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REVIEW ARTICLE

A Comprehensive Review of Biological Agents Against Plant-Parasitic Nematodes

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ABSTRACT

Plant-parasitic nematodes (PPNs) are a massive group of animals that feed on plant tissue and cause a reduction in yield quantity and quality. PPNs affect plants directly by infecting the plant or indirectly breaking the plant's resistance to other pathogens and/or synergistically with different pathogens, causing complex diseases. Additionally, PPNs sometimes carry plant pathogens as viruses and transmit them to hosts. Many strategies were employed to manage PPNs. Biological control is considered the main strategy for controlling PPNs, alternatively to nematicides, which cause harmful effects on humans, the environment, and beneficial microorganisms. Fungi, bacteria, viruses, actinomycetes, mites, predatory nematodes, protozoa, and yeasts were utilized successfully for managing PPNs. These bioagents suppress nematode populations through a variety of direct and indirect mechanisms. These environmentally benign strategies are being progressively incorporated integrated into integrated pest management (IPM) systems to reduce reliance on chemical nematicides and support sustainable agriculture. In this review, the benefits, drawbacks, limitations, and overcomes of applying biological control strategies against PPNs have been discussed and summarized.

Keywords: Biocontrol, nematicides, plant-promoting growth, nematode-trapping fungi, limitations.

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INTRODUCTION

Plant-parasitic nematodes (PPNs) are microscopic roundworms that establish obligate parasitic relationships with plants, feeding on various tissues such as roots, stems, leaves, flowers, buds, and seeds(Ferris and Ferris, 1998; Back *et al.*, 2002; Perry and Moens, 2011). They are aquatic, colonizing a wide range of environments, Furthermore, their body is bilaterally symmetrical and unsegmented (Back *et al.*, 2002). According to Decraemer & Hunt (2013), there are more than 4100 species of PPNs that infect plants and cause losses in yield out of 25,000 described species belonging to the Phylum Nematoda (Back *et al.*, 2002; Decraemer and Hunt, 2013).

PPNs have a special stylet organ, a hollow, needle-like feeding apparatus used to puncture plant cells, inject secretions, and extract nutrients (Yeates *et al.*, 1993; Bird and Koltai, 2000; Perry and Moens, 2011; Jones *et al.*, 2013). According to nematode parasitism (Figure 1), PPNs can divide into sedentary endoparasites entry into the host, reach feeding site and settle within root whole life cycle (root-knot nematodes, *Meloidogyne*), migratory endoparasites which enter the host and migrate through host tissues causing extensive damage (lesion nematode, *Pratylenchus*), semi-endoparasites partially penetrate the host plant to feed at one stage of the life cycle. (citrus nematode, *Tylenchulus*), and ectoparasites that never enter the host (dagger nematode, *Xiphinema*) (Perry and Moens, 2011). Additionally, the other three types of PPN parasitism include nematodes that feed on the bulb and stem (*Ditylenchus*), nematode-infested seeds (seed gall nematode, *Anguina*), and nematodes that feed on foliar parts (*Aphelenchoides*).

Generally, root infection by PPNs causes damage to plant roots (Kantor *et al.*, 2024). Hence, they reduce the ability of plants to absorb water and nutrients. Due to nematode infection of roots, the biomass was reduced, and there was a distortion of root structure and enlargement. So, root galls, stunt root growth, rotting of the root system, cysts found on the root surface, and necrotic lesions in the root cortex may be symptoms of nematode infection (Singh and Phulera, 2015). Furthermore, nematode-damaged plant roots provide an opportunity for other plant pathogens to invade, leading to weakening of the plant. On the other hand, shoot infection with plant nematodes results in reduced vigor, distortion of plant parts, and death of infected tissues. PPNs infecting roots may lead to chlorosis, stunt top growth, small or sparse foliage, wilt, exhibit dieback of larger branches, and failure to respond to fertilizers.

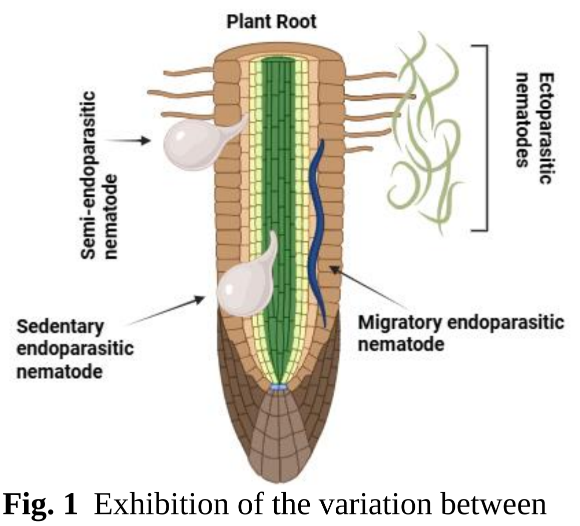

Fig. 1 Exhibition of the variation between nematode feeding habitats.

The life cycle of PPNs consists of five stages: 1st-stage juvenile (mostly inside the eggs), 2nd-stage juvenile hatch from eggs and move towered plant, following the plant exudates (responsible for infection in most PPN species), 3rd-stage juvenile, and 4th-stage juvenile, mostly mid-stage between 2nd-stage and adults, finally adults. Molt should occur between the two following stages to convert from one stage to another (molting four times). Consequently, adult females should lay eggs after mating or by parthenogenesis.

The impact of PPN infection extends beyond yield reduction, affecting plant vigor, nutrient uptake, and increasing susceptibility to other pathogens (Back *et al.*, 2002). The economic consequences are substantial, impacting food security and the livelihoods of farmers worldwide (Nicol *et al.*, 2011). Globally, PPNs are recognized as significant agricultural pests, causing $80 billion in annual crop losses (Jones *et al.*, 2013). However, the crop losses due to nematode infections were estimated at 14.6% in developing countries compared with 8.8% in developed countries (Sasser and Freckman, 1987). Root-knot, cyst, and lesion nematodes were found responsible for more than 50% of crop losses out of the losses caused by PPNs (Jones *et al.*, 2013; El-Qurashi *et al.*, 2023). In addition, root-knot nematodes were observed globally infecting different crops (El-Qurashi *et al.*, 2019; Mohamed *et al.*, 2023).

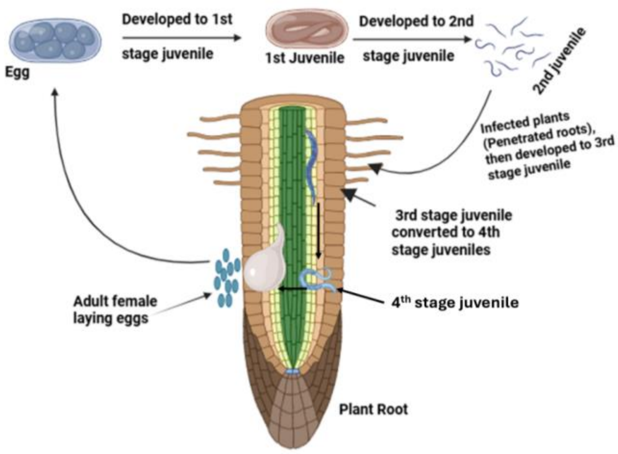

Fig. 2 The life cycle of PPNs (sedentary endo-parasitic nematode).

Understanding the biology and accurate identification of PPNs is crucial for management (El-Qurashi *et al.*, 2017). So, evaluating the nematode population densities, identifying the species, and knowing the irrigation system and cultivated crops are crucial for employing an accurate management strategy (El-Qurashi *et al.*, 2019). Many strategies have been employed to manage plant-parasitic nematodes (El-Qurashi *et al.*, 2023). Chemical methods have received much attention since the 19th century. In recent years, many nematicides have been banned from global markets due to their harmful effects on human health, the environment, and microflora (El-Qurashi *et al.*, 2019; 2025). So, nematologists are seeking alternative strategies for managing PPNs.

Biological control was the best choice and received much attention. Moreover, a plethora studies were carried out under different environmental conditions to screen the effect of different isolated organisms against PPNs. Among these organisms, filamentous fungi were isolated from various niches and examined against different nematode genera worldwide. *Trichoderma, Fusarium, Penicillium, Aspergillus, Arthrobotrys, Drechslerella,* and *Catenaria* were isolated from different nematode stages and varying niches. These genera were examined for their efficacy in controlling PPNs *in vitro* and *in vivo*. Fungal culture filtrate or mycelial mass can be used for this purpose.

Many bacterial isolates were successfully utilized in controlling PPNs worldwide. Additionally, actinomycetes and yeasts have shown potential against PPNs. The success of bioagents in managing PPNs came from their ability to parasitize on nematode eggs or juveniles, compete for niches and food, and/or produce some toxins and enzymes. This review will discuss the biological control of PPNs with different organisms besides their effects on plant growth and/or pathogens. Benefits and limitations of using bioagents against PPNs will be mentioned as well.

Fungi as biocontrol agents against PPNs

Filamentous fungi are a group of microorganisms belonging to the Kingdom Fungi. These organisms are recognized by eukaryotes, heterotrophs, and contain chitin in their cell wall. Fungi are found in different niches. They were isolated from soilborne, seedborne, airborne, and marine pathogens. Depending on their effects, large groups are known as plant pathogens. Groups of them can infect animal cells and cause chronic diseases, and others can be useful for humans and used for controlling plant diseases and/or producing medical supplies.

Nematophagous fungi

Biological control of plant-parasitic nematodes using fungi was studied extensively (Moosavi and Zare, 2012). Fungi that are used for PPNs control are known as nematophagous fungi. Nematophagous fungi consist of three groups: 1) nematode-trapping fungi (NTF), 2) endoparasitic fungi, and 3) egg and cyst-parasitic fungi (Nordbring-Hertz *et al.*, 2006). Nematophagous fungi are classified according to their effect on nematodes into 1) nematode-trapping fungi, which produce special devices to capture nematodes and consume their bodies. These devices include adhesive branches, mycelia, knobs, nets, and spores, and constricting and non-constricting rings. 2) fungi that produce toxins and/or metabolites affecting nematode survival and movement. 3) fungi that infect sedentary stages of nematodes (eggs, cysts, adult sessile females). 4) fungi infect worm-like stages (vermiform) of nematodes by producing sticky spores that adhere to the nematode cuticle, then germinate inside their body and consume their content.

Once a nematode is captured (either by sticky devices or by passes through rings), the fungus penetrates the nematode's cuticle (outer layer) with specialized hyphae (Yang *et al.*, 2007). Then it grows inside the nematode's body, releasing enzymes to digest the internal contents and absorb the nutrients (Jiang *et al.*, 2017). Ecologically, NTFs are commonly found in soil environments rich in organic matter, such as decaying. Many NTF can live as saprophytes (feeding on dead organic matter) when nematodes are scarce (Jiang *et al.*, 2017). The formation of traps is often induced by the presence of nematodes or specific chemical cues (like nematode pheromones or low nutrient conditions) (Hsueh *et al.*, 2013). NTF have significant potential as biological control agents against plant-parasitic nematodes that damage crops (Jiang *et al.*, 2017). The most studied genera of NTF are *Arthrobotrys*, *Dactylellina* (includes species formerly in *Monacrosporium* and *Dactylella*), and *Drechslerella* (Kumar, 2024; Suresh *et al.*, 2024).

Arbuscular mycorrhizal fungi

Arbuscular mycorrhizal fungi (AMF) represent a widespread symbiotic association between fungi and the roots of most terrestrial plants (Castro-Delgado *et al.*, 2020). AMF are the most common type, forming intricate structures within root cells to facilitate nutrient exchange– primarily providing phosphorus and other minerals to the plant in exchange for carbon. There is growing evidence that establishing AMF symbiosis can help plants tolerate or resist PPN attacks, offering a potential biological control strategy (Schouteden *et al.*, 2015).

The protective effect of AMF against PPN is generally considered multifactorial and often indirect, rather than involving direct killing of nematodes (Malviya *et al.*, 2023). Key mechanisms include: 1) Improved plant nutrition and tolerance via enhanced nutrient (especially phosphorus) and water uptake, leading to more vigorous plants (Begum *et al.*, 2019). These healthier plants are better able to compensate for the damage caused by nematode feeding and can tolerate higher nematode populations without substantial yield loss. 2) Competition for resources and space, AMF colonizes the root cortex, potentially competing with sedentary endoparasitic nematodes for space and nutrients (photosynthates) supplied by the plant (Poveda *et al.*, 2020). Heavy AMF colonization might limit suitable feeding sites for nematodes. 3) Induced systemic resistance (ISR) and priming: AMF colonization can trigger the plant's defense mechanisms (Malviya *et al.*, 2023). This involves activating defense-related genes and pathways, leading to systemic resistance throughout the plant. The plant becomes 'primed' to respond more quickly and strongly to subsequent attacks by pathogens, including nematodes (Poveda *et al.*, 2020). This can involve strengthening cell walls or producing protective biochemical compounds (Underwood, 2012). 4) Alteration of root exudates, the symbiosis can change the profile of chemicals released by plant roots (Cameron *et al.*, 2013). These changes might make the roots less attractive to certain nematode species or interfere with their host-finding cues (da Silva Campos, 2024). 5) Changes in root morphology, AMF colonization can sometimes alter root system architecture, potentially influencing nematode penetration and movement within the root (Schouteden *et al.*, 2015).

The effectiveness of AMF in controlling nematodes is not universal and heavily depends on the specific combination of plant species/cultivar, AMF species/strain, nematode species/population density, and environmental conditions (soil type, fertility, climate). Some AMF-nematode interactions may result in suppression, while others might show no effect or even, rarely, increased susceptibility

Endophytic fungi

Endophytic fungi are microorganisms that live inside the tissues of plants (roots, stems, leaves) for all or part of their life cycle without causing any apparent harm or disease symptoms to their host (Wen *et al.*, 2022). These fungi often establish mutualistic relationships, conferring benefits to the host plant such as enhanced growth, improved nutrient acquisition, increased tolerance to abiotic stresses (like drought or salinity), and protection against pests and pathogens, including plant-parasitic nematodes (Watts *et al.*, 2023). Some endophytic fungi produce nematicidal compounds, which are secondary metabolites toxic to nematodes. These compounds can directly kill or paralyze nematodes upon contact or ingestion. Examples include volatile organic compounds, enzymes, and specific toxins (Deng *et al.*, 2022). Furthermore, certain endophytes can induce systemic resistance

(ISR) in plants. This primes the plant's defense mechanisms, making it more resistant to subsequent nematode attacks. The plant may exhibit enhanced production of defense-related enzymes and signaling molecules (Fontana *et al.*, 2021). Competition for resources and space is another way endophytes can indirectly suppress nematode populations. By colonizing the root system, they may limit the availability of infection sites and nutrients for nematodes (Gowtham *et al.*, 2024). Some endophytic fungi can parasitize nematode eggs or juveniles, directly interfering with their life cycle (Schouten, 2016).

Benefits of using fungi as bioagents against PPNs

Fungi are natural components of the soil ecosystem and offer a more sustainable alternative to synthetic chemical nematicides, which can have detrimental effects on non-target organisms and the environment (Bhat *et al.*, 2023). They are generally considered safer for human health and leave no harmful residues in the soil or food products. Fungi employ various mechanisms to control nematodes (Figure 3), including parasitism (trapping and infecting nematodes), production of nematicidal toxins, and induction of plant resistance. This multifaceted approach can lead to more effective and durable nematode control (Rahman *et al.*, 2024). Some fungi can colonize plant roots as endophytes, establishing a long-term association that can provide continuous protection against nematodes throughout the plant's life cycle (Yan *et al.*, 2011). Certain nematophagous fungi can persist in the soil, contributing to the development of nematode-suppressive soils over time. Besides their direct effects on nematodes, some beneficial fungi, like mycorrhizal and certain endophytic fungi, can promote plant growth by improving nutrient and water uptake, leading to healthier and more tolerant plants. In the long run, the use of fungal bioagents can be cost-effective, especially if they can establish and persist in the soil. They are also generally easier and safer for farmers to handle compared to harsh chemical nematicides. It's important to note that the effectiveness of fungal bioagents can vary depending on the specific fungus, nematode species, soil conditions, and application methods. Integrated pest management strategies that combine the use of fungal bioagents with other cultural and biological control practices often provide the most successful and sustainable nematode management.

Disadvantages of using fungi against PPNs

The effectiveness of fungal bioagents can be inconsistent and highly dependent on various factors such as the specific fungal strain, nematode species, soil type, environmental conditions (temperature, moisture, pH), and the application method (Kerry, 2000). Results observed in laboratory or greenhouse studies may not always translate directly to field conditions due to the complexity of the soil ecosystem (Siddiqui and Akhtar, 2008). Some nematophagous fungi may exhibit a degree of specificity towards certain nematode species or life stages, limiting their broad-spectrum applicability (Degenkolb and Vilcinskas, 2016). Fungal growth, survival, and infectivity can be significantly affected by environmental factors. Extreme temperatures, fluctuations in soil moisture, and unfavorable pH levels can reduce their efficacy (Braga *et al.*, 2015). Successful implementation of fungal bioagents often requires specific application techniques and precise timing relative to nematode populations and plant growth stages. Inadequate application can lead to poor establishment and control. Introduced fungal bioagents may interact with the native soil microbial community, potentially leading to competition for resources or even antagonistic effects that reduce their effectiveness. The viability and efficacy of fungal formulations can be affected by storage conditions and their shelf life. Maintaining optimal conditions for mass-produced fungal inoculants can be challenging.

Biological control agents, including fungi, generally have a slower mode of action compared to synthetic chemical nematicides, which can provide rapid knockdown of nematode populations. This may be a disadvantage in situations requiring immediate pest control. While significant progress has been made, further research is needed to optimize the selection, production, formulation, and application of fungal bioagents for consistent and reliable nematode control under diverse field conditions. In some regions, the registration and commercialization of microbial biopesticides, including fungi, can face regulatory hurdles, which may limit their availability to growers. It's crucial to consider these potential disadvantages alongside the advantages when evaluating the suitability of fungal bioagents for nematode management in specific agricultural systems.

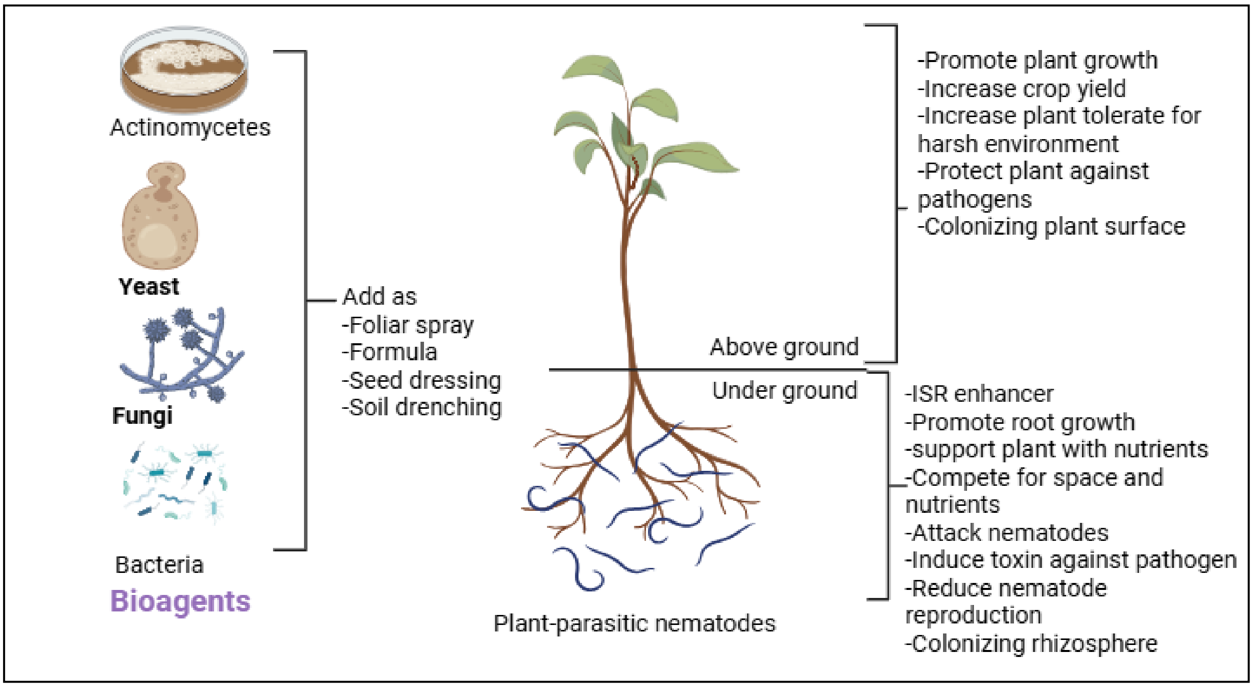

Fig. 3 The effect of bioagents (fungi, bacteria, yeasts, and actinomycetes) on plant growth and PPNs

Bacteria as biocontrol agents against PPNs

Bacteria are single-celled microorganisms ubiquitous in virtually every environment on Earth, from the deepest oceans to the soil beneath our feet, and even within and on other living organisms. They belong to the prokaryotic domain, their cells lack a membrane-bound nucleus and other complex organelles characteristic of eukaryotic cells. The ecological roles of bacteria are immense and critical for the functioning of ecosystems. They act as decomposers, breaking down organic matter and recycling nutrients. They play vital roles in nutrient cycles, such as nitrogen fixation, which is essential for plant growth. In the human body, the gut microbiota, a complex community of bacteria, aids in digestion and plays a role in immunity. While some bacteria are pathogenic, causing diseases in plants and animals, the vast majority are beneficial or harmless. Their diverse metabolic capabilities are harnessed in various biotechnological applications, including the production of antibiotics, enzymes, and biofuels, as well as in bioremediation processes for cleaning up pollutants.

While chemical nematicides have been traditionally used for nematode control, concerns regarding environmental impact and human health have spurred the search for sustainable alternatives. Biological control, utilizing naturally occurring organisms, offers a promising approach, and bacteria have emerged as effective bioagents against these microscopic pests (Vasantha-Srinivasan *et al.*, 2025). Several mechanisms contribute to the nematicidal activity of bacteria (Sarri *et al.*, 2024). Some bacteria, such as certain strains of *Bacillus* and *Pseudomonas*, produce metabolites that are toxic to nematodes (Gallagher and Manoil, 2001). These metabolites can disrupt nematode physiology, leading to paralysis or death (Vasantha-Srinivasan *et al.*, 2025). For instance, *Bacillus thuringiensis* (Bt), well-known for its insecticidal crystal proteins, also produces nematicidal toxins in some strains (Wei *et al.*, 2003). Other bacteria employ different strategies. Certain species are parasitic to nematodes, colonizing and eventually killing them (Tian *et al.*, 2007). *Pasteuria penetrans* is a prime example of an obligate bacterial parasite of root-knot nematodes (Davies, 2009). Its spores attach to the nematode cuticle, germinate, and develop within the nematode body, ultimately preventing reproduction (Dyrdahl-Young and DiGennaro, 2018).

Furthermore, some bacteria can induce systemic resistance (ISR) in plants (Zhu *et al.*, 2022). Colonization of the plant roots by these beneficial bacteria triggers defense mechanisms within the plant, making it less susceptible to nematode attack (Liu *et al.*, 2023). Plant growth-promoting rhizobacteria (PGPR) like certain *Bacillus* and *Pseudomonas* species are known for their ability to elicit ISR (Zhu *et al.*, 2022).

The application of bacterial bioagents can involve seed treatments, soil drenching, or incorporation into the soil (Bonaterra *et al.*, 2022). Research efforts are continuously focused on isolating and characterizing novel bacterial strains with potent nematicidal activity, optimizing their production and formulation, and understanding their interactions within the soil environment to enhance their efficacy in the field (Vasantha-Srinivasan *et al.*, 2025).

Advantages of the utilization of bacteria against PPNs

Using bacteria as bioagents against plant-parasitic nematodes offers a range of significant benefits, making them an attractive alternative or supplement to traditional chemical control methods (Ayaz *et al.*, 2024). Bacterial bioagents are generally considered more environmentally benign than synthetic nematicides (Vasantha-Srinivasan *et al.*, 2025). They are naturally occurring microorganisms and, when used appropriately, pose less risk of soil and water contamination (Vasantha-Srinivasan *et al.*, 2025). This contributes to sustainable agriculture and reduces the ecological footprint of nematode management (Figure 3) (Migunova and Sasanelli, 2021). Certain bacterial bioagents exhibit a degree of specificity towards target nematode species or groups, minimizing harm to beneficial soil organisms like earthworms, mycorrhizal fungi, and other components of the soil food web (Vasantha-Srinivasan *et al.*, 2025). This selectivity helps maintain soil health and biodiversity. Some bacterial bioagents, particularly parasitic ones like *Pasteuria penetrans*, can establish and persist in the soil, potentially providing long-term suppression of nematode populations (Davies *et al.*, 2023). Additionally, many beneficial bacteria can promote plant growth and overall soil health through mechanisms like nutrient cycling and the production of plant growth hormones (Orozco-Mosqueda *et al.*, 2023).

Disadvantages of using bacteria against PPNs

The effectiveness of bacterial bioagents can be inconsistent and highly dependent on environmental factors such as soil type, moisture content, temperature, and pH (Ayaz *et al.*, 2024). A bacterium that performs well in one field might show limited efficacy in another due to these variations. This unpredictability can make it challenging for growers to rely solely on bacterial control. Furthermore, many bacterial bioagents exhibit a narrow host range, meaning they are only effective against specific nematode species or even specific life stages within a species. This specificity necessitates accurate nematode identification and the application of the correct bacterial strain, which can be complex and time-consuming. Broad-spectrum control, often desired by growers facing multiple nematode pests, is less likely with individual bacterial agents.

Introducing effective populations of beneficial bacteria and ensuring their long-term establishment and persistence in the soil can be difficult (Chen *et al.*, 2024). Indigenous soil microbial communities can compete with the introduced bacteria for resources and space, limiting their ability to proliferate and exert sustained nematode control (Mawarda *et al.*, 2022). Moreover, Large-scale, cost-effective production and formulation of viable and stable bacterial bioagents can present technical challenges (Bonaterra *et al.*, 2022). Maintaining the viability and virulence of bacteria during production, storage, and application is crucial for their efficacy (Vasantha-Srinivasan *et al.*, 2025). The shelf life of some bacterial products can also be limited. While generally bioagent bacterial isolates are considered safer than synthetic nematicides, there's a theoretical risk of certain bacterial strains exhibiting off-target effects on non-target organisms within the soil ecosystem (Belousova *et al.*, 2021). Thorough risk assessments are necessary to minimize this potential. Effective nematode control with bacteria often requires specific application methods and timing to ensure the bioagent reaches the target nematodes in sufficient concentrations at the appropriate time. This might involve specialized equipment or application strategies that growers may not be familiar with.

Yeasts as biocontrol agents against PPNs

Yeasts are unicellular eukaryotic microorganisms belonging to the Kingdom Fungi. Unlike most fungi that grow as multicellular filaments called hyphae, yeasts are characterized by their predominantly single-celled, rounded morphology and their typical mode of asexual reproduction through budding or fission. Some species can also exhibit multicellular characteristics by forming pseudohyphae, which are chains of budding cells. Physiologically, many yeasts are known for their ability to perform fermentation, converting sugars into alcohol and carbon dioxide. Yeasts exhibit a remarkable diversity in their natural habitats. They are widely dispersed in nature and can be found in various environments, including plant surfaces, soil, water, animals and insects, and extreme environments. The distribution of yeasts is influenced by the availability of nutrients, particularly sugars, and the presence of suitable vectors for dispersal (Walker, 1998).

Certain yeast species are emerging as promising biological control agents (BCAs) against PPNs, offering a more sustainable alternative to chemical nematicides (Elezaby *et al.*, 2022; D’Addabbo *et al.*, 2024). These microscopic fungi can suppress nematode populations through various mechanisms, such as A) Production of nematicidal compounds: Some yeasts produce metabolites with direct toxicity to nematodes (D’Addabbo *et al.*, 2024). These compounds can inhibit egg hatching, cause juveniles mortality, and disrupt nematode development (Mei *et al.*, 2021). Examples include volatile organic compounds (VOCs) produced by *Saccharomyces cerevisiae* and culture filtrates from species like *Pichia guilliermondii* and *Candida albicans* which have shown nematocidal activity against root-knot nematodes (*Meloidogyne* spp.). B) Competition for resources: Introduced beneficial yeasts can compete with nematodes and other soilborne pathogens for essential nutrients and space in the rhizosphere, indirectly suppressing nematode populations (Freimoser *et al.*, 2019). C) Induction of plant resistance: Certain yeasts can trigger systemic resistance in plants, enhancing their defense mechanisms against nematode attack (Kowalska *et al.*, 2022). This can lead to reduced nematode penetration, development, and reproduction within the plant roots. *S. cerevisiae*, for instance, has been suggested to induce plant resistance similar to hydrogen peroxide(Karajeh, 2013). D) Parasitism:

While less common, some yeasts might exhibit direct parasitism of nematode eggs or larvae. E) Alteration of rhizosphere ecology: Yeasts can modify the soil environment in ways that are unfavorable for nematode survival or activity.

Application of *S. cerevisiae* has shown significant reduction in root galling and nematode reproduction of root-knot nematodes in crops like tomato and cucumber (Karajeh, 2013), and soybean (Elezaby *et al.*, 2022) under both greenhouse and field conditions. Its VOCs have also exhibited nematicidal effects. Culture filtrates of *P. guilliermondii* have shown high egg hatching inhibition and juveniles mortality against *Meloidogyne* spp. (El-Sagheer *et al.*, 2021). *C. albicans* effectively suppressed gall and egg-mass formation of *M. incognita* and promoted tomato plant growth. Culture filtrates of *Sporobolomyces roseus* and *Cryptococcus albidus* have also demonstrated nematicidal properties against *M. javanica* (El-Sagheer *et al.*, 2021).

Advantages of using yeasts against PPNs

Generally, yeasts are considered safer than synthetic nematicides, with lower risks of soil and water contamination. Some yeasts can enhance plant growth and nutrient uptake (Figure 3) (Vargas *et al.*, 2024). Baker's yeast, for example, is readily available and can be applied through soil drenching.

Challenges of using yeasts as bioagents against PPNs

Similar to other bioagents, the effectiveness of yeasts can be influenced by environmental factors, nematode species, and application methods (D'Addabbo *et al.*, 2024). Additionally, more research is needed to optimize application strategies, identify the most effective yeast strains and their mechanisms of action, and develop stable and effective formulations. The long-term impact of introducing specific yeast strains on the soil microbial community needs careful evaluation.

Actinomycetes as biocontrol agents against PPNs

Actinomycetes are a large and diverse group of Gram-positive bacteria characterized by their filamentous, branching growth, resembling the mycelium of fungi (Bowden, 1996). This morphology led to their initial misclassification as "ray fungi." However, they are prokaryotic organisms with typical bacterial cell wall structures and reproduce primarily through spore formation (though not endospores like *Bacillus* and *Clostridium*) (Barka *et al.*, 2016a). These ubiquitous microorganisms are predominantly found in soil, where they play crucial roles in organic matter decomposition and nutrient cycling. They are also found in aquatic environments and can be associated with plants and animals (Van de Water and Carlson, 2024). Actinomycetes are well-known for their ability to produce a wide array of secondary metabolites, many of which have significant antibacterial, antifungal, antiviral, and anticancer activities (Jakubiec-Krzesniak *et al.*, 2018). This has made them a primary source for numerous clinically important antibiotics, including streptomycin, tetracycline, erythromycin, and rifampicin.

Actinomycetes employ several strategies to exert control over nematodes including A) Production of nematicidal metabolites: Many actinomycete species synthesize secondary metabolites with direct toxicity to nematodes. These compounds can interfere with nematode physiology, causing paralysis, mortality, and inhibiting egg hatching. Examples include various antibiotics, enzymes (like chitinases and proteases that can degrade nematode egg shell and cuticles), and VOCs. Genera like *Streptomyces*, *Nocardia*, and *Actinomadura* are particularly known for producing such compounds. Specific metabolites like abamectin (produced by *Streptomyces avermitilis*) are commercially successful nematicides (Huang *et al.*, 2018). B) Enzymatic degradation: Some actinomycetes produce extracellular enzymes capable of degrading nematode structures. Chitinases break down chitin, a major component of nematode egg shell and the outer layer of juveniles. Proteases can digest proteins in the nematode cuticle and eggs. C) Competition and antagonism: Actinomycetes can compete with nematodes for essential nutrients and colonization sites in the rhizosphere. They may also produce substances that inhibit the growth or activity of other soil microorganisms, indirectly impacting nematode populations. D) Induction of plant resistance: Certain actinomycetes can trigger systemic resistance (ISR) in plants, enhancing their defense mechanisms against nematode invasion and development. This can lead to reduced nematode reproduction and damage (Vasantha-Srinivasan *et al.*, 2025). E) Parasitism: While less common, some actinomycetes have been observed to parasitize nematode eggs and juveniles.

Numerous studies have demonstrated the efficacy of various actinomycetes against a range of plant-parasitic nematodes (Silva *et al.*, 2022). Many *Streptomyces* isolates have shown significant suppression of root-knot nematodes (*Meloidogyne* spp.), cyst nematodes (*Heterodera* and *Globodera* spp.), and root-lesion nematodes (*Pratylenchus* spp.) in various crops under greenhouse and field conditions (Shalaby *et al.*, 2021). Specific strains produce nematicidal compounds and enzymes. *Nocardia* species have exhibited nematicidal activity against root-knot nematodes. *Actinomadura* isolates have also shown potential in controlling root-knot nematodes. Application of actinomycete-based formulations or consortia has resulted in reduced nematode populations, improved plant growth, and increased yields in crops like tomato, cucumber, banana, and soybean.

Advantages of using actinomycetes against PPNs

Their multiple modes of action can lead to more effective and sustainable nematode control. They produce stable spores that can offer better shelf life and persistence in the soil compared to some other microbial biocontrol agents. Additionally, some actinomycetes can also exhibit plant growth-promoting activities (Figure 3), such as phosphate solubilization and nitrogen fixation (Chukwuneme *et al.*, 2020). Finally, they offer a more sustainable alternative to synthetic nematicides.

Challenges of using actinomycetes against PPNs

The efficacy of actinomycetes can vary significantly depending on the specific strain and the target nematode species. Soil conditions (temperature, pH, moisture, and organic matter) can influence the establishment and activity of introduced actinomycetes (Barka *et al.*, 2016b). Developing effective and consistent formulations and application methods is crucial for reliable nematode control. More research is needed to identify highly effective strains, elucidate their mechanisms of action, optimize their application, and assess their long-term impact on soil ecosystems.

Viruses as biocontrol agents against PPNs

Viruses are microscopic infectious agents that can only replicate inside the living cells of an organism. They infect a wide variety of life forms, including animals, plants, and microorganisms. They contain either DNA or RNA, which carries the genetic information of the virus. The genetic material is enclosed in a protective protein coat called a capsid. Viruses can only replicate within a host cell, using its cellular machinery. Some viruses can be used as biological control agents, specifically against plant nematodes. These viruses infect and kill the nematodes, offering a potential alternative to chemical nematicides.

The idea of employing viruses to manage plant-parasitic nematodes stems from the high specificity and potential for self-replication inherent in viral infections. If a virus could be identified or engineered to specifically target and debilitate nematode species that cause significant agricultural damage, it could offer an environmentally friendly and sustainable control strategy.

Ultimately, plant viruses were used successfully to encapsulate different biological materials like abamectin (Cao *et al.*, 2015). This technique is important to protect abamectin from degradation and dissolve with the groundwater. Also, deliver abamectin and keep it for a long time attached to PPNs compared with a free one, so a high efficacy in controlling nematodes. The idea is to encapsulate or attach nematode-specific viruses onto or within nanoparticles. This strategy aims to enhance the delivery, stability, and ultimately the efficacy of the viral bioagent against target nematode pests.

Potential advantages of using viruses as bioagents against PPNs

Viruses can be highly specific to their hosts, potentially minimizing off-target effects on beneficial soil organisms (Sun and Peng, 2007). Once introduced, viruses can replicate within the nematode population, potentially leading to long-term control (Ruark *et al.*, 2018). Viruses may offer a different mechanism of action compared to existing nematicides, which could be valuable in managing resistance.

Challenges of using viruses as bioagents against PPNs

Identifying naturally occurring viruses with pathogenicity towards specific nematode pests can be challenging. Thorough investigation of the virus's host range is crucial to ensure it doesn't affect non-target organisms, including other nematodes, insects, or even plants. Furthermore, developing effective methods for delivering the virus to the target nematode population in the soil and ensuring its persistence in the environment are significant hurdles. Also, soil conditions (e.g., pH, moisture, temperature) can influence viral survival and infectivity (Hurst *et al.*, 1980). Rigorous safety assessments are necessary to ensure the virus poses no risk to human health or the broader ecosystem. While genetic engineering could potentially enhance viral pathogenicity or host specificity, it also raises regulatory and public acceptance concerns (Patrick and Barton, 2024).

Predatory nematodes as biocontrol agents against PPNs

Predatory nematodes are free-living nematodes that feed on other nematodes, including many plant-parasitic species. They are found in various soil environments and are part of the natural soil food web. They offer a biological approach to managing PPNs (Bilgrami and Brey, 2005). They belong to several orders, including Mononchida, Diplogasterida, Aphelenchida, and Dorylaimida. They are characterized by having specialized mouthparts (stomata) to capture and consume prey. Predatory nematodes locate their prey, attack, and then consume them. This predation helps to reduce populations of plant-parasitic nematodes, thus minimizing damage to plant roots. They used different mechanisms for attacking nematodes include cutting and sucking type, piercing and sucking type, and cutting type (Bilgrami and Brey, 2005).

Potential advantages of using predatory nematodes as bioagents against PPNs

Predatory nematodes are a natural part of the soil ecosystem. They can provide relatively specific control of PPNs. Also, they offer an environmentally friendly alternative to chemical nematicides.

Challenges and Considerations of using predatory nematodes as bioagents against PPNs

The effectiveness of predatory nematodes in controlling PPNs can vary depending on environmental conditions, soil type, and predator-prey dynamics. Moreover, large-scale production for field applications can be challenging. Also, ensuring their establishment and survival in agricultural fields can be difficult.

Mites as biocontrol agents against PPNs

Spider mites are considered one of the most important organisms belonging to the Kingdom Animalia. Spider mites are tiny arachnids, closely related to spiders and ticks, that are significant agricultural and horticultural pests worldwide. They feed on a wide variety of plants by piercing plant cells with their mouthparts and sucking out the contents, leading to characteristic damage. They play an important role in the environmental hierarchy. Some mites were found feeding on sedentary stages of PPNs, especially eggs. They are distributed in soil and plant parts (Gerson, 2015).

Oribatid mites have considerable diversity in their feeding habits. *Scheloribates species, viz. Scheloribates, S. fimbriatus africanus* and *S. latoincisus* were found have predatory potential and feed on *M. javanica* (Ramakrıshnan and Neravathu, 2019). *M. incognita* is suitable for the growth and reproduction of the predatory mite especially *Protogamasellopsis zaheri* (Prado *et al.*, 2024). This mite was observed as a bioagent against *M. incognita* and significantly reduced the nematode population when applied alone or combined with free-living nematodes. On the other hand, the cunaxid mite, *Cunaxa capreolus,* was found to be a bioagent against PPNs, where it fed on egg masses and juveniles of *M. incognita* and juveniles of the citrus nematode *Tylenchulus semipenetrans*. Cunaxid mite had completed its life span however, the males developed faster than the females (Al-Azzazy and Al-Rehiayani, 2022).

Protozoa as biocontrol agents against PPNs

Protozoa are a diverse group of unicellular, eukaryotic microorganisms (Yaeger, 2011). They are heterotrophic, meaning they obtain nutrients by consuming organic matter, such as other microorganisms or organic tissues and debris, through processes like phagocytosis or osmotrophy. Unlike plants and algae, they lack a rigid cell wall, allowing for flexible movement. Protozoa, particularly certain groups like amoebae and ciliates, have emerged as promising biocontrol agents against plant nematodes.

Protozoa engulf nematodes through phagocytosis, directly reducing nematode populations in the soil. Their feeding can target various nematode life stages, including eggs and juveniles (Esser, 1987; Bilgrami and Brey, 2005). While direct predation is the main mechanism, some protozoa might also indirectly affect nematodes by competing for resources like bacteria, which serve as a food source for certain nematode species (Bonkowski, 2004). A wide range of soil protozoa exhibits nematophagous activity, suggesting a broad potential for biological control. Different protozoan species may have varying degrees of effectiveness against specific nematode pests (Foissner, 1987). As naturally occurring soil organisms, protozoa-based bioagents are generally considered environmentally friendly compared to synthetic chemical nematicides. Protozoa can potentially be integrated with other biological control agents like bacteria and fungi for enhanced nematode suppression. For instance, protozoan grazing on bacteria can influence nutrient cycling and potentially impact nematode-antagonistic bacteria (Griffiths, 1994). While promising, the practical application of protozoa as bioagents faces challenges. Factors like soil conditions (moisture, texture), the specific protozoan and nematode species involved, and the establishment and persistence of introduced protozoa need careful consideration. Further research is needed to optimize their use in field conditions and develop effective application strategies.

Advantages of using biological control

Biological control is a method of managing pests (including insects, mites, weeds, and plant pathogens) by using their natural enemies. These natural enemies can include predators, parasitoids, pathogens, and competitors. Biological control helps to minimize the use of synthetic pesticides, which can have harmful effects on human health, non-target organisms, and the environment. By reducing pesticide use, biological control helps to protect water quality, soil health, and biodiversity. It promotes a more balanced ecosystem. Unlike some chemical treatments that provide only short-term solutions, biological control agents can establish themselves and provide long-lasting pest suppression.

Biological control agents often target specific pests, reducing the impact on beneficial non-target organisms. Additionally, biological control can help to slow down the development of pesticide resistance in pest populations. Lower pesticide residues on crops lead to safer food products for consumers.

Limitations and challenges of using biological control

While bioagents offer a promising and environmentally friendly alternative to chemical nematicides for controlling nematode pests, their use is not without limitations and challenges. The effectiveness of bioagents can be highly variable and often less consistent than chemical controls. This inconsistency is influenced by various biotic and abiotic factors in the soil environment (Kerry *et al.*, 1982; Stirling, 2011). The performance of bioagents is strongly influenced by environmental conditions such as soil type, temperature, moisture, pH, and organic matter content. Optimal conditions for the bioagent might not always coincide with field conditions (Kerry *et al.*, 1982). Many bioagents exhibit specificity towards certain nematode species or even specific life stages. This narrow spectrum of activity might limit their effectiveness in fields with mixed nematode populations (Siddiqui, 2006). Biological control generally takes longer to achieve nematode suppression compared to the rapid action of chemical nematicides. This can be a disadvantage when quick pest control is needed to prevent significant crop damage. Introducing and establishing effective populations of bioagents in the soil rhizosphere can be challenging. Factors affecting colonization include competition with native microflora and the availability of suitable niches (Vasantha-Srinivasan *et al.*, 2025). Developing cost-effective and stable formulations of bioagents with a good shelf life for large-scale application can be difficult. Maintaining viability and virulence of the bioagent during production and storage is crucial (Stirling, 2011). The successful implementation of biological control often requires integration with other pest management strategies and agricultural practices. Incompatibility with certain chemical fertilizers or pesticides can limit their use. Unlike many chemical nematicides that can control a wide range of soil pests, bioagents typically have a more limited spectrum of activity, targeting specific nematode groups. The cost-effectiveness and ease of application are crucial for the adoption of bioagents by growers. In some cases, the production costs might be higher, or the application methods more complex compared to chemical alternatives. While many bioagents have shown promise, the precise mechanisms by which they suppress nematodes are not always fully understood. Further research is needed to optimize their application and enhance their efficacy.

How can we overcome the challenges of using biological control?

Fortunately, several strategies are aimed at overcoming the challenges and limitations of using biological control.

a. Enhancing Consistency in Efficacy

Focus on isolating and selecting more virulent, robust, and environmentally adaptable strains of bioagents. This includes screening for strains with broad-spectrum activity and those effective against multiple life stages of nematodes. Intensify research to elucidate the precise mechanisms by which bioagents suppress nematodes. This knowledge can help optimize their application and predict their performance under different conditions. Explore the use of consortia of different bioagents with complementary modes of action. Combining fungal and bacterial agents, or different strains of the same organism, can lead to more consistent and broader control.

b. Integrated Pest Management (IPM) Approaches

Incorporate bioagents into broader IPM programs that include cultural practices (crop rotation, resistant varieties, soil health management), physical methods (soil solarization), and judicious use of chemical controls when necessary. This holistic approach can buffer the variability of bioagents.

c. Mitigating Environmental Dependency

Identify and select bioagent strains that are effective across a wider range of soil types, temperatures, moisture levels, and pH. Develop formulations that protect bioagents from adverse environmental conditions and enhance their survival and activity in the soil. This includes encapsulation, the use of protective carriers, and the addition of nutrients or attractants. Explore strategies to manipulate the rhizosphere environment to favor the establishment and activity of introduced bioagents, such as through specific soil amendments or the use of PGPR that support the bioagent.

d. Broadening Host Range and Specificity

Continue the search for novel bioagents with activity against a wider range of nematode species. Explore methods to deliver bioagents specifically to the target nematodes or the plant roots where nematodes feed, potentially enhancing their impact even if their host range is somewhat narrow. While requiring careful consideration and regulatory approval, genetic modification of bioagents could potentially enhance their host range or virulence.

e. Accelerating Action

Develop formulations with high concentrations of viable and active bioagents to achieve a more rapid impact on nematode populations. Optimize application methods to ensure quick and effective contact between the bioagent and the target nematodes (e.g., seed treatments, in-furrow application). Investigate the potential of combining bioagents with natural nematicidal compounds that offer a faster initial knockdown of nematode populations while the bioagent establishes for longer-term control.

f. Improving Establishment and Colonization

Select bioagents that are highly competitive and can effectively colonize the rhizosphere, outcompeting native microorganisms and establishing a strong presence. Incorporate additives into formulations that enhance the adhesion, spread, and root colonization by bioagents. Promote overall soil health through organic matter additions and practices that support beneficial microbial communities, creating a more favorable environment for the introduced bioagents.

g. Advancing Mass Production and Formulation

Develop cost-effective and scalable methods for the mass production of high-quality bioagents. Explore novel formulation technologies such as microencapsulation, nano-formulations, and hydrogels to improve the stability, shelf life, and delivery of bioagents. Identify and utilize effective carrier materials that protect the bioagent, enhance its survival, and facilitate its application.

h. Enhancing Integration with Agricultural Practices

Conduct thorough research to assess the compatibility of bioagents with commonly used fertilizers, pesticides, and other agricultural inputs. Design IPM programs that strategically combine bioagents with compatible agricultural practices to maximize their effectiveness. Provide growers with clear guidelines and training on the proper use and integration of bioagents within their farming systems.

i. Achieving Broad-Spectrum Activity

Explore a wider range of microbial sources, including underexplored environments, to discover novel bioagents with broader activity. Formulate products containing a carefully selected mix of bioagents known to target different nematode species or pest complexes.

j. Improving Economic Viability and Grower Adoption

Optimize production and formulation processes to reduce the cost of bioagent-based products. Develop formulations that are easy to handle and apply using existing farm equipment. Conducting field trials and economic analyses clearly demonstrate the return on investment for using bioagents in nematode management.

k. Deepening Understanding of Mechanisms of Action

Utilize advanced omics technologies (genomics, transcriptomics, proteomics, metabolomics) to gain a comprehensive understanding of the molecular interactions between bioagents, nematodes, and plants. Isolate and characterize the specific compounds or enzymes produced by bioagents that are responsible for their nematicidal activity. This can lead to the development of more targeted and effective bio-based control strategies.

CONCLUSION

PPNs are the most important and limited for crop production worldwide. They not only reduce the productivity of the plant, but they also decrease the quality of yield. Consequently, growers used chemical nematicides extensively to manage PPNs for a long time. Recently, many residual effects were observed on human health, environmental microflora, underground water, and beneficial microorganisms due to the extensive use of nematicides. Globally, a plethora of chemical nematicides were banned from marketing. Decades ago, scientists started to seek new eco-friendly strategies alternative to nematicides. Biological control has received much attention as a bio-nematicide. Fungi, bacteria, actinomycetes, and yeasts were used successfully in controlling PPNs. They are characterized by being easy to handle, having a wide variety, and being distributed in all niches. They manage nematodes either directly by attacking different stages of nematodes or indirectly by supporting plant growth. On the other hand, mites, protozoa, predatory nematodes, and viruses have received little attention as biological control agents against PPNs. They can attack nematodes directly and feed on their bodies.

Bioagents should be examined against the pests and studied for their wide range before recommending them. Additionally, sometimes it’s important to evaluate the effect of bioagents on plant growth (Pathogenicity). However, studying the influence of environmental factors and soil community before applying the bioagents. Notably, some bioagents can perform well alone, however other bioagents give the best results when combined with another bioagent or pesticides. Thus, plethora studies should be done before release the bioagents. Ultimately, biological control is a promise as an alternative to nematicides. They play an important role in attacking PPNs and enhancing plant growth.

AUTHOR CONTRIBUTIONS

Majority contribution for the whole article belongs to the author(s). The authors read and approved the final manuscript.

COMPETING INTERESTS

The authors declare that they have no competing interests. The contents of the manuscript have neither been published nor under consideration for publication elsewhere.

DISCLAIMER (ARTIFICIAL INTELLIGENCE)

The author (s) hereby declare that NO generative AI technologies such as Large Language Models (Chat GPT, COPILOT, etc.) and text-to-image generators have been used during the writing or editing of this manuscript.

STATEMENT AND ETHICS DECLARATIONS

The authors declare that they have no known competing financial interests or personal relationships that could have influenced the work reported in this article. Ethical approval was not required for this study.

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