Globodera pallida* in potato, and *Agrobacterium radiobacter* G12 doing the same against *M. incognita* in tomato (Kumar & Dara, 2021).

4.3 Indirect Mechanisms Nutrient Solubilization and Phytohormone Synthesis

Besides direct antagonism and induced resistance, bacterial endophytes can indirectly suppress nematodes by enhancing plant vigor. Improved nutrient availability through phosphate solubilization and nitrogen fixation, together with phytohormone production, promotes healthier root systems that are better able to withstand nematode infection (Banihashemian et al., 2025). Both bacterial and fungal endophytes improve crop health through nitrogen fixation, phosphate solubilization, siderophore production, and phytohormone synthesis, while also helping plants weather abiotic stresses (Chaudhary et al., 2022). The auxins, gibberellins, cytokinins, ethylene, and abscisic acid that these microbes produce do more than stimulate root growth they also feed into the very signaling pathways plants use for defense. This overlap was demonstrated in *Burkholderia seminalis* 869T2, where the endophyte's output of auxin, siderophores, and phosphate-solubilizing activity coincided with altered expression of host genes across the auxin, gibberellin, cytokinin, and abscisic acid transduction pathways (Hwang et al., 2025). The combined ability of endophytic bacteria to promote plant growth and enhance defense is widely recognized. Traits such as phytohormone production, nitrogen fixation, phosphorus solubilization, and nutrient mobilization support plant growth, whereas secondary metabolites, including antibiotics, siderophores, and lytic enzymes, help suppress pathogenic organisms. (Bansal et al., 2025).

4.4 Competitive Colonization and Niche Exclusion

Endophytes that stake out the same intercellular and vascular real estate nematodes need for their feeding sites can physically block infection before it starts. Certain bacteria quickly move into root-knot nematode feeding sites, cutting infection rates by competing for space and nutrients while also tweaking root exudates to trigger plant resistance (Wu et al., 2022). The close association of endophytes with plant tissues makes them promising candidates for bionematicides. Because both endophytes and sedentary plant-parasitic nematodes inhabit the same tissues, endophytes are better positioned to suppress nematodes than non-endophytic biocontrol agents. This advantage is further enhanced by their ability to produce pesticidal secondary metabolites. (Kumar & Dara, 2021). Endophytes can also go on the offensive directly attacking, killing, immobilizing, or repelling PPNs while the nematodes are still hunting for a host, all while competing for space and churning out harmful metabolites such as flavonoids, peptides, quinones, alkaloids, and steroids. Colonization can even reshape the chemical landscape that

nematodes navigate: endophyte presence shifts root exudate composition and output in ways that further interfere with nematode host-finding and establishment (Kumar & Dara, 2021)

4.5 Volatile Organic Compounds (VOCs)

Endophytic and rhizosphere bacteria release low-molecular-weight volatile organic compounds that can fumigate nematodes without ever touching them. In a GC-MS screen of bacterial VOCs, dimethyl disulfide (DMDS) and S-methyl thioacetate (MTA) stood out as the most potent fumigants against *Caenorhabditis elegans*, with LC50 values of 8.57 and 1.43 $\mu\text{g}/\text{cm}^3$ air, respectively. MTA was also highly effective against *Meloidogyne incognita* (Diyapoglu et al., 2022). Pseudomonads have drawn particular attention in this area: VOCs from *Pseudomonas putida* 1A00316 killed *M. incognita* on contact, with 2-octanone, hexenyl acetate, 2-undecanone, DMDS, and 2-nonanone all contributing to the toxicity. Related strains *P. koreensis*, *P. monteilii*, and *P. soli* produced DMDS alongside 1-undecene and pyrazine derivatives that also had nematocidal properties. *Bacillus* endophytes play a similar role: VOCs from *Bacillus atrophaeus* GBSC56, including DMDS, methyl isovalerate, and 2-undecanone, showed strong nematocidal activity (Deng et al., 2022). This volatile-based defense isn't limited to bacteria, either a synthetic blend mimicking compounds from the endophytic fungus *Daldinia cf. concentrica* (3-methyl-1-butanol, 2-methyl-1-butanol, 4-heptanone, and isoamyl acetate) wiped out 99% of *Meloidogyne javanica* juveniles (Liarzi et al., 2016).

5. Nematicidal Biomolecules

Bacillus endophytes are remarkably productive when it comes to cyclic lipopeptide molecules that act through multiple mechanisms by disrupting membranes and killing nematodes at the same time. These bacteria synthesize lipopeptides such as surfactin, bacillomycin D, fengycins, iturins, and bacteriocins, all of which have been shown to suppress *Meloidogyne incognita*. Because they are amphiphilic, these compounds can interact with lipid membranes and contribute to nematode mortality. The major classes of bacterial nematicidal biomolecules, their representative bacterial sources, proposed mechanisms of action, target nematodes, and reported efficacy are summarized in Table 2

5.1 Lipopeptides (Surfactin, Iturin, Fengycin *Bacillus* spp.)

Bacillus endophytes are remarkably productive when it comes to cyclic lipopeptides molecules that act through multiple mechanisms by disrupting membranes and killing nematodes at the same time. These bacteria synthesize lipopeptides such as surfactin, bacillomycin D, fengycins, iturins, and bacteriocins, all of which have been shown to suppress *Meloidogyne incognita*. Because they are amphiphilic, these compounds slip into lipid bilayers and punch holes through them. They are traditionally celebrated for their antifungal and antibacterial punch, but their surfactant and pore-forming abilities also chew through the nematode cuticle and the microbial biofilms that come with it. That versatility makes them the most commonly reported class of nematicidal biomolecules coming from *Bacillus* in endophyte screening studies (Ayaz et al., 2024). Isolated surfactin molecules at 35 ppm caused 85% egg mortality and 83.97% ovicidal activity in *M. incognita* within 96 hours, while strains producing both surfactin and iturin showed synergistic nematicidal activity (Kavitha et al., 2012; Nadeem et al., 2021). Fengycin emerged as the most potent lipopeptide family, with strong membrane-disrupting activity (Chen et al., 2025; Yin et al., 2024).

5.2 Phenazine Compounds

Phenazines stand out as a chemically unique family of nitrogen-containing heterocyclic secondary metabolites that exhibit broad-spectrum antimicrobial activity and play important roles in biological control (Mavrodi et al., 2006). Take phenazine-1-carboxamide (PCN), for instance it was isolated from *Pseudomonas aeruginosa* W-126, an endophyte living inside the medicinal plant *Waltheria indica*. PCN proved highly effective at keeping *Ralstonia solanacearum* in check, with an EC50 of 64.16 $\mu\text{g}/\text{mL}$, and it also killed *Meloidogyne incognita* with an LC50 of 118.63 $\mu\text{g}/\text{mL}$ after 72 hours (S. Wang et al., 2025). A closer look at structure activity relationships across PCN analogues revealed that the phenazine backbone and its acylamide side group were the critical pharmacophores for knocking out *R. solanacearum*. Against *M. incognita*, the top performers were phenazin-1-ylamine, PCN itself, phenazine, and 1-hydroxyphenazine each cutting nematode survival by more than 50% at 125 $\mu\text{g}/\text{mL}$ (S. Wang et al., 2025). In a pot experiment targeting the bacterial wilt-root-knot nematode disease complex in pepper, PCN delivered control efficiencies of 51.41% against the bacterium and 39.80% against the nematode (S. Wang et al., 2025). That dual-targeting performance highlights the broader potential of endophyte-derived phenazines for managing complex diseases involving both nematodes and bacterial pathogens, reinforcing their importance as multifunctional biocontrol metabolites (Chin-A-Woeng et al., 2003).

5.3 High-Efficacy Strains from Culture Filtrates

Cell-free filtrates from several *Bacillus* endophytes and rhizobacteria have produced some of the highest nematode mortality rates on record, which tells us the active compounds are secreted into the surrounding medium and don't require living bacterial cells to make direct contact. Filtrates from *B. subtilis* OKB105 and *B. cereus* 09B18, for example, were powerfully nematicidal killing up to 95% of second-stage juveniles from both *Meloidogyne javanica* and *Heterodera filipjevi* (Ayaz et al., 2024). The same OKB105 strain, along with *B. amyloliquefaciens* B3, also proved lethal to *Aphelenchoides besseyi*, *Ditylenchus destructor*, and *Bursaphelenchus xylophilus*, with mortality rates of 85%, 79%, and 100% respectively (Ayaz et al., 2024). These findings place *Bacillus*-derived culture filtrates among the most potent bacterial nematicidal preparations reported and emphasize the importance of extracellular metabolites in biological control (Migunova & Sasanelli, 2021).

5.4 Coffee-Specific Endophyte Activity

Endophytes drawn from particular crop hosts often display nematocidal activity that is tightly linked to their host or ecological niche. A compelling example is the endophytic bacterium K6, recovered from coffee leaves, which achieved a 65.8% mortality against *Pratylenchus coffeae* (Ayaz et al., 2024). This finding underscores the value of bioprospecting host-associated endophytes, as crop-specific microbial communities often harbor strains adapted to the ecological niche of their host and capable of promoting plant health and suppressing pests and pathogens (Asad et al., 2023). For plantation systems such as coffee, tea, and other perennial crops where lesion nematodes (*Pratylenchus* spp.) remain persistent constraints, host-targeted endophyte bioprospecting offers a promising strategy for identifying crop-adapted biological control agents (Strobel & Daisy, 2003).

5.5 *Serratia plymuthica*

Beyond the well-studied genera *Bacillus* and *Pseudomonas*, *Serratia* endophytes are increasingly recognized as promising sources of nematocidal metabolites, highlighting the expanding diversity of bacterial endophytes with potential for biological control of plant-parasitic nematodes (Kumar & Dara, 2021). *Serratia plymuthica* M24T3, for instance, delivered complete mortality against the pinewood nematode (*Bursaphelenchus xylophilus*). Other *Serratia* strains have also shown promise against root-knot nematodes by suppressing egg hatching and killing juveniles (Ayaz et al., 2024). Together, these findings indicate that *Serratia* represents a valuable yet underexplored bacterial genus with considerable potential for sustainable nematode management alongside more extensively studied genera such as *Bacillus* and *Pseudomonas* (Aioub et al., 2022).

5.6 Enzymes (Proteases, Chitinases)

Hydrolytic enzymes are among the best-characterized nematocidal mechanisms employed by bacterial biocontrol agents, acting by degrading the structural polymers that constitute the nematode cuticle and eggshell. Both rhizobacteria and endophytic bacteria produce a wide range of lytic enzymes, including chitinases, proteases, cellulases, lipases, glucanases, and keratinases, which disrupt nematode development and metabolism by degrading the essential components of the cuticle and eggshell (Ayaz et al., 2024). Chitinases hydrolyze the chitin matrix of the nematode eggshell, leading to eggshell rupture and premature hatching of incompletely developed juveniles, whereas proteases cleave peptide bonds within structural proteins and glycoproteins of the cuticle, resulting in progressive degradation of the nematode body wall (Yang et al., 2013).

Recent studies have provided direct experimental evidence for these mechanisms. A purified protease from *Bacillus cereus* NJSZ-13 exhibited strong nematocidal activity against the pinewood nematode (*Bursaphelenchus xylophilus*), while collagenases produced by *Pseudomonas fluorescens* FP805PU and *Brevibacterium frigoritolerans* FB37BR impaired *Meloidogyne ethiopica* and *Xiphinema index* by degrading the collagen layer of the cuticle (Ayaz et al., 2024; Li et al., 2023).

Similarly, extracellular proteases secreted by *Bacillus cereus* BCM2 caused 100% mortality of *Meloidogyne incognita* second-stage juveniles within 72 hr. Electron microscopy revealed a progressive sequence of damage, beginning with cuticle disruption, followed by eggshell degradation and ultimately destruction of internal tissues, providing compelling evidence that extracellular hydrolytic enzymes are key determinants of bacterial nematocidal activity (Hu et al., 2020).

Table 2. Major classes of bacterial-derived nematocidal biomolecules and metabolites reported from endophytes and other beneficial bacteria

Biomolecule/ metabolite class	Representative bacterium / strain	Mechanism proposed action	Target nematode	Reported efficacy	Biomolecule/ metabolite class
Lipopeptides (e.g., surfactin, iturin, fengycin and bacillomycin D)	<i>Bacillus</i> spp.; surfactin specifically from <i>B. subtilis</i> MTCC441	Amphiphilic interaction with nematode surface membranes/cuticle; surfactin exhibits direct nematocidal/ovicidal activity	<i>Meloidogyne</i> <i>incognita</i>	Surfactin at 35 ppm caused 85% egg mortality and 83.97% ovicidal activity after 96 h	Lipopeptides (e.g., surfactin, iturin, fengycin and bacillomycin D)

Phenazines (phenazine-1-carboxamide, PCN)	<i>Pseudomonas aeruginosa</i> W-126 (plant-associated/endophytic isolate)	Nematicidal and antibacterial activity; phenazine skeleton and acylamide group contribute to bioactivity	<i>Meloidogyne incognita</i> ; <i>Ralstonia solanacearum</i> (co-target)	LC ₅₀ = 118.63 µg/mL at 72 h; 39.80% inhibitory rate against <i>M. incognita</i> in pepper pot experiment	Phenazines (phenazine-1-carboxamide, PCN)
Culture-filtrate metabolites (secreted, cell-free)	<i>B. subtilis</i> OKB105; <i>B. cereus</i> 09B18; <i>B. amyloliquefaciens</i> B3	Extracellular metabolites/proteins can act without direct bacterial-cell contact	<i>M. javanica</i> ; <i>Heterodera filipjevi</i> ; <i>Aphelenchoides besseyi</i> ; <i>Ditylenchus destructor</i> ; <i>Bursaphelenchus xylophilus</i>	Up to 95–100% juvenile mortality reported, depending on bacterial strain, metabolite preparation and target nematode	Culture-filtrate metabolites (secreted, cell-free)
Host-/niche-associated bacterial metabolites	Coffee leaf endophyte K6	Bioactivity associated with a host-adapted endophytic isolate; active metabolite(s) require further characterization	<i>Pratylenchus coffeae</i>	65.8% mortality reported	Host-/niche-associated bacterial metabolites
Serratia-associated nematicidal metabolites	<i>Serratia plymuthica</i> M24T3	Nematicidal activity associated with bacterial metabolites; active compound(s) not fully characterized	<i>Bursaphelenchus xylophilus</i> ; <i>Meloidogyne</i> spp.	100% mortality reported against <i>B. xylophilus</i> under the reported experimental conditions	Serratia-associated nematicidal metabolites
Hydrolytic enzymes (especially proteases and chitinolytic enzymes)	<i>Bacillus cereus</i> BCM2; <i>B. cereus</i> NJSZ-13; <i>Pseudomonas fluorescens</i> FP805PU; <i>Brevibacterium frigoritolerans</i> FB37BR	Enzymatic degradation/damage of nematode cuticle and eggshell components, leading to tissue disruption and mortality	<i>M. incognita</i> ; <i>Bursaphelenchus xylophilus</i> ; <i>M. ethiopica</i> ; <i>Xiphinema index</i>	Crude extracellular proteins from <i>B. cereus</i> BCM2 caused 100% <i>M. incognita</i>	Hydrolytic enzymes (especially proteases and chitinolytic enzymes)

				J2 mortality within 72 h	
Volatile organic compounds (VOCs; e.g., DMDS and MTA)	<i>Pseudomonas putida</i> 1A00316; <i>P. koreensis</i> ; <i>Bacillus atrophaeus</i> GBSC56	Fumigant toxicity through volatile compounds without direct cell contact	<i>Caenorhabditis elegans</i> ; <i>M. incognita</i>	For <i>C. elegans</i> , LC ₅₀ values were 8.57 µg/cm ³ air (DMDS) and 1.43 µg/cm ³ air (MTA) after 24 h fumigation; MTA also showed activity against <i>M. incognita</i>	Volatile organic compounds (VOCs; e.g., DMDS and MTA)

6. Crop Wise Case Studies

6.1 Black Pepper -Endophyte Screening Against *R. similis* Across Three Pepper Varieties

Black pepper (*Piper nigrum* L.) stands out as one of the first crops where researchers systematically hunted for endophytes capable of tackling a migratory endoparasitic nematode. In a landmark study, scientists took endophytic bacteria that had already been isolated from ten different black pepper varieties and tested against *Phytophthora capsici*, and for the first time screened them against the burrowing nematode *Radopholus similis* the culprit behind slow decline disease in black pepper (Aravind et al., 2010). Because *R. similis* is a migratory pest, it largely slips past conventional fungal and bacterial biocontrol agents, which makes endophyte-based suppression particularly attractive for this pathosystem (Aravind et al., 2010).

The team screened seventy-four endophytic bacterial isolates recovered from black pepper tissue, using both lab-based and plant-based bioassays. In vitro results on their own turned out to be unreliable, so the promising candidates were put to the test inside living plants across three black pepper varieties an important step to see whether the host's own genetics might sway how well the endophytes performed (Aravind et al., 2010). This approach of cross-testing the same endophyte candidates against multiple host genotypes before taking them to the field established a methodological blueprint that researchers still follow today in black pepper and coffee studies. That early groundwork eventually paved the way for later discoveries, such as *Bacillus megaterium* BP17 and *Curtobacterium luteum* TC10, which suppress *R. similis* through antibiotic production (Munjal et al., 2016). Collectively, these studies established black pepper as an important model for the discovery and evaluation of endophytic bacteria for sustainable management of migratory plant-parasitic nematodes and highlighted their potential as environmentally friendly alternatives to chemical nematicides (Subhagan et al., 2020)

6.2 Coffee Two-Year Field Application of *T. asperellum* and *P. lilacinum* (Fungal Comparator)

Although *Trichoderma asperellum* and *Purpureocillium lilacinum* are fungi rather than bacteria, their two-year field performance on mature *Arabica coffee* in Kenya provides a valuable establishment benchmark against which bacterial endophyte colonization speed can be judged (Saikai et al., 2023). Across seven field trials spanning two years and trees of different ages, all plots were heavily infested with *Meloidogyne hapla* — the first report of this species on coffee in Kenya. Both fungal biocontrol agents were eventually detected colonizing roots endophytically and were recovered from soil, but only after six months had passed since the initial application. It took a full 12 months before *M. hapla* population densities in treated roots declined significantly, even though soil nematode counts stayed similar across treatments during that entire period. The treatments did leave distinct marks on soil ecology. *T. asperellum* improved soil health and enriched microbial diversity, as shown by maturity and Shannon indices, while *P. lilacinum* increased the abundance of fungivorous nematodes especially *Aphelenchus* species, which seemed to treat *P. lilacinum* as a preferred food source (Saikai et al., 2023). Because the trial soils were stressed and denuded, both the treatment impacts and colonization detection were probably delayed, leading

the study's authors to conclude that longer observation periods are needed to fully capture treatment benefits on perennial crops (Saikai et al., 2023).

This sluggish fungal timeline is not universal a Brazilian study on mature conilon coffee recorded significant reductions in *Meloidogyne incognita* just two months after *Trichoderma harzianum* application but it does highlight a recurrent challenge with fungal biocontrol on established perennials (Zinger et al., 2021). By contrast, bacterial endophytes derived from coffee itself have shown far more rapid action. *Bacillus* isolates from Vietnamese coffee caused 100% nematode mortality within 24 hours in vitro (Duong et al., 2021), while Ethiopian coffee root endophytes *Bacillus pumilus* and *B. mycoides* reduced galling and egg masses under pot conditions (Mekete et al., 2009). In tomato model systems, *Bacillus subtilis* achieves root colonization densities exceeding 10^7 CFU/g within 14 days (Chen et al., 2026) a pace that, if replicated in coffee, would offer growers a genuinely practical advantage over the six-to-twelve-month fungal establishment window, particularly when managing mature, already-infested plantations.

6.3 Coffee and Black Pepper Combined - Genome-Selected *Bacillus velezensis* Strains in Large-Scale Field Trials

This case captures both the upside and the hard reality of genome-guided endophyte selection: even when an isolate is closely related to a proven biocontrol reference strain and carries an impressive arsenal of secondary-metabolite genes, that genetic promise does not automatically translate into equivalent field performance (Thanh Tam et al., 2023). The phenomenon is now recognized as a systematic "translation gap": laboratory and greenhouse assays consistently overestimate efficacy because they ignore microbial competition, rainfall wash-off, and temperature fluctuations that reshape bacterial survival in open tropical fields (Dao & Ho, 2026). Multi-location soybean trials with other *Bacillus*-based inoculants have recorded similarly variable field outcomes despite uniform greenhouse success (Vasconcelos et al., 2025), and colonization studies show that root-associated *Bacillus* strains often achieve stable establishment under sterile conditions yet fragment into heterogeneous, low-density populations in non-sterile field soil (Mendis et al., 2018).

The TL7 failure is not universal for endophytic *B. velezensis*. A rice endophyte, LS123N, persisted from seed to maturity and significantly reduced multiple diseases in field trial (Tu et al., 2024), while Vietnamese BTR11 matched chemical bactericide efficacy against rice bacterial leaf blight in replicated field plots (Do et al., 2023). What distinguished S1 from TL7 in the coffee trial was likely ecological niche: rhizosphere domestication can amplify colonization density by severalfold (Z. Wang et al., 2025), and S1's rhizosphere lifestyle allowed it to achieve the $\geq 60\%$ pathogen reduction in soil that TL7's endophytic strategy could not replicate. The lesson is that genome mining identifies potential, but field efficacy depends on whether that potential is coupled to ecological fitness for the specific niche rhizosphere or endophytic into which the strain must establish.

6.4 Citrus and Kiwifruit (Woody Perennial Comparator)

Woody perennial fruit crops outside the usual plantation staples offer a helpful cross-crop lens for gauging how well bacterial endophytes tackle root-knot nematodes. Take kiwifruit: researchers in Iran isolated thirty-one bacterial endophytes from roots and leaves across twelve genera including *Bacillus*, *Pseudomonas*, *Streptomyces*, *Variovorax*, and *Chryseobacterium* all drawn from nematode-infested growing regions. Two isolates in particular, *Pseudomonas ananatis* 121.en and *Pseudomonas chlororaphis* 54.en, stood out for their antagonism against *Meloidogyne incognita*. They cut down the number of galls and egg masses on roots, reduced second-stage juvenile (J2) populations in the soil, and boosted plant growth parameters compared to untreated controls (Banihashemian et al., 2022).

Follow-up work with the same research group has pushed this from greenhouse discovery to field validation and mechanism. *Bacillus altitudinis* 123.en one of the isolates from the original kiwifruit screen was found to induce systemic resistance, upregulating PR-1 and PR-5 defense genes by 3.9 to 8 fold after nematode challenge (Banihashemian et al., 2023). More importantly, formulated probiotic products containing *Pseudomonas chlororaphis* RO1 and *Bacillus velezensis* RO9 were tested in an actual kiwifruit orchard infested with *M. incognita*. After two applications, RO1 reduced soil J2 populations by 76.7% and the nematode reproduction factor by 60.4%, while RO9 cut root galls by 31% and egg masses by 44% performance statistically equivalent to the chemical nematicide Rugby® (Mirghasemi et al., 2025).

Citrus offers a parallel woody-perennial test case, this time against the slow-decline nematode *Tylenchulus semipenetrans* rather than *Meloidogyne*. On susceptible sour orange rootstock, endophytic *Bacillus safensis* Q.en and *Pseudomonas chlororaphis* P.en significantly reduced nematode females on roots and J2s in soil, while simultaneously improving shoot and root biomass (Banihashemian et al., 2025). *Bacillus* strains from citrus rhizospheres had already shown $\sim 80\%$ J2 mortality in vitro alongside enhanced root development (Labiadh et al., 2023), and a recent review documents at least sixteen bacterial or fungal bionematicides already commercialized for citrus nematode management worldwide (Kumar & Arthurs, 2021).

This one-two punch fewer nematodes alongside healthier plants echoes the dual suppression-and-growth-promotion pattern seen repeatedly in bacterial endophyte studies on other woody perennials, from kiwifruit and citrus to coffee and black pepper. That consistency makes these fruit crops worthwhile benchmark systems: they help validate whether bacterial endophytes can deliver the same paired benefits in plantation systems where success is ultimately measured by both nematode suppression and tangible plant improvement.

7. Formulation and Delivery Challenges Specific to Perennial Plantation Systems

7.1 Long Establishment/Colonization Time in Woody Perennials

Woody perennial fruit crops outside the usual plantation staples offer a helpful cross-crop lens for gauging how well bacterial endophytes tackle root-knot nematodes. Take kiwifruit: researchers in Iran isolated thirty-one bacterial endophytes from roots and leaves across twelve genera including *Bacillus*, *Pseudomonas*, *Streptomyces*, *Variovorax*, and *Chryseobacterium* — all drawn from nematode-infested growing regions. Two isolates in particular, *Pantoea ananatis* 121.en and *Pseudomonas chlororaphis* 54.en, stood out for their antagonism against *Meloidogyne incognita*. They cut down the number of galls and egg masses on roots, reduced second-stage juvenile (J2) populations in the soil, and boosted plant growth parameters compared to untreated controls (Pires et al., 2022). This one-two punch fewer nematodes alongside healthier plants echoes the dual suppression-and-growth-promotion pattern seen repeatedly in bacterial endophyte studies on other woody perennials. That consistency makes kiwifruit a worthwhile benchmark crop: it helps validate whether bacterial endophytes can deliver the same paired benefits in plantation systems like coffee and black pepper, where success is ultimately measured by both nematode suppression and tangible plant improvement. Similar patterns emerge across diverse crops: tomato endophytes including *Bacillus wiedmannii* and *Serratia liquefaciens* reduced galls and egg masses while promoting plant growth, confirming that dual-action biocontrol is a generalizable trait among endophytic taxa (Moslehi et al., 2021).

7.2 Tree Age Effects on Endophyte Establishment

A consistent theme across the kiwifruit, citrus, and coffee case studies above (Sections 6.2 and 6.4) is that endophyte colonization of woody perennial root systems is typically slower to establish, and slower to show measurable nematode suppression, than in annual crops. In the Kenyan coffee trials, fungal biocontrol agents were not detected colonizing roots endophytically until six months after application, and a full 12 months passed before nematode densities declined significantly (Saikai et al., 2023). Bacterial endophytes generally establish faster than fungal agents in comparable systems *Bacillus* isolates from Vietnamese coffee achieved 100% in vitro nematode mortality within 24 hours (Duong et al., 2021) but translating that faster in vitro action into an equally fast in planta colonization timeline in mature, already-established root systems remains far less consistent, as the TL7/S1 divergence in Section 6.3 illustrates.

This lag matters directly for formulation strategy: a product that performs well in a 4-6week pot trial cannot be assumed to colonize and act on the same timescale once applied to a decades-old root system with an established native microbial community. Similar patterns emerge across other crops: tomato endophytes including *Bacillus wiedmannii* and *Serratia liquefaciens* reduced galls and egg masses while promoting plant growth (Moslehi et al., 2021), suggesting that dual-action biocontrol is a generalizable trait among endophytic taxa but the speed at which that dual action becomes measurable in the field is highly system-dependent, and is consistently slower in woody perennials than in the annual or short-cycle systems where most screening is first carried out.

7.3 Nursery-Stage vs. Established-Plantation Application Strategies

Perennial plantation crops present two fundamentally different opportunities for getting endophytes into plants and each comes with its own set of practical trade-offs. The first is nursery-stage inoculation, where young seedlings are treated before they ever hit the field. The second is drench or soil-based application to mature, already-established trees.

For coffee, one of the smartest nematode management moves is simply starting clean: using healthy, resistant, protected seedlings to reduce initial infection from the outset. This approach is actively promoted across Latin America and Asia, where nematode control is built into the nursery phase before problems can take root in mature plantations (Thanh Tam et al., 2023). Recent reviews of coffee endophyte application pipelines confirm that nursery-stage inoculation is particularly suitable for coffee because seedlings can be treated under controlled conditions, colonization can be monitored before transplanting, and candidate strains can be selected before exposure to field-level stress. Concrete examples already exist: *Metarhizium robertsii* coated onto *Arabica* seeds established endophytically and improved seedling growth while suppressing coffee leaf minor damage across generations (Wei et al., 2026).

Once a perennial crop is in the ground and infected, however, the game changes completely. Managing soil-borne pests and diseases on established perennials is notoriously difficult, and once nematode populations settle in, they are virtually impossible to wipe out. The coffee field trials discussed earlier illustrate this uphill battle: biocontrol products were drenched around the base of mature, already-infected trees on a weekly-to-monthly basis over many months, essentially trying to force colonization retroactively into a fully developed root system (Thanh Tam et al., 2023). Comparative work on coffee seedlings shows why this is so much harder than nursery inoculation: when *Beauveria bassiana* was introduced via radicle inoculation, foliar spray, stem injection, or soil drench, direct injection into young tissue yielded the highest endophytic recovery, while drench establishment declined steadily over time (Posada et al., 2007).

Nursery-stage delivery is increasingly recognized as an effective strategy for establishing beneficial endophytes early in plant development. Advances in microbial formulations, including seed and seedling coatings containing carriers, tackifiers, and stabilizing compounds, have improved microbial survival during storage and enhanced early colonization following germination (Kandel et al., 2017; von Maltzahn et al., 2021). Yet scaling up remains stubborn. A multi-laboratory assessment of seed-coated biocontrol agents found that survival during 3-6 months

of storage varies dramatically by microbial group: spore-forming *Bacillus* and *Paenibacillus* strains maintained stable populations for six months, while *Pseudomonas* and non-spore-forming fungi often crashed below efficacy thresholds within a single month (Köhl et al., 2025). The shelf-life of coated seeds for both the seedling and the microbe is still described as an overlooked topic in the literature (Paravar et al., 2023). Given the year-long lag documented for drench applications on mature trees, nursery inoculation offers a mechanistically cleaner entry point, but only if the strain and coating formulation are matched correctly: the same *Bacillus* strain can excel as a seed yet underperform as a drench, or vice versa, depending on its colonization biology (Mattos et al., 2025). The catch is that this requires growers to commit to management years before symptoms would ever push them to act. Still, for perennial plantations where reversing established nematode damage is notoriously difficult, the nursery window may be the only point at which bacterial endophytes can truly get ahead of the problem.

7.4 Consistency of Field Efficacy

If there is one overarching bottleneck choking the pipeline from promising lab discovery to commercial shelf, it is the stubborn inconsistency of endophyte performance in the field. Across horticultural, agricultural, fodder, and forestry systems, numerous *Bacillus* species and some endophytic *Fusarium* strains have shown genuine nematocidal potential in controlled *in vitro* and *in vivo* studies, yet efforts to turn them into commercial bionematicides keep running aground on the same problem (Kumar & Dara, 2021). The major stages involved in translating bacterial endophyte-based nematode management from laboratory discovery to field deployment, together with the key bottlenecks at each stage, are illustrated in Figure 2.

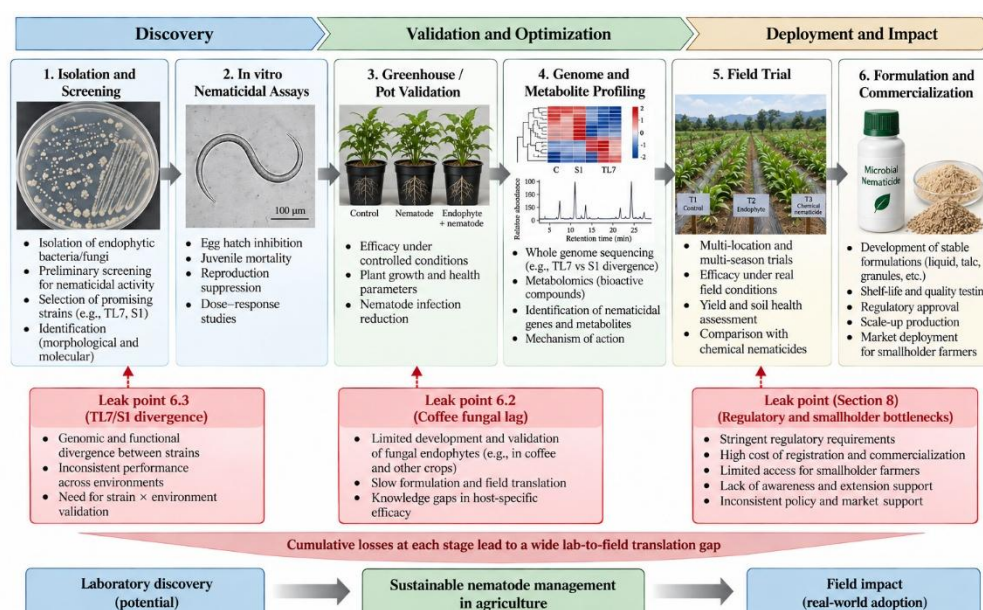
The culprits behind this variability are well documented. Harsh soil conditions, fierce competition from native soil microorganisms, and predatory nematodes that treat the introduced biocontrol agent as lunch all chip away at efficacy. In some cases, endophytes may even release metabolites toxic to herbivorous mammals or throw the resident rhizosphere and phylloplane microbial communities off balance, producing unintended collateral damage (Kumar & Dara, 2021). This is not an endophyte-specific headache. The broader biocontrol world faces the same pattern: microbial strains that look brilliant *in vitro* routinely stumble under field conditions. That gap is reflected in the disappointingly short list of plant-growth-promoting rhizobacteria that have actually made it to market, and the regulatory thicket surrounding biocontrol agent registration only deepens the discouragement, even when field data look promising (Pires et al., 2022). Formulation science is fighting back. Encapsulation technologies both micro and nano-scale are being engineered to shield endophytes from environmental stress and release them in a controlled manner, which has already been shown to boost viability and extend shelf-life enough to make repeated or delayed field applications genuinely practical (Das et al., 2025).

Looking ahead, the proposed fixes are threefold. First, invest in applied research that generates hard field-efficacy data rather than leaning on greenhouse and pot-trial results. Second, keep refining formulation technologies to bring down production costs while improving shelf stability. And third perhaps most promisingly move away from the single-strain silver-bullet mindset and instead assemble consortia of multiple biocontrol agents that can suppress nematodes through complementary and synergistic interactions, so the whole system does not collapse if one strain has an off day (Gowrisudha et al., 2025; Kumar & Dara, 2021).

Figure 2. Schematic representation of the lab-to-field translation pathway for bacterial endophyte-based nematode management, highlighting key stages, validation steps, major bottlenecks, and the progression toward sustainable agricultural application.

8. Research Gaps and Challenges

8.1 Underexplored Crops (Cardamom, Coconut) Relative to Coffee/Pepper



Coffee and black pepper dominate the bacterial endophyte–nematode literature; coconut and cardamom remain comparatively unstudied. Endophytic bacteria have been isolated from coconut tissue *Bacillus subtilis* and *Pantoea dispersa* strains with antimicrobial pigment production and phosphorus solubilization (Salo & Novero, 2020) and antagonistic *Bacillus velezensis* strains from coconut orchard soils have shown activity against fungal pathogens including *Ceratocystis paradoxa*, *Pestalotiopsis menezesiana*, and *Curvularia oryzae* (Zhu et al., 2025). In both cases, the research targeted fungal disease suppression and growth promotion; nematode control was not evaluated, despite coconut's exposure to the red ring nematode (*Bursaphelenchus cocophilus*) and burrowing nematode (*Radopholus similis*) across major production regions (Griffith et al., 2005). Cardamom shows a similar pattern, more pronounced. Entomopathogenic nematodes have been reasonably well studied for cardamom root grub management (Soundarajan et al.), but no dedicated screening of bacterial endophytes against cardamom-associated plant-parasitic nematodes exists in contrast to the multi-decade screening programs built around coffee and pepper. This is an addressable gap: the isolation and genomic characterization pipelines validated on coffee and pepper could be applied directly to cardamom and coconut. What is missing is crop-specific validation targeted screening, varietal cross-testing, and field trials confirming whether these pipelines transfer to nematode suppression in these crops.

8.2 Smallholder-Farmer Accessibility

Strain performance in the lab does not guarantee farmer access. Smallholder systems, which produce a large share of global plantation crops, operate under different economic and informational constraints than research stations. In East African coffee production, nematode awareness among growers is minimal, despite nematodes being one of the most damaging constraints to coffee elsewhere (Saikai et al., 2023). Where management options exist full replanting of aged orchards, for instance cost and practicality put them out of reach for most smallholders (Saikai et al., 2023).

The pattern extends beyond coffee. Across Sub-Saharan Africa, low-cost interventions such as clean seedlings and host resistance could substantially reduce pest and disease pressure and pesticide dependence. In practice, smallholder nurseries are frequently established in nematode-infested fields, so planting stock is often already infected with root-knot nematodes before reaching the field, undermining downstream management (Coyne et al., 2018). For bacterial endophyte technologies, this means efficacy data alone is insufficient. Delivery cost, application complexity, and diagnostic awareness need research attention comparable to strain discovery and formulation not as secondary concerns, but as parallel priorities.

8.3 Regulatory Pathways for Microbial Biopesticides

Regulatory approval timelines for microbial biocontrol agents vary sharply by jurisdiction. The EU and US both reference OECD risk-assessment standards, but EU registration is markedly slower several EU and member-state agencies lack the experience and resources for efficient review, which partly explains the smaller number of microbial biocontrol products reaching the European market compared to the US (Frederiks & Wesseler, 2019). A second issue is that OECD testing guidelines were built for conventional chemical pesticides; microbial-specific guidance is limited, and some existing protocols perform poorly in practice. This leaves developers with limited clarity on the data required for a regulatory dossier on a new bacterial endophyte strain (Wend et al., 2024).

Harmonization efforts exist but are the exception: the East African Community has established shared biopesticide registration guidelines allowing partner states to recognize each other's approvals and pool data (Deeksha et al., 2025). Absent broader adoption of this model, a strain approved for nematode suppression in one region may face an entirely different data and timeline requirement elsewhere a structural bottleneck limiting how quickly research findings reach growers (Deeksha et al., 2025; Frederiks & Wesseler, 2019; Wend et al., 2024).

8.4 Strain Specificity and Environmental Variability Across Plantation Agro-Climates

Biocontrol strains rarely perform consistently across soil types, climates, and cropping systems, which is a particular challenge for plantation crops grown under diverse tropical and subtropical conditions. The efficacy of microbial agents against root-knot nematodes is influenced by habitat characteristics, soil properties, and interactions with native microbial communities, making single-strain strategies difficult to apply uniformly across regions. In particular, soil pH, temperature, moisture, and organic matter content strongly affect the establishment, survival, and performance of introduced biocontrol agents (Sharma et al., 2025).

Temperature is a major variable. In one study of an endophytic bacterial antagonist against a bacterial wilt pathogen, suppression peaked at 20°C and declined sharply as temperatures rose a shift in competitive balance that helps explain inconsistent field results across seasons and elevations (Wei et al., 2017). Single-strain inoculants also often underperform because they cannot outcompete locally adapted native soil bacteria, which has driven interest in multi-strain consortia that spread environmental tolerance across several strains rather than relying on one (Yadav et al., 2025). Together, this indicates that strain selection for plantation-crop nematode management cannot assume portability across regions. Programs need to test candidate strains across the soil types, elevations, and temperature ranges present in the target growing region rather than extrapolating from a single agro-climatic zone (Sharma et al., 2025; Wei et al., 2017; Yadav et al., 2025).

9. FUTURE SCOPE AND CONCLUSION

9.1 Future Scope

Despite the demonstrated potential of bacterial endophytes as nematocidal agents, several areas require further investigation before large-scale field adoption. Genome mining and metabolomic profiling of endophytic and entomopathogenic bacterial strains, as increasingly applied to genera such as *Photorhabdus* (Krithika et al., 2024; Meesil et al., 2023) and *Stenotrophomonas* (Sahu et al., 2026), should be expanded to systematically identify novel biosynthetic gene clusters encoding nematocidal secondary metabolites (Meesil et al., 2023). Coupling such omics-based discovery with functional validation will help move candidate biomolecules from in vitro screening toward field-deployable products. Consortium-based approaches, combining multiple endophytic and rhizosphere bacterial strains, have shown promise over single-strain inoculants in suppressing *Pratylenchus* populations in coffee (Asyiah et al., 2020; Munif & Giyanto, 2015) and warrant further optimization for other plantation crops such as black pepper, banana, and citrus. Integration of endophytic bacteria with complementary strategies nematode-resistant rootstocks and grafting (Banihashemian et al., 2025; Poonia et al., 2025), and biopesticide-compatible nanoformulations such as bacterially-synthesized silver nanoparticles (Khan et al., 2023; Osman et al., 2025) offers a promising route toward durable, multi-tactic nematode management rather than reliance on any single control measure. Formulation stability, shelf life, and delivery methods (seed treatment, soil drenching, or endophyte-based nano-carriers) also need dedicated research to ensure consistent field performance across varying soil and climatic conditions (Abd-Elgawad, 2024; Khan et al., 2023). Finally, comparative field trials across agro-climatic zones, along with regulatory and cost-benefit assessments, are essential to translate laboratory and greenhouse successes into commercially viable, farmer-adopted biocontrol products for plantation systems (Abd-Elgawad, 2024; Nisha, 2024).

9.2 CONCLUSION

Bacterial endophytes represent a scientifically sound and environmentally sustainable alternative to chemical nematocides for managing plant-parasitic nematodes in plantation crops. Their intimate association with host plant tissues allows them to produce nematocidal biomolecules in situ, offering advantages in persistence and target specificity over externally applied rhizobacterial treatments (Aravind et al., 2010; Bertrand et al., 2000; Munif & Giyanto, 2015). Evidence from black pepper, coffee, and citrus systems confirms their efficacy against key nematode genera, including *Radopholus*, *Pratylenchus*, and *Meloidogyne*. Advances in genome mining and metabolomics are now revealing the genetic basis of this nematocidal potential (Krithika et al., 2024; Meesil et al., 2023), strengthening the case for rational, mechanism-guided development of endophyte-based biocontrol products within broader integrated pest management frameworks (Abd-Elgawad, 2024). Realizing this potential at a commercial scale will depend on integrating endophyte-based interventions with resistant germplasm (Banihashemian et al., 2025; Bertrand et al., 2000), precision formulation technologies, and region-specific management strategies, positioning bacterial endophytes as a central pillar of sustainable, chemical-free nematode management in plantation crops in the years ahead.

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CRediT authorship contribution statement

Afreen A: Writing—original draft. **K. Devrajan:** Formal analysis, Conceptualization.
P. Vetrivelkalai: Visualization. **Nakkeeran S:** Visualization, Conceptualization.
Anandham R: Supervision, Visualization.

Declaration of competing interest

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

Data availability

Data will be made available on request

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