FACTORS INFLUENCING THE RELATIONSHIP BETWEEN NEMATODE COMMUNITIES AND EDAPHIC FACTORS ON SELECTED SOIL GROUPS IN KENYA: VERTISOLS, CAMBISOLS AND ARENOSOLS †

[FACTORES QUE INFLUYEN EN LA RELACIÓN ENTRE COMUNIDADES NEMATODE Y FACTORES EDÁFICOS EN GRUPOS DE SUELOS SELECCIONADOS EN KENIA: VERTISOLES, CAMBISOLES Y ARENOSOLES]

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SUMMARY

Background. Inappropriate agricultural practices such as use of heavy machinery, excessive tillage and unbalanced use of inorganic fertilizers, inappropriate irrigation practices and poor water management techniques, pesticide overuse, inadequate crop residue and/or organic carbon inputs, and poor crop cycling negatively affect soil characteristics. **Objective.** Determine the relationship between soil physical-chemical parameters and nematode assemblages, ecological suitability and nutrient recycling potential as influenced by their respective soil ecosystems. **Methodology.** A total of 576 soil samples were collected in areas characterized by small scale subsistence agriculture in Kenya’s Northern and Southern sites during the cold-dry (1), warm-rainy (2) and hot-dry (3) seasons. The sampling points included land under cultivation (disturbed) and the adjoining natural undisturbed land within three soil groups, namely; Vertisols, Cambisols and Arenosols. Nematodes were extracted, assigned to their respective trophic groups and correlated with analyzed soil chemical properties. **Results.** Omnivores and predators were positively influenced by an increase in Mg and soil organic matter content while an increase in soil pH, K and NH_4 content had a linear relationship with bacterivores. Increase in Ca and N concentrations was associated with increased numbers of both herbivores and fungivores. Low ecological disturbance and nutrient cycling potential was favored in natural soils, northern sites and where the soils had an active root growth in season 2. **Implications.** Sustainable soil management practices are recommended in a bid to maintain the favorable soil structure through nematode assemblage. **Conclusion.** Changes in soil properties resulting from anthropogenic activities, have a significant impact on nematode assemblages in their respective food webs.

Key words: Disturbed and undisturbed soils; soil chemical and physical characteristics; soil groups; nematode trophic levels and groups.

RESUMEN

Antecedentes. Las prácticas agrícolas inadecuadas, como el uso de maquinaria pesada, la labranza excesiva y el uso desequilibrado de fertilizantes inorgánicos, las prácticas de riego inadecuadas y las malas técnicas de gestión del agua, uso excesivo de pesticidas, los residuos de cultivos inadecuados o los insumos de carbono orgánico, y la planificación deficiente del ciclo de cultivo afectan negativamente las características del suelo. **Objetivo.** Determinar la relación entre los parámetros físico-químicos del suelo y los conjuntos de nematodos, la idoneidad ecológica y el potencial de reciclaje de nutrientes según la influencia de sus respectivos ecosistemas del suelo. **Metodología.** Se recogieron un

† *Submitted September 24, 2019 – Accepted April 4, 2020.*
ISSN: 1870-0462.

total de 576 muestras de suelo en áreas caracterizadas por la agricultura de subsistencia a pequeña escala en los sitios del norte y sur de Kenia durante las estaciones de frío seco (uno), cálido-lluvioso (dos) y caliente-seco (tres). Los puntos de muestreo incluyeron tierra bajo cultivo (perturbada) y la tierra natural adyacente (no perturbada) dentro de tres grupos de suelo, a saber; Vertisoles, Cambisoles y Arenosoles. Se extrajeron los nematodos, se asignaron a sus respectivos grupos tróficos y se correlacionaron con las propiedades químicas analizadas del suelo. **Resultados.** Los omnívoros y los depredadores fueron influenciados positivamente por un aumento en el Mg y la materia orgánica del suelo, mientras que un aumento en el pH del suelo, K y NH_4 tuvieron una relación lineal con los bacterívoros. El aumento en las concentraciones de Ca y N se asoció con un mayor número de herbívoros y fungívoros. La baja perturbación ecológica y el potencial de ciclo de nutrientes se favoreció en los suelos naturales, los sitios del norte y donde los suelos tuvieron un crecimiento activo de raíces en la temporada 2. **Implicaciones.** Se recomiendan prácticas sostenibles de manejo del suelo en un intento por mantener la estructura favorable del suelo a través del ensamblaje de nematodos. **Conclusiones.** Los cambios en las propiedades del suelo como resultado de actividades antropogénicas tienen un efecto significativo impacto en ensamblajes de nematodos en sus respectivas redes alimenticias.
Palabras clave: suelos perturbados y no perturbados; características químicas y físicas del suelo; grupos de suelo; niveles y grupos tróficos de nematodos.

INTRODUCTION

Soils are vital natural resources that never receive adequate attention from their users. Soils act as genetic and habitat reserves, with a wide array of micro-organisms. They also support a rich body of both biological and chemical processes giving them a “living” characteristic. The different roles the soil plays depends on location, climate and both animals and plant life (Charlotte, 2009). Anthropogenic activities are regarded as the main causative agent for soil health reduction due to their overuse without sustainable management and control leading to soil degradation (Blum, 2002; Karlen and Rice, 2015). The soil is composed of an intricate network of microbes that play a vital role in global cycling of organic matter (OM) and mineralization into CO_2, H_2O, N, P, S, and other nutrients (Bloem *et al.*, 1994; Schimel and Schaeffer, 2012). Nematodes, being among the most abundant microorganisms, have a high diversity in the soil ecosystems and as such have gained attention as potential soil health bio-indicators owing to their ever-present, high abundance, prompt reaction to environmental shifts and close inter-relationship with soil characteristics (Neher, 2001; Fiscus and Neher, 2002). Studies have suggested that these attributes enable agriculturalists to infer vital soil processes using nematodes (Wardle *et al*., 2005; Ettema, 1998; Porazinska *et al*., 1999; Ekschmitt *et al*., 2003; Yeates, 2003). Nematodes act as descriptive indicators of soil condition when applied to reflect variations that arise in agroecosystems (McGeoch, 1998; Walz, 2000).

Nematodes are recognized as useful as most are highly sensitive to disturbances and hence have been used as indicators of overall ecological condition due to a wide range of feeding types, and the fact that they reflect the succession stage of the systems in which they occur (Ferris *et al.*, 2012; Neher, 2001; Chen *et al.*, 2010). Nematodes have are highly ranked as important indicator of soil status in two European projects evaluating soil biological indicators (Bispo *et al.*, 2009; Ferris *et al.*, 2012; Ritz *et al.*, 2009). Nematodes also serve as evaluative indicators of soil conditions when they are used to determine and analyze the causes of soil deterioration (Dale and Beyeler, 2001; Heink and Kowarik, 2010). For instance, bacterivorous and fungivorous nematodes feed on soil bacteria and fungi, respectively, so as to release CO_2 and NH_4^+ hoarded by the later in form of C and N; a process that in tandem influences direct C and N mineralization (Ingham *et al.*, 1985).

In response to limiting any deficiency effects arising from overgrazing of the bacteria and fungi, the bacterivorous and fungivorous nematodes are in turn fed on by predatory nematodes thus enabling nutrient cycling (Yeates and Wardle, 1996). Changes occurring in nematode assemblage have been attributed to seasonal variations and ecological successions (Neher *et al.*, 2005). Colonization and life history enable nematode taxa to be classified on a colonizer-persister (*c-p*) scale either as colonizers (cp-1) or persisters (cp-5). Those with short life cycles multiply faster, are fastidious and hence are considered colonizers or *r* strategists. On the other hand, nematodes that live longer, have low fecundity and have low nutritional needs and are referred to as persisters or *K* strategists (Bongers, 1990; Ferris *et al.*, 2001).

To assess changes in the soil ecosystem, indices such as Plant Parasitic Index (PPI) and The Nematode Maturity Indices (MI) have been developed and utilize nematode survival mechanisms (Bongers, 1990). The MI are used to determine both the nematodes’ life history and functional roles in the soil ecosystem (Ferris and Bongers, 2009; Rosa and Nahum, 2012). In addition, indices such as PPI and Fertility Index (PPI/MI) are also used to evaluate nutrient-stability of ecosystems (Ferris and Bongers, 2009; Rosa and Nahum, 2012). Nematodes act as evaluative bio-indicators by application of basal (BI), structural (SI), enrichment (EI) and channel (CI) indices used for determining the soil food web structure and the nutrient recycling in the soil ecosystem (Bulluck, 2000; Ferris *et al.*, 2001; Ferris, 2010; Rosa and Nahum, 2012). Studies have shown that MI is more suitable than diversity indices in measuring tillage effects (Lenz and Eisenbeis, 2000) while cover cropping has an additive effect on EI and a negative effect on both BI and SI indices (DuPont *et al.,* 2009).

Hence the objective of this study was to determine how association of nematode faunal assemblages and edaphic parameters can be utilized as evaluative and descriptive indicators of soil quality in Vertisols, Cambisols and Arenosols group of soils.

MATERIALS AND METHODS

Soil sampling

Soil sampling was done on three soil groups, namely Vertisols, Cambisols and Arenosols at selected sites in Kenyan counties. Sampling sites located in Makuyu County were designated as Northern sites while sampling sites located in both Machakos and Makueni Counties were designated as Southern sites. For each soil group, two sites were selected with each comprising of a natural untilled and disturbed ecosystem. From the disturbed ecosystem, 12 field-representative composite soil samples and 4 representative composite soil cores were collected from the natural ecosystem and their co-ordinates were recorded for each sampling point. A 1 kg soil sample was collected using a 600 cm^3 soil auger at a depth of 15-30 cm. Geo-referenced samples were repeatedly collected at the original sampling points during the cold-dry (Season 1), rainy-wet (Season 2) and hot-dry (Season3) seasons during the study period.

Nematode extraction, identification and counting

Each soil sample was thoroughly mixed, passed through a 4 mm sieve into a holding pan and partitioned into two: 200 cm^3 for nematode analysis and another 200 cm^3 for soil chemical and physical analyses. Soil nematodes were extracted from the 200 cm^3 soil sub-sample using the centrifugal-floatation method (Jenkins, 1964). Using a mounted nematode counting dish and a standard identification key, morphological and morphometric features identified and enumerated nematodes on a compound microscope (Motic 101 M, AE 2000) at ×400 magnification. The nematodes were identified up to genera level using standard identification keys and tallied three times using a 1ml pipette aliquot each time. These standard nematode identification keys included: The Pictorial Key to Genera of Plant Parasitic Nematodes (Mai *et al.,* 1968), C.I.H. Description of Plant Parasitic Nematodes and the 'Interactive Diagnostic Key to Plant-parasitic and free-living nematodes; available from their identification website (http://nematode.unl.edu/konzlistbutt.htm). The mean count was used to calculate the total number of nematodes in the original 3 ml aliquot as a representative count for each soil sample. All nematodes enumerated were then grouped into feeding groups of herbivores, fungivores, bacterivores, omnivores and predators (Yeates *et al*., 1993; Bongers and Bongers, 1998).

Soil Chemical and physical Analyses

The other 200 cm^3 soil sample was subjected to chemical and physical characterization. Soil pH-H_2O and pH-KCl_2 was determined with a pH meter. The percentage soil organic carbon (% OC) was determined according to Walkley and Black (1934) as described by Nelson and Sommers (1996). Total Nitrogen (TN) was determined by micro-Kjeldhal distillation method (Bremner, 1996) while NO_3^- - N and NH_4^+- N were determined using colorimetric determination from the soil extract as described by Bremner *et al.* (1965). Exchangeable Ca and Mg in the ammonium lactate solution were determined by Atomic Adsorption Spectrophotometry (AAS) while K was by flame photometry (Osborne, 1973). Available P was determined as described by Olsen *et al.* (1954). Soil texture was determined by hydrometer method as described by Glendon and Doni (2002).

Grouping of nematodes in their trophic levels

Nematode trophic levels were established through nematode feeding habits and this enabled grouping into their respective life strategies using the colonizer persister (c-p) scale (Bongers, 1990; Bongers and Bongers, 1998). The scale ranges from a value of 1 (short life cycles, high reproduction rates and tolerance to disturbance) to 5 (long life cycles, low reproduction rates and sensitive to disturbances).

Determination of the relationship between nematodes and soil chemical properties

Detrended canonical correspondence analysis (DCCA) was carried out according to Leps and Smilauer (2003) using CANOCO version 4 to analyze the relationship between the soil chemical properties and nematode assemblage to establish if there are any patterns between the different nematode feeding groups and soil properties.

Determination of ecological disturbances

All plant parasitic nematodes from the soil samples were used to determine the plant parasitic index (PPI) while free living nematodes determined the maturity index (MI). The total maturity index (ΣMI) was determined by combining all plant parasitic and free-living nematodes from c-p1 through c-p 5. Nematodes in c-p 2 through c-p 5 were used to determine the maturity index (MI2-5) for free living nematodes while those in c-p 2 through c-p5 for free living and plant parasitic nematodes were used to determine the combined maturity index (ΣMI2-5) (Bongers, 1990; Yeates, 1994). The plant parasitic index (PPI) and MI were used to calculate the fertility index (FI) (Bongers *et al*., 1997) in order to establish the extent of degradation and disturbance in different soil systems. The indices above were determined through a weighted mean mathematically expressed as $\Sigma (vi \times fi)/n$ where vi = c-p value assigned to family i, fi = frequency of family i in the sample, and n = total number of individuals in sample (Neher *et al*., 2004).

Establishment of soil food web structure

The basal (BI), structure (SI) and enrichment (EI) were calculated according to Ferris *et al*. (2001) and Neher *et al*. (2004). Soil food web graphs were developed using EI against SI to assess the structure and enrichment levels in varied soil groups, seasons and sites under different soil disturbance levels. Ferris *et al*. (2001) were able to apply the c-p scaling and nematode feeding groups into nematode functional guilds to compute the enrichment index (EI), and the structure index (SI). The EI is based on the expected responsiveness of the opportunistic guilds (bacterivores with c-p = 1) to food resource enrichment while the SI represents an aggregation of functional guilds with c-p values ranging from 3-5. Thus, EI describes whether a soil ecosystem is nutrient enriched (high EI) or depleted (low EI). The SI represents an aggregation of functional guilds with c-p values ranging from 3-5 (Figure 1).

Statistical analyses

Data was subjected to a two-way analysis of variance (ANOVA) to investigate the effect and interactions between different seasons, sites, soil groups and disturbance levels. Significant differences ($P \leq 0.05$) among means were determined using the Turkey-Kramer comparison test. All nematode data were log-transformed (*ln* x + 1). Karl Pearson's correlation analysis analyses were carried out between nematode genera, trophic groups and soil physical-chemical properties to determine any significant correlations ($P \leq 0.05$) between them.

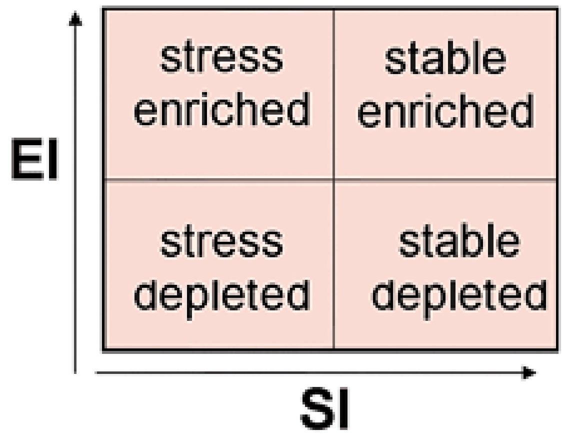

Figure 1. A simplified food web structure on enrichment index (EI) and structure index (SI) trajectories (modified from Ferris *et al*., 2001).

RESULTS

Effect of soil physical and chemical properties on different nematode feeding groups

The seasonal correlations between nematode feeding groups and soil properties are displayed in Table 1 with significant correlations ($P \leq 0.05$) indicated with an asterisk (*). In season one, omnivores were significantly ($P \leq 0.05$) and positively correlated with pH but significantly and negatively correlated with Mg. The predators were significantly ($P \leq 0.05$) and positively correlated with soil organic matter (SOM) and total nitrogen (N). Bacterivores were significantly and positively ($P \leq 0.05$) correlated with SOM but significantly and negatively correlated with potassium (K). Fungivores were significantly and positively ($P \leq 0.05$) correlated with ammonium ions but significantly and negatively ($P \leq 0.05$) correlated with Mg. Herbivores were however significantly and positively ($P \leq 0.05$) correlated with SOM, N and Mg though significantly and negatively correlated with K and P. In season two, a significant and positive ($P \leq 0.05$) correlation between all the nematode feeding groups and N was observed. The same trend was observed with SOM in all feeding groups except for fungivores which was insignificant. Further, omnivores were significantly and positively ($P \leq 0.05$) correlated with K, Ca and Mg while predators with K and NO_3.

Table 1. Correlation coefficients between abundance of nematodes and soil properties in different seasons.

Seasons	Nematode Trophic groups	pH	SOM	TN	P	K	Ca	Mg	NH_4	NO_3
Season 1	OV	0.18*	0.00	-0.08	-0.05	0.04	-0.06	-0.21*	-0.02	0.10
	PR	-0.07	0.22*	0.36*	-0.08	0.10	-0.01	-0.01	0.07	0.03
	BV	-0.12	0.21*	0.13	0.04	-0.14*	-0.02	0.06	0.08	-0.03
	FV	0.01	0.03	0.01	0.12	-0.03	0.00	-0.15*	0.15*	0.11
	HV	-0.03	0.23*	0.18*	-0.16*	-0.10	0.07	0.01*	-0.01	-0.02
Season 2	OV	-0.11	0.43*	0.41*	-0.18*	0.19*	0.21*	0.36*	0.06	0.10
	PR	-0.11	0.36*	0.29*	-0.13	0.19*	0.06	0.13	0.10	0.18*
	BV	-0.27*	0.24*	0.23*	-0.06	0.24*	-0.10	0.00	0.31*	0.05
	FV	-0.22*	0.12	0.17*	-0.08	0.10	-0.07	0.06	0.14*	-0.05
	HV	-0.10	0.40*	0.38*	-0.05	0.08	0.24*	0.21*	0.03	0.12
Season 3	OV	0.01	0.12	0.07	-0.04	0.05	-0.04	-0.01	0.10	-0.08
	PR	0.03	0.16*	0.21*	0.05	-0.10	-0.05	-0.06	-0.03	0.02
	BV	0.08	0.05	0.12	0.11	-0.06	0.05	-0.06	-0.03	0.13
	FV	0.08	-0.05	-0.01	0.08	-0.11	0.29*	0.10	-0.03	0.16*
	HV	0.09	0.11	0.13	0.01	-0.15*	0.15	0.05	-0.24*	-0.09

SOM: Soil organic matter, TN: Total Nitrogen, K: Potassium, Ca: Calcium, Mg: Magnesium, NH_4: available Ammonium, NO_3: Nitrate, * represent significant levels at ($P \leq 0.05$).where OV: Omnivores, Pr: Predators, BV: Bacterivores, FV: Fungivores, and HV: Herbivores.

However, bacterivores and fungivores had a significant and positive ($P \leq 0.05$) correlation with K and NH_4 and a negative with soil pH while herbivores were significantly and positively correlated with Ca and Mg. Omnivores were significantly and negatively correlated with P. In season three, only predators and fungivores were significantly and positively correlated with SOM, TN and Ca and NO_3 while herbivores were significant but negatively related with both K and NH_4.

A significant relationship ($P \leq 0.05$) was observed between the edaphic factors and nematode trophic groups (Table 2). For Arenosols, all nematode feeding groups were significantly and positively correlated with SOM and TN with the exception of the fungivores which were insignificant. Omnivores were significant and positive with K only while predators with K, Ca and Mg, bacterivores and fungivores with NH_4 and NO_3 while fungivores were significant but negative with pH, P and Mg. Herbivores were significantly and negatively correlated with Mg and positively with P. For Cambisols, omnivores, predators and bacterivores were significant and positive with pH and SOM, respectively. Both omnivores and predators had a significant and positive correlation with N while omnivores had a significant and negative correlation with NH_4 but positive with NO_3. Herbivores had a significant and positive correlation with Ca. For Vertisols, omnivores had a significant and positive correlation with SOM, Mg and NO_3, but significantly and negatively correlated with NH_4. Predators had a significant and positive correlation with SOM, N, and NO_3 increases while bacterivores were significantly and positively correlated with N only. On the other hand, fungivores were significant and negatively correlated with SOM, K and NH_4. An increase of SOM, N and Ca significantly and positively correlated with herbivores while K and P increase significantly and negatively influenced them.

Table 2. Correlation coefficients between abundance of nematodes and soil properties in different soil groups.

Soil Groups	Nematode Trophic groups	pH	SOM	TN	P	K	Ca	Mg	NH_4	NO_3
Arenosols	OM	-0.04	0.32*	0.16*	-0.02	0.22*	0.04	0.11	0.09	0.07
	PD	0.10	0.35*	0.22*	0.01	0.18*	0.29*	0.20*	0.13	0.14
	BV	0.03	0.41*	0.22*	-0.03	0.07	0.08	0.14	0.33*	0.15*
	FV	-0.20*	0.36*	0.13	-0.25*	0.05	-0.02	-0.02	0.20*	0.33*
	HV	0.08	0.18*	0.07	0.19*	0.06	-0.06	-0.17*	0.07	-0.13
Cambisols	OM	0.14*	0.26*	0.17*	-0.11	0.06	-0.07	-0.09	-0.17*	0.18*
	PD	0.15*	0.27*	0.21*	-0.13	-0.04	-0.02	-0.11	0.01	0.12
	BV	0.18*	0.16*	0.14	-0.08	0.02	0.06	0.01	0.03	0.10
	FV	0.08	0.03	0.12	-0.03	0.01	-0.10	-0.08	-0.12	0.06
	HV	0.12	0.01	0.03	-0.07	-0.07	0.18*	0.10	-0.07	0.08
Vertisols	OM	-0.05	0.34*	-0.02	-0.12	-0.13	-0.01	0.25*	-0.27*	0.21*
	PD	-0.04	0.25*	0.44*	-0.09	0.01	-0.07	0.07	0.01	0.18*
	BV	0.04	0.06	0.16*	-0.05	-0.04	0.04	-0.01	0.05	0.13
	FV	-0.02	-0.20*	-0.08	0.27	-0.14*	-0.11	-0.03	-0.20*	0.04
	HV	-0.07	0.22*	0.20*	-0.18*	-0.24*	0.16*	0.13	-0.13	0.09

SOM: Soil organic matter, TN= Total nitrogen, K: Potassium, Ca: Calcium, Mg: Magnesium, NH_4: available Ammonium, NO_3: Nitrate. [*****] represents significant levels at $P \leq 0.05$ and where nematode trophic groups OM= Omnivores, PD= Predators, BV= Bacterivores, FV= Fungivores, and HV= Herbivores.

The study also found a significant relationship ($P \leq 0.05$) between nematode trophic groups and their geographical locations and disturbance levels (Table 3). In the Northern site, omnivores, predators and bacterivores were significant and positively correlated to soil pH and NO_3. Also, omnivores, predators and herbivores were significant and positively correlated with the SOM and TN. Bacterivores on the other hand were significant and negatively correlated with Ca and Mg, respectively, but a significant and positive correlation was observed with NH_4 and NO_3. Fungivores and herbivores also had significant and negative correlations with Ca and NH_4, respectively. In the Southern region, all nematode feeding groups had a significant and positive correlation with SOM and Mg except for omnivores which were negatively correlated with Mg. Furthermore, bacterivores had a significant and positive correlation with pH, N, P and Ca while fungivores had a significant and positive correlation with P, Ca and NO_3 and a significant and negative correlation with NH_4. In addition, herbivores had a significant and positive correlation with N and Ca. In the natural undisturbed soils, Fungivores and herbivores had significant and negative correlations with Ca and NH_4. Herbivores and fungivores were the only feeding group that had a significant and positive correlation with NO_3 while predators and bacterivores had significant and positive correlations with N and soil pH, respectively. Fungivores had a significant and positive correlation with NO_3 and a significant and negative correlation with Ca. Herbivores had a significant and positive correlation with both SOM and N but a negative correlation was observed with P and NH_4. In the tilled soils (disturbed), all the feeding groups had a significant and positive correlation with SOM. Also, all feeding groups had a significant and positive correlation to N except for omnivores. However, omnivores had significant and positive correlations with K and NO_3. All nematodes feeding groups had significant and positive correlations with NO_3 with the exception of herbivores.

Relationship between nematode trophic groups and soil chemical properties

The detrended canonical correspondence analysis (DCCA) ordination shows that different nematode feeding groups have varied relationships with various soil chemical parameters (Figure 2). Omnivores and predators increased together with SOM, C and Mg while fungivores decreased as the same soil parameters increased. Furthermore, fungivores also reduced when available K, pH and NO_3 increased. Increase in predators, omnivores and herbivores had an inverse relationship to a reduction in P and NH_4 in soils. For omnivores, an increase in NH4 also reduced their numbers, meaning they need a narrow range for this nutrient. Herbivores on the other hand increased with Ca and N and reduced with high soil levels of K, NO_3 and pH. Predators and Omnivores occupied similar niches while fungivores and bacterivores were found in closely similar conditions.

The detrended canonical correspondence analysis (DCCA) ordination information provided showed that different nematode genera in the study had varied relationships with various soil chemical parameters (Figure 3). An increase in K and NH_4 led to an increase in numbers of *Hoplolaimus*, *Hemicycliophora*, *Tylenchus and Eucephalobus* spp. while an increase in soil pH and available P influenced the occurrence of *Plectus*, *Cervidellus* and *Tylenchorrynchus* spp. An increase in TN and SOM positively influenced the occurrence of *Scutellonema*, *Helicotylenchus*, *Longidorus*, *Xiphinema* and *Criconemella*, *Dorylaimoides, Labronema and Discolaimoides* spp.

Effect of soil group, seasons, sites and soil disturbance on ecological disturbance indices of nematodes

The ecological disturbance indices of significantly different seasons, soil groups, and soil disturbance in the Northern and Southern sites are shown in Table 4. Among the soil groups, the fertility index (FI) was significantly different ($P \leq 0.05$) with Cambisols having a higher FI compared to both Vertisols and Arenosols. Among the seasons, significant differences ($P \leq 0.05$) were observed in maturity indices (MI, MI2-5, ΣMI2-5) where season 2 had significantly highest maturity indices followed by season 3. The northern sites had significantly higher maturity index (MI2-5) compared to the southern ones. The naturally (undisturbed) occurring soils had significantly higher maturity indices (MI, Σ MI, MI2-5, ΣMI2-5) and fertility index (FI) compared to the disturbed. Plant parasitic index (PPI) was notably insignificant amongst the soil groups, seasons, sites and soil disturbance in the study.

Table 3. Correlation coefficients between abundance of nematode feeding groups and soil properties in different disturbance levels in the Northern and Southern sites.

Sites/ Disturbance Levels	Nematode Trophic Groups	pH	SOM	TN	P	K	Ca	Mg	NH_4	NO_3
North	OM	0.17*	0.21*	0.17*	-0.06	0.08	-0.02	0.10	-0.11	0.19*
	PD	0.30*	0.14*	0.14*	0.03	0.13*	-0.02	-0.07	0.00	0.25*
	BV	0.25*	-0.09	-0.05	0.01	0.05	-0.19*	-0.21*	0.16*	0.18*
	FV	0.02	-0.17	-0.10	-0.01	-0.03	-0.24*	-0.09	-0.01	0.05
	HV	0.04	0.19*	0.20*	0.04	-0.06	0.07	0.11*	-0.15*	0.08
South	OM	0.02	0.06	-0.04	0.02	0.04	-0.01	-0.02	-0.17*	0.05
	PD	-0.01	0.26*	0.41*	-0.03	-0.05	0.06	0.21*	0.01	-0.04
	BV	0.15*	0.30*	0.19*	0.12*	-0.06	0.25*	0.38*	0.04	0.00
	FV	0.02	0.21*	0.02	0.20*	-0.03	0.26*	0.16*	-0.14*	0.19*
	HV	0.10	0.26*	0.17*	-0.05	-0.09	0.16*	0.03	-0.05	-0.01
Natural	OM	0.03	0.08	-0.16	-0.06	0.07	-0.04	0.02	-0.15	0.25*
	PD	0.13	0.00	0.23*	-0.03	0.10	-0.15	-0.15	-0.04	-0.03
	BV	0.23*	-0.12	0.07	-0.05	0.13	-0.11	-0.08	0.00	0.08
	FV	-0.03	-0.13	-0.12	-0.07	0.12	-0.20*	-0.13	-0.13	0.18*
	HV	-0.11	0.26*	0.18*	-0.20*	0.04	0.13	0.03	-0.23*	0.12
Tilled	OM	-0.03	0.13*	0.02	-0.02	0.11*	-0.08	0.08	-0.06	0.11*
	PD	0.00	0.25*	0.24*	-0.03	0.09	0.03	0.04	0.10*	0.23*
	BV	0.03	0.19*	0.17*	0.02	0.01	0.02	-0.01	0.19*	0.13*
	FV	-0.05	0.14*	0.17*	0.08	-0.05	0.05	0.05	0.00	0.11*
	HV	0.03	0.12*	0.02	0.03	-0.09	0.07	0.06	-0.04	0.02

SOM: Soil organic matter, N= Total nitrogen, K: Potassium, Ca: Calcium, Mg: Magnesium, NH_4: available Ammonium, NO_3: Nitrate, * represent significant levels at ($P \leq 0.05$).where OM: Omnivores, PD: Predators, BV: Bacterivores, FV: Fungivores, and HV: Herbivores.

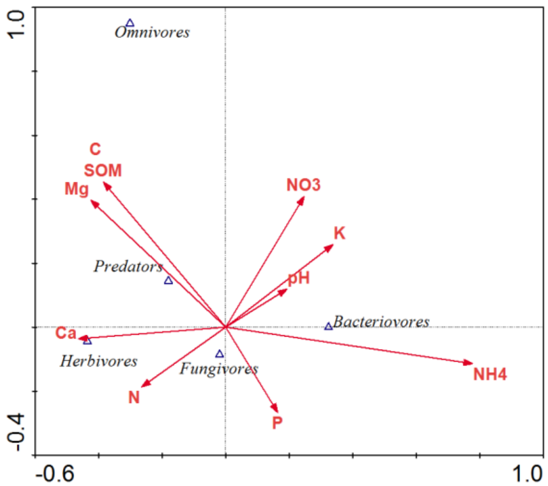

Figure 2. Detrended canonical correspondence analysis (DCCA) ordination diagram showing relationship between nematode feeding groups and soil characteristics (Mg, SOM, C, NH_4^+, P, N, Ca).

Effect of different soil groups, seasons, sites and disturbance levels on soil nematode food web indices and nutrient cycling

The nematode food web and nutrient cycling indices were significantly different ($P \leq 0.05$) among soil groups, seasons, sites and soil disturbance (Table 5). The enrichment index (EI) was significantly higher ($P \leq 0.05$) in both Vertisols and Cambisols compared to that in Arenosols. The seasons had a significant effect on basal (BI), enrichment (EI) and structural (SI) indices. The BI in both season 1 and season 3 was significantly higher ($P \leq 0.05$) than in season 2. The EI in season 1 and 2 were significantly higher than is season 3. In addition, the SI was significantly highest in season 2 and lowest in season 1 while significant differences ($P \leq 0.05$) were observed in the BI, EI and SI between the Northern and Southern sites. The Northern sites had significantly higher EI and SI compared to the Southern sites while BI in the Southern sites was significantly higher. The undisturbed soils had significantly higher SI compared to the disturbed. Conversely, the disturbed soils had a significantly higher BI than the undisturbed soils.

Soil food web and nutrient cycling in the Northern and Southern regions under natural and disturbed soil conditions

Figure 4 indicates the soil food web status in the Southern and Northern soils, respectively. The undisturbed soil in both Northern (c) and Southern (a) sites revealed better structure and less disturbance. The disturbed soils especially in the South (b) revealed to be more nutrient deficient, stressed and unstructured compared to the disturbed soils in the North (Fig. 3d).

Soil food web and nutrient cycling in Arenosols, Cambisols and Vertisols soil groups under natural and disturbed conditions

Figure 5 indicate soil conditions in terms of structure and enrichment of nutrients in the different soil groups under different disturbance levels. The undisturbed Arenosols (a), Cambisols (b) and Vertisols (c) had better structure and enrichment compared to disturbed Arenosols (b), Cambisols (d) and Vertisols (f). However, both Cambisols (d) and Vertisols (f) under cultivation had a better structure and nutrient enrichment compared Arenosols (b) under cultivation.

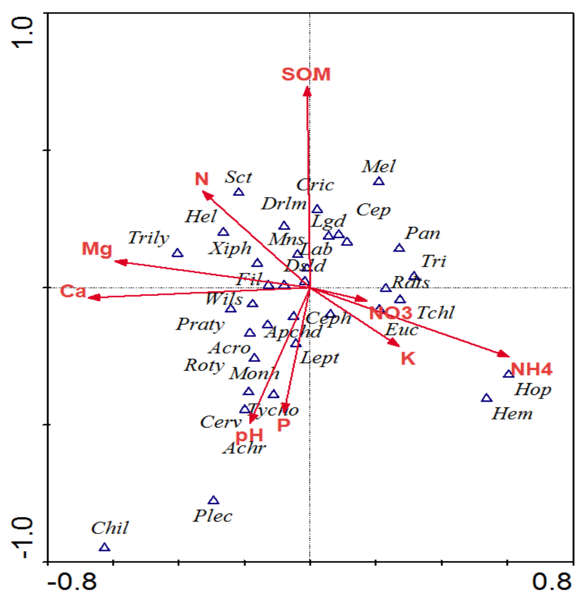

Figure 3. Detrended canonical correspondence analysis (DCCA) ordination diagram showing the occurrence of different nematode genera in relation to soil characteristics. (Hop-*Hoplolaimus*, Hem-*Hemicyclophora*, Euc- *Eucephalobus*, Tchl-*Tylenchus*, Mel- *Meloidogyne*, Pan-*Panagrolaimus*,Tri- *Trichodorus*, Rdts- *Rhabditis*, Sct- *Scutelonema*, Cric- *Criconemella*, Cep-*Cephalobus*, Lgd- *Longidorus*, Lab- *Labronema*, Drlm- *Dorylaimodes*, Mns- *Monhysteridae*, Dsld-*Discolaimoides*, Hel- *Helicotylenchus*, Trily-*Trichotylenchus* ,Xiph- *Xiphinema*, Fil- *Filenchus*, Wils- *Wilsonema*, ,Praty- *Pratylenchus*, Chil-*Chiloplacus*, Plec- *Plectus*, ,Achr- *Achromadora*, Cerv- *Cervidellus*, Tycho- *Tylenchorhynchus*, Monh-*Monhystera*, Roty- *Rotylenchus*, Lept- *Leptonchus* and Apchd- *Aphelenchoides* spp.).

Soil food web and nutrient cycling in different seasons under natural and disturbed conditions

Structural and enrichment changes occurred as influenced by seasonal variations (Figure 6). Undisturbed soils retained their structure across the seasons better than the disturbed soils. It was noted that in the disturbed soils, the structure and enrichment improved from season 1 (b) to season 2 (d) and then both declined in season 3 (f).

DISCUSSION

This study established that soil nematode abundances are influenced by seasons, soil groups, sites and disturbance levels. The significant and positive correlations between bacterivores with SOM, N and NH_4 as observed in season 2 was probably caused by the high abundance of bacteria during the warm/rainy season when detritus was plenty. The increasing number of bacterivores after application of organic materials in Arenosols in the Northern sites agrees with Liang *et al*. (2009) who observed increased bacterivores numbers when soil was amended with organic materials. The organic amendments applied during crop cultivation are known to be rich in N that aids in propagation of soil bacteria and could have led to their high abundances in season 2 when farmers are actively involved in introduction of amendments that will augment crop productivity. Farmers in the Northern Arenosols could potentially be applying high quantities of organic amendments than other farmers in the study. Nematode association with its immediate microenvironment can potentially be used to assess soil health condition and several other soil functions such as its potential to avail required nutrients to its micro-fauna apart from supporting crop growth (Mulder *et al*., 2005).

Omnivores and predators were found to be positively influenced by an increase in SOM, N and K. Omnivores and predators are k strategists and since they don't have high nutritional requirements, they probably were more able to utilize SOM, N and K as compared to bacterivores that are mostly *r*-strategists. Increase in Ca and N concentrations was associated with increased number of herbivores and fungivores. These shifts are characteristic of management practices such as fertilizer additions during intensive cropping which significantly affect abundance of particular nematode taxa. The presence or absence of a particular species is therefore determined by several factors and thus cannot be used as a general indicator of any particular soil type. Gebremikael *et al*. (2016) in their study observed that the presence of nematodes significantly increased plant biomass production (+9%), net N (+25%) and net P (+23%) availability compared to their absence, demonstrating that nematodes link below- and above-ground processes, primarily through increasing nutrient availability.

Table 4. Effects of different soil groups, seasons, sites and disturbance levels on ecological disturbance indices of nematodes.

Soil groups/ seasons/sites/ Disturbance levels		PPI	MI	MI2-5	ΣMI	ΣMI2-5	FI
Soil Group	Cambisols	2.6	2.0	2.1	2.3	2.4	1.3^{a}
	Vertisols	2.5	2.0	2.1	2.3	2.4	1.2^{b}
	Arenosols	2.5	2.1	2.2	2.0	2.3	1.2^{b}
Season	Season 1	2.5	1.9^{b}	2.1 ^{b}	2.2^{b}	2.3^{b}	1.3
	Season 2	2.6	2.1^{a}	2.2^{a}	2.3^{a}	2.4^{a}	1.3
	Season 3	2.5	2.0^{ab}	2.1^{ab}	2.3^{a}	2.4^{ab}	1.2
Site	North	2. 6	2.0	2.2^{a}	2.2	2.4	1.3
	South	2.5	2.0	2.1^{b}	2.3	2.3	1.3
Disturbance	Natural	2.6	2.2^{a}	2.4^{a}	2.4^{a}	2.5^{a}	1.2^{b}
	Disturbed	2.5	1.9^{b}	2.1^{b}	2.2^{b}	2.37^{b}	1.3^{a}

PPI: plant parasitic index, **MI**: maturity index, **MI2-5**: maturity index of c-p 2-5, **ΣMI**: sum of maturity index, **ΣMI2-5**: sum of maturity index of c-p 2-5 under each ecological index. Means followed by different letters within soil groups, regions and soil status in each season, region and nature of soil are significantly different at P ≤ 0.05.

Table 5. Effect of different soil groups, seasons, sites and disturbance levels on soil nematode food web indices and nutrient cycling.

Categories		BI	EI	SI
Soil Group	Vertisols	54.81	33.24[a]	23.51
	Cambisols	55.90	33.78[a]	21.25
	Arenosols	58.18	27.50[b]	22.66
Seasons	Season 1	57.29[a]	34.43[a]	14.80[c]
	Season 2	49.49[b]	34.97[a]	30.96[a]
	Season 3	62.19[a]	25.00[b]	21.71[b]
Sites	North	46.57[b]	41.62[a]	26.68[a]
	South	66.29[a]	21.06[b]	18.16[b]
Disturbance levels	Natural	46.36[b]	30.29	39.63[a]
	Disturbed	59.74[a]	31.91	16.54[b]

Means followed by superscripts indicate significantly different indices at $P \leq 0.05$. Where **BI**= Basal index, **EI** = Enrichment index and **SI** = Structural index.

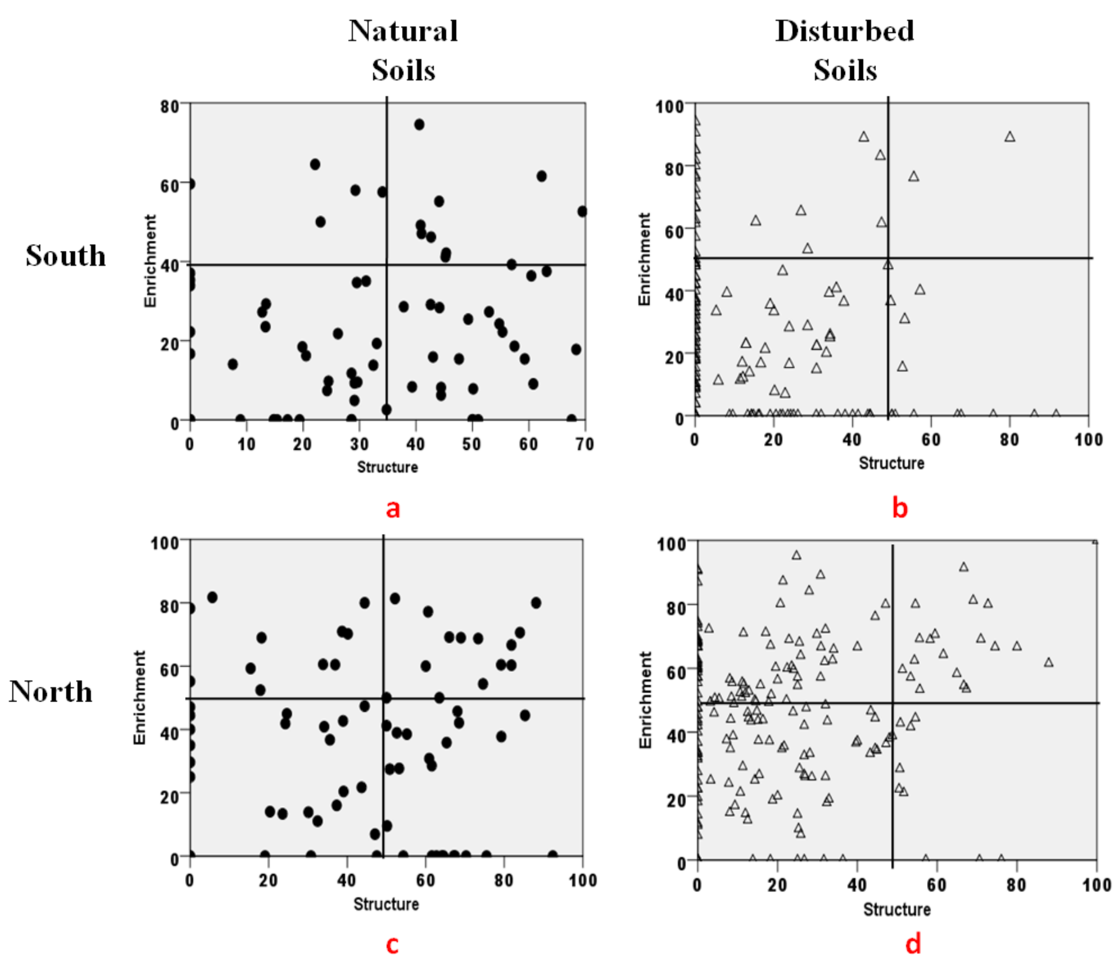

Figure 4. Soil food web structure in natural (a & c [●]) and disturbed (b & d [Δ]) soils in the Southern and Northern sites.

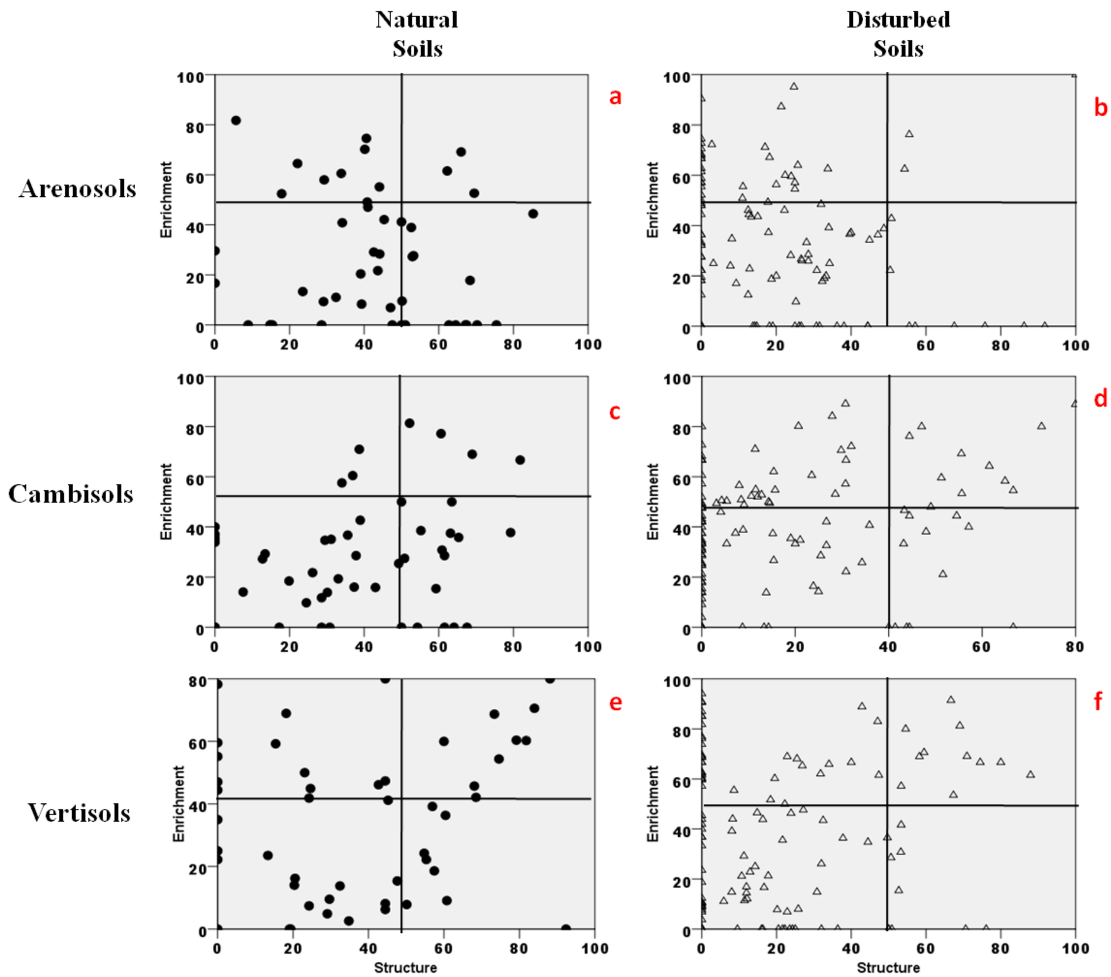

Figure 5. Soil food web structure in natural (a, c & e [●]) and disturbed (b, d & f [Δ]) soils in Arenosols, Cambisols and Vertisols soils groups.

Nematode response to soil disturbance varied within trophic group and soil groups; whereby bacterivores and fungivores were stimulated by NH_4 and TN. The natural/undisturbed soils had higher amounts of NH_4 and TN compared to disturbed (Table 3) and may have favored the propagation of bacterivores and fungivores. Herbivores were generally inhibited by disturbance and an increase in Ca. Predators and omnivores were stimulated by Mg, SOM and C. The few omnivores and predators in the disturbed soils probably represented k strategists that are less tolerant and unsuited in these disturbed soil conditions. Data also indicated that an increase in soil pH, available K and NH_4 was inversely related to bacterivores population growth. This agrees with findings by Fu *et al.* (2005) who posited that bacterivores influence C and N-mineralization by feeding on bacteria and excreting NH_4 and hence aiding propagation of bacteria through the soil.

There is a top-down control of microbes by soil nematodes and is the principle mechanism by which soil nematodes positively contribute to soil processes (Yeates, 2007). Microbial biomass is important for microbivores such as bacterivores and fungivores, and also omnivorous nematodes which in turn feed on microbivores. Zhang *et al.* (2012b) indicated that soil C: N ratio, microbial biomass carbon, and pH were important factors affecting soil nematode communities and suggested that the grazing of soil nematodes on microbes could increase the turnover of microbial populations, which could be the reason why C was one of the main determining factors of the distribution of omnivorous nematodes in this study. Results from the present study indicate that an increase in *Achromadora*, *Tylenchorrynchus*, *Cervidellus* and *plectus* spp. mean counts were positively correlated with an increase in soil available P and soil pH because an increase in soil organic matter causes increases in soil N which corresponds to fungivore abundance. *Rhabditis* and *Eucephalobus* spp. were positively associated with NH_4^+, probably because bacterivores are associated with increased N mineralization (Ferris, 2004). These findings agree with Ferns *et al*. (2004) who reported that *Mesorhabditis* and *Acrobeloides* spp. positively associated with NH_4. When bacterivores predominate in soils, they enhance N mineralization and thus the availability of N for plants (Ferris *et al*., 2004). Nakamoto (2006) noted that TN may be correlated with abundance of certain nematodes and might explain why it was associated only with abundance of fungivores in this study. The discrimination between responses of nematodes in the higher and the lower levels of the soil food web was evident in the DCCA ordination (Figure 2), revealing a link between lower trophic levels and NH_4^+ and total N. Bacteriovores, fungivores and herbivores with low c-p values ordered opposite to predatory and omnivore nematodes.

The maturity index (MI) was higher in the natural/undisturbed soils than the disturbed soils and were significantly affected by seasons due to variability in soil temperature and moisture which affects the abundance of soil nematodes. The study observed that higher values of this index occurred in season 2 than the first and third. The second season which was more humid and rainy had a high MI (2.1), conditions that favored soil nematode reproduction.

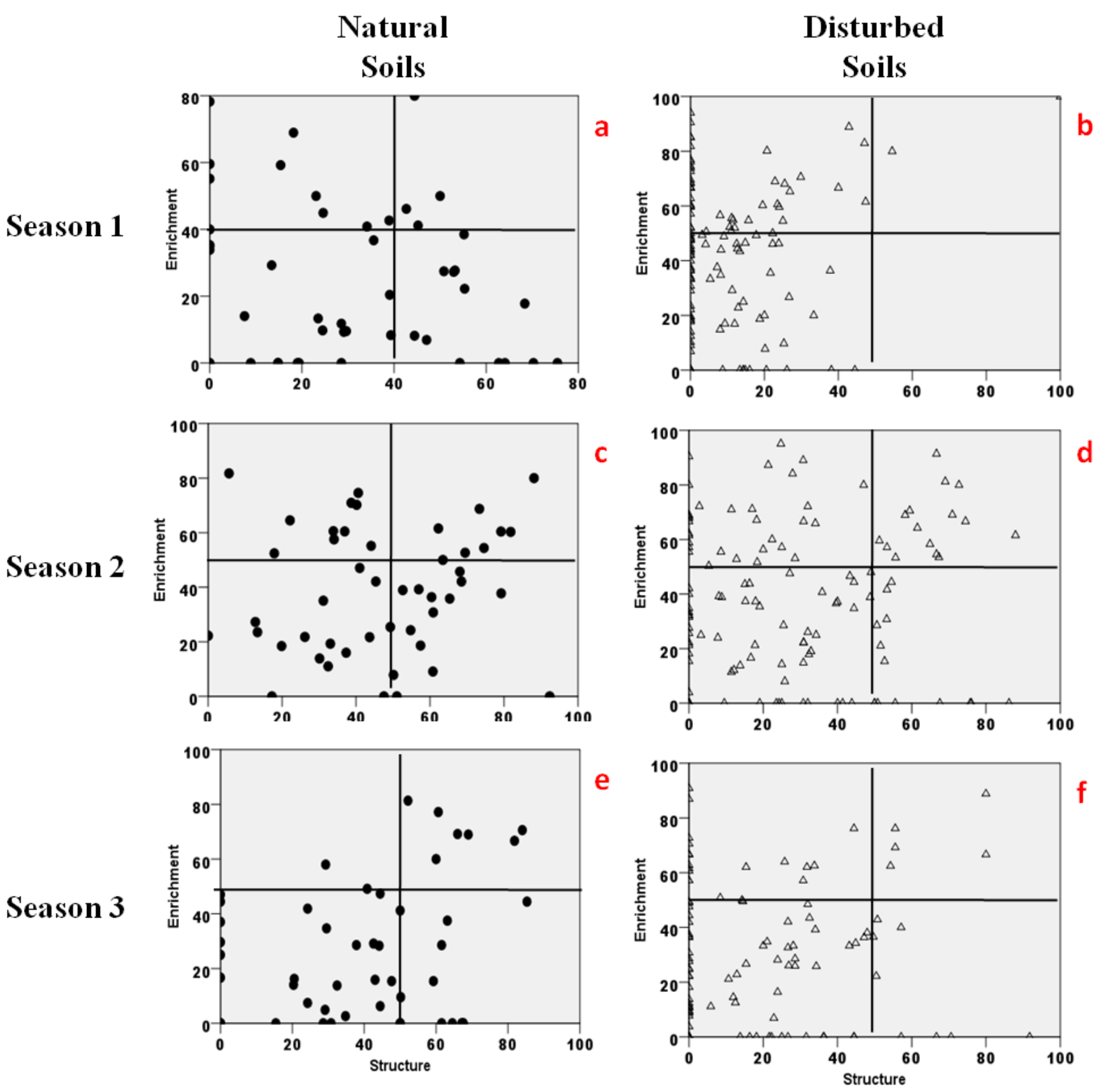

Figure 6. Soil food web structure in natural (a, c & e [●]) and disturbed (b, d & f [Δ]) soils in seasons 1, 2 and 3.

The nematode MI indicates the state of the soil environmental conditions and ecosystems disturbance (Bongers, 1990) and provides useful information on the direction of change within a particular soil, with prospects that the abundance or proportion of c-p groups 1 and 2 may have value as a transferable index. Its higher values reflect the less disturbed sites. Valocka and Sabova (1999) found a similar trend in MI for soil nematodes in grasses and cereals. In the current study, the fertility index (FI) increased from the natural to the disturbed soil. According to Bongers and Korthals (1995) and Bongers *et al*. (1997), the PPI/MI ratio increases gradually from natural/undisturbed habitats to intensively managed agricultural systems and where higher plants make optimal use of nutrient resources, it does not exceed 0.9. The PPI/MI values obtained in the study were above 1.2 thus contradicting this observation.

The EI is based on the weighted abundance of bacterial feeding nematodes (enrichment-opportunistic) relative to longer life cycle bacterial feeders, indicating highly active bacterial-mediated decomposition channels (Sanchez-Moreno, 2006). This study established that seasons and level of soil disturbance significantly affected BI, EI and SI. Increased soil moisture levels and available root systems could have promoted improvement of the soil food web during season two due to higher rainfall realized then and which agrees with Ferris *et al.* (2004) who in their study, modified conditions to suit the propagation of bacterial feeders. The BI was significantly high ($P \leq 0.05$) in tilled soils probably due to addition of organic amendments in the arable lands in bid to increase crop yields. However, the SI was significantly high ($P \leq 0.05$) in natural soils probably because less soil defaunation had occurred to the micro-fauna as compared to the arable land that may have continued to receive human disturbances over time by ploughing, digging, addition of amendments, weeding and rouging from one season to the next, ultimately leading to biodiversity loss. The high EI in the Northern region indicated the prevalence of opportunistic bacterial feeders over other microbial feeders. This may decrease bacterial biomass more than the effect of fungal feeders on fungal biomass, as indicated by the positive association between the EI, the seasons and regions, indicating the prevalence of fungivores over bacterivores.

The basal (BI) and structural (SI) indices were strongly affected by variability between seasons and regions. High BI values indicate a nematode assemblage composed of disturbance-tolerant taxa mainly of the lower trophic levels due probably to their high fecundity and unperturbed reproductive cycles. Farmers in the Northern sites probably had better tillage methods in season two as compared to the Southern farmers with appropriate soil amendment and frequencies that favored BI and SI indices. Bongers (1990) observed that in organically enriched field under intensive crop cultivation phase, nematodes exploit the abundant resources (bacteria and fungi) and increase rapidly in abundance due to their short life cycles and high fecundity. On the contrary, high values of the BI indicate slower, fungal-mediated decomposition pathways. The soil food web indicated that natural undisturbed soil in both the Northern and Southern sites had better structure and nutrient availability compared the disturbed one, an indication that more N is available for plant growth in natural soils. In addition, the Northern soils were less deprived of nutrients to support crop growth than the Southern soils. This could possibly be due to the northern farmers applying more amendments to their farms and in addition incurring less pressure on them through their management practices.

Cambisols and Vertisols had better enrichment and nutrient availability compared to Arenosols perhaps due to the fact that they have higher nutrient retention as observed in the soil physio-chemical analysis (Table 2). Arenosols are sandy in nature and tend to retain very few nutrients as most are leached with percolating waters. This in turn may affect the nutrient availability for nematodes and hence their population and diversity (Karuku and Mochoge, 2016; Karuku and Mochoge, 2018; Karuku, 2019). The nematode analysis was a direct reflection of the fragile nature of Arenosols in terms of nutrient richness and poor structure compared to both Cambisols and Vertisols. Season 2 in both natural and disturbed soils had better structure and enrichment compared to season 1 and season 3. This implied that seasonal changes resulted in improved availability of nutrients for crop sustenance from season 1 to season 2 and depletion of the same as time progressed to season 3. The similarities in the soil food web observed between the natural and disturbed soils also indicate that the natural soils may at one time have been utilized for crop cultivation and were later on abandoned.

CONCLUSIONS

Different seasons, soil groups, sites and disturbance levels have their variable significant influences on the relationship between soil nematode communities and soil properties in their respective ecosystems.

Cambisols, natural soils, moisture presence and active root growth (in seasons 2) and soils in the northern sites favored high diversity and abundance of nematodes. In addition variability between tillage and untilled land in the different sites may also contribute to differences in the soil properties and content of organic matter, ammonium and pH, important factors that affect the soil nematode fauna abundance and assemblage in the study.

Cambisols and Vertisols possess better agricultural potential than Arenosols although all three soil groups should receive equal attention to address their fragile condition for proper utilization in combating degradation as we seek to curb food insecurity.

RECOMMENDATIONS

- Adoption of appropriate cultivation methods and practices by farmers to boost the soil food web nutrient cycling potential, biodiversity to reduce soil and faunal degradation.

- Future carbon studies maybe necessary to establish these changes from C3 to C4 carbonation types as vegetation and cropping interchanges due to human intervention.

Acknowledgement
The University of Nairobi, Kenya that hosted the research and provided facilities and staff in Collaboration with Michigan State University-USA.

Funding. The research project was funded by the Howard G Buffett Foundation through a grant to the last author (MSU RC101172).

Conflict of interest statement. The authors confirm that there is no known conflict of interest associated with this publication.

Compliance with ethical standards. No human participants or animals were used in the study undertaken in the article by any of the authors.

Data availability. Data are available with corresponding author (karuku_g@yahoo.com or gmoe54321@gmail.com) and Andrew Thuo (andy.thuo@yahoo.com or Andrew.thuo@gmail.com) upon reasonable request.

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