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Ecological intensification of maize-kale systems in Kenya by biofertilization and push-pull management shifts nematode communities

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Plant-parasitic nematodes (PPNs) pose a persistent threat to vegetable production in Kenya, contributing to reduced yields and soil degradation. The management of PPNS in vegetables in Kenya has largely remained unaddressed. The integration of ecological intensification strategies such as the vegetable integrated push-pull (VIPP) system and the use of black soldier fly frass fertilizer (BSFF) is gaining traction in sustainable agriculture. The aim of this study was to determine the effects of integrating VIPP and BSFF on nematode abundance and diversity in maize-kale cropping systems. Field trials were conducted in two different agroecological zones in Kenya. Field treatments involved plots with maize and/or kale: control (non-amended monocrops), inorganic fertilizer (DAP and NPK) treated plots, VIPP plots, BSFF treated plots and combined VIPP and BSFF plots. Soil samples were collected from experimental plots and nematode community composition determined using modified Baermann technique. Plots under VIPP augmented with BSFF exhibited significantly higher populations of free-living nematodes and lower densities of PPNS compared to control and inorganic treated plots. The use of VIPP, particularly in combination with BSFF, enhanced the abundance of bacterivorous and fungivorous nematodes, suggesting improved soil health and biological control potential. The findings demonstrate that VIPP and BSFF synergistically promote assemblages of beneficial nematode communities, providing a sustainable pathway for management of nematodes in agroecological farming systems.

KEYWORDS

cropping system, kale, maize, regenerative agriculture, soil health

1 Introduction

The demand for vegetables is increasing as consumers seek to diversify their diets for essential nutrients that form healthy diets (Da Wafi et al., 2023; Dubey et al., 2020). Increased vegetable production also mitigates food insecurity and enhances food and economic self-sufficiency. It also generates income, particularly for youth and women throughout the

vegetable production chain in rural, urban, and peri-urban areas (Bokelmann et al., 2022; Schreinemachers et al., 2018). In Kenya, the main vegetable crops are tomato (*Solanum lycopersicum*), cabbage (*Brassica oleracea*), kale (*Brassica oleracea* var. *acephala*), African nightshade (*Solanum scabrum*), amaranth (*Amaranthus* spp.), French beans (*Phaseolus vulgaris*), carrot (*Daucus carota*), and onions (*Allium cepa*) (Anyega et al., 2021; Lagerkvist et al., 2012; van der Lans et al., 2012; Ngigi et al., 2011). Kale is mainly grown for household consumption and plays an important role in improving the nutritional balance of diets while also serving as an important source of income for peri-urban farming households (Lagerkvist et al., 2012; Ngigi et al., 2011). The production of vegetables is however constrained by pest infestations and poor soil (Mantovani et al., 2017; Mutiga et al., 2010; Ogol and Makatiani, 2007; Tully et al., 2015). Other challenges include increasingly hot and dry weather conditions that lead to low production (Anyega et al., 2021; Nordey et al., 2017).

Insect pests and diseases have long been recognized as important constraints to vegetable production worldwide, and have been subject to extensive research. However, nematodes, are frequently overlooked, as their symptoms are often mistaken for nutrient deficiencies (Coyne et al., 2018a). This is further compounded by the limited awareness of nematode-related problems among smallholder farmers in sub-Saharan Africa (Coyne et al., 2018a). While plant-parasitic nematode (PPNs) are well known for their detrimental effects on vegetable crops (Sandrine et al., 2023), free-living nematodes (FLNs) are valued for their beneficial roles in the rhizosphere and their positive contribution to soil health and crop productivity (Atandi et al., 2022). FLNs are assigned to different trophic groups, namely, bacterivores, fungivores, predators and omnivores. The contribution of FLNs to the acceleration of nutrient mineralization as well as promoting release of the plant-available nitrogen in soils has been reported in previous studies (Kekelis et al., 2022; Lu et al., 2020; Natalio et al., 2024). For this reason, FLNs community composition is increasingly being used as indicator of soil health, with high densities of these organisms often reflecting improved organic matter content and general soil fertility. Predatory and omnivorous nematodes contribute to biological control by regulating the populations of PPNS (Atandi et al., 2022; Khan and Kim, 2007).

Plant-parasitic nematodes attack underground plant parts, causing crop damage and yield losses, and inducing symptoms that are often mistaken for those caused by abiotic factors, which makes their management challenging (Sandrine et al., 2023). Aboveground symptoms of nematode root damage include nutrient inadequacy, wilting, stunting, poor production, and, in extreme cases, plant mortality (Coyne et al., 2018b). Farmers have relied on synthetic nematicides for PPNS management (Kiriga et al., 2018; Stirling and Pattison, 2008), but these are costly and pose adverse effects to human health, the environment and the microbial biodiversity (Agboyi et al., 2016; Bamboriya et al., 2022; De Bon et al., 2009; Nordey et al., 2017). There is therefore a need to develop sustainable and eco-friendly alternatives to address PPNS management practices. Studies of the efficacy of different cropping systems and organic amendments against PPNS have shown promise from both an economic and ecological perspective (Anedo et al., 2025; Atandi et al., 2022; Dawabah et al., 2019; Paudel et al., 2020).

Vegetable integrated push-pull technology (VIPP) has been reported as a promising strategy and sustainable path to pest management, improved crop productivity and nutritional quality (Chidawanyika et al., 2023, 2025). The VIPP is a form of intercropping of vegetable and cereal crops with pest-attractant and repellent fodder

plants. The main crops in these systems are intercropped with leguminous companion plants of the genus *Desmodium* [Fabaceae] to control the pests of the main crop and suppress parasitic weed growth (Chidawanyika et al., 2023; Khan et al., 2001). The push-pull field is then sown with napier grass (*Pennisetum purpureum*) or *Brachiaria* spp. as a border crop, surrounding the whole field (Midega and Khan, 2003). The *Desmodium* plants produce volatiles that repel various pests while the surrounding grasses serve as alternative attractive ovipositional hosts that are not suitable for full development of larvae (Khan et al., 1997). Apart from pest regulation, the benefits of this system are enhanced safe food production, improved soil fertility and improved overall soil health (Drinkwater et al., 2021; Ndayisaba et al., 2021). This cropping system is gaining increasing interest in agricultural production as it employs on-farm crop diversification to manage pests by leveraging chemically and physically mediated interactions with non-host plants, coupled with the presence of natural enemies (Lang et al., 2022). Although the beneficial effects of VIPP against above-ground pests in East Africa has been demonstrated (Chidawanyika et al., 2025; Khan et al., 2001, 2018; Midega et al., 2018), its effect on belowground pests, particularly nematodes, remains under explored.

The potential of using black soldier fly frass fertilizer (BSFF) as an organic amendment for the control of PPNS was reported by Anedo et al. (2024, 2025). The BSFF, a composted byproduct of black soldier fly larvae, is nutrient-rich and suitable as an organic fertilizer (Beesigamukama et al., 2020a; Oonincx et al., 2015; Tanga et al., 2022). Several studies illustrated the value of frass in improving the growth, yield and nutritional quality of vegetables (Abiya et al., 2022; Agustiyani et al., 2021; Anyega et al., 2021; Borkent and Hodge, 2021; Dzepe et al., 2022; Tan et al., 2021) compared to conventional compost or commercial organic and mineral fertilizers. Similarly, the ability of BSFF to suppress PPNS due to the presence of bioactive compounds such as chitin derived from the pupa exoskeleton was reported (Anedo et al., 2024, 2025; Kisaakye et al., 2024). Chitin acts as a substrate for micro-organisms which parasitize nematodes, thereby reducing PPNS numbers (Kisaakye et al., 2024; Ledchumanakumar et al., 2021). BSFF is also rich in organic matter and nutrients that stimulate the activity of beneficial soil microorganisms, including fungi and bacteria (Beesigamukama et al., 2020b; Yang et al., 2020). Some of these microbes produce nematicidal compounds or infect PPNS, while others are root endophytes, which enhances plant resistance to nematode infection (Kiriga et al., 2018).

Previous studies on the belowground effects of companion crops have largely addressed soil health through fixation of nitrogen and the enhanced accumulation of organic matter and available phosphorus for plants and suppression of *Striga* weed (Drinkwater et al., 2021; Ndayisaba et al., 2021). There is limited knowledge on the impact of VIPP on the nematodes, particularly community composition, population abundance and diversity as well as pathogenicity. This study was conducted to determine the diversity and population densities of nematodes associated with kale and maize (*Zea mays*) in VIPP systems augmented with BSFF. Kale crop was used since it is commonly cultivated as leafy vegetable in both regions where the study was conducted. This study presents the first field-based evaluation of a new integration system combining VIPP and BSFF to suppress PPNS in Kenyan vegetable production systems. The objectives were to determine the effects of this integrated system on (i) soil nematode community composition and diversity and (ii) plant-parasitic nematode densities.

2 Methodology

2.1 Description of sampling sites

Trials were conducted on researcher-managed experimental stations (on-station) in two agro-ecologies of Kenya. These stations were at Embu (0° 30.31' S, 37° 27.39' E) at an elevation of 1,512 m above sea level (a.s.l) and at Kiambu (1° 13'23.36" S, 36° 39'45.29" E) at 2301 m a.s.l for two cropping seasons (April to August 2024 and November 2024 to March 2025). Both sites receive bi-modal rainfall, with the long rains between March–July and short rains between October–December. The Kiambu region experiences a cool, sub-humid climate with an annual rainfall amount ranging from 1,000 to 1,400 mm. The temperatures in Kiambu are relatively cool, ranging between 13 and 20 °C with red silt loam well drained soils. The Embu region experiences a sub-humid climate with an annual average rainfall of 900 mm and temperatures that range between 14 and 30 °C. The area is characterized by red loam soils that are well drained, fertile, and classified as humic nitisols.

2.2 Source of fertilizers, seeds and splits

Two fertilizer types were used in this study. These were: BSFF (Evergrow organic fertilizer), and inorganic fertilizer (DAP 18:46:00 and NPK 17:17:17), sourced from Sanergy Limited Kenya and Simlaw Seeds Company Limited in Nairobi, Kenya, respectively.

The maize (SC DUMA 43) and kale seeds were sourced from Seed Co Kenya and Simlaw Seeds Company Limited, respectively. The *Desmodium* seeds were sourced from Simlaw Seeds Company Limited while *Brachiaria* grass splits from ICIPE push-pull fields, Nairobi, Kenya.

2.3 Treatments and experimental setup

The field trials consisted of 12 treatments covering two crops (maize and kale) replicated four times at each of the two locations, for two cropping seasons, following a randomized complete block design (RCBD). For maize and/or kale, the 12 treatments consisted of 6 for each crop and involved the following: 1. control (non-amended monocrops), 2. inorganic fertilizer (DAP and NPK) treated plots, 3. VIPP plots, 4. BSFF treated plots, 5. VIPP and BSFF plots with either maize or kale and 6. VIPP and BSFF plots with both maize and kale. Each plot measured 6 × 6 m with border widths of 1.5 m and 2 m between the plots and blocks, respectively. The intra-row spacing for maize and kales was 30 and 50 cm, respectively. Where applicable, *Desmodium* and *Brachiaria* companion crops were established 3 months before planting the main crops. *Desmodium* seeds were planted in between rows of maize and/or kales while *Brachiaria* grass splits were planted at plant–plant spacing of 50 cm in the plot border. Planting in the control plots followed the same procedure but without *Desmodium* and *Brachiaria* companion crops. Where applicable, the BSFF was applied 1 week before planting, whereas the inorganic fertilizer was applied 1 week after planting. Weeding was done manually. Since *Brachiaria* and *Desmodium* are perennial crops, they were planted once and trimmed back just before planting maize seeds and kale seedlings (the onset of a season).

Both the VIPP and BSFF plots, as well as the control plots were maintained throughout the study period and the companion crops

similarly maintained over seasons. The experimental layout and position of plots were identical for the two cropping seasons.

2.4 Soil sampling, nematode extraction and identification

Nematodes were sampled from each plot prior to planting (7 days before), and again at harvest in both seasons. A total of 48 soil samples were collected from each site and season (totaling to 192 samples). Soil samples were collected using a soil auger to a depth of ~25 cm, after removing the top 3–5 cm of soil (Coyne et al., 2018b). The composite samples from each plot were then placed in a polythene bag, (~1 kg), labelled and stored in a cool box before being transported to the laboratory. Each sample was thoroughly mixed, sieved (2 mm sieve) and 100 mL removed for nematode analysis. Analysis of the soil samples were done using standard laboratory methods following the procedures of Coyne et al. (2018b); and Shurtleff and Averre (2000). Nematodes were extracted using modified Baermann technique. After 48 h the extractions were concentrated to 10 mL in a falcon tube and all nematodes counted under a leica stereomicroscope. Nematodes were then identified to genus level under a compound microscope (X400) (Coyne et al., 2018b).

2.5 Statistical analyses

Prior to analysis, data were checked for normality and homogeneity of variance using the Shapiro–Wilk test and Levene's test, respectively. Where necessary, the data were transformed to their natural log to meet assumptions for parametric analysis. Permutational multivariate analysis of variance (PERMANOVA) was used to analyze differences in nematode community composition among the treatments. We used non-metric distance scaling (NMDS) to visualize how nematode communities differed among treatments, across seasons and crops (maize vs. kale). To see which of the nematodes are causing the difference in the nematode communities, we did SIMPER analysis. The data were subjected to two-way analysis of variance (ANOVA) to investigate the effect and interactions between sites and treatments. General Linear Model procedures with binomial distribution were used to analyze and distinguish the occurrence and distribution of nematodes with the main effects being season, site, treatment and the interaction effects. Significantly different means at $p \leq 0.05$ were separated using Tukey–HSD. Percentage frequency of occurrence was calculated as: $((n/N) \times 100)$, where n = the number samples containing the genus/trophic group and N = sample size. A Pearson correlation analysis was conducted to explore relationships among different nematode genera, trophic groups, and the total abundances of PPNs and FLNs. All data were analyzed using R version 4.4.2 (R Core Team, 2024).

3 Results

3.1 Nematode composition, characterization and percentage incidences relative to baseline levels in Embu and Kiambu field trials across seasons 1 and 2

Nematode characterization revealed presence of various nematode genera and trophic groups occurring at varying frequencies

across the two sites and seasons (Tables 1, 2). A total of 13 and 14 PPNs genera were found in the samples analyzed both for Embu and Kiambu, respectively. Nine genera were present in both seasons and sites (Table 2). These nematode species represented both economically important plant-parasitic genera including *Pratylenchus*, *Meloidogyne*, *Helicotylenchus*, *Xiphinema*, *Trichodorus* and *Paratrichodorus* as well as less economically important taxa. Order Tylenchida was the most diverse and abundant. A total of 15 genera of PPNs representing eight families in the orders Tylenchida, Triplonchida, Dorylaimida and Aphelenchida were identified (Table 2).

The percentage incidence of FLN trophic groups and PPN genera varied between sites and across season 1 and 2 relative to baseline levels (Table 1), with most of the PPNs occurring infrequently. FLNs occurred in varying proportions across all samples. Four trophic groups were identified namely, bacterivores, fungivores, omnivores and predators. Bacterivores and fungivores showed 100% incidence at baseline and remained present in all samples across both seasons and sites (Table 1). Omnivore exhibited a moderate incidence at the baseline and season 1 in Embu (50%) but declined to 39% in season 2, whereas in Kiambu omnivores were absent at the baseline sampling and increased to 46% and 75% in season 1 and 2, respectively. Predators, on the other hand, were absent at the baseline in Embu and occurred in moderately low frequencies in season 1 for both sites (Embu: 18%; Kiambu: 43%) increasing markedly in season 2 (Embu: 75%; Kiambu: 54%).

The most commonly occurring PPN taxa were *Pratylenchus* spp., *Meloidogyne* spp., *Helicotylenchus* spp., *Rotylenchulus* spp., *Trichodorus*

spp., *Filenchus* spp., *Tylenchus* spp. and *Aphelenchoides* spp. (Table 1). At Embu, *Pratylenchus*, *Meloidogyne*, *Helicotylenchus*, *Rotylenchulus*, *Filenchus* and *Aphelenchoides* were present in all the samples (100%) at the baseline while they occurred in over 80% of all samples in both seasons, except *Meloidogyne* and *Filenchus* which declined markedly by the season 2 (32 and 46%, respectively). While no *Hoplolaimus*, *Rotylenchus* and *Criconema* were recorded in baseline and season 1, their frequencies of occurrence in season 2 were low (7–11%). No *Globodera* or *Xiphinema* were recorded at Embu (Table 1).

Similarly, in Kiambu, *Helicotylenchus*, *Rotylenchulus*, *Filenchus*, *Tylenchus* and *Aphelenchoides* were detected in high frequencies with *Rotylenchulus* being present in all samples in baseline and both seasons (Table 1). *Hoplolaimus*, *Xiphinema* and *Rotylenchus* were detected only in season 2 in very low frequencies (4–7%) while *Globodera* juveniles were only recorded in season 1. *Criconema* were not present in the baseline but occurred at very low frequencies (14%) in both seasons while *Pratylenchus*, *Tylenchorhynchus* and *Trichodorus* were recorded in moderate frequencies in baseline and across seasons. *Paratrichodorus* was only detected at Embu season 2 but not in Kiambu (Table 1).

PERMANOVA analysis showed overall significant differences in nematode community composition among the treatments across season and crop at each site ($F_{23} = 11.91$, $p = 0.001$ and $F_{23} = 11.91$, $p = 0.001$, respectively, for Embu and Kiambu) (Supplementary Table 1). Pairwise comparison showed some treatments harboured similar nematode communities across the seasons (Supplementary Tables 2, 3). SIMPER analysis showed that

TABLE 1 Percentage incidence of free-living nematodes trophic groups and plant-parasitic nematodes relative to baseline levels in Embu and Kiambu field trials across seasons 1 and 2, (n = 48).

Trophic groups	Embu			Kiambu			
	Free-living nematodes	Baseline densities	Season 1	Season 2	Baseline densities	Season 1	Season 2
Fungivores		100	100	100	100	100	100
Bacterivores		100	100	100	100	100	100
Omnivores		50	50	39	0	46	75
Predators		0	18	75	100	43	54
Plant-parasitic genera							
<i>Pratylenchus</i>		100	86	57	50	18	54
<i>Meloidogyne</i>		100	36	32	50	54	75
<i>Globodera</i>		0	0	0	0	4	0
<i>Hoplolaimus</i>		0	0	7	0	0	4
<i>Helicotylenchus</i>		100	93	93	100	100	93
<i>Rotylenchulus</i>		100	82	86	100	100	100
<i>Rotylenchus</i>		0	0	11	0	0	4
<i>Tylenchorhynchus</i>		0	46	29	0	54	32
<i>Trichodorus</i>		0	54	61	0	68	39
<i>Paratrichodorus</i>		0	0	36	0	0	0
<i>Xiphinema</i>		0	0	0	0	0	7
<i>Criconema</i>		0	0	11	0	14	14
<i>Filenchus</i>		100	79	46	100	100	39
<i>Tylenchus</i>		75	82	68	100	100	86
<i>Aphelenchoides</i>		100	100	82	100	96	79

TABLE 2 Plant-parasitic nematodes genera recovered from Embu and Kiambu field trial sites in Kenya.

Class	Order	Family	Genus	Common name
Secernentea	Tylenchida	Pratylenchidae	<i>Pratylenchus</i>	Lesion nematode
		Heteroderidae	<i>Meloidogyne</i>	Root-knot nematode
			<i>Globodera</i>	Potato cysts nematodes
		Hoplolaimidae	<i>Hoplolaimus</i>	Lance nematodes
			<i>Helicotylenchus</i>	Spiral nematode
			<i>Rotylenchulus</i>	Reniform nematode
			<i>Rotylenchus</i>	Spiral nematode
		Tylenchidae	<i>Filenchus</i>	
			<i>Tylenchus</i>	
Enoplea	Triplonchida	Dolichodoridae	<i>Tylenchorynchus</i>	Stunt nematode
		Trichodoridae	<i>Trichodorus</i>	Stubby-root nematode
			<i>Paratrichodorus</i>	
	Dorylaimida	Longidoridae	<i>Xiphinema</i>	Dagger nematode
			<i>Criconema</i>	Ring nematode
	Aphelenchida	Aphelenchoididae	<i>Aphelenchoides</i>	Foliar nematode

Pratylenchus, RKN, *Filenchus*, *Trichodorus*, predators, omnivores, *Helicotylenchus*, *Rotylenchus*, *Aphelenchoides* and bacterivores contributed most to the dissimilarity which caused the differences in nematode community composition in different treatments across the two sites. Analysis of nematode communities between the two sites also showed that there were differences between the sites (Embu and Kiambu) with a 24.83% difference in the nematode communities between the sites and the biggest contributor to the difference was *Pratylenchus* sp. (11.91%), RKN (11.39%), predators (10.74%), omnivores (10.4%) and *Trichodorus* sp. (9.86%). The similarity between the communities at both sites were due to the bacterivores and fungivores.

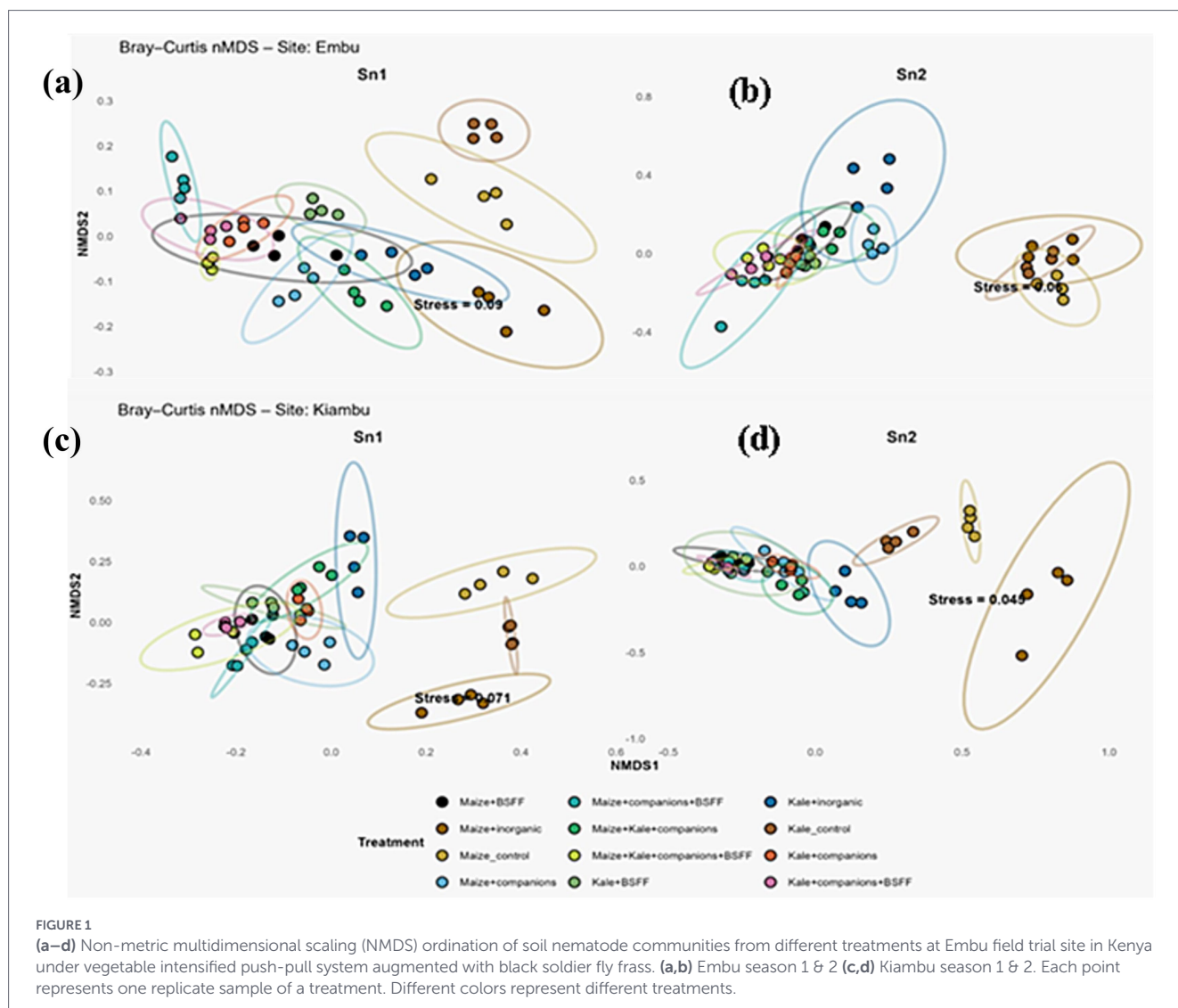
The non-metric multidimensional scaling (NMDS) of Bray–Curtis similarities analysis showed clear temporal differences in nematode assemblages between sites and among the treatments (Figure 1). In Embu season 1, the NMDS (stress = 0.09), control and inorganic fertilizer plots (both kale and maize) clustered separately but showed partial overlap or were closer with the plots treated with either BSFF, companion crops or combinations (Figure 1a). However, in season 2 (stress = 0.06), the ordination displayed a distinct segregation of treatments along the NMDS1 axis (Figure 1b). Control and organic plots grouped together on the right side of the plot, whereas plots with BSFF and/or companion crops formed distinct clusters to the left side, except for kale + inorganic fertilizer which overlapped with maize + companion plots (Figure 1b).

Similarly, NMDS ordinations of Bray–Curtis similarities at Kiambu site, indicated differences in nematode community composition among the treatments and between seasons. In season 1 (stress = 0.071), control, inorganic fertilizer and integrated treatments formed moderately distinct but partly overlapping clusters, showing only initial divergence in community structure (Figure 1c). In season 2 (stress = 0.045), the ordination revealed clearer separation along the NMDS1 axis with the control (kale and maize) and plots with inorganic fertilizer treatments grouping on the right side, while plots with BSFF treatment and/or companion crops distinctively occupying the left side of the plot away from the controls (Figure 1d).

3.2 Relative density of plant-parasitic and free-living nematodes occurrence under different management systems

The overall mean abundance of PPNs varied significantly across seasons, treatments and sites (Figure 2) with significant interaction between the site and seasons ($\chi^2 \geq 89.2$, $p < 0.001$). Across the seasons and locations, the control treatments (both kale and maize) consistently recorded nematodes densities above the baseline populations (dashed line) Figure 2. Control treatments also recorded the highest total PPNs counts ($p < 0.05$) except in Kiambu season 1 where plots treated with inorganic fertilizer showed significantly higher abundance (Figure 2B, Table 3). In contrast, treatments with either BSFF or companion crops alone, or the combinations recorded significantly lower mean numbers ($p < 0.05$) of PPNs in both seasons and sites, relative to the baseline densities as well as compared to the control treatments of both maize and kale (Tables 3, 4). The treatments that had combination of BSFF and companion crops recorded significantly lower PPNs compared to those with BSFF or companion crops only in some cases in the two sites and across the two seasons (Figure 2). Notably, the plots treated with inorganic fertilizer showed significantly lower PPNs densities ($p < 0.05$) compared to controls in both sites but significantly higher PPNs than on BSFF or companion crops separately or combined.

On the other hand, the mean densities of FLNs varied significantly among the seasons, treatments and between the sites ($p < 0.01$) (Tables 5, 6 and Figure 3) with significant interaction between the sites and seasons ($\chi^2 \geq 4.7$, $p = 0.03$). The treatments on control (both kales and maize) recorded significantly lower FLNs compared to other treatments with season 1 ranging between 438.4 and 603.6 nematodes per 100 g (Figures 3A,B) and season 2 between 200.0 and 444.8 in Kiambu and Embu (Figures 3C,D). This was followed by plots with inorganic fertilizer (105.0–730.0) in both seasons. In season 1 in both sites, the FLNs densities in the control (kale and maize) and inorganic fertilizer treated plots remained at or slightly higher above the baseline, whereas in season 2 they were generally below the baseline, with



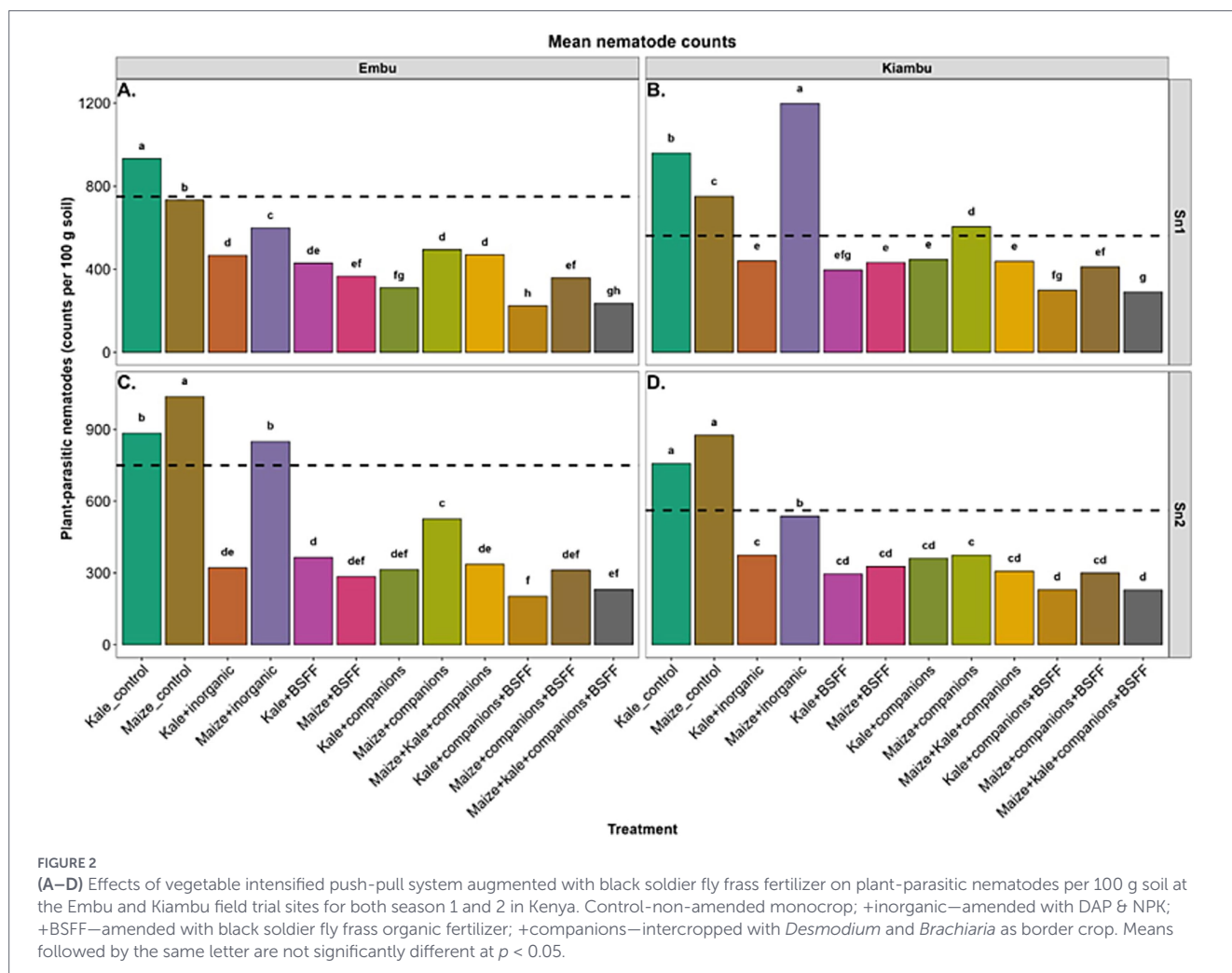
only a few cases reaching the baseline levels. In contrast, treatments amended with BSFF or companion crops alone recorded significantly higher FLNs densities compared to control and inorganic fertilizer treatments at both sites. The treatment that combined BSFF and companion crops recorded even significantly higher densities ($p < 0.01$) than all other treatments, with approximately three-fold increase observed relative to the control treatments (Table 6). All the treatments incorporating BSFF, companion crops or their combination consistently exceeded the baseline nematode populations across both sites and seasons (Figure 3).

3.3 Diversity and densities of plant-parasitic nematodes genera under different management systems

In the first season (Table 3), *Pratylenchus* and *Meloidogyne*, key plant-parasitic genera, were detected in significantly high numbers in the control treatments (both maize and kale) in both sites. In Embu, *Pratylenchus* recorded the highest densities in the kale control plot (207) followed by maize control (152). Notably, *Pratylenchus* was drastically reduced in plots that had companion crops alone or combined BSFF and companion crops but was not detected in kale + maize +

BSFF + companions plots. In Kiambu, it was detected in significant high numbers in maize control (157.0) with other treatments recording significantly low numbers or none at all. RKN, on the other hand, was detected in all treatments in Kiambu except in kale + inorganic fertilizer and maize + BSFF plots. Significantly high densities were recorded in kale control plots (Embu; 186.2, Kiambu; 134.0) followed by maize control plots (64.7) in Embu with very low densities or none at all recorded in the BSFF and companions combined treatments in both sites. *Trichodorus*, also being an important nematode, was detected in low densities in both sites except in maize companions and maize + kale + companions + BSFF in Embu. Other genera, *Helicotylenchus* and *Rotylenchulus*, whose economic importance has not been ascertained in maize and kale were detected in high numbers. They were recorded in high densities in control treatments with densities reducing significantly in either BSFF, companion crops or the combined treatments. Similar results were observed in *Aphelenchoides* and *Filenchus*. Other PPNs, named others, including *Xiphinema*, *Rotylenchus*, *Criconeema*, *Globodera*, *Hoplolaimus*, *Paratrichodorus*, *Tylenchorynchus*, *Tylenchus*, occurred infrequently and remained generally low in abundance across the treatments.

In the second season (Table 4) there was an overall notable reduction in densities of most genera particularly in treatments that



combined companion crops and BSFF compared to control. *Pratylenchus*, was most abundant in the control plots, particularly, in kale control (Embu; 232.5, Kiambu; 124.5) and maize control (Embu; 145.0, Kiambu; 50.0) treatments. The densities were significantly reduced in other treatments compared to the control or totally not detected. RKN followed similar trends as that of *Pratylenchus* except that plots with inorganic fertilizer treatments were not different from the control treatments. *Helicotylenchus* was most prevalent in kale and maize control in Embu while it was similar in all other treatments. In Kiambu, *Helicotylenchus* was prevalent in the control as well as maize inorganic fertilizer treatments while it was reduced significantly in all other treatments particularly, in the integrated treatments. *Rotylenchulus* was most abundant in maize inorganic fertilizer amended plots followed by maize control but showed significantly reduced numbers in the companions, BSFF-amended or combined treatments in Embu. Other PPNs, including *Trichodorus*, *Filenchus* *Aphelenchoides*, and others remained generally low in abundance across the treatments and showed almost similar trends.

3.4 Relative density of free-living nematodes occurrence under different management systems

In general, bacterivores and fungivorous nematodes dominated across seasons, sites and treatments (Tables 5, 6). In the first season

(Table 5), bacterivores nematodes were most abundant in the plots that combined BSFF and companion crops; maize (930.1); maize + kale (814.8), followed closely by +kale (676.2) and maize + companions only (729.8) in Embu. The control plots, both kale and maize controls, recorded the lowest bacterivore counts (251.1 and 209.9 respectively), though this was not significantly different ($p < 0.05$) with the plots that were treated with inorganic fertilizer. In Kiambu, bacterivores followed the same pattern as Embu. Fungivore nematodes followed a similar pattern as bacterivores, with higher densities observed in treatments involving BSFF and companion crops. Omnivore and predator nematodes were generally lower than those of bacterivores and fungivores. Omnivores were not detected in kale inorganic fertilizer plots in Embu and in kale + companions in Kiambu. Predator densities were not different across the treatments in both sites and were not detected at all in some plots.

In the second season (Table 6), bacterivores nematodes were significantly more abundant in plots that had companion crops or were BSFF-amended or that combined BSFF and companion crops in both sites. In contrast, the lowest bacterivore counts were recorded in either control or with inorganic treatments. Fungivore nematodes followed a similar trend, with the highest abundances recorded in maize + companions + BSFF (612.5) in Embu and maize + kale + companions + BSFF (414.8) in Kiambu. Treatments on control, such as maize control (52.5) in Embu and maize + inorganic fertilizer (Embu; 72.5, Kiambu; 47.5), exhibited the lowest fungivore densities. Omnivore and

TABLE 3 Effects of vegetable intensified push-pull system augmented with black soldier fly frass fertilizer on of plant-parasitic nematodes genera feeding groups per 100 g soil at the Embu and Kiambu field trial sites for season 1 in Kenya.

Treatment	<i>Pratylenchus</i>		<i>Meloidogyne</i>		<i>Helicotylenchus</i>		<i>Rotylenchulus</i>		<i>Trichodorus</i>		<i>Filenchus</i>		<i>Aphelenchoides</i>		Others		Total PPNs	
	Embu	Kiambu	Embu	Kiambu	Embu	Kiambu	Embu	Kiambu	Embu	Kiambu	Embu	Kiambu	Embu	Kiambu	Embu	Kiambu	Embu	Kiambu
Kale_control	206.6a	0.0c	186.2a	134.0a	140.0a	193.4bc	49.3cd	207.7b	12.0c	19.4bc	45.5ab	82.6a	127.6bcd	40.6e	166.0a	281.9a	933.1a	959.6b
Maize_control	152.4b	157.0a	64.7b	47.1bc	147.0a	225.5b	130.8b	126.0c	0.0c	40.1a	4.14c	52.7a	184.5ab	72.2cde	50.3cde	30.5e	733.9b	751.1c
Kale + inorganic	53.8d	0.0c	0.0c	0.0e	29.7cd	132.3bcd	100.3b	33.9d	17.9bc	1.3d	47.0ab	25.3b	187.8ab	144.6ab	30.8def	102.7bc	467.3d	440.1e
Maize + inorganic	32.3de	4.2bc	50.5b	11.9de	34.9bcd	427.3a	177.3a	362.4a	26.1b	5.9cd	62.4a	71.2a	150.2abc	185.5a	65.8cd	130.1b	599.4c	1198.6a
Kale + BSFF	114.1c	0.0c	62.5b	12.0de	7.7d	114.7cd	20.3de	37.5d	5.0c	2.5d	9.4c	66.0a	196.4a	27.5e	14.6ef	136.7b	430.0de	396.7efg
Maize + BSFF	53.8d	0.0c	0.0c	0.0e	29.7cd	58.9d	100.3b	41.3d	17.9bc	21.7bc	47.0ab	54.5a	87.8cdef	128.2abc	30.8def	127.5b	367.3ef	432.1e
Kale + companions	55.1d	3.5bc	0.0c	57.0b	25.2cd	139.8bcd	30.3cde	41.7d	48.3ab	14.5cd	30.2bc	49.0ab	57.3ef	44.6e	64.6cd	97.4bc	311.0fg	447.4e
Maize + companions	40.8d	4.0bc	49.4b	35.3bcd	64.9b	203.4bc	59.1c	57.7d	0.0c	31.3ab	66.5a	70.3a	105.8cde	117.3abcd	108.8b	85.9bcd	495.3d	605.0d
Maize + kale + companions	54.3d	0.0c	0.0c	5.2de	40.6bcd	114.7cd	178.1a	32.7d	6.4c	33.4ab	64.4a	53.2a	98.1cdef	158.5a	28.4def	40.7de	470.3d	438.4e
Kale + companions + BSFF	42.2d	13.8b	2.5c	5.2de	56.5bc	56.3d	2.5e	43.6d	26.8b	10.8cd	49.5ab	37.8ab	35.2f	74.9bcde	9.5f	56.3cde	224.6h	298.7fg
Maize + companions + BSFF	56.4d	16.5b	7.3c	22.5cde	22.8d	77.7d	53.6c	67.3d	53.2a	34.5ab	50.2a	57.58a	67.8def	51.6de	48.1cde	83.8bcde	359.5ef	411.5ef
Maize + kale + companions + BSFF	0.0e	0.0c	2.5c	5.1de	36.5bcd	72.2d	20.0de	32.7d	0.0c	28.4abc	6.3c	53.2a	85.6def	58.5cde	85.5bc	40.7de	236.4gh	291.0g

Control-non-amended monocrop; + inorganic—amended with DAP & NPK; + BSFF—amended with black soldier fly frass organic fertilizer; + companions—intercropped with *Desmodium* and *Brachiaria* as border crop. Means within columns followed by the same letter are not significantly different at $p < 0.05$.

TABLE 4 Effects of vegetable intensified push-pull system augmented with black soldier fly frass fertilizer on of plant-parasitic nematodes genera feeding groups per 100 g soil at the Embu and Kiambu field trial sites for season 2 in Kenya.

Treatment	<i>Pratylenchus</i>		<i>Meloidogyne</i>		<i>Helicotylenchus</i>		<i>Rotylenchulus</i>		<i>Trichodorus</i>		<i>Filenchus</i>		<i>Aphelenchoides</i>		Others		Total PPNs	
	Embu	Kiambu	Embu	Kiambu	Embu	Kiambu	Embu	Kiambu	Embu	Kiambu	Embu	Kiambu	Embu	Kiambu	Embu	Kiambu	Embu	Kiambu
Kale_control	232.5a	124.5a	205.5a	54.5abc	170.8a	152.8ab	97.5bcd	230a	12.5ab	47.5ab	12.5c	0c	89ab	48.1bcd	64bc	100.5a	884.2b	757.8a
Maize_control	145b	50b	220a	57.5abc	95ab	187.5a	182.5ab	225a	82.5ab	20ab	60a	110a	62.5abc	145a	190a	81.2a	1037.5a	876.2a
Kale + inorganic	14.8cd	12.5bcd	25b	85ab	71.5b	67.5cd	75bcd	167.5ab	87.5ab	15ab	0c	0c	33.5bc	0d	15c	28a	322.2de	375.5c
Maize + inorganic	45cd	5d	232.5a	107.5a	50b	180a	277.5a	160abc	25ab	0b	0c	0c	70abc	25cd	150ab	60a	850b	537.5b
Kale + BSFF	73c	7.5cd	21.8b	5c	60b	129abc	32.8d	35d	7.5b	0b	41.2ab	42.2b	102.2a	34.5cd	26.8c	43a	365.2d	296.2cd
Maize + BSFF	0d	47.5bc	10b	5c	60b	20d	112.5bcd	62.5bcd	12.5ab	57.5ab	0c	20bc	20c	60bc	70bc	55a	285def	327.5cd
Kale + companions	32.5cd	11.5bcd	0b	45abc	48.8b	70.2bcd	51.5cd	65bcd	55ab	65a	24.5bc	8.2bc	65abc	23.8cd	37.5c	72.5a	314.8def	361.2cd
Maize + companions	20cd	17.5bcd	0b	37.5abc	75b	95bcd	152.5bc	57.5bcd	97.5a	67.5a	0c	0c	60abc	12.5cd	121.2abc	87.5a	526.2c	375c
Maize + kale + companions	22.5cd	27.5bcd	0b	22.5bc	77.5b	27.5d	32.5d	110abcd	75ab	0b	0c	10bc	41.2bc	20cd	87.5abc	90a	336.2de	307.5cd
Kale + companions + BSFF	5d	7.5cd	7.5b	17.5bc	44.2b	60cd	30d	45bcd	0b	0b	0c	0c	37.5bc	38.8cd	79.2abc	61.5a	203.5f	230.2d
Maize + companions + BSFF	2.5d	10bcd	22.5b	17.5bc	45b	37.5d	95bcd	40cd	7.5b	47.5ab	0c	25bc	25c	102.5ab	115abc	20a	312.5def	300cd
Maize + kale + companions + BSFF	0d	0d	0b	22.5bc	22.5b	43.8d	45cd	35d	57.5ab	12.5ab	25bc	27.8bc	12.5c	47.5bcd	70bc	40a	232.5ef	229d

Control—non-amended monocrop; +inorganic—amended with DAP & NPK; +BSFF—amended with black soldier fly frass organic fertilizer; +companions—intercropped with *Desmodium* and *Brachiaria* as border crop. Means within columns followed by the same letter are not significantly different at $p < 0.05$.

TABLE 5 Effects of vegetable intensified push-pull system augmented with black soldier fly frass fertilizer on free-living nematodes feeding groups per 100 g soil at the Embu and Kiambu field trial sites for season 1 in Kenya.

Treatment	Bacterivores		Fungivores		Omnivore		Predator		Total FLNs	
	Embu	Kiambu	Embu	Kiambu	Embu	Kiambu	Embu	Kiambu	Embu	Kiambu
Kale_control	251.1g	293.9f	294.8cde	138.1d	10.6a	0.0d	3.7b	19.75a	560.2h	451.8g
Maize_control	209.9g	157.0g	385.8abc	274.3abc	7.9a	5.0cd	0.0b	2.08a	603.6gh	438.4g
Kale + inorganic	357.1fg	320.9f	377.9bc	242.4bcd	0.0a	10.3bcd	0.0b	17.50a	735.0fg	591.1fg
Maize + inorganic	289.1g	361.0f	185.2ef	289.9abc	10.6a	48.7abc	0.0b	11.88a	484.9h	711.4def
Kale + BSFF	482.9ef	655.2bcd	438.5ab	190.8 cd	3.3a	10.6bcd	26.5a	9.25a	951.1d	865.8 cd
Maize + BSFF	626.2cde	692.0abc	362.5bc	257.8bcd	21.0a	13.9bcd	0.0b	16.51a	1009.7cd	980.3bc
Kale + companions	642.2cd	577.1de	453.8ab	235.8bcd	8.7a	0.0d	0.0b	21.1a	1104.7bc	833.9cde
Maize + companions	729.8bc	594.9cde	168.8f	356.5ab	12.2a	23.5bcd	4.4b	12.7a	915.23de	987.5bc
Maize + kale + companions	539.8de	523.3e	225.9def	165.2cd	12.4a	8.1 cd	0.0b	0.0a	778.02ef	696.6ef
Kale + companions + BSFF	676.2bcd	751.0ab	495.0a	273.5abc	20.3a	7.5 cd	0.0b	4.3a	1191.5b	1036.3ab
Maize + companions + BSFF	930.1a	716.5ab	462.5ab	390.6a	8.1a	81.2a	4.0b	0.0a	1404.7a	1188.3a
Maize + kale + companions + BSFF	814.8ab	787.5a	316.3cd	268.7abc	24.7a	56.1ab	4.4b	21.1a	1160.2b	1133.3ab

Control-non-amended monocrop; +inorganic—amended with DAP & NPK; +BSFF—amended with black soldier fly frass organic fertilizer; +companions—intercropped with *Desmodium* and *Brachiaria* as border crop. Means within columns followed by the same letter are not significantly different at $p < 0.05$.

predatory nematodes occurred in lower densities compared to bacterivores and fungivores. Omnivore nematodes were present in all treatments except in kale + companions + BSFF and maize + inorganic fertilizer plots in Embu and Kiambu, respectively. Predatory nematodes, were most abundant in plots that combined BSFF and companion crops. In contrast, predatory nematodes occurred in significantly lower densities on control or treatments with inorganic fertilizer. Predator nematodes were absent in the maize control and maize + companions plots in Embu and in kale control and maize + kale + companion treatments in Kiambu.

3.5 A Pearson correlation analysis among the genera, total plant-parasitic and free-living nematodes

Pearson correlation analysis revealed strong positive correlations among several PPNs genera (Figure 4). Notably, *Pratylenchus* and RKN numbers showed a moderately high correlation ($R = 0.52$), while *Helicotylenchus* and *Rotylenchulus* abundances were strongly correlated with total PPN numbers ($R = 0.68$ and $R = 0.70$, respectively). On the other hand, a moderate positive correlation was observed between bacterivores and fungivores ($R = 0.46$), and both were strongly associated with total FLN abundance ($R = 0.88$ and $R = 0.77$, respectively). A key finding was the negative correlation between various PPNs and FLNs. Total PPNs were negatively correlated with total

numbers of FLNs ($R = -0.72$), with particularly strong inverse relationships observed between *Rotylenchulus* ($R = -0.59$), RKN ($R = -0.61$), and *Helicotylenchus* ($R = -0.46$) and total FLNs abundance. Similarly, fungivore and bacterivore numbers showed strong negative correlations with total PPNs ($R = -0.65$ and $R = -0.72$ respectively). Omnivores and predators showed weaker or inconsistent correlations with both PPNs and FLNs numbers.

4 Discussion

Our study represents the first known documentation of the diversity and population densities of nematodes under a vegetable integrated push-pull system combined with BSFF in Kenyan agro-ecosystems. Although 15 genera of PPNs were identified during this study, several including, *Globodera*, *Hoplolaimus*, *Rotylenchus*, *Tylenchus*, *Tylenchorynchus*, *Paratrichodorus*, *Xiphinema* and *Criconema* were represented by only a few individuals or low mean densities, suggesting they pose limited or no significant threat to kale or maize crops. Many plant-parasitic genera have previously been reported from vegetable fields elsewhere with some regarded as real threats to the crops (Abiola, 2020; Junior et al., 2021; Ledchumanakumar et al., 2021; Sandrine et al., 2023). This study has demonstrated that PPNs and FLNs are significantly affected by the

TABLE 6 Effects of vegetable intensified push-pull system augmented with black soldier fly frass fertilizer on free-living nematodes feeding groups per 100 g soil at the Embu and Kiambu field trial sites for season 2 in Kenya.

Treatment	Bacterivores		Fungivores		Omnivores		Predators		Total FLNs	
	Embu	Kiambu	Embu	Kiambu	Embu	Kiambu	Embu	Kiambu	Embu	Kiambu
Kale_control	102.5f	220c	140de	192.2de	22.5b	32.5bc	42.5bc	0c	307.5g	444.8e
Maize_control	122.5ef	35d	52.5e	135ef	67.5ab	12.5bc	0c	17.5c	242.5g	200f
Kale + inorganic	270de	264.8c	277cd	274bcd	37.5ab	77abc	8.2c	7.5c	592.8f	623.2d
Maize + inorganic	147.5ef	50d	72.5e	47.5f	40ab	0c	17.5c	7.5c	277.5g	105f
Kale + BSFF	521.8ab	560a	370.2bc	360abc	10b	82.5ab	87.5bc	30c	989.5bcd	1032.5b
Maize + BSFF	450bc	571.2a	310cd	350abc	132.5a	65abc	62.5bc	130ab	955cde	1116.2ab
Kale + companions	502.5abc	415.5b	506.8ab	289.5bcd	30ab	7.5bc	32.5bc	132ab	1071.8bcd	844.5c
Maize + companions	367.5cd	480ab	310cd	265cd	65ab	60abc	0c	62.5bc	742.5ef	867.5c
Maize + kale + companions	507.5abc	548.3ab	290cd	186.4de	22.5b	37.5bc	27.5bc	0c	847.5de	772.3c
Kale + companions + BSFF	647.5a	557.5a	434abc	375ab	0b	75abc	126.2ab	157.5a	1207.8ab	1,165ab
Maize + companions + BSFF	570ab	500ab	612.5a	280bcd	0b	125a	222.5a	132.5ab	1,405a	1037.5b
Maize + kale + companions + BSFF	595ab	556.8a	419.2bc	414.8a	32.5ab	47.5abc	82.5bc	157.5a	1129.2bc	1176.5a

Control-non-amended monocrop; +inorganic—amended with DAP & NPK; +BSFF—amended with black soldier fly frass organic fertilizer; +companions—intercropped with *Desmodium* and *Brachiaria* as border crop. Means within columns followed by the same letter are not significantly different at $p < 0.05$.

integration of VIPP and BSFF relative to the baseline populations with the treatments involving the combinations recording the greatest reduction in total PPNs abundance while enhancing the densities of FLNs. Similarly, application of organic amendments decreased the total densities of PPNs and enhanced beneficial nematode numbers in different crop systems (Akhtar and Mahmood, 1996; Rahman et al., 2014). In contrast, control treatments recorded the highest PPNs densities, confirming the susceptibility of monoculture systems to PPNs infestations. Longer periods of pineapple cultivation as a monoculture were associated with increased densities of PPNs and were reported to be detrimental to the beneficial nematodes (Kiriga et al., 2021). In potatoes, Mburu et al. (2020) showed that continued monoculture without practicing fallow or non-host cropping significantly increased the occurrence and densities of potato cyst nematodes consequently leading to severe yield losses.

We detected lower densities of known vectors of plant viruses, *Xiphinema* (dagger nematodes), *Trichodorus* and *Paratrichodorus* (stubby-root nematodes) in VIPP and BSFF-treated plots. This finding suggests the potential of these practices not only to reduce direct nematode damage but also to mitigate indirect crop losses by reducing the risk of virus transmission. While the overall nematode diversity remained relatively high, some PPNs genera (*Hoplolaimus*, *Globodera*, *Rotylenchus*, *Paratrichodorus*, *Xiphinema* and *Criconema*) were consistently observed at low densities. This indicates that the VIPP and BSFF system regulate nematode communities, where damaging species are suppressed but overall biodiversity is enhanced, an important

aspect of sustainable soil management (Kiriga et al., 2021). The findings align with prior studies reporting the benefits of organic amendments and diversified cropping systems in reducing nematode damage (Stirling, 2014b). They also highlight the potential of integrating local resources, like BSFF, into smallholder farming systems as a cost-effective and environmentally friendly pest management strategy.

Our study revealed strong positive correlation among several PPNs genera (*Pratylenchus*, *Meloidogyne*, *Helicotylenchus* and *Rotylenchulus*), indicating that increases in these PPNs genera contributed significantly to overall PPNs population communities (Figure 4). A strong positive correlation was observed between bacterivores and fungivores indicating that these two groups are key contributors to the FLNs community structure. The inverse relationships between PPNs and FLNs in our study suggest a possible antagonistic dynamic, where higher FLNs population may outcompete or predate upon the PPNs. Our findings were similar with several other studies that revealed negative correlation between PPNs and FLNs where organic amendment and cropping systems such as maize-legume intercropping are incorporated (Atandi et al., 2022; Liu et al., 2020; Roskopf et al., 2020). Omnivores and predators showed weaker or inconsistent correlations with both PPNs and FLNs, implying that their abundance may be influenced by other biotic or abiotic factors. The observed nematode population dynamics in both Embu and Kiambu show contrasting seasonal shifts that likely reflect changes in rhizosphere resource availability, soil structure, and biologically enriched environment. Bacterivores and fungivores remained at 100% occurrence

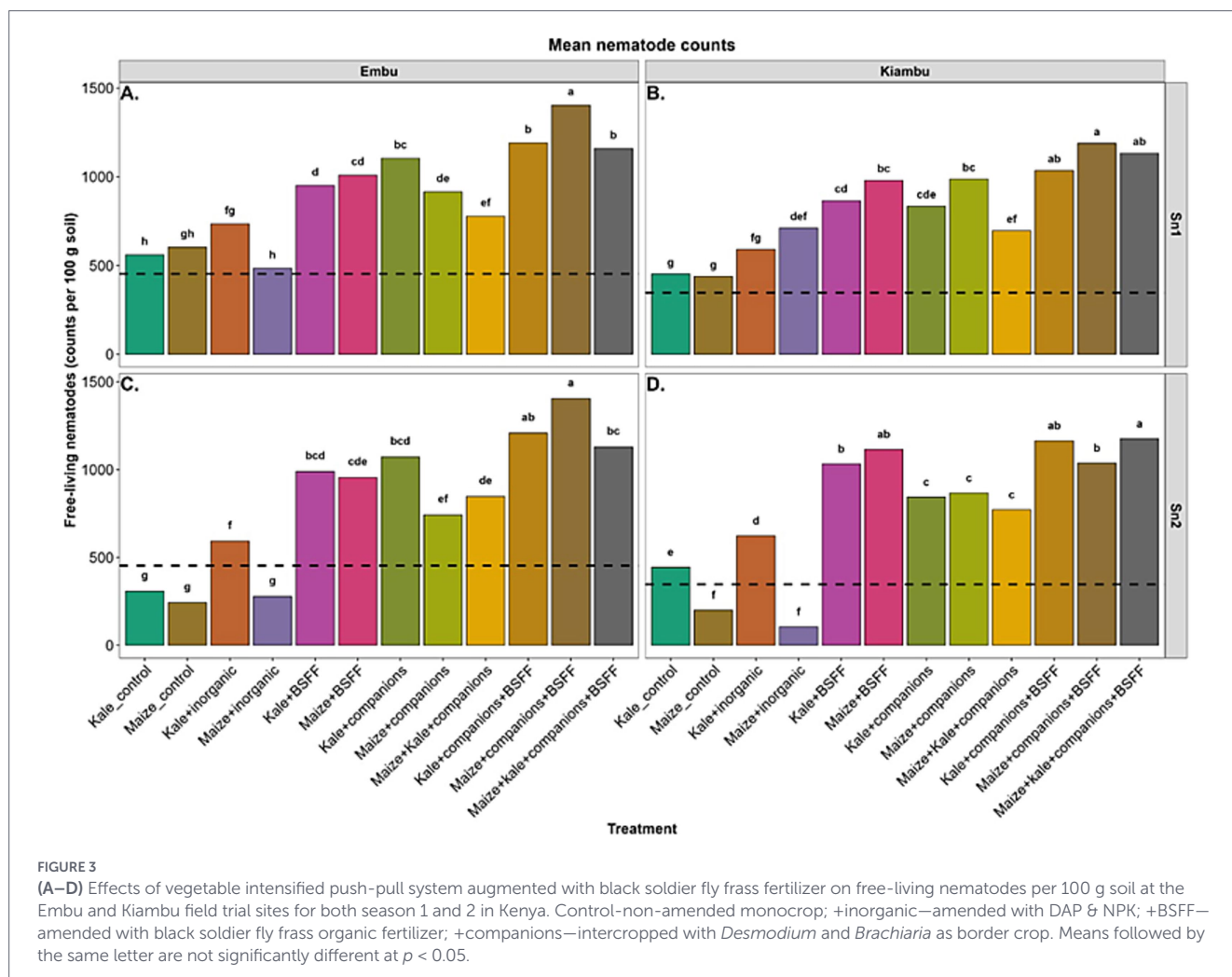


FIGURE 3

(A–D) Effects of vegetable intensified push-pull system augmented with black soldier fly frass fertilizer on free-living nematodes per 100 g soil at the Embu and Kiambu field trial sites for both season 1 and 2 in Kenya. Control–non-amended monocrop; +inorganic—amended with DAP & NPK; +BSFF—amended with black soldier fly frass organic fertilizer; +companions—intercropped with *Desmodium* and *Bracharia* as border crop. Means followed by the same letter are not significantly different at $p < 0.05$.

across both sites and seasons, indicating a consistently active microbial food web and steady availability of microbial resources through time (Ferris et al., 2001). Predatory and omnivorous nematodes showed more variation between sites and seasons. In Embu, predatory nematodes occurrence rose markedly from 18% in season 1 to 75% in season 2, while omnivores declined slightly. This pattern suggests a more structured soil food web and greater top-down regulation during the second season, possibly contributing to the reduction of some plant-parasitic genera. In contrast, Kiambu showed an increase in both omnivores (46–75%) and predators (43–54%), pointing to enhanced soil biological balance and a balanced interaction among trophic groups (Ferris et al., 2001; Neher, 2010).

The NMDS ordinations based on Bray–Curtis similarities demonstrated that nematode community composition was strongly influenced by the management practices involved, cropping system practices and organic amendments, in particular with a clear observation that these effects intensified overtime. Similar to our findings, polyculture systems and use of organic amendments have separately been shown to have a long-term negative effect on pest population buildup due to enhanced soil health producing stronger plants that are less susceptible to pest attack as well as enhancing the activity of natural enemies of pest among other mechanisms (Birkhofer et al., 2008; Mutyambai et al., 2019). In both Embu and Kiambu, control and inorganic fertilizer (maize and kale) treatments formed distinct clusters that differed from plots with BSFF and/or companion crops. This

pattern indicates that integrated management strategies not only reduced PPNs densities but also shifted the overall soil nematode assemblage toward communities more typical of biologically enriched systems (Cole et al., 2020). Temporal comparisons between season 1 and season 2 revealed that treatment effects on nematode community composition became more pronounced with time. In season 1 at both sites, control plots clustered separately from integrated treatments but still exhibited some overlap, while season 2, displayed clearer segregation of treatments along the NMDS1 axis, with combined VIPP–BSFF systems forming the most distinct clusters. This trajectory implies cumulative or residual effects of organic amendments and diversified cropping systems on soil structure (Alletto et al., 2022; Atandi et al., 2022; Bennett et al., 2012; Zhong et al., 2016).

The findings in the present study demonstrate that the integration of these agro-ecological practices can influence nematode community structure, potentially contributing to more sustainable pest management. Despite the increased nematodes suppression observed in the plots with both the VIPP and BSFF systems, the mechanisms involved have not been properly investigated (Atandi et al., 2022; Qiu et al., 2020). However, previous studies have attributed the cropping systems and organic resources on nematode control to enhanced microbial antagonism through production of antimicrobial compounds, release of nematicidal compounds, lifecycle interruption and disruption of PPNs host-seeking due to diversified host plants by companion crops, habitat modification creating a habitable environment for natural

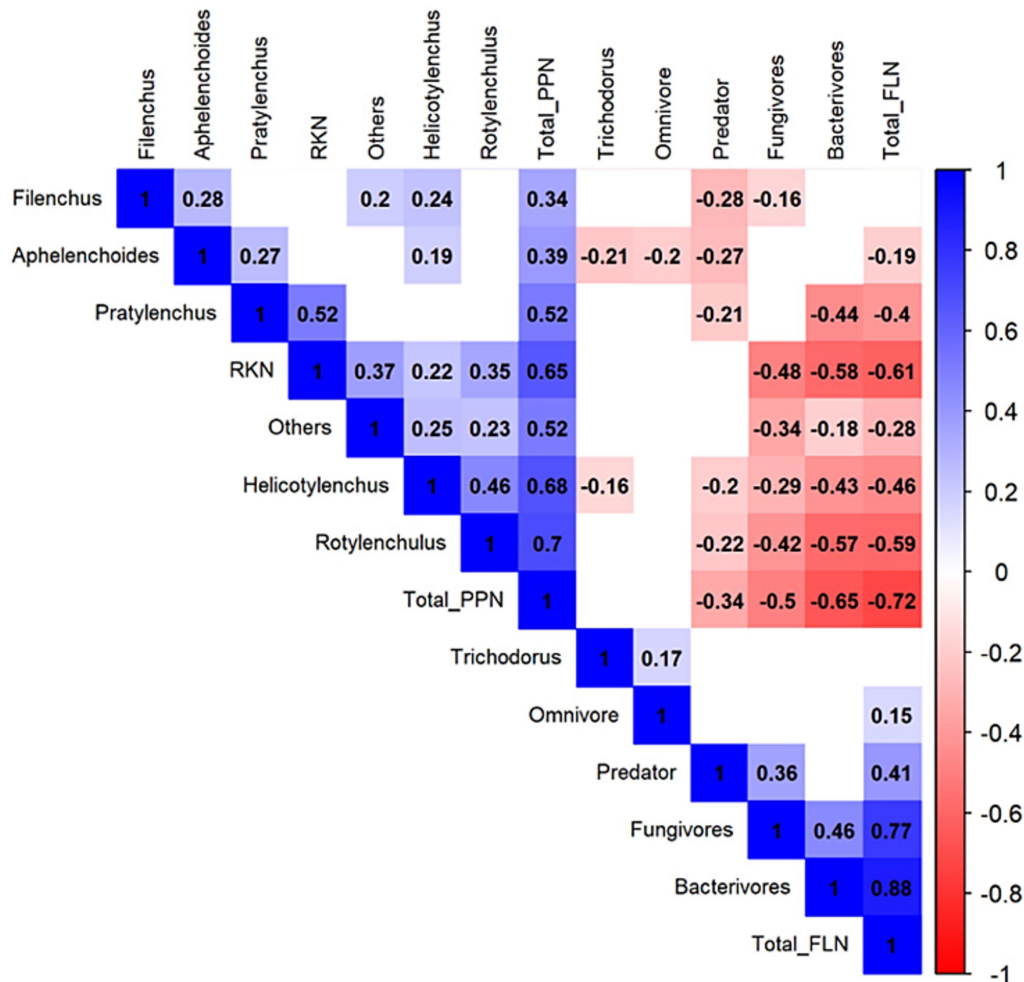


FIGURE 4

Correlation among the genera, total number of plant-parasitic and free-living nematodes at $p < 0.05$ at the Embu and Kiambu field trial sites in Kenya under vegetable intensified push-pull system augmented with black soldier fly frass. Blank spaces indicate non-significant correlations.

enemies. For example, push-pull cropping system has been shown to enhance beneficial soil microbial and arthropod diversity forming distinct community composition which play an important role in pest and nematodes suppression (Jalloh et al., 2024; Mutyambai et al., 2024; Mwakilili et al., 2021). Similarly, long-term responses to organic inputs have been reported elsewhere, where repeated application of chitin-rich amendments gradually increases populations of beneficial bacterivores and nematode-antagonistic microbes (e.g., *Paecilomyces lilacinus*, *Pochonia chlamydosporia*) while suppressing PPNs populations (Zhan et al., 2021).

BSFF is rich in chitin and organic matter. The ability of this fertilizer to reduce nematode numbers has been associated primarily with its high chitin content. Chitin has been linked to increased N levels and low C:N ratios, resulting to nematicidal effects and could lead to enhanced resistance response in plants (Anedo et al., 2024; Roskopf et al., 2020). Similar to our findings on suppression of PPNs, exposure to chitin-fortified BSFF significantly suppressed the potato cyst nematodes by reducing both number of cysts in soil and their reproduction under field conditions (Anedo et al., 2025) and other nematode species in controlled environments (Anedo et al., 2024; Kisaakye et al., 2024). This may indicate a possible synergistic effect that BSFF organic soil amendments of push-pull cropping systems have. BSFF amendment, likely promotes beneficial soil microbes, including bacteria and

fungi that produce nematicidal compounds or act as biological antagonists thereby, leading to competition and predation against PPNs, hence contributing to natural biological control. Previously, chitin has been reported to stimulate populations of nematode-antagonistic microbes, such as *Paecilomyces lilacinus* and *Pochonia chlamydosporia* that parasitize nematode eggs and/or juveniles (Alletto et al., 2022; Kisaakye et al., 2024; Suarez-Fernandez et al., 2021; Zhan et al., 2021). Furthermore, the results also aligns with previous reports highlighting the role of organic amendments in enhancing soil suppressiveness towards PPNs (Anedo et al., 2024; Kisaakye et al., 2024; Liu et al., 2020).

Organic amendments and companion cropping can prime plant defense mechanisms, potentially enhancing the production of compounds that increase their resistance against pests. This could be attributed to the activation of plant signaling pathways and release of secondary metabolites or other chemical defenses (Cardoza and Buhler, 2012; Mutyambai et al., 2019). Moreover, various organic amendments contribute to the formation of distinct communities of symbiotic bacteria and fungi. These microorganisms play a significant role in shaping inducible chemical defenses, and the emission of volatile signals by plants (Rowen et al., 2019). Volatile organic compounds derived from Brassicaceae plants were shown to control PPNs through nematicidal activities (Mazzola et al., 2009; Ploeg and Stapleton, 2001;

Zasada et al., 2009). Plant extracts have demonstrated the ability to induce synthesis of plant defense proteins, leading to a reduction in *Meloidogyne javanica* egg hatch and juvenile penetration into tomato roots (Sholevarfard and Moosavi, 2015). Li et al. (2018) indicated that the influence and efficacy of any organic material on a pest is associated with their chemical composition. Compounds with allelopathic properties, were identified in the exudates of *Crotalaria juncea*, demonstrating nematotoxicity effects (Wang et al., 2001). Likewise, *Desmodium* root releases an array of secondary metabolites that are known to play a role in shaping the nematodes (Hooper et al., 2015; Tsanuo et al., 2003). These chemicals possess allelopathic and antimicrobial properties and are known to interfere with the chemotaxis, egg hatching and survival of PPNs (Rhodes et al., 2014).

In our study, the densities of FLNs increased under BSFF or companions or the integration. Notably, the bacterivores and fungivores were significantly abundant under BSFF or companions or in the integration and so contributed more to the FLNs composition. This suggested that the application of BSFF and the diverse cropping stimulated bacterial decomposition and clearly enhanced bacterivore nematodes, implying the stimulation of bacterial activity and nutrient cycling and potentially contributing to better soil health and pest suppression. Numerous studies have also reported that bacterivores and fungivores dominate in soils amended with organic inputs (Akhtar and Mahmood, 1996; Kimpinski et al., 2003; Liu et al., 2020; Lu et al., 2020; Rahman et al., 2014). Atandi et al. (2022) reported that amending the soil with organic inputs, enhanced the abundance of bacterivore nematodes in the organic systems compared to the conventional and control systems. Similar findings were reported by Kimpinski et al. (2003), in their 7-year study, where they found that compost and manure soil amendments enhanced the densities of bacterial-feeding nematodes in the potato roots rhizosphere.

Omnivores and predatory nematodes were present, although they were generally low across farming systems during the study period. Their occurrence have been well-documented in other studies and have been recorded to significantly reduce PPNs levels in the soil (Askary and Abd-Elgawad, 2017; Atandi et al., 2022; Kanwar et al., 2021; Khan and Kim, 2007). The presence of organic matter can support populations of natural enemies, such as predatory insects or nematodes, which actively prey on soil-dwelling pests (Stirling, 2014a). Enhanced soil organic matter in soils indirectly inhibit pest damage through creating microenvironments that are less favorable for the survival and reproduction of pests and supportive of natural enemies (Yardim and Edwards, 2003). Organic amendments enhance soil fertility and nutrient content. This alteration in soil composition can influence plant health, making them less susceptible to pests (Anedo et al., 2025; Delitte et al., 2021). Similarly, improving the nutritional status of plants results in healthier plants that are more tolerant to herbivores and nematodes (Herms, 2002).

5 Conclusion

This current study demonstrates that integrating cropping systems and insect frass, exert great influence on nematode abundance and community dynamics. Field results demonstrate that this combined approach not only suppresses harmful nematode populations but also enhances the abundance and diversity of beneficial free-living

nematodes, particularly bacterivores and fungivores. Overall, these findings highlight the potential of integrating organic amendments such as BSFF with companion cropping systems as sustainable, environmentally friendly strategies for managing plant-parasitic nematodes while enhancing free-living ones in vegetable-cereal systems (VIPPP) in Kenyan agroecosystems. Further studies are, however, required to establish the long-term effects of vegetable intensified push-pull systems and BSFF farming on the build-up or reduction of important free-living nematodes. Future work should quantify the long-term effects of these practices on crop yields, soil microbial communities, and other soil borne pests. Integrating molecular and chemical analysis techniques could also reveal deeper insights into functional changes within the nematode community and associated microbes.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary material, further inquiries can be directed to the corresponding author.

Ethics statement

The manuscript presents research on animals that do not require ethical approval for their study.

Author contributions

AK: Methodology, Investigation, Formal analysis, Writing – review & editing, Writing – original draft, Data curation. JB: Visualization, Methodology, Validation, Writing – review & editing, Investigation, Supervision. FC: Visualization, Writing – review & editing, Supervision, Investigation, Data curation. SH: Visualization, Validation, Investigation, Writing – review & editing. BG: Validation, Formal analysis, Writing – review & editing. DB: Investigation, Writing – review & editing, Validation. CT: Resources, Validation, Writing – review & editing. SS: Funding acquisition, Writing – review & editing, Project administration, Conceptualization, Resources. DM: Supervision, Data curation, Writing – review & editing, Methodology, Investigation, Writing – original draft, Conceptualization, Formal analysis.

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Conflict of interest

The author(s) declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

The author FC, CT declared that they were an editorial board member of Frontiers, at the time of submission. This had no impact on the peer review process and the final decision.

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