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Review

Nematodes in Agroecosystems: A Review of Their Role and Influence of Farm Management Practices on the Community Structure

Musongora Kambale Muyisa[1,2]*, Keziah Magiroi[3], Njiranjira Pili[4], Abigael Otinga Nakesa[1] and Ruth Njoroge[1]

[1]Department of Soil Science, University of Eldoret, P.O. Box 1125-30100, Eldoret, Kenya; [2]Faculty of Agriculture, Université Catholique du Graben, P.O. Box 29-Butembo, Butembo, Democratic Republic of the Congo; [3]Kenya Agricultural and Livestock Research Organization (KALRO), P.O. Box 450-30200, Kitale, Kenya; [4]Department of Biological Sciences, Moi University, P.O. Box 3900-30100, Eldoret, Kenya.

Abstract | The dynamics of nematode community structure in response to farmland management practices are seldom consistent. In agroecosystems, the economic importance of plant feeding nematodes originates from their direct effect on crop development and yield, reducing produce quality as well as their nutritional value. Moreover, nematode attack can serve as entry points for other soil-borne pathogenic pests and diseases like bacteria, fungi and virus. The destructive potential of plant parasitic nematode results from their feeding habit, preferentially colonizing the meristematic tips of plant feeder roots, underground storage roots and stems of susceptible plants, causing severe anatomical and physiological damage to such crop tissues. Apart from the pathogenic plant feeding nematodes, the soil harbours free-living nematodes that contribute to key ecosystems functions such as nutrient cycling and mineralisation through the control of the decomposing populations of bacteria and fungi. Moreover, free-living nematodes contribute to the regulation of the soil microbial populations through the top-down predation of insects, fungivore and bacterivore nematodes by predator and omnivore nematodes. Farm management practices like cover crop, improved fallow, organic amendments, mulching, crop rotation and agroforestry are associated with increasing nematode abundance and diversity whereas soil tillage and inorganic fertilization have a depressive effect on both abundance and diversity of soil nematodes. How these practices affect plant parasitic nematode populations depends on the diversity and quality of the above ground crop (cover crop, improved fallow, crop rotation and agroforestry) or the quality and amount of the organic amendment. Controversial conclusions have been reported on the effect of inorganic fertilizer on the population of plant feeding nematodes. So far, only scarce information exists on plant parasitic nematodes in agroforestry systems with inconsistent results due to diversity of agroforestry systems and spatio-temporal dynamics of their woody component distribution.

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***Correspondence** | Musongora Kambale Muyisa, Department of Soil Science, University of Eldoret, P.O. Box 1125-30100, Eldoret, Kenya; **Email:** kambalemuyisam@gmail.com, muyisa94@gmail.com
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Links Researchers

Introduction

Currently, more than 25,000 species of nematodes have been identified in terrestrial ecosystems. Soil nematodes represent 35% of the total nematode population and approximately 10% of them are plant-parasitic (Moura and Franzener, 2017). Nematodes are the most abundant metazoans on earth and can be found in all trophic levels of the soil food web. Since they are small in size, nematodes represent only a small portion of the total soil animal biomass accounting for approximately 0.3 gigatonnes (van den Hoogen *et al*., 2019). Factors affecting their abundance, distribution and diversity patterns among biomes and land use are poorly understood (Porazinska *et al*., 2012). Significant influence of latitudinal distribution of nematode community in agroecosystems was reported, with medium-higher latitudes between 30 and 55° recording a higher soil nematode abundance and diversity compared to latitudes between 0- 20° and 70–90° (Song *et al*., 2017). Moreover, a global scale nematode survey reported higher nematode abundances in sub-Arctic regions (38% of total) compared to temperate (24%) and tropical (21%) regions (van den Hoogen *et al*., 2019).

Similarly, land use and land cover change as well as change in the prevailing farming practices can substantially affect the population of soil nematodes (Dong *et al*., 2008; Zhao and Neher, 2013). Generally, a progressive vegetation succession results in an increasing nematode community complexity, abundance and diversity. However, the accumulation of the recalcitrant carbon and soil acidification in the late stage of vegetation succession can negatively affect these characteristics of soil nematode community during this stage (Gao *et al*., 2019). Moreover, ecological conditions like elevation and climate are key in structuring the soil nematode community. In their study, Ding *et al*. (2024), Kouser *et al*. (2021) and Kergunteuil *et al*. (2016) found that the abundance and diversity of the total nematodes and each trophic group of nematodes was significantly higher at high elevations (between 700 and 1500 masl). Increased soil moisture and accumulation of organic matter in the superficial soil horizons at higher elevation offer favourable conditions for nematode abundance and diversity growth at these altitudes (Kergunteuil *et al*., 2016; Kouser *et al*., 2021; Levi *et al*., 2012). However, Afzal *et al*. (2021) found that above 1200 masl, total nematode abundance as well as the nematode abundance in the respective trophic groups (fungivores, herbivores and omnivores) decreased with the increasing elevation in response to cold dry conditions occurring beyond 2500 masl.

Based on their feeding habit, soil nematode communities are classified into five trophic groups namely plant-feeding nematodes (root-feeding nematodes; phytophagous; plant parasites), fungal-feeding nematodes (fungivorous; mycophages), bacterial-feeding nematodes (microbivorous; bacterivorous), predatory nematodes and omnivorous nematodes (Bongers and Bongers, 1998; Steel and Ferris, 2016; Yeates and Bongers, 1999). The pathogenic plant parasitic nematodes are involved in crop disease complexes whereas free-living nematodes contribute to key ecosystems services like nutrient cycling, mineralisation and regulation of soil microbial populations. The magnitude of these functions and their relative importance can be influenced by the above-ground biomass, the prevailing climatic conditions particularly precipitation and temperature (Nisa *et al*., 2021) as well as the soil physico-chemical properties among others soil bulk density, soil moisture content, inorganic nitrogen, soil organic carbon and cation exchange capacity (Nielsen *et al*., 2014; Song *et al*., 2017; van den Hoogen *et al*., 2019). The aim of the present review is to highlight the role of soil nematodes in agroecosystems and the response of their community structure to the most common agricultural practices like the cover crop, mulches, soil amendment, tillage practices, fallowing, crop rotation and agroforestry.

Economic significance of plant parasitic nematodes in crop production

Plant parasitic nematodes are of significant concern in crop production since they not only affect plant growth and crop yield but also reduce produce quality as well as their nutritional value (Kumar *et al*., 2020). However, the accurate estimation of relative importance or pathogenicity of individual species is challenging due to the co-occurrence of several nematode species as well as concurrent attack by other soil-borne pathogens (Coyne *et al*., 2018; Keçici *et al*., 2022; McDonald *et al*., 2017; Ngobeni *et al*., 2011; Talwana *et al*., 2016). Crop growth and productivity reduction as a consequence of nematode attack results from their feeding habit preferentially colonizing the meristematic tips of plant feeder roots, underground storage roots and stems of susceptible plants, causing severe anatomical and physiological damage to such crop tissues (Enyiukwu *et al*., 2021). Severe nematode infestation results in weakened plant anchorage, decreased produce vitality, quality, yield, and marketable value; making them important contributors to both visible and hidden hunger (Coyne *et al*., 2018; Enyiukwu *et al*., 2021). Apart from the induced direct crop yield losses, plant-parasitic nematodes can exacerbate the disease complexity when other pathogens are involved (Kumar *et al*., 2020). Nematode attack can serve as entry points for other pathogenic diseases and predispose crops to cold and frost injury as well as the spread of other pathogens like virus, bacteria and fungi (Coyne *et al*., 2018; Enyiukwu *et al*., 2021; Kumar *et al*., 2020). For instance, the root lesion nematode *Pratylenchus* spp. has been found to be the most damaging to maize causing severe yield loss, particularly when occurring simultaneously with other maize soil-borne pathogens like *Fusarium* and *Rhizoctonia* species (Benjamin *et al*., 2024). The feeding habit of *Pratylenchus* spp facilitates the invasion of opportunistic soil fungi or bacteria exacerbating the root rotting and hence affects maze growth and causes significant yield losses (Da Silva *et al*., 2017).

Plant parasitic nematodes represent a permanent concern in agroecosystems due to their short life cycle and the long-term persistence of eggs. For instance, the golden nematodes *Globodera* spp. can remain viable for up to 30 years (Enyiukwu *et al*., 2021). In most crop production systems, *Meloidogyne spp., Heterodera* spp. and *Pratylenchus* spp. are the most devastating plant parasitic nematodes due to their large host spectrum as well their adaptation to diverse agroclimatic conditions (Coyne *et al*., 2018; Enyiukwu *et al*., 2021; Maina *et al*., 2020). Approximately 13% of total losses in agricultural systems across the world have been attributed to the plant-parasitic nematodes (Moura and Franzener, 2017). In India, a 21.3% annual crop yield loss to nematodes, equivalent to 1.58 billion USD, has been reported with *Meloidogyne graminicola* being the most economically important species causing yield loss in rice, citrus, banana, tomato, brinjal and okra (Kumar *et al*., 2020). In Tunisia, plant parasitic nematodes constitute a severe threat to cereal production, inducing grain yield declines of 19 to 86% in barley and 26 to 96% in wheat (Kachouri *et al*., 2009). Root-knot together with root-lesion nematodes infestation on maize (*Zea mays*), rice (*Oryza sativa*), and sorghum (*Sorghum bicolor*) have shown an 18%–67% reduction in yield (Abdulsalam *et al*., 2021; Benjamin *et al*., 2024); whereas up to 60% yield reduction has been reported in banana in Uganda (Oka, 2010; Speijer and Kajumba, 2000). Significant maize growth reduction has been reported in Central Kenya following an increasing spiral nematode *Scutellonema* spp. infestation (Maina and Ng'endo, 2020). Maize yield loss of up to 27% has been reported in Nigeria due to *Pratylenchus* spp infestation (Abdulsalam *et al*., 2021); up to 50% in Kenya (Desaeger and Rao, 2000, 2003) and 60% in South Africa as a cumulative effect of either single or mixed populations of *Meloidogyne incognita* and *Meloidogyne javanica* (McDonald *et al*., 2017).

Characterization of soil health in agroecosystems: Using nematode community structure as an indicator

Currently, it is believed that a healthy soil is one of the most critical resources for sustainable food production systems as well as the permanent provision of both goods and ecosystem services (Dollinger and Jose, 2018). In the context of the present review, soil health can be considered as its ability to support adequate production of biomass and simultaneously maintain other ecosystem services, such as climate regulation or biodiversity conservation (Kibblewhite *et al*., 2007). Hence, soil health is an integrative soil property that reflects its responsiveness to cropland management by fostering both the agricultural production and the provision of other ecosystem services (Barrios *et al*., 2015). Due to spatial and temporal soil variabilities across the globe, the concept of soil heath has not produced valuable contribution to agroecosystem management practices. Indicators of a healthy soil as well as their threshold levels need to be objectively defined, taking into account their variation with management practices (Cardoso *et al*., 2013). This must take into consideration the different soil characteristics and standards as well as a database of parameters that qualify a good soil health status should be established.

Considering its definition, soil health can be assessed using soil physical, chemical and biological properties (Lu *et al*., 2020). Soil micro-organisms are sensitive to fluctuations in soil management practices; they are specifically involved in valuable soil functions and interconnected with soil physico-chemical properties and can elucidate ecosystem processes (Neher, 2001; Lu *et al*., 2020). Since soil nematodes are ubiquitous, their community structure responsive to soil physico-chemical change as well as farm management practices, their population dynamics can successfully inform about soil health conditions. In fact, nematodes can easily be extracted from soils and identified to significant taxa or functional groups, making them suitable indicators of biodiversity and for assessing the responsiveness of soil conditions to shifting land use (Yeates and Bongers, 1999).

In natural ecosystems as well as agroecosystems, a diverse above-ground vegetation community implies, at some extent, an abundant and highly diverse soil nematode community and can be affected by the management practices (Kimenju *et al*., 2009; Djigal *et al*., 2012; Diakhaté *et al*., 2013; Moura and Franzener, 2017; Yeates and Bongers, 1999). Thus, changes in the aboveground vegetation composition is likely to result in a different soil nematode community structure (Matlack, 2001). The banana growing regions of the Northern Queensland constitute a good illustrative case of the nematode selectivity under different levels of perturbation (Pattison *et al*., 2004). In these regions, higher counts of plant-feeding nematodes but with a declining diversity were recorded in banana pure stand farming systems compared to those less intensively managed such as pastures and forest (Pattison *et al*., 2004). Besides, the incorporation of a cover crop in these banana plantations resulted in increasing nematode counts in all the trophic groups excluding plant-parasitic nematodes, suggesting a likely top-down control of plant-feeding nematodes through the promotion of higher trophic groups (Djigal *et al*., 2012).

Soil biological processes can be understood through the study of the nematode population structure in these soil ecosystems (Neher, 2010). Soil nematode community structure, including free-living as well as plant-feeding nematodes, is indicative of a reaction of biological processes as influenced by ecosystem management (Falkowski *et al*., 2019; Ferris *et al*., 2001; Neher, 2010). Particularly, plant parasitic nematodes (PPNs) are a good indicator of soil health in agroecosystems where they can significantly negatively affect biomass production (Falkowski *et al*., 2019).

Nematode's role in soil-based ecosystem functions

The soil microbial populations are interconnected and the interaction between the diverse soil microorganisms constitutes a soil food web which is indicative of the condition, function and health of the soil (Pinto *et al*., 2024). Ecosystem functions involving soil nematodes include organic matter decomposition and biogeochemical cycles, predation and pest control whose mechanisms can directly or indirectly be affected by either abiotic or biotic factors (Neher, 2010; Pinto *et al*., 2024; Yadav *et al*., 2018).

Role of nematodes in organic matter decomposition and nutrient cycling

In soil food web, bacteria and fungi play a key role in organic matter decomposition with a possibility of nutrient immobilization, making nutrients unavailable for plants uptake (Yadav *et al*., 2018). Though nematodes do not directly decompose the organic matter, their effect results from the alteration of the microbial population, their short lifespan and their contribution to the spread of the inoculum to new substrates (Irshad *et al*., 2011; Yadav *et al*., 2018). The rate of decomposition of the organic matter depends on the diversity of functional groups reflected in the number of trophic levels as well as the interactions among them (Neher, 2010). Apart from the diversity of the decomposing organisms, the organic matter decomposition rate depends also on the quality of the organic residue (C:N ratio) (Ingham *et al*., 1985; De Mesel *et al*., 2006).

Higher populations of bacterivorous and fungivorous nematodes can result in a decreasing decomposition rate due to a compromised overall activity of bacterial or fungal populations when they are excessively fed on by nematodes (Irshad *et al*., 2011; Yadav *et al*., 2018). Under these circumstances, the balanced composition of the soil microbial community improves the organic matter decomposition and nutrient release through the hierarchical structure of the soil food web where generalist predators feed on the bacterivorous and fungivorous nematodes and hence keep their population under control (De Mesel *et al*., 2006; Yadav *et al*., 2018). On the other hand, increasing bacterivorous nematodes can trigger the bacterial population growth and hence accruing their abundance (Jiang *et al*., 2017). The mechanism involved in bacterial population increase or decrease in the presence of bacterial-feeding nematodes is intriguing and may be nematode species-specific (Ingham *et al*., 1985).

Nematodes contribute to nutrient mineralization through processes succeeding predation of bacteria, fungi, nematodes or other microorganisms (Mekonen *et al*., 2017). The absorbed carbon (C) is used for both respiration and assimilation whereas other nutrients (basically nitrogen-N, phosphorus-P and sulphur-S) are merely utilized for assimilation. In general, the C: nutrient (NPS) ratio of the microbial prey (bacterial and fungal) is smaller compared to that of nematodes (Yadav *et al*., 2018). Consequently, the ingested nutrients exceed the nematode requirements. The excesses are excreted in a mineral or readily mineralizable form such as amino acids, NH_4^+ and PO_4^{-3} (Ferris *et al*., 2012). The nutrient mineralization efficiency is nematode trophic group dependent. For instance, N release via predation is due to the fact that bacteria have a lower C:N ratio (approximately 5:1) than bacterivorous nematodes (with approximately 10:1) whereas fungi feeding nematodes tend to immobilize the N as most fungi species present a relatively high C:N ratio (approximately 11:1) (Ingham *et al*., 1985; Yadav *et al*., 2018). Under this hypothesis, nematodes have a relatively higher contribution to N mineralization, making it directly available to plant, compared to bacteria in soil ecosystems (Yadav *et al*., 2018).

The dominant nematode trophic group influences the mineralization rate as well as the availability of the key nutrients. In fact, N mineralization is accelerated in the presence of bacterivorous nematodes whereas P mineralization process is specifically facilitated by fungivorous nematodes (Ferris *et al*., 2012). In conventional and integrated farming systems, bacterivorous and predatory nematodes participate (directly and indirectly) for 8% to 19% to N mineralization, respectively. However, the immobilization by fungi in forest soils and by bacterivorous nematodes in low fertility deserts soils can result in a moderate net N mineralization (Neher, 2010).

Nematodes in the biological control of pests and diseases

Apart from plant parasitic nematodes, soil ecosystems harbour free-living nematodes among which some operate as predators and reduce the population of pathogenic bacteria, fungi or other nematodes (Neher, 2010). For instance, a greenhouse experiment revealed that *Aphelenchus avenae* can significantly reduce *Ralsotnia solani*-induced damping-off of cucumber (Ishibashi, 1991, 2005). Similarly, both *Aphelenchus avenae* and *Steinernema carpocapsae* suppressed gall number (caused by the root-knot *Meloidegyne incognita*) on tomato roots (Ishibashi, 1991).

Apart from their effect on pathogenic bacteria and fungi, an effective control of the population of some soil-born turf insects and several other insects that live in the soil at one of their life cycle stage such as larva, pupa or adult can be achieved using nematodes (Sarwar and Mukhtar, 2021). Two major nematode families have been reported with the entomopathogenic nematodes species: *Steinernematidae* and *Heterorhabditidae* families (Askary, 2010; Gozel and Gozel, 2016; Mahmoud, 2016; Sarwar and Mukhtar, 2021). Due to their large host spectrum, high biocontrol potential, reduced risks to humans as well as other non-target organisms and virtually environment friendly; these nematode families have been extensively studied and used for insect control (Askary, 2010). The death of the insect occurs when the entomopathogenic nematode releases its mutually associated bacteria of the family *Enterobacteriaceae* into the host insect, causing septicaemia (Gozel and Gozel, 2016). Entomopathogenic nematodes of *Steinernema* species have been found effective against more than 250 species of insects from over 75 families and 11 orders among others caterpillar larvae, sod webworms, cutworms, certain borers, and billbug larvae (Askary, 2010; Sarwar and Mukhtar, 2021). On the other hand, *Heterorhabditis* species have been reported effective against more than 200 insect species (Askary, 2010) among others black vine weevil, citrus-infesting root weevils and white grubs (Mahmoud, 2016; Sarwar and Mukhtar, 2021).

Soil nematode community structure in response to some agricultural management practices

Soil nematode community is susceptible to changes in soil physico-chemical properties resulting from farm management practices. The magnitude of change in the soil nematode community depends on the intensity and frequency of disturbances induced by farming practices (Kimenju *et al*., 2009; Puissant *et al*., 2021).

Influence of cover crops and improved fallow on soil nematode community

Cover crop can contribute to the maintenance of a diverse soil nematode community since it promotes a high microbial activity and free-living nematodes feed on these microbes, leading to an increase in nematode population (Akanwari *et al*., 2024). In these conditions, soil nematode community change depends on the above ground diversity of crop used as well as the quality of the resulting litter (Wang *et al*., 2022); with cover crop mixtures hosting a diverse and complex community of free-living nematodes (Garba *et al*., 2024). The increasing population of these free-living nematodes followed by a suppression of plant parasitic nematodes in a mixed cover crop and improved fallow is likely due to the release of biofumigants with nematocidal properties (Akanwari *et al*., 2024; Wang *et al*., 2022).

Under field conditions, Wang *et al*. (2006) reported a depressive effect of methyl bromide, solarisation, and the combination of solarisation and cover crop (*Vigna onguiculata*) treatments on the bacterivore and fungivore nematodes compared to a natural fallow or cover crop (cowpea, *V. onguiculata*) treatments. In this experiment, the effect of this perturbation disappeared before the end of the subsequent intensive cropping season in the plots previously subjected to these treatments (Wang *et al*., 2006). Similarly, DuPont *et al*. (2009) found a total nematode abundance 72% greater in legumes cover crops compared to bare fallow, as a result of resource availability under cover crop treatments. The soil nematode abundance and diversity under cover crop is trophic group dependent (Odeyemi *et al*., 2013). In field conditions, Sánchez-Moreno *et al*. (2006) found that continuous cultivation of cereals suppressed the population of bacterivore and fungivore nematodes while favouring omnivore and predator nematodes. Moreover, the host status of the cover crop, the cultivation season as well as the duration of the improved fallow are the key determining factors of the effectiveness of the cover crop in controlling plant-parasitic nematodes (Cadet and Floret, 1995). Apart from the host status of the cover crop, their effect on other soil physico-chemical properties plays a significant role in the distribution of nematode community and their structure (Kandji *et al*., 2001). Desaeger and Rao (2000) reported an significantly increasing count of root-lesion nematodes (*Pratylenchus* spp.) in the soil after a 12-month *Crotalaria* spp. improved fallow; which resulted in a significant decrease in maize yield in the following cropping season (Desaeger and Rao, 2000). Similarly, a significantly poor growth of beans was reported in the first cropping cycle due to the build-up of root-knot nematodes, *Meloidogyne* spp, following a *Tephrosia* and *Crotalaria* – *Tephrosia* improved fallow (Kandji *et al*., 2003).

Soil nematode community in response to organic amendments, mulching and crop rotation

The use of organic amendments like compost, green manure and animal manure in agroecosystems can stimulate the rapid growth of antagonistic soil organisms, the competitive status of the non-pathogenic organisms and can have toxic effects during the decomposition process and hence negatively affect the population of soil-borne pathogens, including plant-parasitic nematodes (Thoden *et al*., 2011). Controversial results have been reported concerning the effect of organic amendments on the dynamics of plant-parasitic nematodes. However, organic amendments have been consistently associated with the stimulation of soil free-living nematodes whose overall population structure depends on both quality and quantity of organic inputs (Yeates and Bongers, 1999; Puissant *et al*., 2021; Maina *et al*., 2020).

Organic mulches have been reported to have a long-term effect on the structure of the soil nematode population due to their low decomposition rate (Wang *et al*., 2008). In their raspberry orchard experiment, Forge and Kempler (2009) found that the population density of *Pratylenchus penetrans*, a plant-parasitic nematode, can be reduced by 20 % and 34 % by applying broiler dung with overlying mulch of shredded paper and layer dung + yard compost, respectively.

Suppression of plant parasitic nematodes through crop rotation proceeds through either active or passive mechanisms (Enyiukwu *et al*., 2021; Puissant *et al*., 2021). The active effect results from the incorporation, in the rotation cycle, of plant species that produce allelochemicals that interfere with nematodes reproduction or reduce their physiological activities. Passively, crop rotation involving the alternative cultivation of host and non-host plant species interrupts the reproduction cycles of the nematodes (Halbrendt, 1996). When crop rotation is implemented as a management strategy of plant-parasitic nematodes, particular attention should be paid on the host status of plant species in the sequence (Kratochvil *et al*., 2004; Matute and Anders, 2012). In this context, the most recommended crop rotation sequences should prevent the build-up of populations of plant parasitic-nematodes while increasing that of free-living nematode guilds (Matute and Anders, 2012).

Links Researchers

Soil nematode community in response to tillage and inorganic fertilization

Soil physico-chemical and biological properties can differently be influenced by conventional or conservation tillage (Zhang *et al*., 2019). In response to tillage disturbance, soil micro-organisms are highly tolerant compared to macro-organisms or those belonging to high levels of the soil food web (Zhang *et al*., 2019). The soil nematode community structure is highly sensitive to tillage induced disturbances and can be used to assess the stability of the soil ecosystem (Yeates and Bongers, 1999). Experimentally, Okada and Hadara (2007) as well as Wang *et al.* (2022) did not find a significant effect of tillage regime (conservation and conventional) on nematode population density. However, these tillage regimes resulted in highly diverse nematode communities and community indices. The opportunistic bacterivore nematodes are likely to thrive better under conventional tillage regimes. Due to their high sensitivity to physical as well as chemical disturbances, omnivores and predators population do not resist conventional tillage induced disturbances (Sánchez-Moreno *et al*., 2006; Neher, 2010). The accumulation of substantial organic matter in soil under no-tillage regime provides suitable microhabitats with enough moisture and food (microbes and protozoa) for a highly diverse nematode community (Okada and Harada, 2007; Puissant *et al*., 2021).

Studies on the effect of mineral fertilizers on the dynamics of plant parasitic nematodes have reported inconsistent results. Most of the time, mineral fertilizer treatments result in an increase in the root biomass that provide more feeding sites to the herbivorous nematodes (Benkovic-Lacic *et al*., 2013; Okae-Anti *et al*., 2013). However, changes in soil agrochemical properties (soil pH and cation exchange capacity-CEC) subsequent to mineral fertilization can negatively affect the structure of free-living nematode population, particularly those from the high trophic groups (omnivores and predators) (Gruzdeva *et al*., 2007; Benkovic-Lacic *et al*., 2013). In a cropland, the application of inorganic fertilizers consistently decreased the population density of soil free-living nematodes (Puissant *et al*., 2021; Zhao and Neher, 2013). Similarly, P application revealed to be more destructive on the population density of free-living nematodes compared to N addition in secondary tropical forest soils (Zhao *et al*., 2014). However, the application of inorganic fertilizer on soils with a background incorporation of organic manure can preserve the structure of nematode community whereas mineral fertilizer application on plot without manure background can favour plant parasitic nematodes over other trophic groups (Gruzdeva *et al*., 2007).

Dynamics of nematode population as influenced by agroforestry practices

Agroforestry systems are a complex farming system due to multiple spatial and temporal distribution patterns of the woody component. This complexity complicates studies of the effect of specific agroforestry practices on abundance and diversity of soil nematode populations (Falkowski *et al*., 2019). Moreover, most of the studies on soil nematode community as influenced by agroforestry practices in the tropics are limited to some agro-ecological zones as well as agroforestry systems, making result generalization unrealistic (Barrios *et al*., 2012). For this reason, most of the existing studies on the influence of agroforestry on nematode community structure can only improve our understanding of soil ecosystem functioning under these systems without practical implications for decision making.

Studying the influence of scattered single trees as practiced in Lacandon Maya agroforests, Mexico, Falkowski *et al*. (2019) recorded increasing counts of plant parasitic nematodes at increasing radial distance away from the *Lonchocarpus guatemalensis* tree stems. Besides, McQueen and Treonis (2020) found that soil nematode community in cacao agroforestry plots established within old growth rainforest presented a similar structure and diversity compared to the adjacent undisturbed rainforest. This high similarity between nematode community structure and diversity reveals an insignificant perturbation of the natural ecosystem brought about by cacao agroforestry systems (McQueen and Treonis, 2020). In their experiment, Vieira *et al*. (2021) found that the application of cow manure or poultry litter in a coffee agroforestry system increased the population of bacterivore nematodes while suppressing plant parasitic nematodes compared to the naturally fertilized coffee agroforestry systems and the Atlantic rainforest fragment.

The effect of agroforestry trees on the nematode population structure can be affected by the tree size, age as well as tree management practices. In the Lacandon agroforests, nematode community structure as well as soil chemical properties did not show a specific trend in the early successional stages of the Lacandon agroforest (5-12 years after fire-induced perturbation) along an increasing distance gradient from the *Ochroma pyramidale*. In later successional stages (secondary forest), the total nematode population density increased from 8 per 20 g soil at the trunk to over 60 per 20 g at 14 m from the tree trunk. Such a trend is indicative of a potential inhibitory effect of the leaf litter or root exudates of this particular tree species (Diemont *et al*., 2006). These observations reveal that the implemented agroforestry practice as well as the tree species used as woody component play a key role in their effect on soil nematode community structure and diversity. Most of the agroforestry studies based on the introduction of crops under the canopy of indigenous tree species report a stable soil nematode community structure characterised by a significant reduction of plant parasitic nematodes (Falkowski *et al*., 2019; McQueen and Treonis, 2020; Porazinska *et al*., 2012; Puissant *et al*., 2021; van den Hoogen *et al*., 2019). Conversely, practices like improved fallows with exotic tree species like *Sesbania sesban* showed a greater potential to build up the population of root-knot nematode (*Meloidogyne* spp.) when a susceptible bean variety was previously cultivated (Desaeger and Rao, 2000, 2003; Kimenju *et al*., 2007, 2008).

Conclusion

Land use and land cover change as well as change in the prevailing farming practices have been found determinant in shaping soil nematode community and their functional traits. Changes in the soil nematode community structure can result in an alteration of services and functions they are involved in and hence influence ecosystem functioning and productivity. On the other hand, soil nematode community structure as affected by agricultural practices in annual crop smallholder farms on-field conditions of sub-Saharan Africa has not received adequate attention. Whereas studies on the pathogenicity of plant parasitic nematodes are limited to some economically important crops and nematode species, the host status of many cultivated crops and tree species used in these farming systems is not well established. This scarcity of information about plant parasitic nematode host status of cultivated crops and trees represents a risk of increasing alternative hosts and source of infestation of the susceptible intercrops to plant parasitic nematodes. More studies are still needed for a better understanding of soil nematode community structure in response to agricultural practices as implemented in smallholder farm-conditions, implications for ecological functions and the possibility to be accurately used as indicator of soil health and soil quality conditions of these marginal farming systems.

Novelty Statement

Farm management practices like cover crop, improved fallow, organic amendment, mulching, crop rotation and agroforestry can promote beneficial (free-living) nematodes while suppressing plant parasitic nematodes. This ecosystem function can be viable when non-host plants are sequentially introduced in the farming system.

Author's Contribution

Muyisa Kambale Musongora: Conceived the review idea, collected the literature, wrote the first draft of the manuscript, corrected the reviewed manuscript.
Keziah Magiroi: Revised the first draft of the manuscript, corrected the revised manuscript.
Njiranjira Pili: Provided a structural framework of the review, revised the first draft of the manuscript, corrected the revised manuscript.
Abigael Otinga Nakesa: Revised the first draft of the manuscript, corrected the revised manuscript.
Ruth Njoroge: Refined the review idea, revised the first draft of the manuscript, corrected the reviewed manuscript.

Generative AI and AI-assisted technology statement
No generative AI was used in this review.

Conflict of interest
The authors have declared no conflict of interest.

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