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Organic maize and bean farming enhances free-living nematode dynamics in sub-Saharan Africa

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ABSTRACT

Despite their important ecological roles for soil health and soil fertility, free-living nematodes (FLN) have received relatively limited research attention. The present study evaluated the community structure and diversity of FLN in a field setting. The experiments were conducted in on-farm and on-station field plots sown to maize (*Zea mays*) and beans (*Phaseolus vulgaris*) under four cropping practices. These farming systems included organic (compost and biopesticide use), conventional (synthetic fertilizer and pesticide applications), farmer practice (organic and synthetic amendments) and a control (non-amended plots). Nineteen genera of free living nematodes, belonging to bacterivores, fungivores, omnivores and predators were recorded. Among these, bacterivores (Cephalobidae and Rhabditidae) were the most dominant group in the organic systems when compared to the conventional and control systems. Farming systems influenced the abundance and diversity of free living nematodes, with the organic farming system having higher values of maturity, enrichment and structural indices than other farming systems. This would indicate greater stability in soil health and improved soil fertility. This implies that the organic farming systems play a key role in improving the biodiversity and population buildup of FLN, compared with other systems. Our study helps to improve our understanding of how farming systems influence soil biodynamics, while studies on the longer-term effects of organic and conventional farming systems on the build-up or reduction of free living nematodes for improved ecosystem services are needed.

1. Introduction

Soil-dwelling nematodes comprise a diverse range of genera that can be grouped according to their feeding habits (Yeates et al., 1993); the two major groupings include plant-parasitic nematodes (PPN) and free-living nematodes (FLN). For the FLN, trophic groups are assigned as fungivores, bacterivores, omnivores and predators (Ingham et al., 1996). Traditionally, PPN have received much greater attention than FLN (Andrássy, 2009), despite FLN generally occurring in higher densities than PPN, whether in the presence or absence of crops (Buckley and Schmidt, 2003; Ferris et al., 2012). This is changing however, as knowledge and awareness on the benefits of FLN are gained, stimulating interest and activity in this area.

Whereas plant-parasitic nematodes are recognized for causing damage to crops, free living nematodes have been credited for their beneficial contribution to the rhizosphere and importance for crop production (Neher and Darby, 2009; Sanchez-Moreno and Ferris, 2018). For example, when FLN are present in high densities, higher levels of soil mineralization are observed, particularly nitrogen, which has been attributable to the activities of bacterivores and predators (Ferris et al., 1998). Furthermore, fungivores are reported to play a leading role in facilitating the release of available nitrogen in the soil during feeding (Ingham et al., 1996). This role of FLN has been recognized and increasingly used as indicators of soil health (Tabarant et al., 2011; Ürkmez et al., 2014; Tamburini et al., 2016; Sanchez-Moreno and Ferris, 2018).

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Aside from their role as bioindicators of soil health, some free living nematodes have been exploited for their biocontrol potential (Ester and Wilson, 2005; Denno et al., 2008). Some entomopathogenic bacterivore nematodes, for example, have been reared and produced as commercial biocontrol products for insect pests (Gaugler et al., 1997; Hominick, 2002; Adams et al., 2006) and mollusc pest control (Ishibashi, 2005; Zolfagharian et al., 2016; El-Danasoury and Iglesias-Piñeiro, 2017; Saeedizadeh and Niasti, 2020). On the other hand, predatory nematodes have been well-documented to significantly reduce PPN levels in the soil (Bilgrami and Brey, 2005; Bilgrami et al., 2006; Khan and Kim, 2007; Bilgrami, 2008; Askary and Abd-Elgawad, 2017). For example, Diplogasterids are considered the most suitable for biocontrol of PPN, due to their short life cycle (Khan and Kim, 2007), although their generalistic feeding nature has limited their use for PPN management (Bilgrami et al., 2008).

In soils, the natural decline in free living nematode densities has been attributable to various biotic and abiotic factors (Wachira et al., 2009). The availability of food, competition with other soil microorganisms and predation by other organisms (such as nematophagous fungi, tardigrades, insects, mites, and predatory nematodes) can be the major factors responsible for their rapid decline (Bouwman et al., 1996; Stirling, 2014; Moosavi and Zare, 2020). Numerous other factors, however, such as soil contamination with synthetic pesticides and fertilizers, drought and soil disturbance from tillage practices can also severely impact their densities and diversity (Sanchez-Moreno and Ferris, 2018). Wang et al. (2006) demonstrated, for instance, that nitrogen fertilizer (ammonium nitrate) application reduces FLN densities, especially omnivores. Neher (2010) and Sanchez-Moreno and Ferris (2018) also showed that the use of synthetic nematicides for the management of PPN, have over time adversely affected FLN community structure and diversity.

Organic farming and the application of organic matter is known to effectively stimulate soil biodiversity, compared to conventional farming – depending on management practices, land use and climatic conditions (Tuck et al., 2014; Lori et al., 2017; Anyango et al., 2020; Stein-Bachinger et al., 2021). The application of manure can enhance microbial activity, which in turn provides food for bacterivores and their rapid multiplication (Neher, 1999; Sanchez-Moreno and Ferris, 2018). Furthermore, the application of organic amendments, such as neem, leads to the reduction of PPN, and conversely, an increase in predatory nematodes and free living nematodes in general (Akhtar and Mahmood, 1996; Bulluck et al., 2002; Thoden et al., 2011). Separate studies, however, have shown the opposite, with decreased densities of bacterivores and fungivores following the addition of manure (Hasna et al., 2007; Okada and Harada, 2007; Villenave et al., 2010). Consequently, although organic amendments have a positive impact on FLN assemblages and incidence in general, reports and recommendations can be conflicting and inconclusive (Kimpinski et al., 2003; Nahar et al., 2006; Villenave et al., 2010; Thoden et al., 2011). In part, this is likely due to the limited number of studies in this area, although this is beginning to change. In particular, there is very limited understanding of how such amendments affect FLN assemblages in the longer term in tropical regions, such as across sub-Saharan Africa (Liang et al., 2009; Yeates and Newton, 2009; Villenave et al., 2010).

Using an on-going long term study, the objectives of the current study were to examine the influence of (i) farming systems (organic and conventional) and cropping sytems (maize intercropped with beans in rotation with sole bean cropping) on the abundance and diversity of free living nematode communities; (ii) to identify key nematode parameters or indices that may be linked to soil health; and (iii) to determine the effect of farming systems on nematode genera over time. The study was conducted in the Participatory On-farm Research (POR) plots in Kenya, within the framework of the "Farming systems comparison trials in the tropics" (SysCom). A related study on PPN from the same trials is reported separately (Atandi et al., 2017).

2. Methodology

2.1. Study area

The study was conducted in the mid-altitude (1458 m), central highlands of Kenya at Chuka, Tharaka Nithi County (0.3229° S, 37.6546° E) (Atandi et al., 2017). The area receives a bi-modal mean rainfall of 2000 mm: long rains (Mar-Jun) and short rains (Oct-Dec) with a temperature range of 19.2–20.6 °C. The area is characterized by red loam soils that are well drained, fertile, and classified as humic nitisols (Wagate et al., 2010). The ratio of sand, silt and clay aligns with reported values of 9.4%, 16.6% and 74.0%, respectively (Adamtey et al., 2016). The soil quality appears to have degraded over the duration of the experiment and soil chemical analyses were therefore undertaken to establish baseline information (Table 1). Farming is primarily conducted by smallholder farmers on 0.5–1 ha of land with potatoes (*Solanum tuberosum*), maize (*Zea mays*), beans (*Phaseolus vulgaris*), sorghum (*Sorghum bicolor*), bananas (*Musa* spp.) and avocado (*Persea americana*) as the predominantly grown crops (Adamtey et al., 2016).

2.2. Experimental design

Under ongoing participatory on-farm research (POR), established in March 2013 to compare farming systems, two trial designs were conducted: "on-farm" (researcher designed but farmer managed) and "on-station" (researcher designed and managed), with assessments for the current study made over two consecutive cropping seasons between March 2015 and February 2016. The on-farm trial was divided between four farmer fields in close proximity (approximately 0.5–0.8 km between farms), with each farmer field representing a replicate of four treatments. The on-station trial, located 1 km maximum from the farms, was arranged in a randomized complete block design (RCBD) with four replicates. In each trial, there were four plots with four practices: organic (1) and conventional management (2) alongside farmer practice (combined application of organic and industrial amendments including pesticides) (3) and a non-amended plot (designated as control) (4). The details of the amendments are as shown in (Table 2): organic (entirely avoided the use of synthetic pesticides and inorganic fertilizers), conventional (received industrial fertilizer and pesticides) and farmer practice (received organic and conventional treatments). Table 3 shows the chemical properties of the amendments that were applied.

2.3. Cropping system and management practices

In the first season (long rains), maize (cv H513) and beans (cv KAT B9) were row intercropped, with a spacing of 60 cm within rows and 75 cm between rows of maize and 30 cm within rows and 75 cm between rows of beans. Two seeds of each crop were sown per planting hole after hand tillage to a depth of 20 cm using a hoe. In the second season (short rains), beans were sown as a sole crop at a spacing of 30 × 45 cm. All

Table 1
Initial soil chemical characteristics of the study areas in Chuka, Kenya (Atandi et al., 2017).

Parameter[a]	On-farm	On-station
pH	5.82 ± 0.19	5.18 ± 0.05
Electrical conductivity(S) (μS/cm)	80.00 ± 8.03	99.00 ± 0.58
Cation exchange capacity (meq/100 g)	16.74 ± 0.86	16.10 ± 0.03
Soil organic carbon (%)	23.60 ± 0.80	23.20 ± 0.90
Nitrogen total (%)	2.30 ± 0.10	2.40 ± 0.70
Phosphorus (Olsen) (mg kg^{-1})	28.38 ± 4.27	29.48 ± 5.16
Potassium (Cmolc kg^{-1})	0.90 ± 0.16	0.31 ± 0.02
Calcium (Cmolc kg^{-1})	8.59 ± 1.09	5.85 ± 0.26
Magnesium (Cmolc kg^{-1})	2.58 ± 0.25	2.25 ± 0.16
Sodium (Cmolc kg^{-1})	0.25 ± 0.03	0.19 ± 0.01

[a] μS – micro siemens, meq – milliequivalent.

Table 2
Soil amendments applied at planting time in each season to the four designated farming systems in Chuka, Kenya (Atandi et al., 2017).

Farming system	Fertilizer	Pesticides
Farmer practice	2640 kg ha^{-1} FYM[a] and 256 kg ha^{-1} DAP[b]	8000 kg ha^{-1} Wood ash
Organic	4640 kg ha^{-1} Compost and 4312 kg ha^{-1} Tithonia mulch	448 kg ha^{-1} Neem cake
Conventional	512 kg ha^{-1} CAN[c] and 294.4 kg ha^{-1} DAP[b]	4000 kg ha^{-1} Marshal[d] EC
Non-amended Control	Fertilizer not applied	Pesticides not applied

[a] FYM = Farmyard manure.
[b] DAP = Di-ammonium phosphate.
[c] CAN = calcium ammonium nitrate.
[d] Marshal – active ingredient used as seed coat and applied at planting.

plots measured 5 × 5 m with a 1 m buffer zone between plots.

Depending on the treatment, the trial plots received different types of fertilizers to boost plant growth (Table 2). No additional water was added as the trials were strictly rainfed. The trials were hand weeded twice per season to manage weed species, which were similar across plots. Apart from the pesticides applied during planting (Table 2), no additional chemical pesticides were applied. In this manuscript, we describe the management practices together with the crops and the cropping pattern as a farming system.

2.4. Nematode sampling and analyses

Soil was sampled at pre-plant, vegetative, flowering and crop harvest, from five sample-points per plot, using a cross-diagonal pattern, which were bulked (Atandi et al., 2017). Nematodes were extracted from 100 ml sub-samples per plot using a modified Baermann technique (Coyne et al., 2014), killed and fixed using 60 °C water and 37% formaldehyde (Bezooijen, 2006) and densities estimated from 3 × 1 ml aliquots from a 10 ml suspension under a Leica MZ12 stereo-microscope. Using the first 100 nematodes per sample, nematodes were identified to genus level (KSU, 2016; UNL, 2016).

2.5. Nematode community structure

2.5.1. Nematode characterization

Nematode abundance was based on trophic groups (Yeates et al., 1993) and assigned to functional guilds, then classified along the colonization-persistence gradient (cp values) (Table 3) according to Bongers (1990), Bongers and Bongers (1998) and Ferris et al. (2001).

2.5.2. Nematode faunal indices

The FLN possess attributes that can reflect below-ground modifications from changes in land management (Dong et al., 2008). Therefore, a range of indices (genus richness, Shannon diversity index, maturity index, enrichment index and structural index) were computed according to Neher et al. (2004) for use as soil health indicators as described below:

2.5.2.1. Genus richness and Shannon index. To determine the number of taxa present in each sample, genus richness was calculated using the formula:

$$Genusrichness(d) = (S–1)logN$$

where S = number of genera and N = total number of nematodes.

However, because genus richness merely represents the number of taxa, without mentioning the identity or ecological diversity of the genera, the Shannon index was additionally calculated. The Shannon wiener, sometimes called the Shannon weaver index, is a measurement of diversity that accounts for both the genus richness and the proportion of each genus within a community (Begon et al., 1996) and calculated as:

$$\text{Shannonindex}\left(H'\right) = -\sum Pi\left(\ln Pi\right)$$

where $_{\text{Pi}}$ = proportion of trophic group i in the total nematode community.

2.5.2.2. Maturity index. To determine the effects of organic and conventional farming on the condition of the soil food web, a maturity index was determined, which is a measure of soil disturbance, based on the life history of soil nematodes (Neher et al., 2014). Low maturity index (< 2) typically indicates a disturbed environment, low soil food web maturity but rapid organic matter decomposition, whereas high maturity index indicates a less disturbed environment with high food web maturity (Sánchez-Moreno et al., 2011; Neher et al., 2014; Sanchez-Moreno and Ferris, 2018) (Table 4). It is calculated as:

MI = $\frac{\sum(V_i X f_i)}{\sum N}$ where V_i = colonizer-persister value of genus i, f_i = frequency of genus i in the sample, and N = total number of nematodes in the sample (Ürkmez et al., 2014).

2.5.2.3. Enrichment and structural indices. To compare the effects of farming systems on nutrient enrichment and soil stability, enrichment index and structural index were calculated (Ferris et al., 2001). Both indices are considered important descriptors of the food web. Bacterivores and fungivores in cp1 and cp2, respectively, are known to be indicators of enrichment (*e*); cp3–5 nematodes are indicators of structure (*s*); while cp2 nematodes are considered basal (*b*) to both enrichment and structure. The nematodes are weighted according to growth and resource utilization (Neher and Darby, 2006), where cp1 weight (W) = 3.2, cp2 = 0.8, cp3 = 1.8, cp4 = 3.2 and cp5 = 5.0.

Therefore:

$$Enrichment\ index = 100xe/e + b$$
$$Structural\ index = 100xs/s + b$$

Table 3
Properties of the soil amendments applied each season to the four designated farming systems in Chuka, Kenya.

Property	N[a] (%)	P[b] (%)	K[c] (%)	OC[d] (%)	Ca[e] (%)	C:N[f] Ratio	Dry matter (%)	pH
DAP	18	46	0	0.28	–	–	–	8
Compost	1.15	0.24	2.03	14.61	1.42	12.7	94.8	9
Manure	1.41	0.26	1.52	35.23	1.24	9.86	94.8	8.78
Neem cake	2.16	0.87	1.46	28.90	2.68	–	90	–
Tithonia	0.17	0.30	1.30	29.97	–	–	–	–
Ash	–	5.40	0.40	4.56	0.24	–	–	–

[a] N = Nitrogen.
[b] P = Phosphorus.
[c] K = Potassium.
[d] OC = Organic Carbon.
[e] Ca = Calcium.
[f] C:N = Carbon to nitrogen ratio.

Table 4
Proposed threshold for determining ecological quality of an environment (adapted from Sanchez-Moreno et al., 2011).

Indicator	High	Good	Moderate	Poor	Bad
MI	> 2.8	2.8–2.6	2.6–2.4	2.4–2.2	≤ 2.2
cp	cp2 ≤ 50% cp4 > 10%	cp2 ≥ 50% cp4 > 10%	cp2 ≥ 50% cp3 < cp4 < 10%	cp2 > 60% cp4 < 3%	cp2 > 80%

MI – Maturity index; cp – colonizer-persister value (cp values represent the nematode generation cycle where 1 is shortest while 5 is longest).

where b = (Bacterivore cp2 + Fungivore cp2) x Weight cp2e = (Bacterivore cp1 x Weight cp1) + (Fungivore cp2 x Weight cp2) s = (Bacterivore n x Weight n) + (Predator n x Weight n) + (Fungivore n x Weight n) + (Omnivore n x Weight n) where n = 3–5.

2.5.3. Effect of time on nematode genera

Principal response curves (PRC) were used to show the effect of farming systems over time on individual FLN genera. The non-amended control was used as the reference treatment to show the baseline relative to which other treatments are compared (Vendrig et al., 2017). This was calculated from the abundance of each genus as a sum of three terms: mean abundance in the control, a month-specific treatment effect (farming system), and an error (van den Brink and Ter Braak, 1999). Owing to limitations in standard PRC to have a minimum number of time-points (four), PRC was used for the maize-bean intercrop season only, which had five time-points (bean sole crop was invalid as it only had three time-points) following the formula:

$$Y_{d(j)tk} = y_{0tk} + b_k c_{dt} + \sum_{d(j)tk}$$

where $Y_{d(j)tk}$ = abundance of genus k (=19) in replicate j (=4) of treatment d (=4) at time t (0–5 months); y_{0tk} = mean abundance of genus k in month t in the control; b_k = genus weight; c_{dt} = least-squares estimate of the coefficients; and $\sum_{d(j)tk}$ = a random error term.

2.6. Statistical analyses

To meet assumptions of normality, nematode data were first transformed to their natural log [ln(x + 1)], where necessary, before analysis. Abundance data were subjected to a two-way analysis of variance (ANOVA) to compare farming systems and trial sites. Fisher's least significant difference (LSD) test was used to separate means, where differences at $P \leq 0.05$ were considered significant, using the package "agricolae" (De Mendiburu, 2015). The statistical package R version 3.2.3 was used for all analyses (R Core Team, 2015). The package "vegan" was used to assess the significance of the PRC model (Oksanen et al., 2015).

3. Results

3.1. Effect of farming systems on free-living nematode composition

Throughout the study, a total of 19 genera from four nematode trophic groups (Bacterivores, fungivores, omnivores and predators), representing 11 families were identified: Aphelenchoididae (*Aphelenchoides*) (fungivore); Aphelenchidae (*Aphelenchus*) (fungivore); Cephalobidae (*Acrobeles, Cephalobus, Chiloplacus* and *Eucephalobus*) (bacterivores); Diplogasteridae (*Diplogaster*) (bacterivore), Dorylaimidae (*Discolaimus* and *Dorylaimus*) (omnivores); Thornematidae (*Prodorylaimus*) (omnivore); Monhysteridae (*Monhystera*) (bacterivore); Mononchidae (*Mononchus*) (predator); Plectidae (*Plectus* and *Wilsonema*) (bacterivores); Rhabditidae (*Mesorhabditis*, *Oscheius* and *Rhabditis*) (bacterivores); and Qudsianematidae (*Eudorylaimus* and *Labronema*) (omnivores) across the farming systems. These 19 genera were recovered during the maize-bean intercropping season, while only 13 genera were recorded from bean sole crop trial plots (Table 5).

From the on-farm trials, 18 and 13 nematode genera were recovered during the maize-bean intercropping trial and bean sole cropping trial, respectively. Maize-bean intercrop trial had a total of 12, 13, 15 and 16 genera of FLN identified in the control, conventional, farmer practice and organic systems, respectively (Table 5). On the other hand, the bean sole crop trial showed a total of 9, 10, 11 and 12 genera recovered from the farmer practice, control, conventional and organic farming system, respectively (Table 5). The abundance of fungivores *Aphelenchus,* omnivores *Dorylaimus* and *Labronema* and bacterivores *Monhystera* and *Rhabditis* varied considerably, with higher ($P \leq 0.05$) values recorded across the various farming systems (Table 6).

From the on-station trials, 15 and 13 nematode genera were recovered from the maize-bean intercropping trial and bean sole cropping trial, respectively. From the control, conventional, farmer practice and organic farming systems, 7, 10, 10 and 12 FLN genera were identified, respectively, during the maize-bean intercrop. Similarly, under bean sole crop trial 7, 9, 11 and 11 genera were identified from farmer practice, conventional, control and organic farming systems, respectively (Table 7). Significant differences ($P \leq 0.05$) were observed in the densities of nematode genera among the farming systems. Bacterivore nematodes belonging to the genera *Cephalobus*, *Rhabditis* and *Monhystera* were more abundant in the organic system, whereas omnivorous nematodes belonging to the genera *Dorylaimus* and *Labronema* dominated the conventional system (Table 7).

3.2. Effect of farming systems on trophic groupings and soil health parameters

On-farm trials showed a significant variation ($P \leq 0.05$) in trophic group composition among the farming systems under both maize/bean intercropping and bean sole cropping. Farming system influenced trophic group composition, with higher ($P \leq 0.05$) FLN densities, especially bacterivores, which consisted of up to three times the combined number of omnivores, fungivores and predators in organic systems (Table 8). The highest densities of bacterivores occurred in the organic system in both cropping systems, whilst a three-fold and two-fold decrease in bacterivores was observed in the conventional farming under intercrop and sole crop system, respectively. Densities of omnivores and predatory nematodes remained relatively low ($P \leq 0.05$) during the research period, across the trials, when compared to other trophic groups under intercrop and sole crop.

No significant differences were observed for genus richness or Shannon diversity between farming system in either intercrop or sole crop systems. However, maturity index varied ($P \leq 0.05$) among the farming systems under both intercrop and sole cropping system (Table 8). maturity index was especially higher under non-amended control and organic farming than in the conventional farming under both cropping systems. Under the intercrop system, the enrichment index and structural index showed variation with significantly ($P \leq 0.05$) higher values recorded in the organic farming. However, no variation in enrichment index and structural index was observed under the sole cropping system.

In the on-station trials, a similar trend was observed with trophic group variation and soil health parameters among the farming systems under the two cropping sytems. Abundance of bacterivore nematodes was consistently higher ($P \leq 0.05$) than other trophic groups with organic farming recording up to three times the combined number of fungivores, omnivores and predators under both cropping systems (Table 8). Densities of predatory and omnivorous nematodes were

Table 5
Presence and classification of free-living nematodes recovered from trials at Chuka in Tharaka Nithi county, Kenya under intercropping and sole cropping systems.

Family	Genus	cp value*	Trophic group	On-farm		On-station	
				Maize/Bean intercrop	Bean sole crop	Maize/Bean intercrop	Bean sole crop
Aphelenchoidae	Aphelenchoides	2	Fungivore	+	+	+	+
Aphelenchidae	Aphelenchus	2	Fungivore	+	+	+	+
Cephalobidae	Acrobeles	2	Bacterivore	+	+	+	+
	Cephalobus	2	Bacterivore	+	+	+	+
	Chiloplacus	2	Bacterivore	+	–	–	–
	Eucephalobus	2	Bacterivore	+	+	+	+
Diplogasteridae	Diplogaster	1	Bacterivore	–	–	+	–
Dorylaimidae	Discolaimus	5	Predator	+	+	+	+
	Dorylaimus	4	Omnivore	+	+	+	+
Monhysteridae	Monhystera	1	Bacterivore	+	–	+	–
Mononchidae	Mononchus	4	Predator	+	+	+	+
Plectidae	Plectus	2	Bacterivore	+	+	+	+
	Wilsonema	2	Bacterivore	+	–	–	–
Rhabditidae	Oscheius	2	Bacterivore	+	–	+	–
	Rhabditis	1	Bacterivore	+	+	+	+
	Mesorhabditis	1	Bacterivore	+	–	–	–
Thornematidae	Prodorylaimus	5	Omnivore	+	+	–	+
Qudsianematidae	Eudorylaimus	4	Omnivore	+	+	+	+
	Labronema	4	Predator	+	+	+	+

*cp value represents the nematode generation cycle where 1 is shortest while 5 is longest.

Table 6
Percentage contribution of free-living nematode genera to the nematode assemblage in different farming systems under maize/bean intercrop and bean sole crop at POR on-farm trials in Chuka, Tharaka Nithi County, Kenya.

Genus	cp	Farmer practice		Organic		Conventional		Control	
	value	Maize/Bean intercrop	Bean sole crop	Maize/Bean intercrop	Bean sole crop	Maize/Bean intercrop	Bean sole crop	Maize/Bean intercrop	Bean sole crop
Acrobeles spp.	2	0.13 b	0.00 b	4.27 c	1.30 b	0.00 c	0.00 c	0.00 c	0.00 c
Cephalobus spp.	2	34.63 a	10.98 b	23.33 a	27.94 a	30.65 a	8.71 bc	12.57 bc	6.23 bc
Diplogasterid spp.	1	0.00 b	0.00 b	0.00 c	0.00 b	0.00c	0.00 c	0.00 c	0.00 c
Chiloplacus spp.	2	1.68 b	0.00 b	0.93 c	0.00 b	0.00c	0.00 c	0.00 c	0.00 c
Eucephalobus spp.	2	8.32 b	7.90 b	1.86c	8.43 b	2.75c	6.48 c	5.66 c	6.43 bc
Monhystera spp.	1	0.00 b	0.00 b	16.98 b	0.00 b	0.00 c	0.00 c	0.00 c	0.00 c
Oscheius spp.	2	0.00 b	0.00 b	0.30 c	0.00 b	0.07 c	0.00 c	2.28 c	0.00 c
Plectus spp.	2	0.67 b	7.10 b	1.91 c	8.43 b	2.74 c	0.00 c	2.31 c	5.46 bc
Rhabditis spp.	1	9.83 b	14.81 b	19.31 ab	25.95 a	5.42 c	9.33 bc	6.66 c	10.92 b
Mesorhabditis spp.	1	1.33 b	0.00 b	0.00 c	0.00 b	0.00 c	0.00 c	0.00 c	0.00 c
Wilsonema spp.	2	3.41 b	0.00 b	8.72 c	0.00 b	0.00 c	0.00 c	0.00 c	0.00 c
Aphelenchoides spp.	2	0.36 b	0.99 b	3.56 c	0.05 b	7.31 c	5.94 c	0.00 c	5.46 bc
Aphelenchus spp.	2	4.98 b	0.99 b	10.66 bc	7.78 b	15.42 b	11.03 b	0.72 c	12.28 b
Dorylaimus spp.	4	29.66 a	52.31 a	2.17 c	7.78 b	0.13 c	12.72 b	4.13 c	12.29 b
Eudorylaimus spp.	4	0.46 b	2.96 b	0.00 c	0.00 b	0.89 c	2.54 c	1.00 c	0.00 c
Labronema spp.	4	1.71 b	0.00 b	1.42 c	4.54 b	32.13 a	20.35 a	37.83 a	27.29 a
Prodorylaimus spp.	5	1.33 b	0.00 b	0.67 c	3.24 b	0.71 c	10.18 bc	21.71 b	2.73 c
Discolaimus spp.	5	0.00 b	0.00 b	1.25 c	1.95 b	0.52 c	3.39 c	1.00 c	0.00 c
Mononchus spp.	4	1.50 b	1.97 b	2.66 c	2.59 b	1.26 c	9.33 bc	4.13 c	10.92 b

cp values represent the nematode generation cycle where 1 is shortest while 5 is longest. Means separated by least significant difference; means followed by same letter (s) along columns indicate no significant differences at $p \leq 0.05$.

constantly low or completely absent across the farming systems during both intercrop and sole crop systems. Genus richness and Shannon diversity were similar across farming systems and cropping systems. Non-amended control and organic farming recorded significantly higher maturity index values under inter- and sole crop systems. Organic farming again recorded higher values of enrichment index and structural index under the intercrop system but no differences between the farming systems were observed under the sole cropping system.

3.3. Effect of farming systems on the dynamics of free-living nematode genera over time

From the on-farm trials, the multivariate PRC showed bacterivore (*Monhystera* spp.), omnivore (*Eudorylaimus* spp.) and fungivore (*Aphelenchus* spp.) nematodes as the main drivers of the curve (Fig. 1a). The genus *Discolaimus* (predator) was least affected by farming system. Farmer practice recorded the highest abundance of nematodes throughout the season, whereas a similarly low abundance of nematodes was recorded from organic and conventional farming systems.

On-station trials showed a similar trend on the PRC with differences observed on individual nematode genera abundance. Here, the bacterivore genera *Oscheius*, *Diplogasterid* and *Plectus* as well as the fungivore *Aphelenchus* spp. were responsible for the PRC curve but the predatory nematodes *Discolaimus* spp. were again scarce (Fig. 1b). Farmer practice again recorded the highest abundance of nematodes, while organic and conventional systems remained low. The densities of nematodes constantly fluctuated following planting (month 1.5) and remained low until harvest (month 5) in both the organic and conventional system.

Table 7
Percentage contribution of free-living nematode genera to the nematode assemblage in different farming systems under maize/bean intercrop and bean sole crop at POR on-station trials in Chuka, Tharaka Nithi County, Kenya.

Genus	Cp	Farmer practice		Organic		Conventional		Control	
	value	Maize/Bean intercrop	Bean sole crop	Maize/Bean intercrop	Bean sole crop	Maize/Bean intercrop	Bean sole crop	Maize/Bean intercrop	Bean sole crop
Acrobeles spp.	2	0.00 c	0.00 d	2.85 c	3.35 d	1.45 c	1.74 c	0.00 d	2.91 c
Cephalobus spp.	2	17.75 b	13.20 b	18.96 b	31.12 a	21.00 b	15.32 b	35.64 a	0.00 c
Diplogasterid spp.	1	1.25 c	0.00 d	0.00 c	0.00 d	0.00 c	0.00 c	0.00 d	0.00 c
Chiloplacus spp.	2	0.00 c	0.00 d	0.00 c	0.00 d	0.00 c	0.00 c	0.00 d	0.00 c
Eucephalobus spp.	2	5.89 c	6.05 c	4.11 c	10.61 c	0.00 c	5.37 c	3.28 d	9.85 b
Monhystera spp.	1	0.00 c	0.00 d	4.11 c	0.00 d	0.00 c	0.00 c	0.00 d	0.00 c
Oscheius spp.	2	0.17 c	0.00 d	12.54 bc	0.00 d	0.00 c	0.00 c	0.00 d	0.00 c
Plectus spp.	2	2.69 c	2.58 cd	5.66 c	12.13 c	8.98 c	1.32 c	0.00 d	1.86 c
Rhabditis spp.	1	13.11 bc	16.81 ab	35.78 a	21.43 b	7.56 c	30.07 a	11.43 c	16.42 a
Mesorhabditis spp.	1	0.00 c	0.00 d	0.00 c	0.00 d	0.00 c	0.00 c	0.00 c	0.00 c
Wilsonema spp.	2	0.00 c	0.00 d	0.00 c	0.00 d	0.00 c	0.00 c	0.00 d	0.00 c
Aphelenchoides spp.	2	0.78 c	0.00 d	0.00 c	0.00 d	36.71 a	0.00 c	0.00 d	4.38 bc
Aphelenchus spp.	2	16.45 b	25.13 a	0.00 c	8.18 cd	11.31 c	23.67 ab	16.63 bc	20.80 a
Dorylaimus spp.	4	29.22 a	22.28 a	8.67 c	1.78 d	2.71 c	10.70 bc	25.62 b	8.76 b
Eudorylaimus spp.	4	0.00 c	0.00 d	0.17 c	1.79 d	2.71 c	0.00 c	0.00 d	0.00 c
Labronema spp.	4	9.55 c	13.95 b	5.21 c	2.34 d	7.24 c	6.44 c	5.29 cd	16.42 a
Prodorylaimus spp.	5	0.00 c	0.00 d	0.00 c	0.00 d	0.00 c	0.00 c	0.00 d	0.00 c
Discolaimus spp.	5	0.00 c	0.00 d	1.27 c	2.82 d	0.33 c	5.37 c	0.00 d	1.09 c
Mononchus spp.	4	3.14 c	0.00 d	0.67 c	4.44 d	0.00c	0.00 c	2.11 d	4.38 c

cp values represent the nematode generation cycle where 1 is shortest while 5 is longest. Means separated by least significant difference; means followed by same letter (s) along columns indicate no significant differences at $p \leq 0.05$.

4. Discussion

The present study demonstrates that farming systems have an influence on the abundance and diversity of FLN with organic farming showing a positive effect on the FLN community structure as well as nematode trophic dynamics over relatively long durations of time. Overall, however, there were no significant differences in the abundance and diversity of FLN between the on-farm and on-station trials. This may be attributed to the close proximity of the sites, which is estimated at < 1 km between the two farthest fields. The sites are consequently in the same agro-ecological zone (AEZ 2) with similar rainfall, temperatures and nitisol soils (Ministry of Agriculture, 2013). This may also confirm that the treatments and crop establishment at the on-farm trials were well executed and highly comparable to the more controlled conditions for the on-station trial.

In our study, the bacterivore family Cephalobidae (*Cephalobus*, *Eucephalobus* and *Acrobeles*) contributed more to the FLN composition across all farming systems and especially under organic farming. In addition, the bacterivore genus *Rhabditis,* and fungivores *Aphelenchoides* and *Aphelenchus* were significantly abundant in organic systems. This may be attributable to the addition of compost and tithonia mulch, which helps to raise soil organic matter and nitrogen content, which provides a suitable organic substrate to nourish bacteria (Bulluck et al., 2002; Dong et al., 2008) and favors the multiplication of bacterivores (Ferris et al., 1996). This corroborates studies by Neher (1999), Gomes et al. (2003) and Dong et al. (2008), who found Cephalobids to be predominant among the bacterivores, which reflects the study by Ferris and Matute (2003), who also observed increased Rhabditidae and Aphelenchoididae following soil amendment with organic matter. Numerous studies have also reported that bacterivores dominate in soils amended with organic substrates (Wang et al., 2004; Liang et al., 2005; Briar et al., 2007; Neher, 2010).

Under organic farming, bacterivores remained consistently high, whereas their presence was much lower in the conventional system, while conversely, fungivore abundance was high under the conventional farming. This may be due to the application of synthetic fertilizers (DAP and CAN), which can boost fungal growth and, in turn, support fungivore multiplication (Nakhro and Dkhar, 2010). This enables the build-up of fungivores, especially *Aphelenchoides* spp. and *Aphelenchus avenae* under conventional farming (Ferris et al., 1996; Neher, 1999; Langat et al., 2008). Consequently, despite being suspected to have a negative impact on the whole nematode assemblage, chemical fertilizers may indeed facilitate the build-up of FLN (Sanchez-Moreno and Ferris, 2018). The densities of omnivorous and predatory nematodes were generally low across farming systems during the study period, and completely absent on a few occasions under organic farming. Despite studies showing that predators and omnivores respond positively to the addition of organic matter (Wachira et al., 2009), they are slow reproducers (termed *k*-strategists) that do not perform well in disturbed soils, unlike more rapid reproducers (*r*-strategists), such as bacterivores (Ferris and Bongers, 2009).

In our study, the genus richness and Shannon diversity were relatively similar between organic and conventional farming systems in both on-farm and on-station trials, and cropping systems. Similar findings were observed in studies assessing nematode diversity and richness between plots amended with organic and chemical inputs (Neher, 1999; Bulluck et al., 2002; Cheng et al., 2008; Porazinska et al., 1999). This is not surprising, given the diversity of contrasting conditions under which many of these studies have been conducted. However, for the maturity indices, the non-amended control and organic farming system in both the on-farm and on-station trials had values indicating a suitable and stable environment, while values for farmer practice and conventional farming systems indicated a seriously disturbed environment (Neher, 2010; Sánchez-Moreno et al., 2011; Sanchez-Moreno and Ferris, 2018). Soils dominated by cp2 nematodes (most bacterivores and fungivores) and having more than a few cp4 nematodes (omnivores and predatory nematodes) indicate stable environments (Sánchez-Moreno et al., 2011) and therefore, the high abundance of bacterivores in organic systems may be responsible for this stability. Similarly, the ecological and structural indices for organic farming also supported the maturity index results, indicating a more nutrient enriched and stable soil environment than conventional farming systems, but only under the intercrop system. Enrichment and structural indices are known to be affected by cp1–2 and cp3–5 nematodes, respectively, which explains the higher values observed under organic farming at on-farm and on-station trials - organic farming had the highest abundance of cp1–5 nematodes,

Table 8
Effect of farming systems on soil nematode population densities and ecological indices on maize-beans intercrop and beans sole crop at Chuka, Tharaka Nithi county, Kenya.

Trial and cropping	Farming system	Total FLN[1]	Bacterivores[2]	Fungivores[3]	Predators[4]	Omnivores[5]	Genus richness[6]	Shannon diversity[7]	MI[8]	EI[9]	SI[10]
On-farm	F-practice	379.83 cd	226.25 cA	74.84 bB	48.11 cBC	30.63 bc	7.25 a	2.07 a	1.94 c	58.03 b	40.71 c
(intercrop)	Organic	1238.99 a	885.94 aA	124.76 aB	105.12 bB	123.17 aB	8.32 a	2.12 a	2.74 b	85.52 a	87.42 a
	Conventional	558.99c	226.62 cA	125.08 aBC	174.03 abB	33.26 bD	7.31 a	2.56 a	1.91c	62.32 b	64.97 b
	Control	933.69 b	547.75 bA	70.32 bCD	205.69 aB	109.93 aC	7.53 a	2.22 a	3.13 a	37.71 c	38.00 c
On-farm	F-practice	850.08 b	451.75 bA	177.55 cB	125.40 cB	95.38 bBC	6.76 a	2.06 a	2.23 b	55.45 a	22.87 a
(sole crop)	Organic	1771.35 a	932.18 aA	359.64 bB	120.46 cC	359.07 aB	7.02 a	2.16 a	3.16 a	56.85 a	20.14 a
	Conventional	1586.44 a	433.53 bB	681.00 aA	471.91 a B	0.00cC	7.12 a	2.67 a	2.10 b	64.21 a	20.85 a
	Control	874.52 b	330.33 bcA	203.91 bcB	266.80 bB	73.48 bc	6.89 a	2.24 a	3.39 a	57.65 a	17.10 a
On-station	F-practice	397.97 c	205.89 bA	123.48 bB	54.89 aBC	13.71 aC	7.49 a	2.35 a	1.49 b	54.18 c	43.36 c
(intercrop)	Organic	1331.75 a	1184.31 aA	147.44 bB	0.00 bc	0.00 aC	6.81 a	1.88 a	3.09 a	82.04 a	89.90 a
	Conventional	735.33 b	428.38 bA	294.50 aB	12.45 bc	0.00 aC	6.42 a	1.47 a	1.30 b	67.22 b	72.61 b
	Control	60.9 d	30.45 cA	30.45 cA	0.00 bA	0.00 aA	6.55 a	2.16 a	3.96 a	20.00 d	37.90 c
On-station	F-practice	663.42 b	444.13 bA	153.52 aB	43.84 bc	21.93 aC	6.22 a	2.13 a	2.59 b	43.66 a	19.38 a
(sole crop)	Organic	1480.15 a	1243.23 aA	115.58 aB	92.45 aB	28.89 aBC	6.71 a	2.92 a	3.71 a	67.90 a	23.27 a
	Conventional	626.79 b	417.89 bA	109.00 aB	99.90 aB	0.00 bc	7.03 a	2.85 a	2.37 b	63.21 a	15.66 a
	Control	344.94 bc	100.86 cA	155.23 aA	62.44 abAB	26.41 aB	6.10 a	1.97 a	4.15 a	51.19 a	15.12 a

Key to parameters: FLN – Free living nematodes; MI – Maturity index; EI – Enrichment index; SI – Structural index; F-practice – Farmer practice. Data in columns 1–5 represent nematode densities in 100 ml soil.
Means separated by least significant difference.
Column 1: Means followed by same lowercase letter(s) along columns within the same trial and cropping system indicate no significant differences at $p \leq 0.05$.
Columns 2–5: Means followed by same lowercase letter(s) along columns within the same trial and cropping system indicate no significant differences at $p \leq 0.05$.
Columns 2–5: Means followed by same uppercase letter(s) along rows within the same trial and cropping system indicate no significant differences at $p \leq 0.05$.
Columns 6–10: Means followed by same letter(s) along columns within the same trial and cropping system indicate no significant differences at $p \leq 0.05$.

generally. In spite of this, the enrichment and structural indices remained similar when maize/bean intercrop was rotated with bean sole crop The high enrichment index figures are reflected in studies by Dong et al. (2008) and Thoden et al. (2011) but not by Cheng et al. (2008), who reported a significantly higher enrichment index when nitrogen input was high. Zhang et al. (2017) have shared concerns about enrichment index being merely based on proportional abundances and thus may not be a suitable indicator of the activities of a functional guild of nematodes.

The PRC revealed differences in the reaction of different nematode genera to farming systems over time. In the on-farm trials, the abundance of various bacterivore genera were numerically dominant across all the farming systems (*Monhystera*, *Oschieus* and *Plectus*). On the other hand, predatory and omnivorous nematodes were in much lower in densities (*Discolaimus* sp. and *Mononchus* sp.). This may be attributed to the life strategies of different nematode genera and their ecological requirements (Moser et al., 2007). The cp1 nematodes, to which Monhystera nematodes belong, are known for their rapid multiplication and colonization of the rhizosphere, owing to their short generation time and quick response to nitrogen availability (Bongers and Bongers, 1998). Within 1.5 months of crop planting, the total abundance of FLN increased slightly under all farming systems. Ferris et al. (1996) observed a similar pattern with bacterivores, whereby pre-planting densities strongly influenced their abundance. Also, Papatheodorou et al. (2004) and Briar et al. (2007) observed an increase in bacterivore density at two months after planting. A general decline in the omnivores and predators (*Discolaimus* sp. and *Mononchus* sp.) was observed over time, across both trials. This may be due to their low reproduction rates, slow movement, low metabolism and sensitivity to pollutants (Neher, 1999; Pen-Mouratov and Steinberger, 2005; Pokharel et al., 2012). Similar observations were made by Bulluck et al. (2002) and Briar et al. (2007). Nematode composition though can be influenced by season and current crop (Mendoza et al., 2008; Karuri et al., 2013).

5. Conclusion

The current study demonstrates that of the different farming systems, organic and conventional farming, in particular, exert the greatest influence on nematode abundance and community dynamics. We observed a higher abundance of free living nematodes under organic farming systems dominated by bacterivores, which are directly associated with organic amendments. The varying ecological indices, especially the enrichment index and index also suggest that the organic system may be rich in soil nutrients and is highly stable under intercrop systems. Organic farming systems, therefore, appear to provide an enabling environment for the improvement of beneficial nematodes and consequently improved soil structure, soil quality and soil health. Greater awareness of such benefits by extension and agricultural officers should therefore be highlighted, towards the promotion and encouragement by farmers in sub-Saharan Africa to practice organic farming. Overall, this study provides a strong contribution to our otherwise scant knowledge of free living nematode dynamics in African cropping

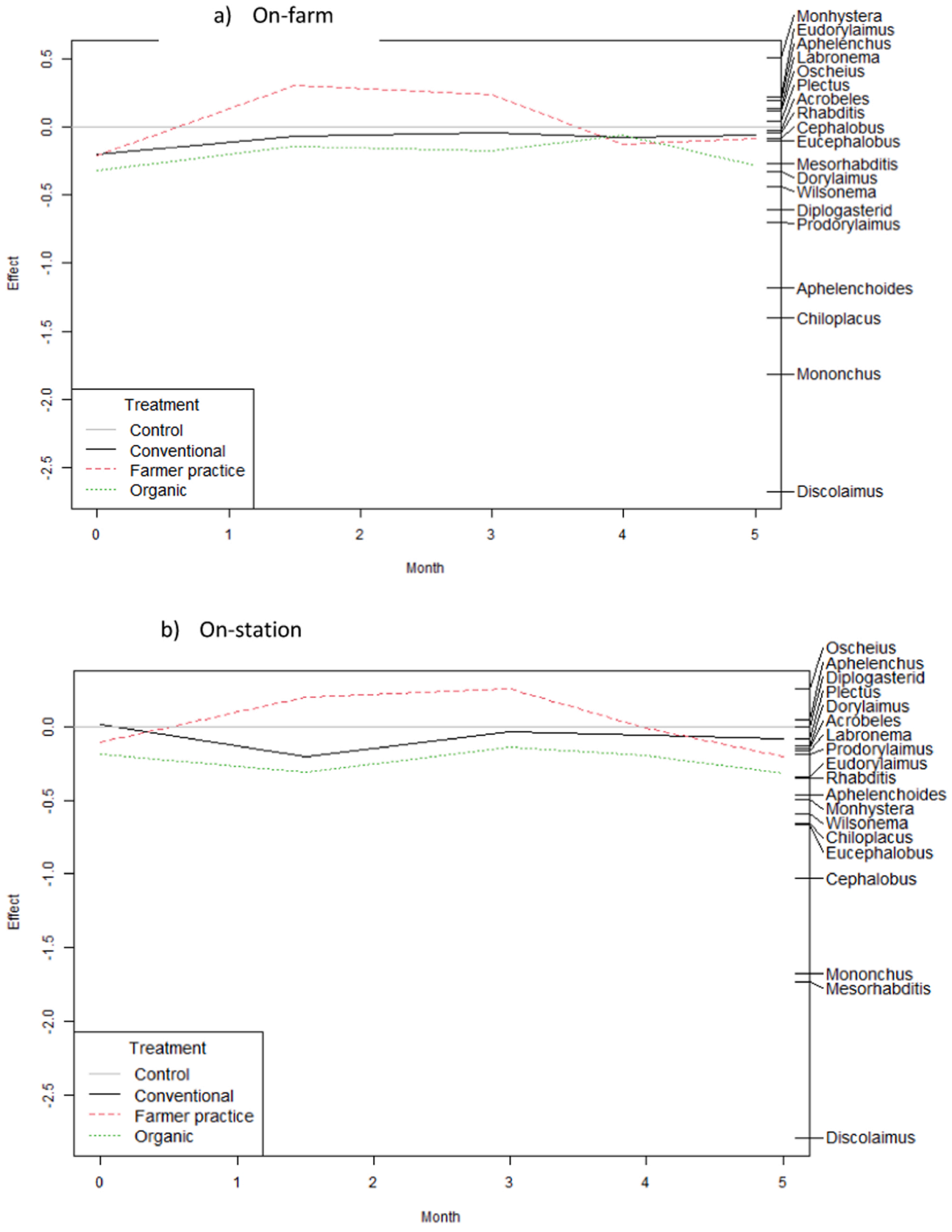

Fig. 1. Principal response curves of the free-living nematode genera showing the effects of farmer practice, conventional and organic farming, compared to the control in on-farm (a) and on-station (b) trials during maize-bean intercrop season in Chuka. The ordinate axis represents the first principal component of the variance due to treatment effect, whereas the abscissa axis represents the sampling time (in months). The horizontal line at 0 shows the response of the free-living nematodes in the control. The genera scores that were associated with the reference system (control) are shown on the right axis.

systems. Further studies are, however, required to establish the long-term effects of organic and conventional farming on the build-up or reduction of important free living nematodes.

Declaration of Competing Interest

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

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