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Review

Implications of Fertilisation on Soil Nematode Community Structure and Nematode-Mediated Nutrient Cycling

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Abstract

Soil nematodes are essential components of the soil food web and are widely recognised as key bioindicators of soil health because of their sensitivity to environmental factors and disturbance. In agriculture, many studies have documented the effects of fertilisation on nematode communities and explored their role in nutrient cycling. Despite this, a key gap in knowledge still exists regarding how fertilisation-induced changes in nematode communities modify their role in nutrient cycling. We reviewed the literature on the mechanisms by which nematodes contribute to nutrient cycling and on how organic, inorganic, and recycling-derived fertilisers (RDFs) impact nematode communities. The literature revealed that the type of organic matter and its C:N ratio are key factors shaping nematode communities in organically fertilised soils. In contrast, soil acidification and ammonium suppression have a greater influence in inorganically fertilised soils. The key sources of variability across studies include differences in the amount of fertiliser applied, the duration of the fertiliser use, management practices, and context-specific factors, all of which led to differences in how nematode communities respond to both fertilisation regimes. The influence of RDFs on nematode communities is largely determined by the fertiliser's origin and its chemical composition. While fertilisation-induced changes in nematode communities affect their role in nutrient cycling, oversimplifying experiments makes it difficult to understand nematodes' functions in these processes. The challenges and knowledge gaps for further research to understand the effects of fertilisation on soil nematodes and their impact on nutrient cycling have been highlighted in this review to inform sustainable agricultural practices.

Keywords: fertiliser impact; inorganic fertiliser; nematode diversity; nematode ecology; nutrient cycling; nutrient dynamics; recycling derived fertiliser; sustainable agriculture; soil health

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1. Introduction

The world population is projected to reach 10 billion by 2060, highlighting the need for continued fertiliser supply to meet the rising food demand [1,2]. In agriculture, fertilising products are generally categorised as organic, inorganic, and recycled-derived fertilisers (RDFs), distinguished either by their chemical composition or the sources of their components [3]. Inorganic fertilisers are manufactured from mineral sources such as phosphate rock and contain high concentrations of readily available nutrients for crops [4]. Organic fertilisers, also called biobased fertilisers, are products made from organic carbon

and nutrients from biological sources. They include compost, waste, animal manure, and plant remains. Organic waste is rich in nutrients and can therefore be further reprocessed through nutrient recovery technologies to obtain high concentrations of nutrients, producing recycling-derived fertilisers (RDFs) [5–9]. To develop better farming practices that support food security while protecting the environment and ensuring the soil remains healthy, it is paramount to understand the impacts of fertilisation on soils.

Nematodes are the most widespread and abundant phylum on Earth, exhibiting diverse feeding strategies and responding rapidly to environmental disturbance [10–12]. They can be studied by analysing their communities using advanced techniques such as metabarcoding for precise identification, and nematode-based indices, which help interpret their ecological roles and responses to environmental changes [11,13–17]. Nematodes are ecologically classified according to their feeding groups, which determine their functional roles within the soil ecosystem [12,18]. They include plant-parasitic nematodes (PPN), bacterivores, fungivores, predators, and omnivores [12]. They are also classified along a five-scale coloniser-persister (C-P) continuum based on their life history strategies [14,19]. R-selected nematodes are opportunistic, produce many eggs, have short lifespans, and flourish with increased food resources; they include bacterial and fungal feeders. In contrast, k-strategists have longer lifespans, reproduce less, and are more sensitive to environmental changes, for example, omnivores and predatory nematodes [14,19].

Nematode assemblage characteristics, such as community abundance, diversity, and composition, serve as key indicators of environmental conditions and soil ecosystem health [11,13,17]. For instance, the presence and dominance of nematodes with low C-P values indicate resource availability or disturbance, while a high abundance of taxa with higher C-P values signifies stability and complex interactions [14]. Therefore, changes in nematode populations across the C-P scale are used to assess environmental disturbance or resource levels [10]. Nematode functional indices are calculated using weighted means of the C-P values, allowing ecologists to represent nematode families proportionally and assess environmental conditions, enhancing our understanding of soil health, nutrient cycling, and soil food web dynamics [13–15,17,19]. For example, the maturity index (MI) is used as an indicator of succession setback after a disturbance [19]. The structural index (SI) describes the complexity and stability of the food web after a disturbance, the enrichment index (EI) measures resource availability, while the channel index (CI) helps identify the prominent decomposition pathway in the presence of organic matter [13,14]. The community indices, such as the Shannon diversity index and Simpson index, are also used to explain the nematode diversity and dominance, respectively [15]. The nematode functional and community indices have been used in agriculture to assess soil health and monitor farming practices [20–24].

In the soil ecosystem, nematodes play a crucial role in decomposing organic matter and cycling nutrients, thereby enhancing plant nutrient availability and uptake [25–27]. Anthropogenic practices such as fertilisation are therefore likely to disrupt these crucial processes. Several studies have quantified the involvement of nematodes in nutrient cycling [25–37]. Many studies have also reported on the impacts of fertilisation on soil nematodes [22,38–42]. While these two areas have been well studied independently, a gap remains in understanding the consequences of fertilisation on the nematode communities and their ecosystem's functional role in nutrient cycling. Therefore, we reviewed the literature to understand the key drivers that shape nematode communities in fertilised soils and how the impacts caused by fertilisation could influence their ecosystem functions. The key objectives were as follows: 1. to understand the mechanisms through which nematodes interact with soil organisms to contribute to nutrient cycling; 2. to explore the impacts of

different fertilisers on nematodes; 3. to discuss how changes in nematode communities caused by fertilisation affect nematode-mediated nutrient cycling.

2. Mechanisms Through Which Nematodes Contribute to Nutrient Cycling

2.1. Direct Contributions of Nematodes to Nutrient Cycling

Nematodes play a crucial role in nutrient cycling by mediating the mineralisation of key elements, such as nitrogen (N) and phosphorus (P), thereby enhancing soil fertility and plant nutrient availability. Several experiments have found that in the presence of nematodes, the amounts of plant nutrients mineralised increase, enhancing plant growth. For instance, in the presence of the entire nematode community, the total nitrogen and phosphorus in the soil increased by 25% and 23%, respectively, in *Lolium perenne* soils amended with clover [26]. Nematodes contribute to nutrient cycling through two major mechanisms. Directly, grazing on bacteria and fungi, to release nutrients to the soil through excretion in the form of nitrates and phosphates, which are plant-available nutrients. The process starts when a carbon or nutrient source, either as a dead organism or a soil amendment, is introduced into the soil. It is broken down by either bacteria or fungi through the bacterial and fungal decomposition pathways, respectively, to release nutrients in excess in the form of plant-available nutrients [25–27,29,43]. However, microbes can also contribute to nutrient immobilisation when they do not release the nutrients through excretion, increasing the competition for nutrients with plants (Figure 1). This implies that an increase in opportunistic bacteria and fungi reduces the available plant nutrients for uptake [43]. According to Ferris et al. [25], under nitrogen-limited conditions, microbes can compete with plants for available nutrients, and any uptake by these microbes upon increasing organic material with high Carbon (C)/Nitrogen (N) leads to the immobilisation of nutrients and consequently reduces plant uptake. Therefore, when microbivorous nematodes (bacterial and fungal feeders) ingest microbes, they release the nutrients in excess through excretion, making them available for plant uptake. Several studies have reported that the presence of microbial-feeding nematodes increases the amount of mineralised N and P, and the amount of both N and P taken up by plants [28,33,44–46]. For instance, the presence of bacterial feeding nematodes, *Mesorhabditids* spp. and *Acrobeloides* spp. increased the amount of soil labile phosphorus, aboveground phosphorus accumulation and enhanced wheat dry biomass compared to their absence [33]. The presence of the fungivore nematode *Aphelenchoides* spp. noticeably increased soil exchangeable potassium (K), by enhancing fungal gene abundance and activity, consequently increasing plant available K in the soil [47]. At higher trophic levels within the food web are the predator and omnivore nematodes, which, as they feed on herbivores, bacterivores, and fungivores, release nutrients in excess, contributing to nutrient cycling [26,48].

2.2. Indirect Effects of Nematodes to Nutrient Cycling

Indirectly, nematodes influence ecosystem functions through the food web [25]. They graze on bacteria and fungi, and their activity influences the structure and activity of the lower trophic-level organisms. Bacterial-feeding nematodes have been found to increase the total bacterial abundance and alter their community composition [26,32,33,46,49]. This happens due to the complex interactions between nematodes, bacterial prey, and plants. The presence of bacterial-feeding nematodes was found to (1) increase bacterial abundance, (2) modify the community's composition, and (3) diversify it [34]. For instance, the selective feeding of bacterial-feeding nematodes on the bacteria is known to change the bacterial community [33,46]. Xiao et al. [46] found that the selective grazing behaviour of bacterial-feeding nematodes on *Nitrosomonas* spp. increased the abundance of other bacterial groups.

These changes in bacterial composition and abundance can lead to more efficient nutrient cycling, as different bacterial species have varying capabilities in processing nitrogen compounds. Nematodes can also influence nutrient cycling through predation on bacteria, which creates positive feedback between the bacterial communities, contributing to increased bacterial turnover and mineralisation. Confirming this was Jiang et al. [33], who explained that the increase in bacterial abundance and diversity in the presence of bacterial-feeding nematodes is due to a positive connectance between bacterial communities, leading to more efficient nutrient cycling and increased nutrient availability. The involvement of nematodes in nutrient cycling is complex and is also influenced by the type of nutrient substrate in the soil. Generally, the bacterial decomposition pathway is favoured by soil inputs with a low C:N ratio, while the fungal decomposition pathway is favoured by soil inputs with a high C:N ratio [25]. This determines whether bacterial or fungal-feeding nematodes play a bigger role in mineralisation and nutrient cycling after fertilisation. Fertilisers with a high C:N ratio are rich in carbon and decompose slowly will be decomposed by fungi promoting their growth. In contrast, fertilisers with low C:N ratio such as manure and compost are rich in nitrogen and decompose rapidly will be decomposed by bacteria promoting their growth. Both fungivore and bacterivore nematodes will feed selectively on their respective prey releasing excess nutrients in form of plant available nutrients, thus determining which group of nematodes will contribute more to mineralisation [25,50].

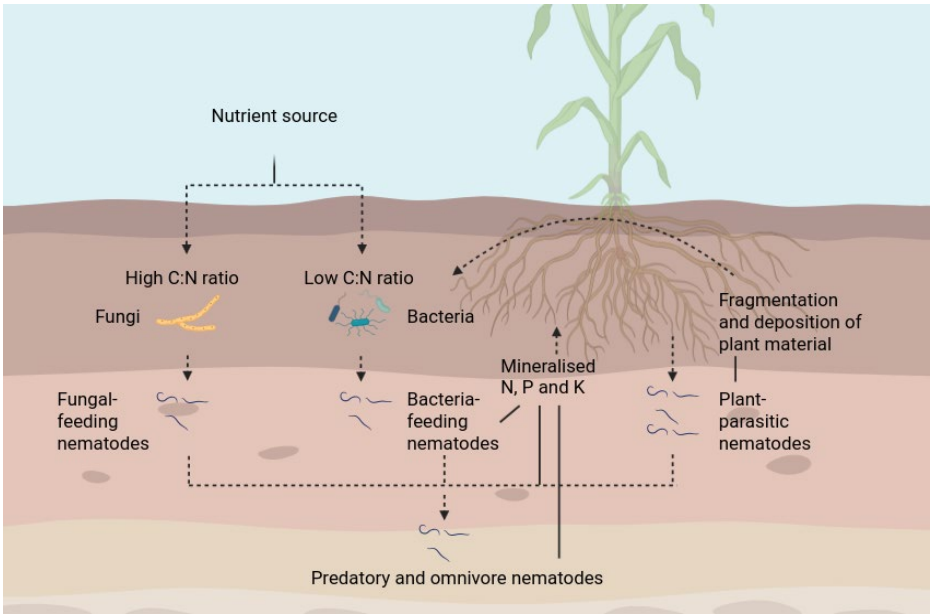


Figure 1. The contribution of nematode feeding groups to nutrient cycling. Dashed lines with arrows indicate trophic relationships, with direction of the arrows indicating the direction of the energy flows. Continuous lines indicate excretions. Diagram designed in Created in BioRender.com. Atira, L. (2025) [Unique Figure URL: https://BioRender.com/c0gag6w].

The role of plant parasitic nematodes (PPNs) in nutrient cycling is through their interactions with plant roots and soil microbes [26,51] (Figure 1). They do this by increasing the amount of carbon in the soil when they feed on plants, causing fragmentation and deposition of plant material back into the soil, which increases microbial activities and carbon turnover [51], contributing to mineralisation and nutrient cycling. For instance, root parasitic nematode *Rotylenchus reniformis* was associated with enhanced nitrogen mineralisation through increased root damage, which facilitated the release of carbon and nutrients back to the soil [51]. On the other hand, their presence and increased infestation of plants could lead to suppressed plant growth, reduced plant nutrient uptake

and consequently low yield in agriculture. However, the presence of PPNs in low numbers can enhance microbial activity in the soil, balancing the negative effects [26].

3. Impacts of Organic Fertilisation on Free-Living Nematodes

3.1. Heterogeneity Within Organic Amendments Shapes Nematode Communities

The impact of fertilisation on different nematode functional groups varies based on the group's life strategy, feeding preference, and sensitivity to ecological changes, composition, and structure. In the soil ecosystem, free-living nematodes (bacterivores, fungivores, omnivores, and predators) are used as bioindicators [12]. Bacterial and fungal feeding nematodes are both microbial feeders and are used as indicators of resource availability [12]. Omnivores and predators are k-strategists, sensitive to disturbance, and are used to indicate the maturity and stability of a soil ecosystem [13]. Organic, inorganic, and recycling-derived fertilisers have distinct effects on nematode community composition and structure. However, these effects differ not only between fertiliser types but also within each type depending on the regime. Generally, organic fertilisation increases the total abundance of nematodes, especially bacterivores and fungivores, driven by increased microbial biomass associated with favourable carbon-to-nitrogen (C:N) ratio conditions [50]. Studies have shown that soil organic matter positively correlates with total nematode abundance, as well as bacterivorous, fungivorous, and omnivore-predator nematode populations [52]. The addition of organic fertilisers such as compost, manure, plant residues, straw, and other organic materials boosts soil organic matter [53–55]. This increased organic matter enhances microbial activity through both bacterial and fungal pathways, resulting in a rise in populations of opportunistic bacterial and fungal feeders, which further contributes to higher total nematode abundance [24,52,56–58]. Zhang et al. [59] reported a positive correlation between bacterial and bacterivore biomass carbon in soils fertilised with nitrogen, phosphorus and potassium (NPK) combined with either manure or straw. The bacterivore biomass carbon was also higher in these soils compared to those treated solely with NPK and unfertilised soils. Similarly, the abundance of fungivore nematodes is influenced by the presence of fungal communities. Nahar et al. [24] observed an increase in fungivore abundance following fertilisation with either raw or composted manure. Other studies have also documented increases in bacterivore and fungivore populations in organically fertilised soils [24,52,58–68]. Omnivorous and predatory nematodes, on the other hand, tend to increase in abundance under more mature, biologically stable conditions where complex food webs can supply a variety of prey. In organically fertilised soils, their abundance has been reported to rise, which coincides with an increase in their herbivore and bacterivore prey populations [24,54,56,69,70].

Despite the expected overall positive effects, organic fertilisers vary in nutrient content and decomposition stage, which influence the abundance of microbivores, omnivores, and predators. For instance, composts derived from different feedstocks, such as willow wood chips or partial popular barks, had higher total nematode abundance compared to those from farm manure and green waste [71]. These different observations were due to variations in organic matter content and the C:N ratio of the fertilisers. The composts derived from feedstocks had a high organic content, a moderate C:N ratio, and relatively low EC values (62–75%, 18.9–30.1, 284–983 μS cm^{-1}, respectively), compared to those derived from green waste (OM 28.4% and the highest EC 1254 μS cm^{-1}). This suggests that soils with high organic matter content tend to support a greater number of microbial communities, resulting in higher total nematode abundance.

The extent to which organic fertilisers influence the abundances of microbivores, omnivores, and predatory nematodes also depends on the quality of organic matter, particularly its carbon-to-nitrogen (C:N) ratio and level of decomposition. Organic materials with a

high C:N ratio promote fungal decomposition pathways, whereas those with a low C:N ratio favour bacterial decomposition pathways [13,17]. This suggests that organic fertilisers with high organic matter and a high C:N ratio will promote the density of fungivorous nematodes. In contrast, those with a low C:N ratio will enhance bacterivorous nematode populations. A higher abundance of bacterivores and overall nematodes was observed in soils that received compost incorporated with effective microorganisms compared to those fertilised only with traditional compost [56].

Organic fertilisers with a high C:N ratio have, in some cases, been linked to increased numbers of omnivore and predator nematodes. For example, the application of organic fertilisers such as sugarcane refinery sludge, sewage sludge, sugarcane bagasse, and plant residues was found to have varying effects on the populations of free-living nematodes [70]. Sugarcane bagasse and plant residues had high C:N ratios of 39 and 25, respectively, and recorded a high abundance of fungivores and omnivore-predators. In contrast, sugarcane refinery sludge and sewage sludge fertilisers had low C:N ratios of 17 and 7, respectively, and exhibited high abundances of bacterivores. The differences in omnivore-predator numbers were linked to increased predation resulting from a highly diverse environment in lower trophic groups after organic fertilisation. Zhang et al. [59] observed that the biomass carbon of fungivores, omnivores and predators was lower in soils treated with NPK incorporated with manure compared to NPK incorporated with straw. Other studies have observed similar trends (Table 1), such as a high abundance of omnivores and predators in popular leaf and maize straw compared to cow manure [64], and a higher abundance of fungivores in plant residue-fertilised coffee plantations than in cow manure-fertilised ones [57].

Raharijaona et al. [69] suggest that combining organic fertilisers can also boost the populations of omnivore and predator nematodes more than applying them individually. They found that soils receiving a high combination of organic fertilisers, such as conventional farmyard manure (CFM), compost (COM), vermicompost (VCT), and bat guano, supported more omnivorous and predatory nematodes than soils treated with each organic fertiliser alone. The combined usage of organic fertilisers creates a synergistic effect from the complementary nutrients provided by the different organic fertilisers, fostering richer and stable food webs than when used separately [69].

The application rates of organic fertilisers also significantly influence the overall abundance and relative proportions of free-living nematodes. Given the opportunistic nature of microbial communities, increased breakdown of organic matter results in a proliferation of their populations, which in turn positively impacts the number of microbial-feeding nematodes. Therefore, how much of the organic fertilisers applied affects both the total and microbivore populations [52,56,61,68]. For instance, the abundance of bacterivores increased as more compost was added in a wheat–maize crop rotation system fertilised with either traditional methods or compost incorporated with effective microorganisms [56]. However, the introduction of more effective microorganisms did not affect bacterivore abundance, indicating that it is the quantity of organic matter, rather than the presence of more microorganisms, that influences microbial activity blooms. Su et al. [52] also observed an increase in fungivore abundance with higher amounts of manure applied to jackfruits. Several studies have also recorded a higher total nematode abundance correlating with the quantities of compost applied [52,60,67,71]. Similarly, high abundances of omnivores and predators have been noted to increase with the rising amount of manure fertilisation in some studies (Table 1) [52,72].

Table 1. Summary of various impacts of different organic fertilisers on soil nematode feeding groups (BF—bacterial feeders, FF—fungal feeders, OM/PR—omnivore-predators and PPN—plant parasitic nematodes), diversity and nematode indices (CI—channel index, EI—enrichment index, MI—maturity index, SI—structural index). For diversity, only the Shannon diversity index was considered. NPK = nitrogen, phosphorus and potassium; ↑ = increase; ↓ = decrease in nematode abundance.

References	Organic Fertilisers	Management Practice and Crop	BF	FF	OM/PR	PPN	Diversity	Nematode Indices
[52]	Organic manure applied at various rates, along with chemical fertilisers at different rates	Greenhouse (jackfruit)	↑ high levels of manure than synthetic fertiliser	↑ high levels of manure than synthetic fertiliser	↑ high levels of manure: synthetic fertiliser	↓ with high levels of manure than synthetic fertiliser	↑ high levels of manure than synthetic fertiliser	↑ MI, EI, SI, high levels of manure than synthetic fertiliser
[58]	Manure (M), manure + urea (M + U), straw (S), straw + urea (S + U)	Monoculture (sorghum)	↑ straws than manures	↑ straws than manures	No effect	↑ manure than straw	not reported	No effect on CI, EI, SI though SI varied with development stage
[73]	Cow manure plus rice straw compost, Sugarcane filter cake compost plus urea	Different cropping patterns (rice, sesame, soybean)	No effect	No effect	No effect	No effect	No effect	No effect
[64]	Poplar leaf, maize straw, cow manure + NPK to all	Monoculture (soybean)	↑ cow manure than straw and poplar leaf	↑ cow manure than straw and poplar leaf	↑ straw and poplar leaf than manure	↑ poplar leaf and maize than straw	↑ Poplar leaf and straw than manure	No effect on MI; ↑ PPI in poplar leaf than straw and manure ↑ SI in straw compared to manure and poplar leaf
[70]	Sugarcane bagasse (SCB), sewage sludge (SES), plant residues (PLR), Sugarcane Refinery Sludge (SCS)	Greenhouse (banana)	↑ SCB, SCS, and SES than PLR	↑ SCB at planting ↓ at the final stage. ↑ in PLR at final	No effect; ↑ in SCB at final stage	↓ in all except vs. control no effect in SES; ↓ at the final stage in SCB	Not reported	↑ in MI in all except SES; ↑ CI in SCS and PLR
[74]	Beef manure (BM), Horse manure (HM), swine manure (SM), poultry manure (PM)	Monoculture (corn)	↑ horse and beef manure, than swine, while poultry manure had the lowest	↑ swine and poultry manure than beef, while horse manure had the lowest	↑ beef and swine manure were the highest, followed by poultry and then horse manure	↑ in all manures	No effect	No effect in PPI, EI, CI; ↑ MI in swine and poultry manure compared to beef, while horse manure had the least MI; beef and swine manure had higher SI than poultry, while horse had the lowest

Table 1. *Cont.*

References	Organic Fertilisers	Management Practice and Crop	BF	FF	OM/PR	PPN	Diversity	Nematode Indices
[75]	Plant based compost, plant-based compost + urea at different ratios (3:1, 1:1, 1:3)	Monoculture (carrot)	No effect	No effect		No effect	No effect	No effect
[69]	Conventional Farmyard Manure (CFM), Compost (COM, Improved Farmyard Manure (IFM), Kraal Manure (KM), Vermicompost (VCT) applied at different rates and in various combinations (16 treatments) with mineral fertilisers in some combinations	Monoculture (rice)	No effect	No effect	↑ organic treatments, especially those incorporating bat guano and high rates of organic materials	↑ organic treatments, especially those incorporating bat guano and high rates of organic materials; ↑ compost only than manure only treatments	No differences between all organic treatments	No effect on MI, PPI, CI, EI; ↑ high rates of organic inputs, kraal manure, low input conventional farmyard manure with NPK
[72]	Fermented manure (FM) and sawdust (SAW), both individually and in combination with inorganic nitrogen	controlled pot experiment (sugar beet)	↑ in both FM treatments than SAW treatments; ↑ high levels of FM	↑ in both FM treatments than SAW treatments; ↑ high levels of FM	↓ in both FM and SAW	↓ in FM; no effect SAW	Not reported	Not reported
[59]	Cattle Manure Compost + NPK (NPKM), Maize Straw + NPK (NPKS)	Crop rotation (wheat and maize)	↑ BF biomass carbon in both manure and straw	↑ FF biomass carbon in straw than manure in wheat	↓ OM-PR biomass carbon manure than straw	↑ PPN biomass carbon; however lower biomass carbon in both manure and straw in maize season	Not reported	↑ in enrichment footprint in straw than manure under wheat. SI footprint lower in maize
[24]	Raw Manure, Composted Manure	Monoculture (tomato)	↑ in both raw and composited manure	↑ in both raw and composited; more in compost	↑ in both raw and composited; more in compost	↓ Raw manure than compost	↑ in compost than raw manure	↓ in ∑MI in both; lower in raw manure

Table 1. *Cont.*

References	Organic Fertilisers	Management Practice and Crop	BF	FF	OM/PR	PPN	Diversity	Nematode Indices
[57]	Naturally fertilised (NF)-plant residues, Poultry Litter (PL), Cow Manure (CM)	Agroforestry (coffee, banana, royal palm, avocado, peanut)	↑ in PL and cow manure (CM) lower in NF	↑ in NF than PL lowest in cow manure	No effect	↑ NF less in PL and lowest in CM.	↑ in NF than PL; lowest in cow manure	↑ in MI in NF than CM; lowest in PL; ↑ in EI in CM than PL, lowest in NF; ↑ in SI in NF than PL, lowest in CM
[62]	Traditional compost (C), compost with effective microorganisms (EMC), and chicken dung compost with effective microorganisms (EMCDC). Each was applied at two rates of 7.5 t/ha and 15 t/ha	Crop rotation (wheat and maize)	↑ in both EMC and EMCDC compared to traditional compost at both rates	No effect	↓ at high rates. Effective microorganisms have no effect	↓ in both EMC and EMCDC vs. traditional compost at high rates	affected by the amount of compost, not effective microbes	Low MI; PPI; ∑MI not affected by effective microbes; EI, SI affected by the amount of compost.
[56]	Traditional Compost (C), Traditional Compost with Effective Microorganisms (EMC)	Crop rotation (wheat and maize)	↑ in both composts, but higher in the compost with microbes	↓ in compost with microbes than traditional compost	↑ in compost with microbes than in traditional compost	↑ in both composts, higher in the compost with microbes	Not reported	Not reported

3.2. Factors Driving Variation in Free-Living Nematode Communities Under Organic Fertilisation

Organic fertilisers are expected to increase the abundances of bacterivores, fungivores, and the total number of nematodes. However, several studies have reported little to no increase, with some indicating a decrease, particularly in fungivorous, omnivorous, and predatory nematodes [42,56,59,61,64,67,69,73,76–78]. This discrepancy is related to factors such as compost maturity and quality, low application rates, or experimental variables, such as short-term observation periods, that may overshadow differences between taxonomic groups. For instance, Herren et al. [42] did not observe differences in the abundances of bacterivores, fungivores, omnivores, and predators following the application of compost. The lack of significance was attributed to low-quality compost, as indicated by a nematode index of compost maturity of 2.06, which was below the standard biological compost maturity requirement of 3. This suggests that the effectiveness of compost in promoting microbivore abundance is influenced not only by the C:N ratio and quantity applied, but also by the maturity of the compost. The application of different organic manures (conventional farmyard manure, improved farmyard manure) and composts (landfill materials and vermicompost), whether applied individually or in combination, did not affect fungivore abundance compared to unfertilised soils in rice fields of Madagascar [69]. The authors attribute the lack of significance to high variability in data caused by local experimental challenges, such as the stressful acidic, nutrient-deficient environment of farrelsols, and low application rates. Low amounts of organic fertiliser might not stimulate microbial growth, hence the abundance of microbivores, while stressful in acidic environments could have affected the nematode's physiology, therefore suppressing the fungivores.

Contradictory results have also been reported, where the abundances of fungivores declined under organic fertilisation with high C:N ratios (Table 2). For example, a higher abundance of fungivores was observed in soils fertilised with manure, which had a lower C:N ratio, compared to soils fertilised with maize straw and poplar leaf, which had higher C:N ratios [64]. The unusual observation may be explained by the fact that manure is more decomposed than straw and contains readily available organic matter, which can promote fungal growth and consequently increase the abundance of fungivores. Hu et al. [56] also reported a significant decline in fungivore abundance in soils amended solely with compost as well as those fertilised with compost incorporated with effective microorganisms, compared to unfertilised soils in one of the growing seasons. The extreme decline in abundance could be due to increased competition for carbon resources by the bacterial and fungal communities. Indeed, the researchers observed an increase in the abundance of bacterivorous nematodes, which was promoted by high bacterial growth. However, the researchers did not observe these differences in other seasons, suggesting that seasonal differences, such as shifts in moisture and temperature, controlled the abundances of the microbivores. However, in the humid nitisols of Kenya, the use of organic fertilisers also reduced the abundance of fungivores compared to conventional fertilisers [76]. The lower number of fungivores in organically fertilised soils could be due to the neem cake applied, which has been shown to reduce fungal abundance, the primary food source for fungivores [79].

Management strategies, such as tillage and crop rotation, also affect nematode communities, particularly the fungivores, omnivores, and predators. The decline or lack of significance in the abundance of omnivore and predator nematodes has been linked to management practices. In tilled soybean crop rotation soils amended with biosolids, composts, and vetch, the abundance of omnivore and predatory nematodes was found to be lower compared to untilled soils with the same crops and fertilisers [67]. Briar et al. [77] observed an initial increase in omnivore-predator populations following organic fertilisation, but these populations decreased with continued tillage. Other studies have observed similar declines in the two groups following organic fertilisation [59,61]. The sensitive nature of

omnivores and predators to changes in the soil environment following disturbance is the primary contributor to the decrease in numbers. Viera Junior et al. [57] also reported a higher abundance of fungivore nematodes in unfertilised forested soils and those fertilised with natural plant residues compared to those fertilised with manure and poultry litter (Table 1). Forest litter and plant residue fertilisers have high concentrations of lignin and cellulose, which are high in organic matter. Fungi require a stable substrate to thrive, and continued tillage breaks their mycelia, impacting their abundance and thus reducing the abundance of fungivores [80]. The substrates in forested and naturally fertilised soils support fungal growth, therefore supporting more fungivore nematodes as their food source. These findings also suggest that fertilisation, even with inorganic fertilisers, alters the nematode community structure. The lack of difference in fungivore abundance between open-field and controlled high tunnel tomato farming was also linked to environmental factors such as temperature, sunlight, and moisture in controlled settings that may boost fungal populations [78].

Table 2. Summary of how different factors influence the nematode feeding groups (bacterivores—BF, fungivores—FF, omnivore-predators—O-P) and nematode indices (CI—channel index, EI—enrichment index, MI—maturity index, SI—structural index) under organic and inorganic fertilisation. C = carbon; N = nitrogen ↑ = increase; ↓ = decrease in nematode abundance.

Factor	BF	FF	O-P	Nematode Indices
Organic Fertilisation				
Type of organic matter based on (C:N)	↑ at low C:N in organic	slow ↑ at high C:N in organic	↑ at high C:N in organic	↑ CI at high C:N; MI varies; ↑ in EI; SI varies; no impact on PPI
Application rate	↑ at high-rate organic	↑ at high-rate organic	↑ at high-rate organic	MI varies across studies
Quality (compost maturity)	No impact at low maturity	No impact at low maturity	No impact at low maturity	
Experimental factors	varies based on conditions	varies based on conditions	varies based on conditions	
Tillage	↑ under tillage	↓ under both organic and inorganic under tillage	↓ under both organic and inorganic under tillage	
Crop type	May favour some taxa in some crops	May favour some taxa in some crops	May favour some taxa in some crops	
Inorganic fertilisation	BF	FF	O-P	Nematode indices
Changes in soil chemistry (soil pH)		↓ under inorganic at low pH	↓ under inorganic at low pH	
Application rate	↑ at low application rates	↓ under inorganic at a high application	↓ under inorganic at a high application	↓ in MI
Ammonium suppression	↓ at high rates of N	↓ at high rates of N	↓ at high rates of N	
Predator–prey abundance	↑ in the presence of more bacteria	↑ in the presence of more fungi	↑ in the presence of prey	↑ in SI with more omnivore-predator nematodes
Tillage	↑ under tillage and even higher under no tillage	↓ under tillage lower than under organic	↓ under no tillage	↑ SI under no tillage; ↓ in EI under tillage
Method of nematode analysis	No effect	No effect	Sensitive to metabarcoding than morphological identification	

Crop type is also a critical factor influencing the populations of omnivorous and predatory nematodes. Fertilisation does not affect the abundances of omnivore and predatory nematodes, but crop type does [73]. This variation is due to the environmental conditions created by different crops, which generate specialised environments that favour specific nematode taxa. For instance, a greater abundance of predatory nematodes, *Brevitobrilus*, was found in rice fields compared to sesame and soya bean fields, despite all having received the same type and amounts of organic fertilisers. The variation in this case was associated with rice fields, which might have created conducive conditions for the *Brevitobrilus* nematodes, such as increased predator abundance [73]. The researchers observed a high abundance of herbivores, including *Hirschmanniella* and *Bitylenchus*, which are commonly found in rice fields and might have provided food for the predators [81].

4. Impacts of Inorganic Fertilisation on Free-Living Nematodes

4.1. Changes in Soil Chemistry Alter Nematodes Under Inorganic Fertilisation

In inorganically fertilised soils, nutrients are in more readily available forms, which can quickly alter soil chemistry and microbial communities, consequently affecting the total and microbivore nematodes abundances. However, the responses are varied and are influenced by factors such as application rate and soil characteristics, resulting in both negative and positive effects on nematode communities [23,38,40,62]. The decline in total and microbivore nematode abundance following inorganic fertilisation compared to unfertilised soils has been linked to the negative effects of the fertilisers on the overall microbial communities [38,40]. The effect extends to higher trophic nematode groups, which also decline due to reduced food availability, contributing to a decrease in total nematode abundance. Additionally, inorganic fertilisers negatively impact both total and free-living nematode populations, primarily because nematodes are sensitive to soil chemical changes caused by fertilisation, such as acidification, increased salt concentration, and reduced carbon levels [40,82].

Fertilisation with both inorganic N and P leads to a decline in fungivorous, omnivorous, and predatory nematodes due to changes in soil pH [22,38,40,42,52,68,76,83–89]. Some studies have documented a strong positive correlation between the abundance of fungivores and soil pH [38,52,90]. Additionally, several studies have observed a decline in fungivore populations following inorganic nitrogen (N) addition [38,62]. This suggests that at low pH levels, acidification resulting from inorganic N fertilisation negatively impacts fungivores by impairing their physiological conditions or suppressing microbial communities [49,91]. In P-fertilised soils, the abundance of fungivores was found to decrease and continued with more amount and duration of fertiliser application [87]. This decline was attributed to a shift in microbial communities from fungal to bacterial, evidenced by a decreasing ratio of fungal to bacterial phospholipid fatty acid levels (PLFAs). A similar decline in fungivore abundance was observed in soils fertilised with NPK fertilisers compared to those fertilised with either straw or manure incorporated with inorganic fertilisers [52].

Wu et al. [83] reported a decline in nematode total abundance after P enrichment that continued to decline and did not recover even after a long-term P application. Several studies have observed a decline in omnivore and predator abundance in inorganically fertilised soils that worsened with high quantities of fertiliser (Table 2) [38,40,68,92,93]. The decline in abundance was attributed to changes in soil pH and nutrient-related dynamics [38,83]. However, the short-term application of P does not impact nematode total abundance [84]. This implies that long-term use of inorganic fertilisers modifies the soil's chemical properties, significantly impacting nematode abundance, especially at higher trophic levels. Several studies have also reported a decline in bacterivore nematode abundance following

inorganic fertilisation compared to unfertilised and organically fertilised soils linked to changes in soil pH caused by fertilisation [38,66,74,76,77,84,94].

While the abundance of the bacterial community is the main factor influencing bacterivore numbers, other factors, such as the amount of fertiliser applied, plant biomass, and tolerance to disturbance, also contribute to the variation in the abundance of total and microbivore nematodes. Studies have documented an increase in total and bacterivore feeding nematodes after inorganic fertilisation [23,41,54,62,63,85,86,88,92,95]. Studies by Wang et al. [23] and Azpilicueta et al. [92] found that adding nitrogen increases the total nematode abundance, with positive effects observed at application rates of up to 25.45 g N m^{-2} yr^{-1} (equivalent to 254.5 kg N ha^{-1} yr^{-1}) and up to 300 kg N ha^{-1} yr^{-1}, respectively. However, these findings contradict those of Wei et al. [40], who observed a decline in nematode abundance following inorganic fertilisation. The discrepancy likely stems from the fact that the application rates used in the first two studies were much lower than the 4.0 mol m^{-2} yr^{-1} (or 560 kg ha^{-1} yr^{-1}) applied by Wei et al. [40]. This suggests that while some N application may increase nematode abundance, exceeding a certain threshold triggers negative effects of N addition, such as acidification, which adversely affect nematode populations. Similar trends have been observed in other studies where the total, microbivorous, fungivorous, and predatory nematode abundance was found to continue to decline with increasing quantities of inorganic fertiliser [39,40,64].

In contrast, when N is combined with phosphorus (P) or potassium (K) at moderate application rates, typically between 150 NPK kg ha^{-1} and 300 NPK kg ha^{-1}, nematode total abundance has been found to increase [62,85,95]. This increase could be due to a combination of nutrients, enhancing plant growth and microbial abundance, consequently impacting some nematode groups. Qi et al. [88] reported that the abundance of bacterivores increased after inorganic N fertilisation but decreased with the addition of an inorganic NP blend. Similarly, Wei et al. [40] observed an increase in bacterivores after inorganic N fertilisation caused by enrichment; however, it declined at higher application rates. This decline was linked to top-down controls by predatory soil organisms or ammonium suppression caused by low soil pH after N fertilisation, indicating that application rate influences bacterivore nematode abundance in inorganically fertilised soils [49,82]. Other studies have observed contradictory results, with inorganic fertilisers having no effect or increasing the abundance of fungivores [68,74,76,89]. For instance, the application of inorganic nitrogen either increased or had no effect on the abundance of fungivores, despite acidification being known as a factor limiting their abundance [58,74,76,89,92]. The observation could be due to the low application rates used in these studies. As stated above, nematodes were sensitive to high nitrogen application rates above 500 kg ha^{-1} yr^{-1}, which were lower in these studies. Atandi et al. [76] found contradictory results, with an increase in fungivore abundance in inorganically fertilised soils, despite the high rate of N applied. The increase in fungivores was caused by the synthetic fertilisers, used to stimulate fungal growth, promoting fungivore abundance.

4.2. The Role of Disturbance and Ecological Interactions Under Inorganic Fertilisation

Discerning the factors contributing to the abundance of omnivores and predators can be challenging because their populations are also influenced by the abundance of herbivores and bacterivore prey, as well as microbial biomass. Ammonium toxicity from inorganic nitrogen fertilisation was not identified as a factor affecting the abundance of omnivores and predators, but their populations are regulated by the populations of their herbivore and bacterial prey [23]. Zhang et al. [59] found that the carbon flow from herbivores to omnivore-predator nematodes contributed the most to carbon biomass compared to bacterivores and fungivores. This made PPN the higher trophic level, contributing to the carbon biomass of

omnivores and predators. In their study, reduced prey abundance led to a decline in the abundance of both omnivores and predators. This may explain why some studies observed an increase in predatory nematode abundance at high inorganic fertilisation rates or with long-term use, which had the highest number of herbivore nematodes [23,54,87,89].

Wang et al. [23] observed a decline in omnivorous nematode abundance with increasing fertilisation despite the high abundance of herbivores. The drop in this case was associated with changes in plant diversity and microbial biomass, which might have increased specialised herbivores, leading to a decline in omnivore abundance. However, the long-term application of inorganic fertilisers does not impact the omnivorous and predatory nematode abundance [41,72]. Tillage and agricultural management practices, such as ploughing and continuous cropping, also control the abundance of omnivores and predators [52,77]. For instance, the abundances of omnivorous nematodes were higher in sesame crops than in rice fields, and specific predatory nematodes, such as *Brevitobrilus*, were more common in rice paddy fields than in other crops in Vietnamese fluvisols applied with the same fertilisers [73]. The observations imply that environmental conditions created by different cropping patterns have a more pronounced effect on these nematode groups than the application of inorganic fertilisers. Stressful environments, such as low baseline soil carbon, nitrogen, phosphorus, and other nutrients, as well as clay soils and drought conditions, can also contribute to low abundances of omnivore and predator nematodes [69,86]. Siebert et al. [86] reported that the application of NPK fertilisers under drought conditions decreased the abundances of omnivores and predators. Nematodes need water to move through the soil, and drought conditions must have created unfavourable conditions for both groups. The low abundance of omnivores and predators in ferralsols under inorganic fertilisation was associated with the stressful nature of the soils, coupled with the effect of inorganic fertiliser [69]. The study reported that initial low soil organic matter and other nutrients might have limited biological activity, reducing the potential for a more diverse soil biota to support the higher trophic levels.

Other studies did not find any differences in omnivore and predator nematode abundances following inorganic fertilisation [42,58,93]. The lack of significance was attributed to factors such as the method of identification in nematode analysis. Herren et al. [42] observed a significant drop in predator abundances in metabarcoding data that did not show in morphological data. This implies that metabarcoding may be a more sensitive method for detecting changes in specific nematode groups that might not be captured in morphological data. The lack of significance could also be due to soil disturbance from tillage overshadowing the effects of inorganic fertilisers [58]. In a Japanese soya bean field with no-tillage, the abundance of fungivore nematodes was high compared to tilled farms with fertilised and unfertilised soil [54]. As discussed in Section 3.2 above, disturbance caused by tillage can break the fungal mycelia, reducing their abundance and, consequently, the abundance of fungivores. Overall, the nematode community under inorganic fertilisation is also driven by functional and broader environmental factors. While inorganic fertilisation can promote quick microbial turnover, sustaining more bacterivores, the continued use can also lead to acidification and nutrient imbalance, which can significantly impact the sensitive groups. Management practices such as application rates and tillage can intensify these effects (Table 2).

5. Impacts of Fertilisation on Plant-Parasitic Nematodes

5.1. Interacting Factors Shaping Plant Parasitic Nematodes in Fertilised Soils

Plant-parasitic nematodes (PPNs) are a concern in agricultural systems due to their damage to crops and adverse effects on crop yield [96]. Generally, fertilisation influences PPN abundance indirectly by altering the soil chemistry, nutrient availability, plant growth,

and root chemical characteristics. Studies have shown that there is a strong positive relationship between plant biomass and herbivore abundance [68]. Additionally, Chen et al. [97] observed that in the absence of plants, the abundance of PPN declines due to a lack of plant roots, which serve as their primary food source. Studies have documented an increase in PPN abundance associated with enhanced plant biomass or crop yield stimulated by both organic and inorganic fertilisation [39,42,52,54,58,68,74,77]. For instance, in Gainesville, FL, USA, the abundance of PPN increased in nitrogen-fertilised plots, which had high squash yields (3.69 kg m^{-2}) compared to unfertilised soils (1.78 kg m^{-2}) [68]. The populations of plant parasitic nematodes were observed to increase under urea application, and that of PPN *Pratylenchus* and *Tylenchorhynchus* were observed to rise under manure compared to straw [58]. The increase in abundance of PPNs was possibly due to enhanced host availability and greater root proliferation [58,68,74].

The influence of environmental factors and management practices, such as crop type and crop rotation, also determines PPN population dynamics, influencing host availability and soil conditions. For instance, inorganic N fertilisation suppressed white clover in pasture soils, favouring nematode genera such as *Pratylenchus* and *Paratylenchus* while suppressing *Meloidogyne*, known parasites of white clover [39]. In Irish grasslands, the abundance of PPNs was found to increase with increasing amount of P applied and become more pronounced with time compared to unfertilised soils. The increase in abundance was associated with fertilised soils, promoting the growth of different grasses such as *Lolium perenne* and *Poa trivialis* that dominated with time, different from those in unfertilised soils. Instead, the unfertilised soils were dominated by *Agrostis capillaris* and *Holcus lanatus* [87]. The shift in plant community to *Lolium perenne* and *Poa trivialis* due to fertilisation may have favoured PPNs associated with these two plants compared to those found in unfertilised soils. Similar observations have been made where a high abundance of *Pratylenchus penetrans* in organically fertilised soils was found in potato root zones compared to those of barley [98]. Zhang et al. [59] also reported that even though the biomass carbon of plant feeders increased in organic fertilised soils mixed with NPK, it was higher in wheat-planted soils than in maize-planted soils. All these patterns imply that the plant species impact the PPN abundance.

Plant growth stage also influences the abundance of PPNs, especially endoparasites. Vestegard [89] observed that NPK fertilisation initially decreased endoparasite *Pratylenchus* spp. at growth. However, the population later increased at the flowering stage in spring barley. This implies that at planting, there was no host and enough plant biomass for the nematodes. However, as the crops grew to the vegetative flowering stage, the endoparasites increased in numbers. The authors did observe an initial increase in other PPN species from the initial stages. Some studies have suggested that inorganic fertilisation reduces PPN abundance caused by changes in the root characteristics [40,60,88,92]. Wei et al. [40] elaborate that there is a negative relationship between ammonium concentration in the soil and the abundance of PPNs along the N addition gradient, hinting that ammonium toxicity is a factor in reducing the number of PPNs by affecting the root fluids. Considering ammonium toxicity as a factor affecting herbivore nematode abundance, the amount of N fertiliser applied negatively affects the PPN population further [52]. This could explain why the abundance of the PPN *Pratylenchus crenatus* and *Paratrichodorus renifer* declined at higher N application rates. Similarly, Ni et al. [91] observed a decrease in the abundance of PPNs with increasing amount of N. The suppression is attributed to ammonium changing the root chemical characteristics, with excessive amounts of ammonium being toxic to the plant feeders [49,91]. Other studies have suggested the use of ammonium to suppress PPNs [99,100]. The long-term application of P also reduces the abundance of plant feeders [22,83,84]. The mechanisms driving PPN abundance remain unclear; however, this

could be that, unlike nitrogen, acidification from phosphorus addition depends on the form of the fertiliser applied. For instance, superphosphate is readily available in an acidic form and can cause a decline in soil pH over time, which negatively affects nematodes [83].

In some studies, fertilisation either increased or had no significant impact on PPN abundances and was linked to factors related to management strategies such as crop rotation. In Japanese soybean fields, for instance, inorganic fertilisation coupled with no tillage increased the densities of PPN *Pratylenchus* compared to tilled soils [54]. Vieira Júnior et al. [57] also found that soils fertilised with natural plant residues had significantly more PPNs than those fertilised with either manure or poultry litter, but not the natural nearby forests. Okada et al. [54] also reported that untilled soils with more weeds promote PPN abundance, which provides alternative hosts to them. The increase in abundance of PPNs in fertilised soils has also been attributed to low application rates, especially in inorganically fertilised soils. Herren et al. [42] and Villenave et al. [58] found that inorganic fertilisation with 120 kg N ha^{-1} yr^{-1} and 60 kg N ha^{-1} yr^{-1}, respectively, increased the abundance of PPNs. These low application rates may not significantly impact soil chemistry, causing ammonium toxicity to PPNs, as suggested by Wei et al. [40]. In contrast, Azilicueta et al. [92] observed a drop in PPN abundance at 100 kg N ha^{-1} yr^{-1}, which increased at 200 kg N ha^{-1} yr^{-1} in apple orchards on aridisols. This could imply other factors, such as soil type or the presence of PPN specialised to apple orchards.

5.2. Plant Parasitic Nematodes Suppression by Organic Fertilisers

Several studies have reported that the application of organic fertilisers suppresses PPN. For instance, Nahar et al. [24] observed a decrease in the abundance of plant feeders after either raw or composite manure application. The decline in PPN here was linked to the release of nematicidal substances from organic manure, such as methane, ammonia, and nitrogen dioxide, which are toxic to nematodes. Soils fertilised with fermented manure suppressed the abundance of PPN, while those fertilised with sawdust had little to no effect in a sugar beet pot experiment [72]. The decrease in abundance was due to biocidal effects in green and fermented manures, such as isothiocyanates that suppress the PPN populations [64]. Fertilisation of squash plants with *Crotalaria juncea* fertiliser also suppressed the populations of PPNs, and they decreased with increasing amount of organic fertiliser applied [68]. The decline was associated with the fertiliser producing allelopathic compounds that are antagonistic to plant parasites [101]. The number of PPN also decreased with higher amounts of organic manure applied to jackfruits, indicating that the amount of organic manure influences their abundance [52]. Stimulation of microbial biomass could also enhance ecosystem diversity, creating unfavourable conditions for the plant-parasitic nematode through increased predation. Similar suppressive effects have been observed in composts [56,67,77,78,102], in manure [52,59,72,103], industrial by-products such as plant residues, sewage sludge, and sugarcane bagasse (Table 1) [70].

In contrast, other studies have documented an increase in plant-parasitic nematodes in organically fertilised soils. For instance, in soils fertilised with several organic fertilisers either in combinations or singly and at different rates, the abundance of PPNs increased especially in treatments that received composts and combinations of composts such as vermicompost, farmyard manure, and bat guano and high rates of composts [69]. Several factors can contribute to this increase, for instance, a reduced abundance of predators, initial dominance of PPN, or even the presence of a suitable host. Other studies have also documented an increase in PPN abundances under organic fertilisation [54,56,58,60,70]. Several studies did not observe changes in PPN abundance following either organic or inorganic fertilisation, attributed to several factors masking the effect of fertilisation. For instance, Herren et al. [42] did not find any significant difference in PPN abundance

between composited and unfertilised soils, attributing the effects to both low compost maturity and confounding effects of crop rotation. Other studies have attributed the lack of significance to short experimental periods [93] and masking effects of both cover crops and crop rotation [102].

Factors controlling PPN abundance in fertilised soils are diverse and often vary between studies. Contradictory outcomes suggest that the impacts of organic fertilisers might be context dependent. Variability in fertiliser type, quality, chemical properties, and application rate, as well as the presence of suitable hosts, antagonistic microbes, and management strategies, plays a crucial role in determining the response. All these imply that the reliance on organic fertilisers for suppression of PPNs may not be guaranteed.

6. Impacts of Recycling Derived Fertilisers on Nematode Communities

Analogous to organic and inorganic fertilisers, recycling-derived fertilisers have different effects on the composition and structure of the nematode community. Usually, they contain nutrients in their fully mineral form with low carbon content, which is easily accessible to plants, much like inorganic fertilisers, influencing their impact on soil nematodes [8,9]. At the same time, they vary significantly depending on their source materials, leading to differences in their nutrient content and nematode communities. For instance, RDFs such as potato waste struvite (PWS) derived from potato waste, municipal waste struvite (MWS) derived from municipal waste, poultry litter ash (PLA) derived from poultry litter, and sewage sludge ash (SSA) derived from sewage sludge are rich in phosphorus (P) [5,8,9,104]. On the other hand, RDFs derived from ReNure, such as ammonium nitrate (AN), ammonium sulphate (AS), and pig urine (PU), are rich in nitrogen (N) [9,105]. Vinasse, a product of the sugarcane processing industry, is rich in both N and potassium (K) [106] (Figure 2). Other factors, such as management strategies and experimental conditions, also contribute to the differences observed between studies. Unlike organic and inorganic fertilisers, which have been extensively studied, there is comparatively limited literature on the impacts of recycling-derived fertilisers on nematode communities [5,104–106]. The most abundant nematode taxa found in RDF-fertilised soils include orders Rhabditida, Triplonchida, Monhysterida, and Dorylaimida [104], Diplogasterida, Araelolaimida, Enoplida, and Tylenchyda [105], and genera *Mesocriconema*, *Meloidogyne*, *Helicotylenchus*, and *Pratylenchus* [106].

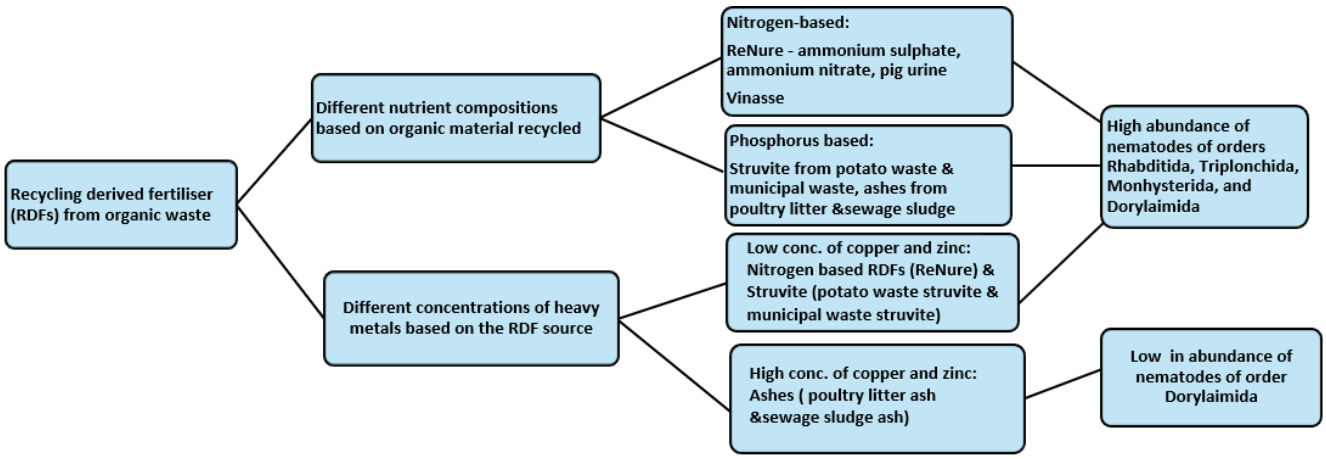


Figure 2. Flow chart illustrating the impacts of recycling derived fertilisers on nematode communities, highlighting differences in responses based on fertiliser source and chemical composition according to [5,8,9,104,105].

Recycling-derived fertilisers seem to promote the bacterial feeding nematodes, and this increase varies with RDF type, just like other fertilisation regimes [5,104–106]. In Irish grasslands, soils fertilised with phosphorus-based RDFs, potato waste struvite, municipal waste struvite, poultry litter ash, and sewage sludge ash, the abundance of bacterivores of orders Rhabditida and Mohysterida was reported to be significantly higher compared to soils fertilised with inorganic phosphorus and unfertilised soils [5,104]. Saju et al. [105] documented that bacterial-feeding nematodes from the orders Rhabditida, Monhysterida, and Diplogasterida are among the most dominant in nitrogen-based ReNure-based RDF soils (Figure 2). This confirms that RDFs, like other fertilisers, enrich the soil by promoting bacterivorous nematodes, and the extent of the increase varies between RDF types.

The RDF source also influences the responses of omnivore and predatory nematodes to the application of RDFs [5,104,105]. Apart from RDFs, poultry litter ash, and sewage sludge ash, all soils fertilised with other RDFs, whether P-based or N-based, had a high abundance of nematodes in the order Dorylaimida [5,104–106]. The abundances of nematodes from the order Dorylaimida were significantly lower than those of other RDFs and inorganic fertilisers. The differences were linked to high concentrations of Zinc and Copper heavy metals in these RDFs that affected the sensitive nematode taxa compared to other RDFs (Figure 2) [8]. The nematodes *Thonus*, *Aporcelaimellus*, and *Alaimus* of orders Dorylaimida and Alaimida, respectively, have been reported to be sensitive to copper and zinc concentrations above 50 mg/kg in a toxicity test performed on sandy soils [107]. However, no significant differences were observed in the abundances of nematodes in the order Dorylaimida in other RDFs compared to either unfertilised or inorganically fertilised soils. Nematodes of the order Dorylaimida are known to favour undisturbed environments, and an increase in their abundance indicates stability, while a decline in their abundance indicates disturbance or pollution of the habitat [10].

A recent study reveals that the impacts of RDFs are linked to variability in their sources and composition. In a similar study evaluating the effectiveness of RDFs as alternatives for conventional inorganic fertilisers in Irish grasslands, the RDFs derived from sewage sludge ash and poultry litter ash recorded high concentrations of zinc and copper. However, these concentrations were reported to be lower than the EU-accepted limits for inorganic fertilisers [8]. In contrast, the RDFs derived from potato and municipal wastes were reported to meet the safety standards. The findings align with the observed reductions and increases in the abundances of nematodes of the order Dorylaimida under the two ashes and struvites, respectively, reported by Ryan et al. [5] and Karpinska et al. [104]. Furthermore, no heavy metals were reported for the ReNure-based RDFs. The evidence suggests that some RDFs, such as struvites and ReNure, can be sustainable options for minerals, and that the impacts of RDFs on soil nematodes are context-dependent, with chemical composition being a significant factor to consider.

A significant gap exists in the current understanding of how RDFs influence fungivorous nematodes, with limited literature available on this specific feeding group. Nonetheless, Costa et al. [106] reported that the abundance of fungivores was low across different RDF vinasse application durations compared to the other nematode groups. However, the authors found that fungivore abundance increased over 10 years of application and declined after 15 years of vinasse application. The fluctuations in the abundance of fungivores with increased use of RDF suggest that at high application rates, vinasse fertilisation probably reduces fungal communities, which are food sources for these nematodes.

The most dominant plant feeders in RDF fertilised soils are from the order Tylenchida [5,104–106]. This could mean that, just like organic and inorganic fertilised soils, RDFs increase plant biomass, providing more food resources for the PPNs. The response of PPNs to RDFs also varies depending on environmental conditions. For in-

stance, Ryan et al. [5] found that in grassland soils fertilised with RDF sewage sludge ash and potato waste struvite, there was a high abundance of nematodes from the order Tylenchida compared to the unfertilised soils. However, this contradicts findings by Karpinska et al. [104], where no differences in the abundance of nematodes from the order Tylenchida were observed between RDFs in similar Irish grasslands. The differences in observations could be due to variations in physical and chemical properties of the soil, likely caused by different amounts of nutrients applied [104]. In soils fertilised with N-based RDFs, nematodes of the order Tylenchida were also among the most abundant. Specifically, in vinasse-fertilised soils, plant parasitic nematodes increased in abundance with continued use of the RDF, with the highest abundances recorded after 5 and 10 years of use [106].

7. Impacts of Fertilisation on Nematode Diversity

Fertilisation alters nematode diversity directly by affecting the physicochemical properties of the soil and indirectly through factors associated with above-ground processes. Inorganic fertilisation leads to a decline in nematode diversity and worsens with the addition of more fertiliser. Certain studies have reported increased levels of inorganic fertilisation and reduced nematode diversity in parallel, due to the impact on individual nematode trophic groups [22,23,38,40,52,64,69,83,88,89]. As discussed in Section 4, inorganic fertilisation negatively affects omnivores, predators, and fungivores, while bacterivores remain dominant in some cases, reducing the complexity of the nematode community. For instance, Niu et al. [95] recorded the dominance of rhabditid and tylenchid nematodes in inorganically fertilised soils, which led to a decline in diversity.

Changes in microbial biomass can significantly alter nematode diversity by decreasing the abundance of microbivorous nematodes. Long-term usage (18 years) of inorganic fertilisers was reported to lead to a decline in nematode diversity due to changes in fungal and bacterial biomass affecting the populations of the dominant genera [83]. In an Irish grassland column experiment, a distinct separation in nematode community was observed in soils fertilised with inorganic nutrients and those with organic fertilisation. It was attributed to the dominance of bacterial feeders in inorganically fertilised soils and reduced beneficial microbes [63].

Changes in plant diversity can also drive a reduction in nematode diversity in inorganically fertilised soils. Wang et al. [23] found that total nematode abundance increased due to the high number of herbivores, which coincided with increased plant productivity. As discussed in Sections 4 and 5, fertilisation is not a significant factor controlling the abundance of herbivorous, omnivorous, and predatory nematodes [108–110]. This means that, under high plant diversity, the abundance of herbivorous, omnivorous, and predatory nematodes will be impacted, influencing nematode diversity. The decline in nematode diversity found by Wang et al. [23], despite the increased total nematode abundance, could be attributed to a decreased plant diversity after fertilisation. The authors suggest that this might have resulted in a high abundance of specialised herbivores, increasing competition for food with the omnivores, affecting nematode diversity. The study established that plant diversity was positively impacted by the abundance of omnivorous nematodes, altering the community diversity [83]. However, Qi et al. [88] reported a contradictory increase in nematode diversity in N-fertilised soils compared to P-fertilised soils, likely caused by the low amounts of fertiliser used in the study.

Conversely, organic fertilisation is likely to enhance nematode diversity [57,69,111]. However, this increase is affected by the type of organic fertiliser. For example, soils fertilised with cow manure were found to be less diverse and dominated by rhabditids compared to those fertilised with poultry litter, plant residue, or natural forest soils that were not fertilised (Table 1) [57]. Nahar et al. [24] observed a lower nematode Shannon

diversity index in soils amended with raw manure compared to those that were not amended, associated with high numbers of bacterivores. In contrast, plots amended with composited manure had no significant difference in nematode Shannon diversity compared to unamended soils. This means that composted manure has less impact on the nematode community than raw manure. These differences indicate variations in how the type of organic fertiliser can shift the nematode community. Other studies have observed similar trends [42,61].

Some studies have found no significant differences in nematode diversity following either organic or inorganic fertilisation [66,74,75,103]. Management strategies such as crop type, crop rotation, tillage, and soil characteristics like soil texture were crucial factors that influence nematode diversity. A higher diversity of nematodes was observed in sesame and soybean crops compared to rice fields of fluvisol soils fertilised with the same NPK fertilisers [73]. This was caused by crops altering the physical and chemical properties of the soil, favouring specific taxa. Natalio et al. [103] reported that soils with medium texture had higher nematode diversity than those with coarse soil texture supplied with the same fertilisers. Disturbance caused by tillage can also overshadow any diversity changes caused by fertilisation [66].

Fertilisation with RDFs also has varied impacts on nematode alpha diversity and varies between RDFs. Saju et al. [105] and Ryan et al. [5] reported that RDF fertilisation did not affect the nematode alpha diversity compared to synthetically and unfertilised soils. The lack of significance may be because RDFs contain similar mineral forms to inorganic fertilisers, promote microbial communities, and therefore have the same effect on nematode diversity. Another reason could be the harsh weather conditions experienced in the study by Saju et al. [105], caused by a lack of rain, which might have affected nematode community composition and structure, overshadowing the effects of fertilisation [105]. Karpinska et al. [104] documented varied impacts of RDFs on nematode alpha diversity depending on the source. They found that soils fertilised with RDF poultry litter ash recorded the highest alpha diversity, while RDF sewage sludge ash reduced the nematode alpha diversity compared to inorganically fertilised soils. The reduced diversity in soils fertilised with sewage sludge ash resulted from high soil pH and heavy metal contents caused by the fertilisers, which affected the sensitive nematodes of the order Dorylaimida.

Beta diversity in RDF fertilised soils consistently indicated differences in nematode community composition between fertiliser treatments [5,104,105]. For instance, based on weighted Unifrac beta diversity, all phosphorus-based RDFs had different nematode communities compared to fertilised soils, except those fertilised with municipal waste struvite [5]. However, municipal struvite did not alter the nematode community compared to potato waste struvite or inorganically fertilised soils. Sewage sludge ash had distinct nematode communities compared to other RDFs. This demonstrates that struvite has similar effects on the nematode community structure as inorganic fertilisers, while sewage sludge ash alters the community differently. All three nitrogen-based RDFs from ReNure (ammonium sulphate, pig urine, and ammonium nitrate) showed no significant differences in beta diversity based on weighted Unifrac compared to inorganically fertilised farms [105]. These various observations demonstrate that using RDF can alter nematode community structure, with the differences affected by the type of recycling-derived fertiliser employed.

8. Impacts of Fertilisation on Nematode Functional Indices

The MI reflects the proportion of nematodes at high trophic levels in the community. In a range from 1 to 5, it indicates the stability of the soil food web after a disturbance [112]. If the MI value is less than 2, this indicates a temporary increase in nutrient availability. However, if the value is close to 2, it indicates a low soil food web structure with a high level

of disturbance. Inorganic fertilisation has a negative impact on the maturity index, which continues to decline if more fertiliser is applied, leading to a dominance of opportunistic nematodes as a result of enrichment (Table 2) [23,40,54,74,85,86]. However, Wang et al. [68] observed an increase in MI at a high rate of inorganic N fertilisation application, following a decrease at low application rates. This recovery could have been caused by a high PPN abundance, which increases with high plant biomass, altering the balance of trophic groups within the nematode community and impacting the MI [14]. The application of P fertiliser alone was found to have no significant impact on MI, due to the overriding influence of nematode genera on other experimental factors, such as water conditions and plant type [84].

Several studies have also recorded a lower MI in organically fertilised soils; however, it varies based on the type of organic material [24,57,61,68,74]. In Croatian corn fields, soils fertilised with swine manure had a higher MI than those fertilised with beef manure (BM) [74]. In contrast, those fertilised with horse manure (HM) had the lowest, suggesting that the degrees of community succession differ between manures. Vieira Júnior et al. [57] observed a higher MI in unfertilised forest soils and those fertilised with natural plant material compared to those fertilised with cow manure and poultry litter. This means that unfertilised forests and naturally fertilised soils provide more stable environments for the nematode community than fertilised soils. This was supported by lower sigma maturity index (∑MI) values in organically fertilised soils, especially in those fertilised with poultry litter, indicating a more disturbed environment. However, it is worth considering that ∑MI is less sensitive to enrichment in agricultural soil [112]. Similar differential trends in MI have been observed in other studies based on the organic material (Table 1) [70].

Incorporating effective microorganisms into organic fertilisers such as compost had no significant effect on MI compared to unfertilised soils, suggesting a more stable soil ecosystem [62]. Similarly, neither the long-term application of organic fertilisers nor the incorporation of inorganic fertilisers affects MI [42,64]. Surprisingly, the rate of organic matter application does not appear to be a factor influencing succession, with variable observations recorded in MI between studies [52,68,69,85]. Other studies have also shown no differences in MI between soils managed organically and inorganically, or conventionally. The contradictory results could be caused by factors such as similar levels of disturbance between strategies [60,66], highly decomposed organic fertiliser or composts with a low biological maturity index [42,54], prevailing stressful soil conditions [69], or other experimental variables [85].

The enrichment index (EI) is a soil health indicator matrix with values ranging from 0 to 100, indicating equivalent levels of nutrient enrichment and food availability in a soil ecosystem, based on the presence of opportunistic nematodes [112]. Both organic and inorganic fertilisers have varying impacts on the EI [22,84]. Several studies show an increase in EI under inorganically fertilised soils [41,74,95]. For instance, Pan et al. [41] found that inorganic fertilisation increased EI in a wheat, corn, and soybean rotation system in Mollisols. This was linked to the increased dominance of bacterivorous nematodes, especially those in the C-P1 (Ba2) and C-P2 (Ba2) groups, indicating a nutrient-rich environment resulting from the use of inorganic fertilisers. Other studies have documented that inorganic fertilisation decreases the EI, influenced by several factors such as a decline in bacterivore abundance, interactions between fertilisation and other management factors [54,68,111]. For instance, Okada et al. [54] reported that the EI was low in untilled land compared to that of the tilled land supplied with the same inorganic fertiliser, which promoted the enrichment of opportunists. Some studies documented that inorganic fertilisation does not seem to impact the EI compared to unfertilised and organically fertilised soils [23,58,69,75,77,86,92]. Fertilisation with urea in *Sorghum bicolor* farms did not impact the EI compared to unfertilised

soils [58]. Neither the application of nitrogen fertilisers at varying levels nor phosphorus impacts on the EI [23,84].

On the other hand, the impact of organic fertilisation on the EI varies depending on different factors. For instance, increases in nematode EI in organically fertilised soils have been observed in several studies [52,60,64,76,94]. This increase is due to an increased abundance of opportunistic microbivores following a bacterial bloom after organic fertilisation, depending on fertiliser type and quality [24,56,57,59]. Fertilisation with either straw or manure incorporated with NPK resulted in a greater nematode enrichment footprint compared to inorganic fertilisation alone [59]. The high enrichment footprint is attributed to the better resource availability provided by organic fertilisers, which increases the metabolic activity of nematodes, also resulting in a high EI. The condition of organic matter can also cause an increase or decrease in EI. At an early stage of development, the EI in soils fertilised with straw combined with urea fertiliser was higher than in cow manure combined with urea. However, as the development stage continued, the EI decreased by the final stage [58]. This means that as decomposition and crop growth continued, soil enrichment decreased. However, the EI remains constant after long-term organic fertilisation [60]. Other studies that did not observe differences in EI between conventional and organic fertilisation were caused by experimental differences [111]. For instance, the lack of significant changes in EI between organically and inorganically fertilised soils of Argentina was attributed to soil type and a complex interplay of various management practices [92].

The Channel Index (CI), which evaluates the decomposition pathway after enrichment, declines after fertilisation. With values ranging from 0 to 100, values below 50 indicate increasing bacterial decomposition, while values above 50 indicate fungal decomposition, characterised by a slow breakdown of complex organic matter [112]. The CI in inorganically fertilised soils is unpredictable, with several studies documenting a lower value in inorganically fertilised soils than either organically fertilised or unfertilised soils [41,95]. Inorganic fertilisers have a low C:N ratio that does not support more fungivorous nematodes (Section 4 above). However, other studies have reported contradictory results where the CI increased or showed no impact compared to unfertilised and organic fertilisers [22,58,68,84]. For instance, fertilisation with inorganic ammonium nitrate under squash recorded an increase in CI compared to soils fertilised with organic *Clotalaria juncea* hay (Sunn hemp) [68]. In this case, hemp may have provided readily available organic carbon and nitrogen, which strongly stimulated the abundance of bacterivores, making the type of fertiliser a key factor at the study level. Organic fertilisers with materials of a high C:N ratio will have a high CI compared to those with low C:N [70]. Soils fertilised with swine manure and poultry manure had a high CI compared to those fertilised with beef manure and horse manure [74]. The varying CI levels among organic fertilisers suggest that different organic materials promote different microbial communities and decomposition channels. Other studies have found no differences in CI between organic and inorganically fertilised soils [69,75,77,102].

The use of organic fertiliser does not seem to have a significant impact on plant parasitic index (PPI) despite several studies reporting an increase in the abundance of PPNs after such fertilisation (Table 2) [40,52,54,60,64,73,74,92,103]. PPI is an indicator of the assemblage of plant parasitic nematodes, with low levels indicating a dominance of small and medium ectoparasites, while high levels indicate a dominance of medium and large endo- or ectoparasitic nematodes [112]. The PPI values were found to be similar across different soils, including those fertilised with cow manure and poultry litter and in unfertilised forested areas [57]. This lack of significance was attributed to the high C:N ratio found in agroecosystems, which causes plants to have a smaller root volume, thereby reducing the available food resources for PPNs. The dominance of some taxa of PPN across all fertilisation regimes can also contribute to the lack of significance observed in

these studies [69]. Neher et al. [66] found that the PPI was higher in organically fertilised soils than in inorganically fertilised soils. Li et al. [64] found that PPI was high in soils fertilised with straw chemical fertilisers and cow manure compared to those fertilised with poplar leaf. The increase in PPI could indicate conducive conditions for the PPN. Chen et al. [87] observed a higher PPI in organically fertilised soils, followed by that in inorganically fertilised soils, while unfertilised soils had the lowest PPI. However, statistically, no significant differences were found across the three. This confirms that PPI is not impacted by fertilisers themselves, and especially not by the type of fertiliser, but rather indirectly by other factors that control the plant-parasitic nematode population.

The Structural Index (SI) is an indicator of soil food web structure, complexity, and disturbance, with values that range from 0 to 100, with lower levels indicating a perturbed soil food web [112]. This indicator is influenced by omnivores and predators, which are sensitive to disturbance. In inorganically fertilised soils, the SI decreases and declines even further with increasing amounts of fertiliser compared to soils that are organically fertilised or unfertilised [22,23,41,52,76,92,95]. This indicates a perturbed soil food web structure due to reduced nematode diversity after fertilisation. However, other studies have observed an increase in SI following inorganic fertilisation. For example, Wang et al. [23] documented that long-term inorganic nitrogen fertilisation resulted in the recovery of SI with increasing amounts of fertilisation. Higher fertilisation leads to an increase in predator numbers, linked to a rise in herbivores and bacterivores, which serve as prey for the predators, resulting in a distinct nematode community structure and an increase in the SI. On the other hand, organically fertilised soils have been found to have more structured nematode communities than inorganically fertilised soils [52,58,59,61,64,69,76]. However, differences in the magnitude of this increase in SI between organic fertilisers of varied materials have also been documented (Table 2). For instance, in a continuous soybean monoculture, soils fertilised with straw combined with chemical fertiliser had the highest SI, followed by those fertilised with poplar leaf. In contrast, those fertilised with cow manure had the lowest SI, not differing from poultry manure fertilised soils (Table 1) [64]. The nematode community structure also improves with more amount of fertiliser applied [56]. Hu & Qi [61] found that soils receiving the highest amount of compost were the most structured and diverse in nematode communities, due to more organic matter provided. However, the incorporation of more microorganisms did not shift the nematode community. The lack of significance could be attributed to the experimental factors [61].

Vieira Júnior et al. [57] observed the highest SI in soils fertilised with plant residues, poultry litter, and unfertilised forested soils. Several other studies have observed a SI decrease in organically fertilised soils compared to the unfertilised [65,77]. This indicates that fertilisation, even with organic fertilisers, results in a less complex nematode community structure compared to natural soils. In soils fertilised with *Crotalaria juncea* hay (Sunn hemp), a higher SI was observed compared to those fertilised with inorganic ammonium nitrate, which later declined with continued use in a two-year squash farm [68]. The initial increase was attributed to residual effects of the previous oat cover crop, which increased the soil's carbon and masked the impact of fertilisation. The drop in SI with continued use of the Sunn hemp organic fertiliser suggests a simple food web promoted by this fertiliser. Other studies have shown that the use of both organic and inorganic fertilisers had no impact on the SI [58,60,77]. The lack of significance has been associated with the influence of tillage, with high values of SI recorded under no tillage systems [54].

Soils fertilised with RDF sewage sludge ash had the highest CI and the lowest EI compared to the other RDFs and unfertilised soils, reflecting a slow fungal decomposition pathway [104]. The CI increased with continued vinasse use but declined after 15 years, indicating a shift to bacterial decomposition [106]. The EI also increased after five years of

application, declined after 10 years, and increased again after 15 years of application. The fluctuations in the continued use of vinasse could indicate differences in environmental conditions. Despite fluctuations in CI and EI, the community remained more stable with ongoing vinasse application, as demonstrated by the SI remaining steady over the 15-year period [106].

9. Impacts of Fertilisation on Nematode-Mediated Nutrient Cycling

Nematode-mediated nutrient cycling has been studied under controlled conditions, and the effects of fertilisation on nematode communities have also been examined. However, these two areas have been investigated separately, and no research has connected them to examine how fertilisation-driven changes influence nematode-mediated nutrient cycling. Fertilisation can impact nematode-mediated nutrient cycling in two major ways. Directly, by affecting the relative abundances of microbivore nematode communities, and indirectly through their impact on microbial communities. Fertilisation, by modifying the community structure and stability in the soil ecosystem, influences nematode-mediated nutrient cycling. Organic fertilisers promote bacterivore and fungivore nematode abundance, increasing nematode-mediated nutrient cycling [52,59]. Microbivores (bacterivores and fungivores) and omnivorous nematodes directly influence nutrient cycling by grazing on bacteria and fungi, releasing excess nitrates and phosphates to the soil through excretion, increasing mineralisation and plant nutrient uptake [29]. Bacterial-feeding nematodes were found to mineralise nitrogen at rates ranging between 0.0012 and 0.0058 µg- N nematode^{-1} day^{-1} in the form of ammonium [25]. Bacterial feeding nematodes Rhabditidae and Cephalobidae increased the amount of water extractable P in sand samples containing bacteria and amended with tricalcium phosphate compared to those without nematodes (21 and 15.67 mg per 250 g of soil, respectively) [45]. These soils also recorded a high phosphatase activity compared to those without nematode inoculation. By increasing the abundance of bacterivores and fungivores, organic fertilisers and RDFs promote the amount of nutrients mineralised back into the soil [24,61]. RDF fertilisation promotes the abundance of bacterivorous nematodes, while their impact on fungivores is not well known; however, the CI was reduced under RDF fertilisation, suggesting reduced fungal decomposition activity by nematodes [5,105,106]. This implies that RDFs promote bacterivore-mediated mineralisation over fungivore. Inorganic fertilisers also promote bacterivore-mediated mineralisation over fungivore-mediated mineralisation. They could also limit nematode-mediated mineralisation by reducing the abundance of bacterivores and fungivores [83,97]. Changes in enrichment index caused by fertilisation can directly influence the nematode-mediated nutrient cycling process. An increase in enrichment index will increase the amount of nutrients mineralised in an ecosystem, while a decline will mean reduced nutrients available for plant uptake.

At higher trophic levels within the soil food web are the predatory and omnivorous nematodes. As they feed on herbivores, bacterivores, and fungivores, they release nutrients in excess, contributing to nutrient cycling [26,48]. The high sensitivity of omnivorous and predatory nematodes to fertilisation negatively impacts mineralisation by reducing their abundance [40,48,56,83,84]. In the absence of omnivorous and predatory nematodes, the populations of microbivorous nematodes will be high. The rise in abundance of microbivores will increase the amount of immobilised nutrients in microbivorous nematode body biomass, hence influencing plant nutrient availability and uptake [26,48]. The high amount of immobilised nutrients in microbivorous body biomass will reduce the amount of nutrients available for plants in the soil [38,40,83,84]. The ratio of fungivore: (bacterivore + fungivore) is usually low in fertilised soils and most especially in inorganically fertilised ones [23]. This implies a transition of the decomposition pathway from

fungal to bacterial [13]. This happens primarily because inorganic fertilisation leads to a decline in the C:N ratio of soils, favouring bacterial growth (Figure 1) [113]. It is expected that organic fertilisation brings a balance between the influence of bacteria and the influence of fungal nematodes by increasing the abundance of both fungal and bacterial communities. Yet, the bacterial decomposition pathway seems to be dominant in organic fertilised soils [41,59]. This probably happens because, unlike fungi, the opportunistic nature of bacteria allows them to consume resources faster, increasing competition for fungal communities [12]. This leads to an increase in both bacterivore and fungivore nematodes in these soils, but much more for the bacterial-feeding group, hence the bacterial decomposition pathway becomes the most dominant in organically fertilised soils [24]. While this might seem favourable for increasing plant nutrient availability from increased mineralisation in the soil, it also implies that the increased amount of available plant nutrients could be lost through other pathways, such as leaching and surface runoff, causing environmental degradation [114]. In this case, the slow fungal decomposition pathway could be efficient in slowly releasing nutrients to the plants.

Acidification due to fertilisation has been proposed as a crucial factor that negatively affects nematode abundance [115]. Omnivorous and predatory nematodes are known to modulate the lower trophic populations, increasing the amount of nutrients released to the soil for plant uptake (Figure 1) [26,48]. Some studies have also shown that N enrichment promotes bacterial biomass and diversity [116,117]. Changes in soil pH after N fertilisation reduce the omnivorous and predatory nematodes, which will otherwise increase the amount of nutrients immobilised by microbes and microbivorous nematodes as discussed in Section 2 above [115]. This will result in increased competition for nutrients between plants and microbes, reducing plant nutrient uptake. Fertilisation by organic, inorganic, and RDFs promotes the abundance of plant-parasitic nematodes [23,61,106]. Some studies have shown that plant-parasitic nematodes contribute to nutrient cycling through interaction with their plant host, adding organic matter to the soil (Figure 1) [26,51]. While this might be the case, these positive effects may only be acceptable to a certain extent, as excessive invasion of PPN on plants can lead to significant economic losses rather than benefits [118].

A shift in the nematode community composition caused by fertilisation can negatively impact the nematode-mediated nutrient cycling. For instance, a shift towards the plant-parasitic nematodes over the free-living nematodes will reduce the relative efficiency of nutrient mineralisation. In bare soil microcosms, the presence of the entire nematode community increased the total mineral nitrogen by 32% compared to soils without nematodes [29]. This was linked to an increased number of bacterial feeders that persisted throughout the experiment. In contrast, soils that were planted with *Lolium perenne*, the nematode community shifted in favour of PPNs by 70% [29]. In these soils, there was no significant increase in total nitrogen mineralised compared to those without nematodes. This demonstrates that shifts in the community towards plant feeders in fertilised soils may reduce the efficiency of nematode-mediated nutrient cycling. Given that fertilisation alters the nematode community structure, any fertiliser-induced shifts are likely to influence their ecosystem functions, such as nutrient cycling. While this review explores the potential links between fertiliser impacts on nematode communities and nematode-mediated nutrient cycling, a clear gap remains in knowledge of how much nematodes mineralise plant nutrients under different fertilisation regimes.

10. Perspectives, Challenges, and Opportunities

All fertilising products are designed to maximise yields by increasing available nutrients in the soil. Understanding the impacts of fertilisation on soil nematodes and how these

impacts influence nematode-mediated nutrient cycling is important for sustainable crop production and food security. Unfortunately, the mechanisms through which soil fauna contribute to nutrient cycling have been underexplored, especially in real field conditions. The main hurdle in understanding the role of nematodes in nutrient cycling has always been the oversimplification of experiments, which do not reflect realistic and complex interactions in soil ecosystems. Most experiments quantifying the role of nematodes in nutrient cycling involve a limited number of nematode species and their interactions with their specific prey [33,34,44–46]. While these experiments have improved our understanding of the mechanisms through which nematodes participate in nutrient mineralisation and plant uptake, they do not account for the entire nematode community and, therefore, are far from emulating reality. This oversimplification occurs because nematodes participate in nutrient cycling through indirect interactions with soil microbes, such as modulating microbial populations. This requires designing and conducting mesocosm experiments that involve eliminating nematodes and other fauna from soil and reintroducing them without altering microbial communities.

Constructing complex mesocosms can be challenging because methods used for soil defaunation either kill or reduce the abundance of microorganisms. Kane et al. [44] reported that defaunation decreased microbial biomass by 28% compared to fresh soil. Another method of eliminating nematodes from the soil is through autoclaving at high temperatures, which kills all soil organisms [31]. Additionally, plant inclusion in the experiments makes the experiments more complex. Therefore, researchers prefer simplified experiments with specialised nematodes and their prey. However, these simplifications hinder the exploration of real-world situations. Defaunation using gamma irradiation at low radiation doses has been explored to effectively kill soil fauna while preserving soil microbes, allowing the entire role of nematodes in nutrient cycling to be quantified [26,29]. However, these experiments require specialised equipment, which is expensive and hard to maintain. In addition, most studies conducted on the role of nematodes in nutrient cycling have been ecologically localised, showing a geographical bias towards temperate regions. More studies in different areas with different soils and climates are needed to better understand the contribution of nematodes to nutrient cycling in different ecological contexts. Factors such as nematode body size and feeding behaviour can vary based on their habitat, influencing their effects on microbial communities in other environments [119]. While mesocosm experiments represent real situations, they are still controlled experiments and vary from complex and real situations.

All experiments examining the role of nematodes in nutrient cycling have been conducted on a short-term basis. Long-term field trials on the effects of nematodes on microbial communities and nutrient cycling will give more insights into how nematodes consistently influence this process over time, capturing seasonal and cumulative effects not addressed in short-term experiments [32]. Utilising DNA metabarcoding in multitrophic mesocosms for quick and precise identification of nematodes will allow complex food web interactions involving nematodes to be easily quantified and monitored over time. Jiang et al. [33] reported that there is variability in how different nematode species enhance nutrient availability and plant performance. From this review, we have established that fertilisation modifies nematode communities, influencing mineralisation and nutrient cycling. It will be beneficial to understand how different nematode species interact with bacteria and plants to contribute to the nutrient-cycling process. While several studies have explored these through simplified experiments, there remain many more nematode species and bacteria to be studied, especially under P-limited conditions [33,49]. Moreover, fertilisation through variation in the C:N ratio and carbon sources influences nematode community structure and complexity, and consequently, the nutrient cycling process. Until now, the

research quantifying the involvement of nematodes in nutrient cycling has focused on model substrates such as tricalcium phosphate and soil amendments, such as plant residues, manure [26,27]. There is a need to explore different types of amendments to better understand how the source and type of fertiliser influence the role of nematodes in nutrient cycling. Experiments quantifying the contribution of nematodes to nutrient cycling under different fertilisation regimes will fill this gap.

Globally, many farmers rely on synthetic fertilisers for maximum crop production. These fertilisers are produced either through the physical mining of mineral rocks or chemical industrial processes. For instance, P fertilisers are sourced through the mining of the phosphate rock [120], and nitrate fertilisers through the Haber–Bosch process from atmospheric nitrogen and hydrogen [121]. These processes are expensive, and their mining, production, transportation, and use result in serious environmental challenges such as loss of biodiversity, soil acidification, eutrophication, and increased greenhouse gas emissions. Organic fertilisers have been encouraged as the most sustainable option because they enhance soil health and crop productivity. However, factors such as varied nutrient levels and slow nutrient release from organic fertilisers limit their effectiveness for quick, short-term crop production [122]. Recycling-derived fertilisers recovered through nutrient recovery technologies from surplus nutrient sources, such as organic waste streams from industries, municipalities, and agriculture, can also serve as sustainable options. However, a key limitation is that RDFs are highly variable in composition; even an RDF from the same category might differ in composition based on its source material or treatment process. For instance, the concentrations of heavy metals can vary significantly based on the origin of the waste [8,9]. As such, the effects observed on nematode communities in one case may not be similar to those in another. The few studies we reviewed here clearly show that RDFs from various sources have different nutrient composition based on their sources, hence differences in their impacts on nematodes [5,104,105].

Legislative limitations also impede the adoption of RDFs by farmers, as they are not considered at the same standard as synthetic fertilisers, despite the further processing involved in their production [9]. Yet these fertilisers do not meet the total carbon requirement to be considered organic fertilisers [8]. For example, according to the Nitrate Directive 91/676/EEC, RDF derived from further processing of animal manure to produce nitrate-rich fertilisers still retains the status of 'manure', hindering the possibility of these nutrients being optimised to the same status as synthetic fertilisers [105]. Nevertheless, there are anticipated revisions of such regulations to facilitate and encourage farmers to use RDF, such as the nitrogen fertilisers derived from manure, as options to synthetic fertilisers in Nitrate Vulnerable Zones (NVZs) [123]. To address these challenges, future research that provides ecological data on how RDFs from various sources impact soil ecosystems using sensitive bioindicators such as nematodes can inform the development of standardised RDF safety production protocols. Standardisation of protocols by setting limits will reduce variability in the composition of RDFs and establish standard application rates that will not cause ecological harm, enabling legislative bodies to consider recognising these fertilisers on the same legal status as inorganic fertilisers [8].

11. Conclusions

All fertilisers disrupt the soil nematode community composition. Bacterial-feeding nematodes are the most tolerant to disturbance and seem to thrive by dominating all fertilisation regimes, even at a high fertilisation rate. Inorganic fertilisers seem to have the most severe impact on soil nematode abundance, diversity, community composition, and consequent nutrient cycling. Inorganic fertilisers are the most used due to their immediate and precise nutrient release for maximum crop production. However, their production,

transportation, and use cause adverse effects on the environment. Organic fertilisers, on the other hand, are the safest and most environmentally friendly by enhancing microbial activity, nematode abundance, diversity, and community composition, and consequently improving nematode-mediated nutrient cycling. However, in production systems where immediate nutrient availability is required to support short-term crop yields, organic fertilisers may not supply nutrients quickly; therefore, they may not be the ideal fertiliser in these contexts. Recycling-derived fertilisers may offer a sustainable option to synthetic mineral fertilisers for providing essential minerals for plant growth. They also contribute to closing the nutrient loop in agriculture by promoting a circular economy and reducing waste. There is a need to provide more data through research on the impacts of RDF on soil nematode communities and how they influence nematode-mediated nutrient cycling to guide farmers and policymakers towards making informed decisions regarding fertiliser use and soil management practices.

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Abbreviations

The following abbreviations are used in this manuscript:

RDF	Recycled-derived fertiliser
PPN	Plant parasitic nematodes
C-P	Coloniser-Persister
MI	Maturity index
CI	Channel index
SI	Structural index
EI	Enrichment index
C	Carbon
N	Nitrogen
P	Phosphorus
K	Potassium
NPK	Nitrogen, Phosphorus, and Potassium

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