Heliyon 8 (2022) e10189

Contents lists available at ScienceDirect

Heliyon

journal homepage: www.cell.com/heliyon

Research article

Nematode assemblages, food web indices and metabolic footprints in maize-pigeon pea agro-ecosystems

Samuel Maina, Hannah Karuri *, Julius Mugweru

Department of Biological Sciences, University of Embu, P.O Box 6-60100, Embu, Kenya

ARTICLE INFO

Keywords:
Cajanus cajan
Metabolic footprint
Nematode community assemblages
Soil health
Zea mays

ABSTRACT

Pigeon pea (*Cajanus cajan* L.) and maize (*Zea mays* L.) are important food crops in developing countries due to their multiple benefits. However, their production is constrained by plant-parasitic nematodes (PPN) which cause significant yield losses. Understanding the nematode-based soil food web structure in maize-pigeon pea agro-ecosystems will allow sustainable PPN management by improving soil health. This study explored nematode community assemblages, indices and metabolic footprints in maize-pigeon pea agroecosystems in Mbeere South, Embu County, Kenya. Soil samples were collected from Gachuriri, Irabari, Kanduu, Kangeta, Kangungi, Kaninwathiga, Karimari and Mutugu regions. The recovered nematodes were identified to the genus level. There were 41 nematode genera across the eight regions. *Longidorus* spp., *Heterocephalobus* spp., *Cervidellus* spp., *Mesorhabditis* spp. and *Mononchus* spp. differed significantly across the regions. *Meloidogyne* spp., *Scutellonema* spp., *Rotylenchulus* spp. and *Pratylenchus* spp. were the most prevalent genera although their abundance was not statistically different across the regions. Using the structure and enrichment indices, soil food web in Irabari was degraded, whereas the other seven regions were structured. The main energy channel of organic matter decomposition in the studied regions was dominated by fungivores. There were no differences in metabolic footprints expect for bacterivore footprint. The occurrence of *Hoplolaimus* spp. and *Xiphinema* spp. showed a negative correlation with N, C, Mg and Na. This work provides useful insights into the maize-pigeon pea nematode soil food web structure and function which can be used in improving their yields and soil health.

1. Introduction

Pigeon pea (*Cajanus cajan* L.) is a food crop that is a valuable source of dietary proteins to millions of people in developing countries (Singh et al., 2020). Besides human consumption, it serves as nutritious feed for livestock, fish and pigs (Rao et al., 2002). Despite these benefits, pigeon pea is often regarded as an "orphan crop" in terms of the amount of research done on it (Varshney et al., 2017). The current leading world producer of pigeon pea, India, contributes about 67% of the world's pigeon pea, while other producers, including Malawi, Tanzania and Kenya, contribute 6.3%, 5.3% and 4.6%, respectively (Rawal and Navarro, 2019). In Kenya, pigeon pea ranks as the third most important grain legume after common bean (*Phaseolus vulgaris* L.) and cowpea (*Vigna unguiculata* L.) (Ministry of Agriculture, 2015; International Trade Centre, 2016; Ojwang et al., 2021). It is mainly cultivated as a subsistence and cash crop by smallholder farmers either as an intercrop with maize (*Zea mays* L.) or as a sole crop (Snapp et al., 2003). The total area cultivated with pigeon pea in Kenya has decreased annually from 158,746 ha in 2010 to 133,525 ha in 2020 (FAOSTAT, 2020). The current pigeon pea yield in Kenya is 0.54 t ha^{-1}, which is relatively lower than the potential yield of 1.5–2.5 t ha^{-1} (Esilaba et al., 2021). Maize, together with wheat and rice, provides around 30% of the food calories to >4.5 billion people in 94 developing countries (Shiferaw et al., 2011). Maize plays a key role in national food security in Kenya and accounts for 65% of the calories that are consumed (Ministry of Agriculture, 2015). Due to population growth along with increasing animal feed usage, demand for maize is rapidly growing. The total area cultivated with maize in Kenya has slightly increased from 2.10 Mha in 2015 to 2.19 Mha in 2020, but the overall yields per ha have been fluctuating since 2010 (FAOSTAT, 2020).

Previous work has shown that pigeon pea and maize suffer from low yields due to biotic and abiotic stresses (Saxena et al., 2014; Macauley and Ramadjita, 2015). Among the biotic constraints, considerable yield loss in pigeon pea and maize worldwide is due to plant-parasitic nematodes (PPN) such as the reniform nematodes (*Rotylenchulus reniformis*), root-lesion nematodes (*Pratylenchus* spp.), root-knot nematodes (*Meloidogyne* spp.) and cyst nematodes (*Heterodera* spp.) (Sikora et al., 2018;

* Corresponding author.
E-mail address: hwkaruri@gmail.com (H. Karuri).

https://doi.org/10.1016/j.heliyon.2022.e10189
Received 25 February 2022; Received in revised form 8 May 2022; Accepted 2 August 2022
2405-8440/© 2022 The Author(s). Published by Elsevier Ltd. This is an open access article under the CC BY-NC-ND license (http://creativecommons.org/licenses/by-nc-nd/4.0/).

Kimenju et al., 2022). Globally, PPN cause 13.2% annual yield losses in pigeon pea (Abd-Elgawad and Askary, 2015). In Kenya, PPN contributes to about 35% and 50% of the yield losses in pigeon pea and maize, respectively (Hillocks et al., 2000), with *Rotylenchulus parvus*, *Meloidogyne javanica, Pratylenchus* spp. and *Scutellonema unum* being the most harmful species (Sharma et al., 1993). Compared with other pests of pigeon pea and maize, PPN remains one of the most abandoned organisms in terms of research in spite of inducing considerable yield losses (Askary, 2017; Mc Donald et al., 2017). To counteract economic losses correlated with these nematodes, adoption of effective management techniques for the suppression of these PPN is paramount (Abuzar and Haseeb, 2009). Use of nematicides is the main control method of nematodes in sub-Saharan Africa (Coyne et al., 2018). However, due to negative effects associated with nematicides on environment, non-target organisms, and high cost of production, there is need for sustainable PPN management practices in maize-pigeon pea agroecosystems. Input of organic amendments has been shown to possess multiple benefits such as enhancing soil suppressiveness ability and regulation of PPN (Sánchez-Moreno and Ferris 2018). Tenuta and Ferris (2004) and Steel and Ferris (2016), for instance, demonstrated that exogenous organic amendments suppressed PPN through an increase in the number of predatory nematodes. It has been established that under optimal conditions including the appropriate amount of resources (Ferris et al., 2012a) and ideal spatial and temporal location of predatory nematodes and their prey (Steel and Ferris 2016), generalist and specialists predators effectively reduce the population of PPN in soil.

Free-living nematodes (FLN) perform key ecological functions such as nutrient mineralization, nutrient cycling and decomposition (Ferris and Bongers, 2009). They are also bioindicators of ecosystem health and suppress harmful pests such as PPN. The suppressive function of these nematodes can be enhanced for management of PPN (Ferris et al., 2012b; Ferris and Tuomisto, 2015). Further, the suppressive ability of soil in management of PPN requires an understanding of the nematode soil food web (Ferris et al., 2001). Nematode metabolic footprints have been developed to quantify the contributions of nematodes to soil functioning (Ferris, 2010). Information on nematode community composition and soil food web status is essential for improving maize-pigeon pea productivity and in management of PPN in Kenya. This study was performed in maize-pigeon pea agro-ecosystems in Mbeere South, Embu County, Kenya, and the objectives were; (i) to examine the nematode community assemblages and (ii) to assess the nematode-based soil food web indices and metabolic footprints.

2. Materials and methods

2.1. Site description and soil sampling

The study was conducted in Mbeere South Sub-County, Embu County, Kenya (Table 1). The average rainfall and temperature recorded in the area during the sampling period were 550 mm and 20 °C, respectively. In this study, we sampled fields (0.5–2 acres) that were cultivated with maize (Pioneer)-pigeon pea (KAT 60/8 variety) intercrop for more than five years in January 2021. Cow manure was applied in the sampled fields at an approximate rate of 4640 kg/ha. The 24 fields (8 regions) were in Gachuriri, Irabari, Kanduu, Kangeta, Kangungi, Kaninwathiga, Karimari and Mutugu in Mbeere South sub-county, Embu County, Kenya (Table 1). In each field, three soil samples were taken using a soil auger (3.5 cm in diameter) at a depth of 25 cm. Each soil sample was collected along 3 separate W-shaped "sample walks", composed of 30 sampling points. The distance between two sampling points was 10 m. Three 250 g soil composite cores were taken for nematode extraction, whereas one kilogram of soil subsamples were used for soil physico-chemical analysis (Wiesel et al., 2015).

Table 1. Soil sampling sites in Gachuriri, Irabari, Kanduu, Kangeta, Kangungi, Kaninwathiga, Karimari and Mutugu, Mbeere South, Embu County, Kenya.

Province	County	Sub-county	Region	Latitude	Longitude
Eastern	Embu	Mbeere south	Gachuriri	0°42′49.4″S	37°31′57.8″E
			Irabari	0°41′58.4″S	37°40′51.9″E
			Kanduu	0°41′13.3″S	37°29′19.1″E
			Kangeta	0°40′31.1″S	37°30′36.4″E
			Kangungi	0°39′30.6″S	37°33′29.3″E
			Kaninwathiga	0°38′20.1″S	37°31′17.0″E
			Karimari	0°39′27.9″S	37°35′36.6″E
			Mutugu	0°42′23.4″S	37°39′56.4″E

The soil physical and chemical characteristics, including soil pH, total organic carbon, nitrogen, sand, clay, silt, pH, phosphorus, potassium, calcium, magnesium, manganese, copper, iron, zinc, and sodium were evaluated at the Kenya Agriculture and Livestock Research Organization, National Agricultural Research Laboratories as described (Gallaher et al., 1975; Gee and Bauder, 1985; Jackson, 1958; Smith and Doran, 1996). Temperature and rainfall data were acquired from the Kenya Meteorological Department, Kenya.

2.2. Nematode processing and enumeration

A 250 g soil sample was placed in filter trays for nematode extraction following the modified Baermann method for 48 h (Hooper et al., 2005). After extraction, 10 ml of nematode suspension were heat killed by adding an equal volume of fixative (Golden solution) which was prepared according to the protocol by Hooper et al. (2005). The extracted nematodes were counted and identified at the genus level using light compound microscope (model DM750 Leica, Wetzlar, Germany).

2.3. Calculation of ecological and functions indices and metabolic footprints

The identified nematode genera were grouped into bacterivores, omnivores, fungivores, herbivores and predators (Yeates et al., 1993). They were further ordered into their respective colonizer-persister guilds ranging from *r*- (colonizers) to *k*- (persisters) strategists (Yeates et al., 1993; Bongers and Bongers, 1998). Maturity index (MI), Maturity index of nematodes in cp2-5 (MI2-5) and plant-parasitic index (PPI) were calculated for each region (Bongers and Bongers, 1998). Channel index (CI), basal index (BI), enrichment index (EI) and structure index (SI) were also computed (Ferris et al., 2001). The EI and SI were plotted into a fauna profile which depicts the structure and state of the soil food web as either disturbed, degraded, maturing or structured (Ferris et al., 2001). The nematode metabolic footprints were also examined (Ferris, 2010). The computation of metabolic footprints and indices was executed using the online program, Nematode Indicators Joint Analysis (Sieriebriennikov et al., 2014).

2.4. Data analysis

The Shapiro-Wilk test was used to assess normality of the nematode abundance data. Data transformation (log (x+1)) was done as needed before analysis. Differences in nematode genera, indices and metabolic footprints in the eight regions were examined using one-way analysis of variance (ANOVA). Significantly different means were separated using Tukey's HSD test. Nematode community structure in the eight regions was assessed using the hierarchical cluster analysis in the R package vegan. The relationship between nematode community structure and soil characteristics was explored using canonical correspondence analysis (CCA) using the vegan package.

3. Results

3.1. Nematode assemblage composition and structure

A total of 41 nematode genera belonging to five trophic levels were identified across the eight regions. Abundance of *Longidorus*, *Cervidellus*, *Heterocephalobus*, *Mesorhabditis* and *Mononchus* varied considerably ($P <$

Table 2. Nematode genera abundance (mean ± standard error) in 250 g of soil obtained from Gachuriri, Irabari, Kanduu, Kangeta, Kangungi, Kaninwathiga, Karimari and Mutugu, Kenya.

Genus	Cp-value	Gachuriri	Irabari	Kanduu	Kangeta	Kangungi	Kaninwathiga	Karimari	Mutugu	*F*-vale	*P*-value
		Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE		
Herbivores											
Helicotylenchus	3	8.7 ± 8.7	8.7 ± 8.7	52.0 ± 27.1	47.7 ± 24.1	4.3 ± 4.3	52.0 ± 27.1	21.7 ± 11.5	21.7 ± 15.6	0.508	0.816
Hoplolaimus	3	0	4.3 ± 4.3	0	0	0	0	0	0	1.000	0.466
Longidorus	5	17.3 ± 8.7	30.3 ± 4.3	0	0	21.7 ± 4.3	4.3 ± 4.3	8.7 ± 4.3	4.3 ± 4.3	3.890	0.012*
Malenchus	2	4.3 ± 4.3	8.7 ± 8.7	17.3 ± 11.5	0	0	21.7 ± 15.6	0	8.7 ± 8.7	1.121	0.398
Meloidogyne	3	13.0 ± 13.0	65.0 ± 58.6	0	30.3 ± 24.1	164.7 ± 158.2	13.0 ± 13.0	17.3 ± 11.5	65.0 ± 46.9	0.614	0.737
Pratylenchus	3	0	21.7 ± 11.5	13.0 ± 7.5	99.7 ± 86.7	4.3 ± 4.3	26.0 ± 15.0	52.0 ± 32.7	56.3 ± 33.8	1.533	0.226
Psilenchus	2	4.3 ± 4.3	0.0 ± 0.0	0	0	0	17.3 ± 8.7	0.0 ± 0.0	0	2.573	0.056
Rotylenchulus	3	21.7 ± 4.3	17.3 ± 4.3	26.0 ± 19.9	52.0 ± 45.7	34.7 ± 15.6	95.3 ± 48.8	17.3 ± 11.5	30.3 ± 30.3	0.656	0.705
Scutellonema	3	8.7 ± 4.3	13.0 ± 7.5	8.7 ± 4.3	39.0 ± 19.9	34.7 ± 15.6	69.3 ± 17.3	104.0 ± 71.6	30.3 ± 30.3	1.366	0.285
Trichodorus	4	0	8.7 ± 8.7	0	0	0	0	0	0	1.000	0.466
Tylenchorhynchus	3	0	4.3 ± 4.3	0	0	0	0	4.3 ± 4.3	0	0.857	0.559
Tylenchus	2	91.0 ± 32.7	65.0 ± 34.4	151.7 ± 45.9	39 ± 19.9	60.7 ± 15.6	34.7 ± 28.4	91.0 ± 45.7	60.7 ± 18.9	0.669	0.696
Xiphinema	5	60.7 ± 33.8	13.0 ± 7.5	0	0	39.0 ± 39.0	8.7 ± 4.3	0	0	1.701	0.179
Bacterivores											
Acrobeles	2	73.7 ± 24.1	108.3 ± 51.1	21.7 ± 15.6	30.3 ± 8.7	91.0 ± 65.0	164.7 ± 41.3	190.7 ± 78.1	134.3 ± 75.9	2.247	0.085
Alaimus	4	0	4.3 ± 4.3	8.7 ± 8.7	4.3 ± 4.3	13.0 ± 7.5	39.0 ± 7.5	21.7 ± 15.6	4.3 ± 4.3	1.745	0.169
Cephalobus	2	138.7 ± 30.3	238.3 ± 41.3	117.0 ± 34.4	86.7 ± 31.2	138.7 ± 75.2	208.0 ± 60.0	164.7 ± 67.7	117.0 ± 7.5	0.907	0.525
Cervidellus	2	0	8.7 ± 4.3	8.7 ± 4.3	4.3 ± 4.3	34.7 ± 22.9	60.7 ± 15.6	21.7 ± 4.3	13.0 ± 0.0	3.189	0.026*
Chiloplacus	2	52.0 ± 27.1	13.0 ± 13.0	26.0 ± 26.0	8.7 ± 8.7	13.0 ± 13.0	34.7 ± 34.7	39.0 ± 15.0	26.0 ± 19.9	0.497	0.823
Drilocephalobus	2	8.7 ± 4.3	0	0	0	4.3 ± 4.3	17.3 ± 8.7	0	0	2.408	0.069
Eucephalobus	2	0.0 ± 0.0	4.3 ± 4.3	4.3 ± 4.3	26.0 ± 19.9	0	17.3 ± 4.3	13.0 ± 13.0	17.3 ± 17.3	1.245	0.336
Geomonhystera	2	21.7 ± 11.5	13.0 ± 7.5	4.3 ± 4.3	34.7 ± 17.3	26.0 ± 15.0	13.0 ± 7.5	13.0 ± 7.5	34.7 ± 17.3	0.266	0.959
Heterocephalobus	2	86.7 ± 8.7	112.7 ± 22.9	91.0 ± 34.4	60.7 ± 24.1	21.7 ± 21.7	117.0 ± 32.7	143.0 ± 61.4	173.3 ± 18.9	3.812	0.013*
Mesorhabditis	1	0	4.3 ± 4.3	0	0	0	0	0	56.3 ± 33.8	2.920	0.036*
Panagrolaimus	1	4.3 ± 4.3	8.7 ± 4.3	13.0 ± 13.0	34.7 ± 22.9	0	17.3 ± 17.3	13.0 ± 13.0	30.3 ± 18.9	0.587	0.758
Plectus	2	30.3 ± 18.9	43.3 ± 11.5	39.0 ± 15.0	26.0 ± 15.0	39.0 ± 19.9	86.7 ± 17.3	8.7 ± 8.7	56.3 ± 33.8	1.163	0.376
Prismatolaimus	3	30.3 ± 4.3	34.7 ± 17.3	47.7 ± 11.5	8.7 ± 8.7	21.7 ± 15.6	78.0 ± 0.0	21.7 ± 15.6	21.7 ± 8.7	1.469	0.247
Rhabditis	1	17.3 ± 8.7	21.7 ± 8.7	8.7 ± 4.3	21.7 ± 4.3	30.3 ± 15.6	21.7 ± 4.3	21.7 ± 8.7	13.0 ± 7.5	0.459	0.850
Wilsonema	2	8.7 ± 8.7	8.7 ± 8.7	17.3 ± 4.3	8.7 ± 8.7	21.7 ± 11.5	43.3 ± 15.6	21.7 ± 15.6	13.0 ± 7.5	0.866	0.553
Fungivores											
Aphelenchoides	2	30.3 ± 11.5	39.0 ± 19.9	52.0 ± 7.5	99.7 ± 37.0	47.7 ± 18.9	60.7 ± 4.3	65.0 ± 7.5	117.0 ± 45.0	1.049	0.437
Aphelenchus	2	52 ± 13.0	39.0 ± 19.9	143.0 ± 58.6	177.7 ± 33.8	160.3 ± 73.7	65.0 ± 32.7	82.3 ± 11.5	95.3 ± 18.9	1.398	0.272
Filenchus	2	26.0 ± 15.0	8.7 ± 8.7	21.7 ± 21.7	4.3 ± 4.3	21.7 ± 4.3	0	21.7 ± 4.3	4.3 ± 4.3	1.618	0.201
Omnivores											
Aporcelaimellus	5	4.3 ± 4.3	0	0	0	0	8.7 ± 8.7	0	0	0.861	0.556
Eudorylaimus	4	69.3 ± 51.1	8.7 ± 8.7	60.7 ± 33.8	60.7 ± 41.3	117.0 ± 15.0	82.3 ± 15.6	78.0 ± 19.9	30.3 ± 11.5	1.639	0.195
Labronema	4	30.3 ± 8.7	39.0 ± 22.5	65.0 ± 13.0	52.0 ± 34.4	8.7 ± 8.7	78.0 ± 49.2	17.3 ± 11.5	52.0 ± 39.0	0.707	0.667
Mesodorylaimus	4	0	4.3 ± 4.3	8.7 ± 8.7	0	0	8.7 ± 8.7	4.3 ± 4.3	0	0.579	0.763
Prodorylaimus	4	0	8.7 ± 8.7	0	17.3 ± 17.3	0	4.3 ± 4.3	4.3 ± 4.3	26.0 ± 19.9	0.850	0.564
Predators											
Discolaimus	5	0	0	0	0	8.7 ± 4.3	0	0	4.3 ± 4.3	2.214	0.089

(*continued on next page*)

Table 2 (*continued*)

Genus	Cp-value	Gachuriri	Irabari	Kanduu	Kangeta	Kangungi	Kaninwathiga	Karimari	Mutugu	*F*-vale	*P*-value
		Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE		
Mononchus	4	0	0	0	0	0	0	0	8.7 ± 4.3	4.000	0.010*
Nygolaimus	5	43.3 ± 22.9	34.7 ± 11.5	56.3 ± 18.9	104.0 ± 7.5	34.7 ± 11.5	39.0 ± 32.7	69.3 ± 24.1	86.7 ± 52.7	0.604	0.744
Prionchulus	4	8.7 ± 8.7	0	4.3 ± 4.3	8.7 ± 4.3	17.3 ± 8.7	4.3 ± 4.3	0	34.7 ± 8.7	2.364	0.073
Tripyla	3	0	0	0	0	0	0	0	4.3 ± 4.3	1.000	0.466

Cp = colonizer-persister scale (Cp1-5). *$P < 0.05$.

0.05) across the regions. In all regions, bacterivorous genera (15) were more abundant compared with herbivores (13), omnivores (5), predators (5) and fungivores (3). Majority of bacterivore genera belonged to cp-1 and cp-2 guilds except *Prismatolaimus* and *Alaimus*. Across all fields, herbivores belonging to the cp-3 guild were the most dominant. *Meloidogyne*, *Scutellonema*, *Rotylenchulus* and *Pratylenchus* were the most prevalent genera but their abundance was not statistically different across the regions (Table 2).

Following the heatmap analysis, the eight studied regions were clustered into three major groups with the bigger cluster containing six regions. The PPN and FLN genera were grouped into two major clusters. The smallest cluster was composed of *Mesorhabditis*, *Mononchus*, *Tripyla*, *Tylenchorhynchus*, *Hoplolaimus* and *Trichodorus*; fungivores and bacterivores were excluded from this cluster (Figure 1).

3.2. Nematode ecological indices, metabolic footprints and soil physico-chemical properties

The MI, MI2-5, EI, SI, CI and BI did not differ statistically ($P > 0.05$) among the eight regions. However, the PPI, descriptor of herbivore pressure, varied significantly ($P = 0.049$), with the highest being observed in Gachuriri and the lowest in Kanduu. Apart from bacterivore footprint ($P = 0.033$), all the other footprints did not vary significantly (Table 3). Based on the values of EI and SI, the soil food web in Gachuriri, Kanduu, Kangeta, Kangungi, Kaninwathiga, Karimari and Mutugu was structured (quadrat C), while Irabari was degraded (quadrat D) (Figure 2).

Soil nitrogen ($P = 0.023$), calcium ($P = 0.005$) and silt ($P = 0.011$) differed significantly across the eight regions (Table 4). Canonical correspondence analysis revealed a significant association ($P < 0.05$) between nematode genera and some soil physico-chemical properties. The first (eigen value = 0.07) and second axes (eigen value = 0.06) explained 25.2% and 20.6% of the observed variation, respectively. The genus *Hoplolaimus* was negatively associated with N, C, K, Ca, Mg and Na, whereas *Psilenchus* was positively associated with silt. *Xiphinema* exhibited a positive correlation with Cu and Fe as well as a negative correlation with Zn. *Drilocephalobus* showed a negative correlation with pH and a positive correlation with silt. There was a negative association between the abundance of *Trichodorus* and N, C, Mg, Ca and Na (Figure 3).

4. Discussion

The most abundant PPN genera in the present work are estimated to cause around $173 billion per annum in crop yield losses worldwide (Elling, 2013; Zhao et al., 2022). The 13 PPN genera recorded across the eight regions was consistent with observations by Abuzar and Haseeb (2009). In Kenya, Sharma et al. (1993) reported a higher number (25) of PPN genera associated with pigeon pea. The differences between these two studies may be due to different agro-ecological zones (AEZs). This study was conducted in the lower midland (LM3), LM4 and inner lowland (IL5) zones, whereas Sharma et al. (1993) conducted their study in LM3, LM4, LM5, upper midland (UM3) and UM4 AEZs. The AEZs LM3, UM3 and UM4 are high potential agricultural areas with an annual mean rainfall of >1000 mm, altitude of 1070–1460 m and mean temperature of 19.6–22.0 °C. The LM4 and LM5 are low potential agricultural areas characterized by < 1000 mm of rainfall, mean annual temperature of 21.0–23.9 °C and an altitude of 830–1220 m (Jaetzold et al., 2007; Gummadi et al., 2020). For the IL5, the annual mean rainfall is <900 mm, mean annual temperature is 24.0–25.4 °C and the altitude is 600–850 m (Jaestzold et al. 2007). An additional difference with the study by Sharma et al. (1993) is that it focused on PPN in monocrop pigeon pea in different agro-ecological zones in northeastern Kenya, while the present work provides data on nematode community assemblages and food web structure in maize-pigeon pea intercrop systems.

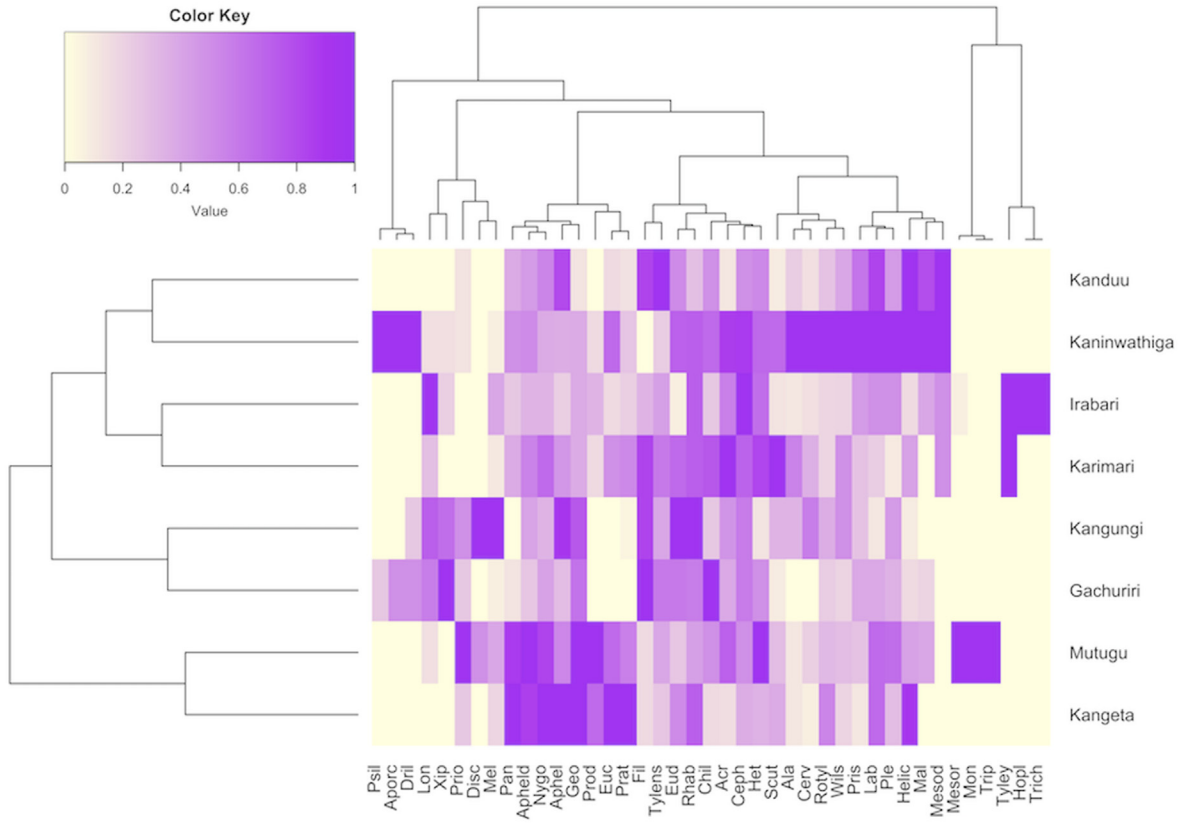

Figure 1. Heatmap of nematodes in maize-pigeon pea fields in Kanduu, Kaninwathiga, Irabari, Karimari, Kangungi, Gachuriri, Mutugu and Kangeta regions, Mbeere South, Embu County, Kenya. The dendrogram along the left axis reflects the sampled maize-pigeon pea fields in eight regions whereas the dendrogram in the upper part indicates the nematode genera. The color key scale represents the abundance of nematode genera. Nematode genera abbreviations are: Acr (*Acrobeles*), Acrd (*Acrobeloides*), Apheld (*Aphelenchoides*), Aphel (*Aphelenchus*), Aporc (*Aporcelaimellus*), Ceph (*Cephalobus*), Cerv (*Cervidellus*), Chil (*Chiloplacus*), Disc (*Discolaimus*), Dril (*Drilocephalobus*), Euc (*Eucephalobus*), Eud (*Eudorylaimus*), Fil (*Filenchus*), Geo (*Geomonhystera*), Helic (*Helicotylenchus*), Het (*Heterocephalobus*), Hopl (*Hoplolaimus*), Lab (*Labronema*), Lon (*Longidorus*), Mal (*Malenchus*), Mel (*Meloidogyne*), Mesod (*Mesodorylaimus*), Mesor (*Mesorhabditis*), Mon (*Mononchus*), Nygo (*Nygolaimus*), Pan (*Panagrolaimus*), Ple (*Plectus*), Prat (*Pratylenchus*), Prio (*Prionchulus*), Pris (*Prismatolaimus*), Prod (*Prodorylaimus*), Psi (*Psilenchus*), Rhab (*Rhabditis*), Rotyl (*Rotylenchulus*), Scut (*Scutellonema*), Trich (*Trichodorus*), Trip (*Tripyla*), Tyley (*Tylenchorhynchus*), Tylens (*Tylenchus*), Wils (*Wilsonema*) and Xip (*Xiphinema*).

Table 3. Nematode indices and log-transformed metabolic footprints in Gachuriri, Irabari, Kanduu, Kangeta, Kangungi, Kaninwathiga, Karimari and Mutugu, Mbeere South, Embu County, Kenya.

Index/footprint	Gachuriri	Irabari	Kanduu	Kangeta	Kangungi	Kaninwathiga	Karimari	Mutugu	*F-value*	*P - value*
	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE		
MI	2.54a±0.13	2.33a±0.08	2.59a±0.18	2.64a±0.07	2.59a±0.19	2.55a±0.09	2.54a±0.07	2.50a±0.23	0.452	0.854
M12-5	2.60a±0.12	2.40a±0.06	2.64a±0.18	2.76a±0.02	2.68a±0.25	2.61a±0.10	2.62a±0.12	2.64a±0.18	0.512	0.812
PPI	3.32a±0.44	3.07ab±0.09	2.36b ± 0.16	2.77ab±0.14	3.10ab±0.06	2.88ab±0.03	2.84ab±0.16	2.72ab±0.11	2.679	0.049*
CI	53.76a±12.04	39.99a±4.90	73.58a±17.41	60.31a±13.75	67.56a±18.48	49.93a±16.02	62.75a±12.18	41.38a±11.98	0.660	0.702
BI	32.48a±5.10	40.42a±2.92	29.79a±6.98	23.35a±0.84	30.65a±10.94	32.27a±5.44	31.87a±6.47	26.94a±3.69	0.677	0.689
EI	30.13a±2.32	30.02a±4.87	37.13a±3.77	48.44a±6.73	42.24a±9.04	27.27a±4.68	34.28a±9.35	45.92a±6.14	1.439	0.258
SI	61.94a±6.78	50.48a±4.66	63.39a±9.29	69.59a±0.78	62.24a±13.02	63.62a±5.69	62.63a±6.26	62.04a±8.31	0.500	0.821
ComposFP	6.27a±0.12	6.67a±0.40	6.19a±0.21	6.60a±0.18	6.90a±0.64	6.61a±0.27	6.49a±0.18	6.96a±0.29	0.696	0.675
EnrichFP	3.92a±0.30	4.07a±0.26	4.15a±0.06	4.66a±0.12	4.63a±0.27	4.20a±0.24	4.23a±0.30	4.49a±0.10	1.459	0.250
StrucFP	5.11a±0.30	4.79a±0.31	5.39a±0.27	5.59a±0.19	5.10a±0.34	5.54a±0.38	5.17a±0.15	5.66a±0.26	1.123	0.396
HerbFP	4.93a±0.13	5.80a±0.69	3.82a±0.28	4.78a±1.09	5.92a±1.10	5.18a±0.37	5.12a±0.32	5.44a±0.94	0.851	0.563
FungFP	2.76a±0.24	2.52a±0.25	3.62a±0.32	3.94a±0.13	3.54a±0.60	2.79a±0.46	3.28a±0.10	3.48a±0.13	2.395	0.070
BacterFP	5.35ab±0.00	5.58ab±0.13	5.22ab±0.31	5.11ab±0.24	4.98b ± 0.03	5.75a±0.18	5.63ab±0.25	5.86a±0.03	2.997	0.033*
PredFP	3.03a±1.52	3.52a±0.42	4.21a±0.22	4.87a±0.12	3.92a±0.62	2.78a±1.43	4.25a±0.33	5.03a±0.29	1.011	0.460
OmnFP	4.55a±0.35	3.14a±1.58	4.87a±0.31	4.73a±0.45	4.56a±0.24	5.12a±0.41	4.47a±0.10	4.81a±0.28	0.892	0.535

Means with the same letter across the row are not statistically different.
Maturity indices (MI and MI2-5), Plant parasitic index (PPI), Channel index (CI), Basal index (BI), Enrichment index (EI), and Structure index (SI). ComposFP = Composite footprint, EnrichFP = Enrichment footprint, StrucFP = Structure footprint, HerbFP = Herbivore footprint, FungFP = Fungivore footprint, BacterFP = Bacterivore footprint, PredFP = Predatory footprint and OmnFP = Omnivore footprint. *$P < 0.05$.

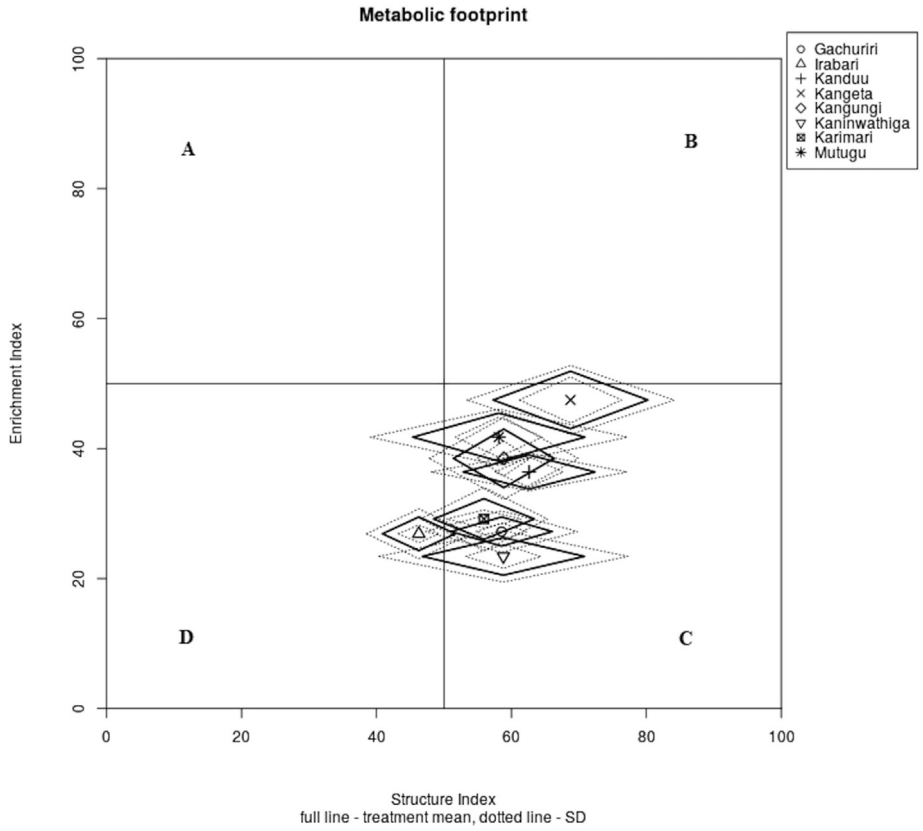

Figure 2. Soil food web condition in Gachuriri, Irabari, Kanduu, Kangeta, Kangungi, Kaninwathiga, Karimari and Mutugu regions, Mbeere South, Embu County, Kenya. The meeting point at the middle of the rhombus indicates the intersection of structure and enrichment indices.

In this study, *Tylenchus* occurred in great abundance with the highest population being recorded in Kanduu region. Among pulse and cereal crops, including pigeon pea and maize, *Tylenchus* is often considered of less economic importance in terms of yield and quality reduction (McDonald and Nicol, 2005; Askary, 2017). *Meloidogyne,* a sedentary endoparasitic nematode, was the second most dominant genus corroborating reports by Sharma et al. (1993). *Meloidogyne* is among the most harmful nematodes (Jones et al., 2013) and it causes 8%–35% yield losses in pigeon pea (Hillocks et al., 2000; Askary, 2017). This nematode has also been reported in association with pigeon pea in Malawi, Brazil and India (Reddy et al., 1993; Sikora et al., 2005; Askary, 2012). *Meloidogyne javanica* population levels of 10,000 J2/kg of soil were linked to a significant drop in pigeon pea plant growth indices such as plant height, plant weight, chlorophyll content and pod number (Askary, 2012). Mc

Table 4. Soil physico-chemical characteristics in Gachuriri, Irabari, Kanduu, Kangeta, Kangungi, Kaninwathiga, Karimari and Mutugu, Mbeere South, Embu County, Kenya.

Soil property	Gachuriri	Irabari	Kanduu	Kangeta	Kangungi	Kaninwathiga	Karimari	Mutugu	*F-value*	*P-value*
	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE		
pH	5.88 ± 0.06	6.08 ± 0.01	6.24 ± 0.17	6.21 ± 0.20	6.11 ± 0.11	5.86 ± 0.05	6.07 ± 0.03	6.17 ± 0.07	1.810	0.154
Total nitrogen %	0.12 ± 0.01	0.08 ± 0.02	0.14 ± 0.00	0.14 ± 0.00	0.11 ± 0.00	0.13 ± 0.01	0.12 ± 0.01	0.13 ± 0.00	3.277	0.023*
Total organic carbon %	1.30 ± 0.12	0.81 ± 0.34	1.56 ± 0.03	1.49 ± 0.04	1.14 ± 0.08	1.47 ± 0.15	1.35 ± 0.14	1.42 ± 0.07	2.539	0.058
Phosphorus	37.67 ± 6.67	21.33 ± 4.33	33.33 ± 0.67	33.00 ± 1.00	45.33 ± 5.67	32.33 ± 0.33	37.00 ± 7.00	31.33 ± 1.33	2.497	0.061
Potassium	0.91 ± 0.11	0.58 ± 0.34	1.45 ± 0.09	1.37 ± 0.17	1.02 ± 0.34	1.19 ± 0.07	1.07 ± 0.19	1.41 ± 0.15	1.989	0.121
Calcium meq%	3.40 ± 0.00	1.73 ± 0.33	2.60 ± 0.20	3.00 ± 0.20	3.00 ± 0.40	2.20 ± 0.00	2.73 ± 0.33	2.33 ± 0.07	4.788	0.005**
Magnesium meq%	4.06 ± 0.66	2.34 ± 0.68	3.63 ± 0.10	3.62 ± 0.11	4.75 ± 0.63	3.08 ± 0.34	4.26 ± 0.56	3.63 ± 0.07	2.462	0.064
Manganese meq%	0.52 ± 0.02	0.42 ± 0.11	0.78 ± 0.12	0.77 ± 0.13	0.60 ± 0.04	0.64 ± 0.11	0.61 ± 0.02	0.65 ± 0.02	1.888	0.138
Copper ppm	1.19 ± 0.90	0.67 ± 0.11	0.13 ± 0.02	0.20 ± 0.05	2.34 ± 0.65	0.40 ± 0.30	1.60 ± 0.70	0.94 ± 0.04	2.505	0.061
Iron ppm	25.73 ± 10.03	16.73 ± 1.83	19.40 ± 0.40	18.43 ± 1.37	37.80 ± 8.00	20.13 ± 1.53	28.87 ± 8.47	20.87 ± 0.47	1.613	0.202
Zinc ppm	3.27 ± 0.01	4.88 ± 1.26	7.38 ± 0.54	5.65 ± 1.19	3.80 ± 0.51	7.36 ± 1.10	6.03 ± 1.37	6.54 ± 0.86	2.559	0.057
Sodium meq%	0.31 ± 0.05	0.09 ± 0.05	0.28 ± 0.00	0.27 ± 0.01	0.34 ± 0.08	0.25 ± 0.03	0.27 ± 0.07	0.19 ± 0.01	2.616	0.053
Sand	54.67 ± 1.33	57.33 ± 9.33	68.00 ± 10.00	70.67 ± 7.33	53.33 ± 1.33	52.00 ± 4.00	68.00 ± 8.00	69.33 ± 6.67	1.396	0.273
Clay	35.33 ± 1.33	35.33 ± 8.67	24.00 ± 10.00	20.67 ± 6.67	37.33 ± 0.67	38.00 ± 6.00	24.67 ± 6.67	24.00 ± 6.00	1.224	0.346
Silt	10.00 ± 0.00	8.00 ± 0.00	8.00 ± 0.00	8.67 ± 0.67	10.00 ± 0.00	10.00 ± 2.00	6.00 ± 0.00	6.67 ± 0.67	3.935	0.011*

Note: meq = milliequivalent. ppm = parts-per million.
$^{**}P < 0.01$, $^{*}P < 0.05$.

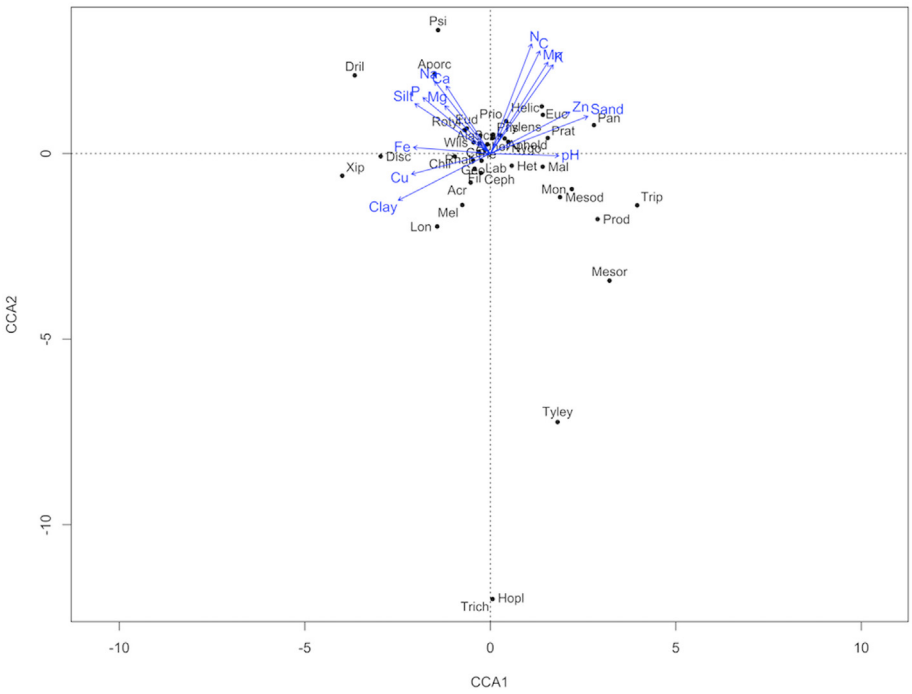

Figure 3. Canonical correspondence analysis of soil variables and nematode genera abundance in Gachuriri, Irabari, Kanduu, Kangeta, Kangungi, Kaninwathiga, Karimari and Mutugu regions, Mbeere South, Embu County, Kenya. The first and second axes (CCA1 and CCA2) explain 25.2% and 20.6% of the variance, respectively. Soil variables are represented by arrows, including Carbon (C), Nitrogen (N), Calcium (Ca), Copper (Cu), Zinc (Zn), Sodium (Na), sand (Sa), Magnesium (Mg), silt (Si), Phosphorus (P), Iron (Fe), clay (Cl), Potassium (K), Manganese (Mn) and soil Ph (pH). Nematode genera abbreviations include: Acr (*Acrobeles*), Acrd (*Acrobeloides*), Apheld (*Aphelenchoides*), Aphel (*Aphelenchus*), Aporc (*Aporcelaimellus*), Ceph (*Cephalobus*), Cerv (*Cervidellus*), Chil (*Chiloplacus*), Disc (*Discolaimus*), Dril (*Drilocephalobus*), Euc (*Eucephalobus*), Eud (*Eudorylaimus*), Fil (*Filenchus*), Geo (*Geomonhystera*), Helic (*Helicotylenchus*), Het (*Heterocephalobus*), Hopl (*Hoplolaimus*), Lab (*Labronema*), Lon (*Longidorus*), Mal (*Malenchus*), Mel (*Meloidogyne*), Mesod (*Mesodorylaimus*), Mesor (*Mesorhabditis*), Mon (*Mononchus*), Nygo (*Nygolaimus*), Pan (*Panagrolaimus*), Ple (*Plectus*), Prat (*Pratylenchus*), Prio (*Prionchulus*), Pris (*Prismatolaimus*), Prod (*Prodorylaimus*), Psi (*Psilenchus*), Rhab (*Rhabditis*), Rotyl (*Rotylenchulus*), Scut (*Scutellonema*), Trich (*Trichodorus*), Trip (*Tripyla*), Tyley (*Tylenchorhynchus*), Tylens (*Tylenchus*), Wils (*Wilsonema*) and Xip (*Xiphinema*).

Donald et al. (2017) found between 12% and 60% yield losses in maize due to *Meloidogyne* spp. in South Africa.

Scutellonema is an important PPN in sub-Saharan Africa which attacks numerous crops including pigeon pea and maize (Bridge and Starr, 2007; Coyne et al., 2018). In root tissues, this nematode feeds intracellularly, producing cell wall breakage and loss of cell contents (Bridge et al., 1995). In the current study, *Scutellonema* was recorded in all regions with a higher prevalence in Karimari, which is consistent with observations made by Sharma et al. (1993) and Mc Donald et al. (2017). Although pigeon pea has been shown to be an excellent host of *Scutellonema clathricaudatum* (Sharma et al., 1993), the relationship between yield loss and pathogenicity of *Scutellonema* spp. remains unknown. Similar to *Scutellonema*, *Rotylenchulus* occurred across the eight regions as documented in pigeon pea agroecosystems in Zambia, South Africa, Brazil and India (Furstenberg and Heyns, 1978; Sharma and McDonald, 1990; Araújo et al., 2010). According to Gaur et al. (2001) and Ali and Singh (2005), *Rotylenchulus* infestation can cause between 14% and 29% yield loss in pigeon pea, depending on the growth stage of the crop and initial pathogenic level of nematodes. It has been recently recorded in exceptionally high numbers of >10,000 J2 50 g roots^{-1} in maize under both conventional and conservation management practices (Mc Donald et al., 2017). This nematode can cause between 40% and 60% yield losses in tropical environments (Jones et al., 2013).

Pratylenchus was most abundant in Kangeta but occurred in low numbers in Gachuriri. High *Pratylenchus* density causes lesions on feeder roots and affects shoot and root growth in pulse crops (Askary, 2017). In maize, yield losses of more than 10% have been linked to *Pratylenchus* spp. (McDonald and Nicol, 2005; Kimenju et al., 2022). However, there are pigeon pea varieties that are resistant to *Pratylenchus* spp. (Araújo et al., 2010; Souto et al., 2011). It would be important to identify the major *Pratylenchus* species in Kenyan maize-pigeon pea agroecosystems which was not considered in the current study. Contrary to previous reports, the abundance of *Tylenchorhynchus*, *Hoplolaimus* and *Trichodorus* was lower in this study (Jena and Mahalik, 2020).

Characterizing nematode assemblages with similar life history characteristics allows their use in an integrative analysis of soil food web conditions (Tenuta and Ferris, 2004; Ferris et al., 2012b). According to the life-history traits analysis, bacterivores (cp-2) and predators (cp-4 and cp-5) were more abundant across the eight regions in this study. The cp-2 nematodes are highly tolerant to disturbances and can survive in depleted ecosystems (Bongers and Bongers, 1998; Yeates, 2003). On the other hand, cp-4 and cp-5 predators are associated with long life cycle, long generation time, low number of offspring and sensitivity to environmental degradation (Sánchez-Moreno and Ferris, 2018). Ferris et al. (2001) pointed out that high density of predators and omnivores leads to the development of a larger SI. Herein, the SI was greater in Kangeta and lower in Irabari, although the difference was not statistically significant. These results suggests that Kangeta soil food web is well structured with greater trophic connectance than that of Irabari which was characterized as depleted (Ferris et al., 2012a). In addition, the fauna analysis predicted the soil food web status in Kangeta, Gachuriri, Kanduu, Kangungi, Kaninwathiga, Karimari and Mutugu as structured, while Irabari was degraded. In order to improve the structure of Irabari food web, it will be essential to minimize physical and chemical disturbances. This will favor the increase of higher nematode trophic groups, especially omnivores and predators that are important in pest regulation (Ferris et al., 2012b). Berkelmans et al. (2003) and Steel and Ferris (2016) observed that both generalist and specialist predators can curb PPN species. Further, Oka (2010) found that application of organic material makes the soil less conducive to PPN species. Maintenance of soil health is paramount in order to support critical ecosystem functions and services such as pest regulation and nutrient cycling (Siebert et al., 2020).

The CI and EI provide a useful tool for evaluating levels of soil fertility and nutrient resource availability (Ferris et al., 2001). The CI values <50% and >50% denote bacterial and fungal mediated decomposition pathways, respectively (Ferris et al., 2009; Sánchez-Moreno and Ferris, 2018). In the present study, the CI values ranged from 39.99 ± 4.90 to 73.58 ± 17.41 indicating the occurrence of both bacterial and fungal decomposition channels across the eight regions. However, the most predominant decomposition pathway was mediated by fungivores. This implies that incorporation of labile organic matter particularly in Irabari, Kaninwathiga and Mutugu will be crucial so as to improve bacterial mediated decomposition (Ferris and Matute, 2003). The two decomposition pathways should be active and coupled in a healthy agricultural system (Sánchez-Moreno and Ferris, 2018). The EI values in our study were similar among the eight regions as previously reported (Okada and

Harada, 2007; Villenave et al., 2010). To further explore the extent of soil food web conditions across the eight regions, we also examined the nematode metabolic footprints, which allows quantification of ecosystem services provided by different nematode trophic groups (Ferris, 2010). Bacterivore footprint, an indicator of carbon and energy entering the soil food web via bacterial channel, was markedly higher in Mutugu compared with the other regions. This observation could be due to the high density of *Heterocephalobus* and *Mesorhabditis* that was recorded in the region.

Understanding the relationship between nematodes and soil properties is key for development of effective and environmentally-friendly nematode management programs. Several studies have elucidated the influence of soil properties on abundance, structure, composition and distribution of nematode assemblages (Pokharel, 2009; Maina et al., 2020; Lazarova et al., 2021). These properties may have been one of several factors that contributed to the structure of nematode communities that was depicted in the heatmap. In the current study, *Hoplolaimus* and *Xiphinema* showed a negative correlation with N, C, Mg and Na. This is consistent with the findings obtained by Wang et al. (2004) and Ngeno et al. (2019). There was a positive correlation between Cu and Fe with abundance of *Xiphinema,* contrary to reports by Wang et al. (2004). However, Zoubi et al. (2022) reported a positive relationship between the abundance of *Xiphinema* and Fe.

5. Conclusion

This study gives information on the nematode composition and soil food web structure in Kenyan maize-pigeon pea fields. Soil food web in Irabari region was degraded and in order to improve its status, it will be essential to integrate practices that improve the population of nematode functional groups that contribute to stability and resilience of an ecosystem. The main energy channel of organic matter decomposition in the studied regions was dominated by fungivores. For sustainable and active energy flow from organic material across some of the studied regions, there is need to incorporate suitable labile organic material at a rate required for crop growth.

Declarations

Author contribution statement

Samuel Maina: Performed the experiments; Analyzed and interpreted the data; Wrote the paper.

Hannah Karuri: Conceived and designed the experiments; Analyzed and interpreted the data; Contributed reagents, materials, analysis tools or data; Wrote the paper.

Julius Mugweru: Analyzed and interpreted the data; Contributed reagents, materials, analysis tools or data; Wrote the paper.

Funding statement

This work was supported by the CIRCLE research uptake fund.

Data availability statement

Data will be made available on request.

Declaration of interest's statement

The authors declare no conflict of interest.

Additional information

No additional information is available for this paper.

Acknowledgements

The authors thank the farmers from Embu County who participated in this work.

References

Abd-Elgawad, M.M.M., Askary, T.H., 2015. Impact of Phytonematodes on Agriculture Economy. Biocontrol Agents of Phytonematodes. CABI, Wallington, pp. 1–49.

Abuzar, S., Haseeb, A., 2009. Bio-management of plant-parasitic nematodes in pigeon pea field crop using neem-based products and manurial treatments. World Appl. Sci. J. 7 (7), 881–884.

Ali, S.S., Singh, B., 2005. Nematodes of Pigeonpea and Their Management. Advances in Pigeonpea Research. DK Agencies Pvt Limited, New Delhi, India, pp. 284–314.

Araújo, F., Inomoto, M.M., Godoy, R., Ferraz, L., 2010. Host response of Brazilian pigeonpea lines to *Rotylenchulus reniformis* and *Pratylenchus zeae*. Nematol. Bras. 34 (4), 204–210.

Askary, T.H., 2012. Management of root-knot nematode *Meloidogyne javanica* in pigeonpea through seed treatment. Indian J. Ecol. 39, 151–152.

Askary, Tarique Hassan, 2017. Diversity of plant parasitic nematodes in pulses. In: Plant Biodiversity: Monitoring, Assessment and Conservation. CAB International, pp. 239–274.

Jena, P. Sahoo, Mahalik, N.K., 2020. Occurrence, distribution and community analysis of plant parasitic nematodes associated with vegetable crops in the state of Chhattisgarh, India. J. Emerg. Technol. Innovat. Res. 4 (7), 1447–1457.

Berkelmans, R., Ferris, H., Tenuta, M., Van Bruggen, A.H.C., 2003. Effects of long-term crop management on nematode trophic levels other than plant feeders disappear after 1 year of disruptive soil management. Appl. Soil Ecol. 23 (3), 223–235.

Bongers, T., Bongers, M., 1998. Functional diversity of nematodes. Appl. Soil Ecol. 10 (3), 239–251.

Bridge, J., Starr, J., 2007. Plant Nematodes of Agricultural Importance: a Colour Handbook. Manson Publishing Ltd, 73 Corringham Road, London NW11 7DL, UK.

Bridge, J., Price, N.S., Kofi, P., 1995. Plant parasitic nematodes of plantain and other crops in Cameroon, West Africa. Fundam. Appl. Nematol. 18 (3), 251–260.

Coyne, D.L., Cortada, L., Dalzell, J.J., Claudius-Cole, A.O., Haukeland, S., Luambano, N., Talwana, H., 2018. Plant-parasitic nematodes and food security in Sub-Saharan Africa. Annu. Rev. Phytopathol. 56, 381–403.

Elling, A.A., 2013. Major emerging problems with minor *Meloidogyne* species. Phytopathology 103 (11), 1092–1102.

Esilaba, A.O., Nyongesa, D., Okoti, M., Otipa, M., Wasilwa, L., 2021. KCEP-CRAL Pigeon Peas Extension Manual. Kenya Agricultural and Livestock Research Organization. Elsevier, Nairobi, Kenya.

Faostat, 2020. Production/yield quantities of Pigeon peas and Maize in Kenya [WWW Document]. URL. https://www.fao.org/faostat/en/#data/QCL/visualize (accessed 4.5.22).

Ferris, H., 2010. Form and function: metabolic footprints of nematodes in the soil food web. Eur. J. Soil Biol. 46 (2), 97–104.

Ferris, H., Bongers, T., 2009. Indices developed specifically for analysis of nematode assemblages. In: Wilson, M.J., Kakouli-Duarte, T. (Eds.), Nematodes as Environmental Indicators. CABI Publishing, Wallingford, pp. 124–145.

Ferris, H., Matute, M.M., 2003. Structural and functional succession in the nematode fauna of a soil food web. Appl. Soil Ecol. 23 (2), 93–110.

Ferris, H., Tuomisto, H., 2015. Unearthing the role of biological diversity in soil health. Soil Biol. Biochem. 85, 101–109.

Ferris, H., Bongers, T., De Goede, R.G.M., 2001. A framework for soil food web diagnostics: extension of the nematode faunal analysis concept. Appl. Soil Ecol. 18 (1), 13–29.

Ferris, H., Pocasangre, L.E., Serrano, E., Muñoz, J., Garcia, S., Perichi, G., Martinez, G., 2012a. Diversity and complexity complement apparent competition: nematode assemblages in banana plantations. Acta Oecol. 40, 11–18.

Ferris, H., Sánchez-Moreno, S., Brennan, E.B., 2012b. Structure, functions and interguild relationships of the soil nematode assemblage in organic vegetable production. Appl. Soil Ecol. 61, 16–25.

Furstenberg, J.P., Heyns, J., 1978. The effect of cultivation on nematodes. Part I. *Rotylenchulus parvus*. Phytophylactica 10 (3), 77–80.

Gallaher, R.N., Weldon, C., Futral, J., 1975. An aluminium block digester for plant and soil analysis. Soil Science Society of America 39, 803–806. Proceedings.

Gaur, H.S., Singh, R.V., Kumar, S., Kumar, V., 2001. Search for nematode resistance in crops. In: AICRP on Plant Parasitic Nematodes with Integrated Approach for Their Control. IARI. Indian Agriculture Research Institute, Division of Nematology, New Delhi, India.

Gee, G.W., Bauder, J., 1985. Particle Size Analysis. In: In a Kluteed Methods of Soil Analysis Part 1 Agronomy Monograph No 9, second ed. American Society of Agronomy, Madison WI, pp. 385–411.

Gummadi, S., Kadiyala, M.D.M., Rao, K.P.C., Athanasiadis, I., Mulwa, R., Kilavi, M., Legesse, G., Amede, T., 2020. Simulating adaptation strategies to offset potential impacts of climate variability and change on maize yields in Embu County, Kenya. PLoS One 15, e0241147.

Hillocks, R.J., Minja, E., Mwaga, A., Nahdy, M.S., Subrahmanyam, P., 2000. Diseases and pests of pigeonpea in eastern Africa: a review. Int. J. Pest Manag. 46 (1), 7–18.

Hooper, D.J., Hallmann, J., Subbotin, S.A., 2005. Methods for extraction, processing and detection of plant and soil nematodes. In: Luc, M., Sikora, R.A., Bridge, J. (Eds.), Plant Parasitic Nematodes in Subtropical and Tropical Agriculture. CAB International, Wallingford, pp. 53–86.

International Trade Centre, 2016. Pulses sector investment profile Kenya. Kenya Pulses Sector Investment Profile.
Jackson, M.L., 1958. Soil Chemical Analysis. Prentice hall engelwood Cliffs NJ, USA.
Jaetzold, R., Schmidt, H., Hornetz, B., Shisanya, C., 2007. Farm Management Handbook of Kenya, Vol II, Natural Conditions and Farm Management Information. Ministry of Agriculture, East Kenya, p. 573.
Jones, J.T., Haegeman, A., Danchin, E.G.J., Gaur, H.S., Helder, J., Jones, M.G.K., Kikuchi, T., Manzanilla-López, R., Palomares-Rius, J.E., Wesemael, W.M.L., 2013. Top 10 plant-parasitic nematodes in molecular plant pathology. Mol. Plant Pathol. 14 (9), 946–961.
Kimenju, J.W., Wendot, P.K., Thuo, A.K., 2022. Cumulative demage impact of parasitic nematodes in smallholder maize cropping systems in East Africa. Integr. Nematode Manag. State-of-the-art visions Futur 48.
Lazarova, S., Coyne, D., Rodríguez, M., Peteira, B., Ciancio, A., 2021. Functional diversity of soil nematodes in relation to the impact of agriculture—a review. Diversity 13 (2), 64.
Macauley, H., Ramadjita, T., 2015. Cereal Crops: Rice, maize, Millet, Sorghum, Wheat, Feeding Africa. Abdou Diouf International Conference Center, Dakar, Senega, pp. 1–36.
Maina, S., Karuri, H., Ng'endo, R.N., 2020. Nematode metabolic footprints, ecological and functional indices in tropical maize-beans agro-ecosystems under different farming practices. Acta Oecol. 108, 103622.
Mc Donald, A.H., De Waele, D., Fourie, H., 2017. Nematode pests of maize and other cereal crops. In: Fourie, H., Spaull, V.W., Jones, R.K., Daneel, M.S., De Waele, D. (Eds.), Nematology in South Africa: A View from the 21st Century. Springer. Springer, Cham, Switz, pp. 183–199.
McDonald, A.H., Nicol, J.M., 2005. Nematode parasites of cereals. In: Luc, M., Sikora, R.A., Bridge, J. (Eds.), Plant Parasitic Nematodes in Subtropical and Tropical Agriculture. CAB International, Wallingford, pp. 131–192.
Ministry of Agriculture, 2015. Economic Review of Agriculture [ERA] 2015. Central Planning and Monitoring Unit, MoA. Ministry of Agriculture, Nairobi, Kenya.
Ojwang, J.D., Nyankanga, R., Ganga Rao, N.V.P.R.G., Imungi, J., 2021. Evaluation of vegetable pigeonpea [*Cajanus cajan* (L.) millsp] genotypes for yield stability. CABI Agricul. Biosci. 2 (1), 41.
Oka, Y., 2010. Mechanisms of nematode suppression by organic soil amendments - a review. Appl. Soil Ecol. 44, 101–115.
Okada, H., Harada, H., 2007. Effects of tillage and fertilizer on nematode communities in a Japanese soybean field. Appl. Soil Ecol. 35 (3), 582–598.
Pokharel, R.R., 2009. Damage of root-knot nematode (*Meloidogyne graminicola*) to rice in fields with different soil types. Nematol. Mediterr. 37 (2), 203–217.
Rao, S.C., Coleman, S.W., Mayeux, H.S., 2002. Forage production and nutritive value of selected pigeonpea ecotypes in the southern great plains. Crop Sci. 42 (4), 1259–1263.
Rawal, V., Navarro, D.,K., 2019. The Global Economy of Pulses. Food and Agriculture Organization of the United Nations, Rome. http://www.fao.org/3/i7108en/I7108EN.pdf.
Reddy, M.V., Subrahmanyam, P., Likoswe, A.A., Saka, V.W., Msuku, W.A.B., 1993. Pigeonpea diseases in Malawi. Plant Prot. 41 (2), 101–106.
Sánchez-Moreno, S., Ferris, H., 2018. Nematode ecology and soil health. In: Sikora, R.A., Coyne, D., Hallmann, J., Timper, P. (Eds.), Plant Parasitic Nematodes in Subtropical and Tropical Agriculture, third ed. CAB International, pp. 62–83.
Saxena, R.K., Von Wettberg, E., Upadhyaya, H.D., Sanchez, V., Songok, S., Saxena, K., Kimurto, P., Varshney, R.K., 2014. Genetic diversity and demographic history of *Cajanus* spp. illustrated from genome-wide SNPs. PLoS One 9 (2).
Sharma, S.B., McDonald, D., 1990. Global status of nematode problems of groundnut, pigeonpea, chickpea, sorghum and pearl millet, and suggestions for future work. Crop Protect. 9 (6), 453–458.
Sharma, S.B., Siddiqi, M.R., Omanga, P., Singh, L., 1993. Distribution and potential importance of plant-parasitic nematodes associated with pigeonpea in Kenya. Afro-Asian J. Nematol. 3 (2), 182–187.
Shiferaw, B., Prasanna, B.M., Hellin, J., Bänziger, M., 2011. Crops that feed the world 6. Past successes and future challenges to the role played by maize in global food security. Food Secur. 3, 307.
Siebert, J., Ciobanu, M., Schädler, M., Eisenhauer, N., 2020. Climate change and land use induce functional shifts in soil nematode communities. Oecologia 192 (1), 281–294.
Sieriebriennikov, B., Ferris, H., De Goede, R.G.M., 2014. NINJA: an automated calculation system for nematode-based biological monitoring. Eur. J. Soil Biol. 61, 90–93.
Sikora, R.A., Greco, N., Silva, J.F.V., 2005. Nematode parasites of food legumes. Plant Parasit. Nematodes Subtropical Trop. Agric. 259–318.
Sikora, R.A., Greco, N., Silva, J.F.V., 2018. Nematode parasites of food legumes. Plant Parasit. Nematodes Subtropical Trop. Agric. 259–318.
Singh, N., Rai, V., Singh, N.K., 2020. Multi-omics strategies and prospects to enhance seed quality and nutritional traits in pigeonpea. Nucleus 63 (3), 249–256.
Smith, J., Doran, J., 1996. Measurement and use of electrical conductivity for soil quality analysis. In: Doran JW. Soil Science Society of America: Jones AJ Eds. Methods for Assessing Soil Quality. Soil science society of America special publication Madison WI, pp. 169–185.
Snapp, S.S., Jones, R.B., Minja, E.M., Rusike, J., Silim, S.N., 2003. Pigeon pea for Africa: a versatile vegetable-and more. Hortscience 38 (6), 1073–1079.
Souto, T.G., Godoy, R., Inomoto, M.M., 2011. Additional list of pigeon pea lines resistant to *Pratylenchus zeae*. Nematol. Bras. 35 (3/4), 78–81.
Steel, H., Ferris, H., 2016. Soil nematode assemblages indicate the potential for biological regulation of pest species. Acta Oecol. 73, 87–96.
Tenuta, M., Ferris, H., 2004. Sensitivity of nematode life-history groups to ions and osmotic tensions of nitrogenous solutions. J. Nematol. 36 (1), 85–94.
Varshney, R.K., Saxena, R.K., Jackson, S.A., 2017. The pigeonpea genome: an overview. In: The Pigeonpea Genome. Springer, pp. 1–4.
Villenave, C., Saj, S., Pablo, A., 2010. Influence of long-term organic and mineral fertilization on soil nematofauna when growing Sorghum bicolor in Burkina Faso. J. Biol. Fertil. Soils 46, 659–670.
Wiesel, L., Daniell, T.J., King, D., Neilson, R., 2015. Determination of the optimal soil sample size to accurately characterise nematode communities in soil. Soil Biol. Biochem. 80, 89–91.
Yeates, G.W., 2003. Nematodes as soil indicators: functional and biodiversity aspects. Biol. Fertil. Soils 37 (4), 199–210.
Yeates, G.W., Bongers, T.D., De Goede, R.G.M., Freckman, D.W., Georgieva, S.S., 1993. Feeding habits in soil nematode families and genera an outline for soil ecologists. J. Nematol. 25 (3), 315–331.
Zhao, D., Wang, Y., Wen, L., Qu, H., Zhang, Z., Zhang, H., Jia, Y., Wang, J., Feng, Y., Li, Y., 2022. Response of soil nematode community structure and function to monocultures of pumpkin and melon. Life 12 (1), 102.
Zoubi, B., Mokrini, F., Dababat, A.A., Amer, M., Ghoulam, C., Lahlali, R., Laasli, S.-E., Khfif, K., Imren, M., Akachoud, O., Benkebboura, A., Housseini, A.I., Qaddoury, A., 2022. Occurrence and geographic distribution of plant-parasitic nematodes associated with citrus in Morocco and their interaction with soil patterns. Life.