



Research article

Food web structure of nematode communities in irrigated rice fields

Dorcas Mokuah, Hannah Karuri^{*}, Justine M. Nyaga

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



ARTICLE INFO

Keywords:

Ecological indices
Metabolic footprints
Oryza sativa
Paddy

ABSTRACT

Nematodes are a key component of the soil food web and they play an important role in the provision of ecosystem services. Rice cultivation in Mwea, Kenya involves the intensive use of fertilizers and pesticides which may affect the complexity of the nematode-based soil food web. This study examined the nematode diversity and food web structure in irrigated rice fields in Nyangati and Tebere in Mwea, Kirinyaga County, Kenya. Nematodes were identified up to the genus level and soil physico-chemical properties were also determined. *Aphelenchoides* and *Longidorus* occurred in significantly greater proportions in Tebere, while in Nyangati there was a high abundance of *Helicotylenchus*. *Aphelenchoides* was positively correlated to soil electrical conductivity. From additive diversity partitioning of genus richness, the α and β components contributed 33.7% and 66.3% of the γ diversity, respectively. For Shannon and Simpson diversity indices, the largest contribution to overall diversity was from α component. Soil food web indices were similar across the two regions. Channel and basal indices were below 30% while Enrichment (EI) and Structure (SI) indices were above 50%. There was no variation in metabolic footprints except for the fungivore footprint which was significantly higher in Tebere. Based on the EI and SI, the soil food web in paddy rice fields in Mwea was structured and enriched with moderate disturbance. Due to the high prevalence of economically damaging parasitic nematodes in the rice fields, appropriate management schemes that enhance specific components of the soil food web and increase the suppressive ability of soil against plant-parasitic nematodes should be implemented.

1. Introduction

In Kenya, rice, the third most important staple crop, is grown in Kirinyaga, Kisumu, Mombasa and Tana River Counties [1,2]. Despite the 12% annual increase in consumption (300,000 tonnes), yield is comparatively low (45,000 to 80,000 tonnes) and the gap is covered through import [2,3]. Yield decreases have been reported despite increased application of nitrogen fertilizers [4]. There are several biotic constraints in Kenyan rice production systems such as viruses, fungi [5–7] and plant-parasitic nematodes (PPN) [8]. In addition to these constraints, irrigated areas that account for 80% of rice production in Kenya, pose additional stress such as high salinity and low fertility. Agricultural intensification affects the soil food web [9] which influences crop productivity [10,11]. A global meta-analysis showed that the application of pesticides and chemical-based fertilizers lowers the structural complexity of the nematode-based soil food web [12]. On the other hand, judicious use of inorganic fertilizers enhances food web structure and increases

^{*} Corresponding author.

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

<https://doi.org/10.1016/j.heliyon.2023.e13183>

Received 22 September 2022; Received in revised form 11 January 2023; Accepted 20 January 2023

Available online 26 January 2023

2405-8440/© 2023 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

soil suppressiveness against PPN [13]. In some cases, nematode functional guilds provide a greater contribution to the structure of the soil food web compared to other microorganisms as demonstrated by Li et al. [14] in an agricultural field trial.

Nematodes play important ecological roles and they are used as indicators of soil health. Nematode trophic groups in higher levels such as omnivores and predators can suppress PPN that reduce crop yields [15]. There are several PPN that have been reported in rice such as *Helicotylenchus* spp., *Trichodorus* spp., *Xiphinema* spp. (Cote d'Ivoire; [16]), *Aphelenchoides* spp., *Ditylenchus* spp., *Heterodera* spp., *Hirschmanniella* spp., *Meloidogyne* spp. and *Pratylenchus* spp. (recorded in different regions of the world; [17]). Nematode genera that cause significant yield losses in rice include *Aphelenchoides* spp., *Ditylenchus* spp., *Criconemoides* spp., *Heterodera* spp., *Hirschmanniella* spp., *Hoplolaimus* spp., *Meloidogyne* spp., *Paralongidorus* spp., *Pratylenchus* spp. and *Xiphinema* spp. [18]. Certain economically damaging nematodes prefer irrigated areas [19]. For instance, the number of *Hirschmanniella oryzae* [20] and *Meloidogyne graminicola* second-stage juveniles were higher in irrigated areas compared to upland fields in Myanmar [21]. Similarly, in Côte d'Ivoire, the number of *Basiria*, spp. *Filenchus* spp. and *Coslenchus* spp. was greater in high moisture paddy fields [22]. Irrigation in rice cropping systems also affects the nematode-based food web [23] which has a regulatory role against PPN [24].

Disturbance in rice fields alters the food web structure by reducing nematode trophic levels, number of predatory nematodes, enrichment and structure indices [25]. Wang et al. [26] reported alterations in nematode trophic groups and the Plant-Parasitic Index (PPI) due to elevated carbon dioxide in rice paddy fields. Okada et al. [27] revealed that flooding increases the abundance of *k* strategists, lowers the EI and increases the SI. Salinity in irrigated rice fields affects nematode assemblages and trophic groups and reduces the complexity of the food web structure [28]. In order to sustainably control PPN, maintain soil health and related ecosystem functions in Kenyan rice ecosystems, it is important to have information on nematode diversity and its contribution to the soil food web. The aim of this study was to examine the nematode diversity, soil food web indices and metabolic footprints in irrigated rice fields in Mwea, Kenya.

1.1. Methodology

1.1.1. Study area and soil sampling

Irrigated rice fields in Nyangati (0°36'47.4"S 37°21'11.4"E) and Tebere (0°38'10.9"S 37°21'44.0"E) regions of Mwea, Kirinyaga County (Fig. 1) were sampled in April 2022. The soil in the fields is classified as Eutric Nitisols [29]. Annually, the region has two rainy seasons with approximately 930 mm rainfall and average temperature between 14 °C - 31 °C [30]. For this study, fields that were cultivated with monoculture rice for 10–15 years were selected. The sampled fields had the same management practices whereby they had received a basal fertilizer input (NPK; 17:17:17) and ammonium sulfate top dressing after 45 days of transplanting. In addition,

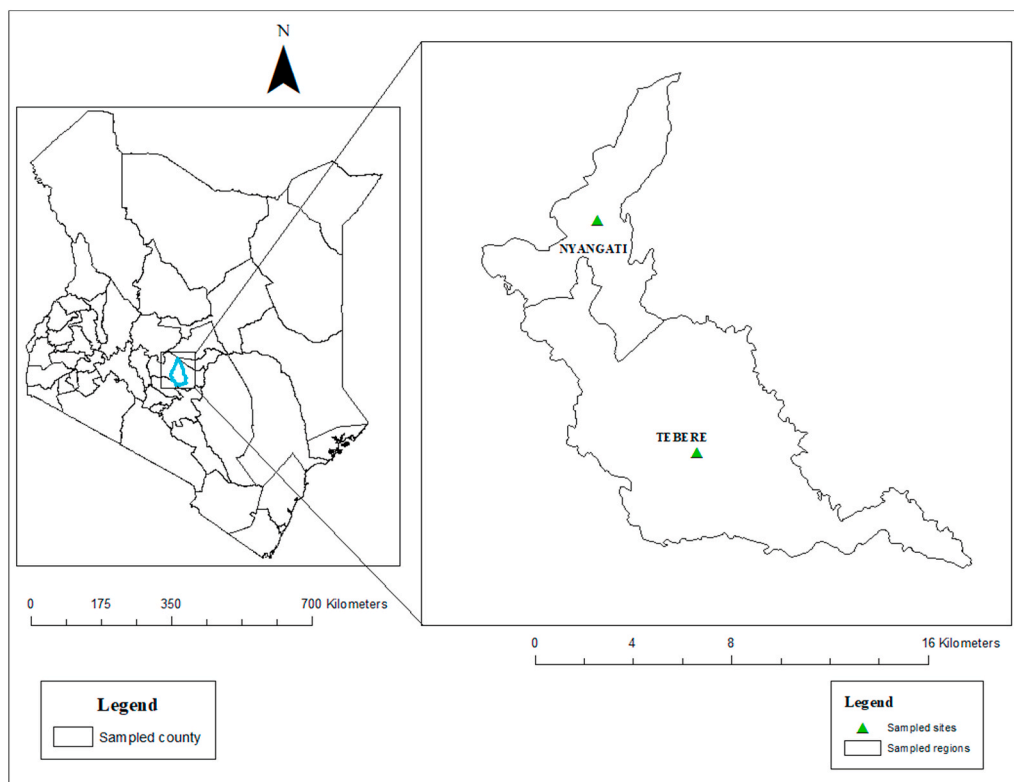


Fig. 1. Study areas at Nyangati and Tebere, in Mwea, Kirinyaga County, Kenya where nematode samples were obtained.

insects were controlled with applications of Oshothion 50EC and Diazol 60EC. Soil samples were collected from fields cultivated with the rice variety Basmati 370 at four months after planting. Thirty fields in Nyangati (15) and Tebere (15) were sampled. Based on the sampling protocol described by Wiesel et al. [31], soil samples from each field were collected from three W shaped “sample walks” at 25 cm depth. From each field one 4 kg composite soil sample was collected for analysis of nematode communities and soil physico-chemical properties.

1.1.2. Nematode analyses

From the composite soil sample, three 250 g sub-samples were used for nematode extraction using the modified Baermann technique [32] for 48 h. Nematodes were fixed using a hot mixture of formaldehyde and glycerin [33]. They were then placed in a counting dish for enumeration. The nematodes were identified to the genus level [34,35] using a compound microscope. Soil physico-chemical properties were assessed at the Kenya Agricultural and Livestock Research Organization, National Agricultural Research Laboratories. The hydrometer technique [36] was used to examine the soil texture while Mn, Mg, Ca, K, Na, P and pH were assessed following the method by Mehlich et al. [37]. The amount of N and C was determined using Kjeldahl digestion method [38] and colorimetric technique [39], respectively. Atomic Absorption Spectrophotometer was used to analyze Zn, Cu and Fe content [37].

1.1.3. Data analysis

From the triplicate samples, the average number of nematodes was used in subsequent analyses. Nematode indices (PPI, maturity index of nematodes belonging to colonizer-persister group 1–5; MI, Maturity index excluding cp1 nematodes; MI 2–5, SI, EI, basal index; BI and channel index; CI) and metabolic footprints were computed using the Nematode Indicators Joint Analysis online program [40]. The MI, MI 2–5, SI, BI and CI provide information on the level of disturbance in the ecosystem and the condition of the soil food web. On the other hand, metabolic footprints indicate the ecosystem services provided by different nematode trophic groups [41]. Prior to analysis, the Shapiro-Wilk test was used to assess normality of the nematode abundance data which was subsequently $\log(x+1)$ transformed. One-way analysis of variance (ANOVA) with Tukey post hoc test was used to evaluate differences in number of nematode genera, indices and metabolic footprints in Nyangati and Tebere. Rényi diversity ordering of nematode genera [42] in the two regions was conducted using the Rényi function in R vegan package. The Rényi diversity index represents four indices (species richness, Shannon, Simpson and Berger-Parker indices) and gives a scalable comparison of diversity at four scale parameter (α) values. At 0, 1, 2 and infinity, the value of the Rényi index represents the logarithm of species richness, Shannon index, logarithm of the reciprocal Simpson index and Berger-Parker index, respectively. If the diversity profiles intersect, the communities cannot be unequivocally ordered. When there is no intersection of the profiles, a community is more diverse if its profile is above the other one [43,44]. Additive diversity partitioning [45] of genus richness, Shannon and Simpson diversity indices was used to compute the contribution of α and β components to overall γ diversity using vegan package. Spatial distribution of nematode communities in Nyangati and Tebere was examined using Jaccard index-based non-metric multidimensional scaling (NMDS). Differences between the two regions were assessed using permutational multivariate analysis of variance (PERMANOVA) and permutational multivariate analysis of dispersion (PERMDISP) [46–48]. Relationships between nematode genera abundance and soil properties were determined using canonical correspondence analysis (CCA). Vegan package in R was used for NMDS and CCA analyses. All analyses were done in R version 4.0.2 [49].

Table 1

Mean number of nematode genera in 250 g of soil from Nyangati and Tebere, Kirinyaga, Kenya. Cp-Colonizer-persister values from 1 to 5. Pr – predators, Ba – bacterivores, Fu-fungivores, Pp – herbivores and Om – omnivores. SE - standard error.

Genus	Cp value	Functional guild	Nyangati		Tebere		F value	P value
			Mean	SE	Mean	SE		
<i>Panagrellus</i>	1	Ba ₁	7.9	6.6	3.9	3.9	0.3	0.6
<i>Rhabditis</i>	1	Ba ₁	19.8	5.1	22.2	8.9	0.6	0.5
<i>Acrobeloides</i>	2	Ba ₂	2.6	2.6	5.3	3	0.9	0.4
<i>Anaplectus</i>	2	Ba ₂	13.1	5.7	4	2.1	1.1	0.3
<i>Aphelenchoides</i>	2	Fu ₂	1.3	1.3	15.7	6.4	4.1	0.05 ^a
<i>Cephalobus</i>	2	Ba ₂	4	2.1	2.7	1.8	0.2	0.6
<i>Eucephalobus</i>	2	Ba ₂	3.9	2.8	1.3	1.3	0.5	0.5
<i>Heterocephalobus</i>	2	Ba ₂	9.1	5.7	17.1	5.7	2.1	0.2
<i>Helicotylenchus</i>	3	Pp ₃	70.4	18.2	15.9	5.2	6.1	0.02 ^a
<i>Meloidogyne</i>	3	Pp ₃	10.5	4.7	10.5	6.3	0.4	0.6
<i>Pratylenchus</i>	3	Pp ₃	9.2	6.6	0	0	3.3	0.1
<i>Labronema</i>	4	Om ₄	20.9	8.2	9.2	5.4	1	0.3
<i>Mesodorylaimus</i>	4	Om ₄	33.9	10.7	34	12.7	0.3	0.6
<i>Mylonchulus</i>	4	Pr ₄	2.7	1.8	2.6	2.6	0.2	0.7
<i>Prodorylaimus</i>	4	Om ₄	57.4	13.3	58.7	13.7	0.01	1.0
<i>Aporcelaimus</i>	5	Om ₅	30	12.4	7.9	4.6	1.2	0.3
<i>Longidorus</i>	5	Pp ₅	14.3	9	23.7	6.4	5.6	0.03 ^a

^a = P < 0.05 – One-way analysis of variance.

1.2. Results

There were variations in the nematode genera in the two sampled regions. Cumulatively, there were 17 nematode genera in Tebere (16) and Nyangati (17) rice fields. Bacterivores were predominantly in the Ba₂ functional guild and herbivores were mainly represented by Pp₃. *Panagrellus* and *Rhabditis* were the only enrichment opportunist bacterivores. *Aphelenchoides* ($P = 0.052$) and *Longidorus* ($P = 0.026$) occurred in greater abundance in Tebere, and the number of *Helicotylenchus* ($P = 0.020$) was higher in Nyangati. The omnivore, *Prodorylaimus* occurred in high numbers in both regions (Table 1).

From the Rényi diversity profiles, the two regions could not be unequivocally ordered due to crossing of the profiles along the scale parameter (Fig. 2). Genus richness partitioning, showed that the α and β components contributed 33.7% and 66.3% of the γ diversity, respectively. For Shannon and Simpson diversity indices, the largest contribution to overall diversity was from the α component. The observed β diversity for Shannon (37.5% of γ diversity) and Simpson (15.9% of γ diversity) diversity indices was higher than expected ($P < 0.0001$) (Fig. 3).

Soil food web indices were similar across the two regions with MI2-5 ranging between 3.39 and 3.72. Channel and basal indices were below 30% while the EI and SI were above 50%. There was also no variation in metabolic footprints except for fungivore footprint which was significantly higher ($P = 0.041$) in Tebere (Table 2). Based on the EI and SI, the soil food web in both regions was structured, moderately enriched, and with low to moderate disturbance (Fig. 4).

Nematode communities in Nyangati and Tebere were different with an average dissimilarity of 71.8% (Fig. 5; PERMANOVA, $R^2 = 0.06$, $F = 1.8$, $P = 0.02$; PERMDISP, $F = 0.17$, $P = 0.69$). The observed difference in ordination of nematode communities in the two regions was due to differences in abundance of *Aporcelaimus*, *Helicotylenchus*, *Labronema*, *Longidorus*, *Mesodorylaimus*, *Prodorylaimus* and *Rhabditis*.

Phosphorus, pH and Electrical Conductivity (EC) were significantly different in the two regions. Tebere had the highest pH ($P = 0.005$) and EC ($P = 0.0001$) while P was high ($P = 0.001$) in Nyangati (Table 3). The first two axes in the CCA of soil properties and abundance of nematode genera accounted for 18.2% of the variation. There was a significant positive correlation between *Aphelenchoides* and EC while *Helicotylenchus* was negatively correlated (Fig. 6). In the CCA examining the relationship between nematode-based indices and soil properties, a significant negative correlation was observed between MI 2–5, SI and K, Zn and sand. The BI was positively correlated with K while the CI showed a significant positive correlation with Na. The first and second axes represented 36% of the observed variation (Fig. 7).

1.3. Discussion

Irrigated rice cropping systems are ecosystems with environmental variables that differentially shape soil communities [27,28]. In this study, *Panagrellus* and *Rhabditis* were the only bacterivorous enrichment opportunists. *Rhabditis* has been previously reported in paddy areas [50] but Korobushkin et al. [25] did not observe the genus in irrigated rice fields. The abundance of enrichment opportunists in the family Rhabditidae may be attributed to increased breakdown of organic matter by bacteria and the availability of labile food sources [27]. In this study, the numbers of *Aphelenchoides* and *Longidorus* were significantly higher in Tebere while the abundance of *Helicotylenchus* was greater in Nyangati. However, *Aphelenchoides* made up a small proportion of the entire nematode community; 0.4% in Nyangati and 6.7% in Tebere. This nematode is generally prevalent in upland rice fields [27,51] while *Longidorus* is more common in irrigated areas [52]. The PPN *Helicotylenchus* made up the highest proportion (22.6%) of nematode genera in Nyangati. High prevalence of *Helicotylenchus* was also reported in the Philippines, where it occurred in 80% of the sampled regions [53]. According to Coyne et al. [22] *Helicotylenchus* is positively correlated to irrigation compared to *Meloidogyne incognita* and *Pratylenchus zaeae* as similarly observed by Bambaradeniya et al. [54]. Control of *Helicotylenchus* in Mwea is imperative since it significantly affects rice grain yield [55] and concomitant infection of paddy rice by *Criconebella onoensis* and *H. dihystra* causes 63–72% yield losses [56]. Only one predatory genus, *Myonchulus* was present in both regions probably due to the negative effects of flooding on

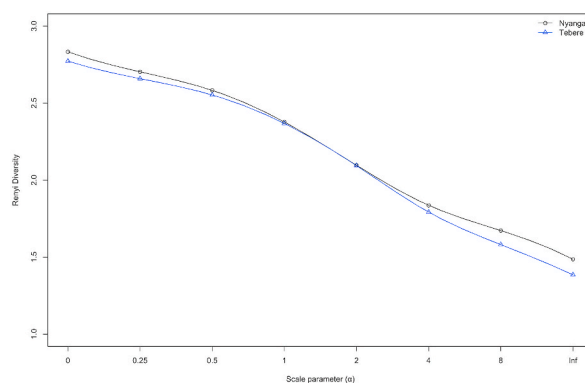


Fig. 2. Rényi diversity profiles of nematode communities in Nyangati and Tebere rice fields in Kirinyaga, Kenya. Scale parameter values are 0-logarithm of species richness, 1- Shannon index, 2- logarithm of the reciprocal Simpson index, and infinity- Berger–Parker index.

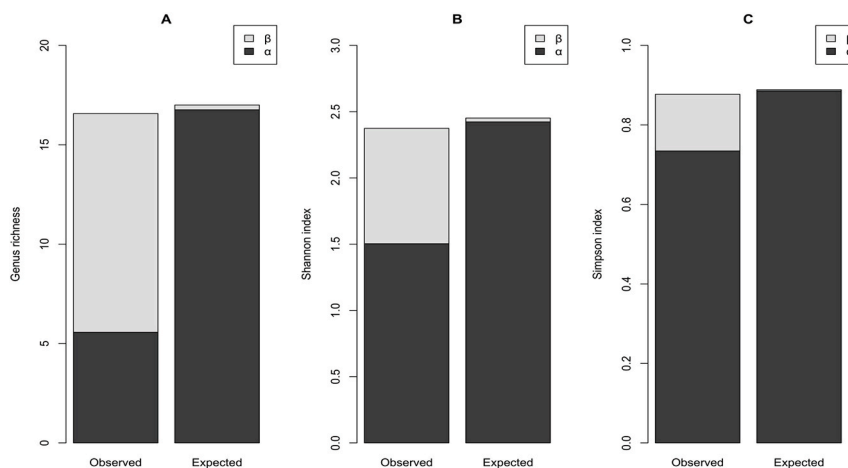


Fig. 3. Additive γ diversity partitioning (alpha, α and beta, β) components) of A) nematode genus richness B) Shannon diversity and C) Simpson diversity index in Nyangati and Tebere rice fields in Kirinyaga, Kenya.

Table 2

Soil food web indices and metabolic footprints (log-transformed) in Nyangati and Tebere rice fields in Kirinyaga, Kenya.

Index/footprint	Nyangati		Tebere		F value	P value
	Mean	SE	Mean	SE		
Maturity Index (MI)	3.34	0.13	3.03	0.17	2.28	0.14
Maturity Index 2–5 (MI2-5)	3.72	0.14	3.39	0.14	2.55	0.12
Plant-Parasitic Index (PPI)	2.99	0.24	3.8	0.34	1.2	0.28
Channel Index (CI)	6.67	6.67	28.5	11.66	3.26	0.08
Basal Index (BI)	7.82	3.87	9.75	2.44	1.27	0.27
Enrichment Index (EI)	58.09	11.02	54	10.07	0.04	0.84
Structure Index (SI)	91.62	3.86	86.54	3.28	0.48	0.5
Composite footprint	6.02	0.2	5.68	0.21	1.43	0.24
Enrichment footprint	2.81	0.51	2.69	0.51	0.03	0.87
Structure footprint	5.28	0.3	4.59	0.28	2.78	0.1
Herbivore footprint	3.38	0.48	3.88	0.46	0.57	0.45
Fungivore footprint	0.06	0.06	0.48	0.19	4.58	0.04 ^a
Bacterivore footprint	3.83	0.33	3.8	0.32	0.01	0.95
Predator footprint	0.31	0.21	0.2	0.2	0.16	0.7
Omnivore footprint	5.26	0.31	4.4	0.4	2.97	0.1

^a = $P < 0.05$ – One-way analysis of variance.

predaceous nematodes [25]. The extraction method used in this study favored the extraction of majority of genera from the nematode community but is not optimal for extraction of some genera that have low motility.

Soil food web indices were similar across the two regions with the CI and BI having values below 30% while the EI and SI were above 50%. Contrary to these observations, Korobushkin et al. [25] reported significant regional effects on EI and SI in rice fields. Similar to observations made in this study, Okada et al. [27] reported high SI values with great abundance of cp 3–5. Moderate values of EI that were observed in both Nyangati and Tebere are expected due to fertilizer application that increases the level of fertility and consequently the number of enrichment opportunists [57]. In addition, under irrigated conditions in rice fields, bacterial decomposition is dominant and organic matter from rice litter acts as a source of nutrients to cp1 bacterivores which is reflected in high EI [27]. Rice cultivation as with other forms of agriculture comprise a source of disturbance to soil nematode communities and food web structure [24]. Based on the EI, there was moderate disturbance in Nyangati and Tebere, probably due to fertilizers and pesticides application [12]; however, the soil food web showed some level of complexity due to the presence of omnivorous nematodes which also contributed to the observed high SI [57]. The intensive use of fertilizers and pesticides in Mwea rice fields is increasing [4,58] which forms a potential source of disturbance that can reduce the complexity of the nematode soil food web [9].

The omnivores, *Prodorylaimus*, *Labronema*, *Mesodorylaimus* and *Aporcelaimus* were present in both regions. They belong to cp4 and cp5 groups which are sensitive to disturbance—the observed high number is therefore unexpected although it has been observed in other studies [27,28]. Sinh et al. [59] hypothesized that an increased population of omnivores in paddy rice fields receiving chemical fertilizers may be due to an increase in food supply. Nematodes in higher trophic groups have a regulatory role against PPN [15] and it is therefore important that low levels of disturbance are maintained in Nyangati and Tebere in order to sustain a structured food web that suppresses the parasitic nematodes. In both regions, the channel index was low which is indicative of low levels of complex material and the reduced role of fungivores in decomposition [57]. Fungivore footprint was also reduced which may be due to the

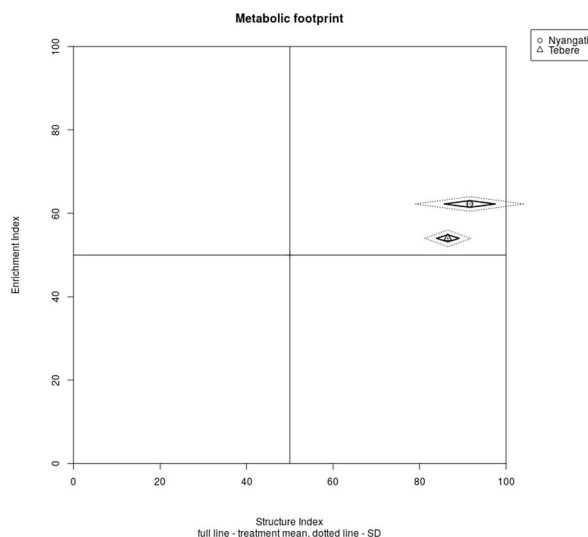


Fig. 4. Soil food web condition in Nyangati and Tebere rice fields in Kirinyaga, Kenya based on the enrichment and structure indices.

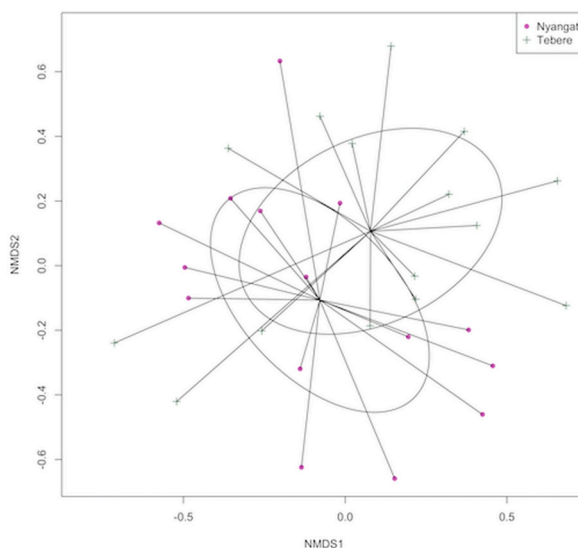


Fig. 5. Non-metric multidimensional scaling ordination of nematode communities in rice fields in Nyangati and Tebere, Kirinyaga, Kenya (PERMANOVA: $P = 0.02$; NMDS Stress = 0.2).

anaerobic conditions in paddy fields that inhibit fungal growth [23].

Diversity partitioning of Shannon and Simpson diversity indices showed a higher contribution of α component while between region differences (β) contributed more to genus richness. In addition, Rényi diversity profiles could not be unequivocally ordered due to overlap in nematode diversity measures. Nematode alpha and beta diversity can be affected by variables such as soil, climate [60] and agricultural intensification [61]. In this study, regional variability may have been a stronger driver of differences in specific nematode genera than on the computed diversity indices. This was shown in the NMDS where certain nematode genera had a greater contribution to the dissimilarity between regions. Some of the genera showed correlation with soil properties. Soil pH and EC, which are linked to salinity, are properties that greatly influence nematode communities in paddy rice fields. Nguyen et al. [51] observed that bacterial and fungal feeders were positively correlated to EC while PPN showed a negative correlation which was not significant. Enrichment opportunists in the cp2 class can tolerate soils with high EC [28]. This may explain the positive correlation that was observed between *Aphelenchoides* and EC. The tolerance of this genera to high salinity was also reported in rice fields with alluvial soils containing high salt content [28]. Contrary to our results, Wang et al. [62] did not observe a correlation between the structure index, K, Zn and sand. In the same study the CI was negatively correlated with Na unlike our observations. A positive correlation between silt and structure index was reported by Landi et al. [63]. Correlation of specific nematode indices with soil properties provides an insight

Table 3
Soil physico-chemical properties of Nyangati and Tebere rice fields in Kirinyaga, Kenya.

Soil property	Nyangati		Tebere		F value	P value
	Mean	SE	Mean	SE		
pH (H ₂ O)	6.2	0.2	6.9	0.2	9.3	0.005 ^a
Total Nitrogen (%)	0.3	0.01	0.3	0.01	2.3	0.1
Total Organic Carbon (%)	3.1	0.1	2.8	0.2	2.0	0.1
Phosphorus (mg kg ⁻¹)	38.4	2.4	23.8	3.3	12.9	0.001 ^a
Potassium (mmol L ⁻¹)	0.2	0.03	0.4	0.1	3.6	0.1
Calcium (mmol L ⁻¹)	19.6	3.1	24.7	4.3	1	0.3
Magnesium (mmol L ⁻¹)	5.6	0.1	5.4	0.2	0.6	0.5
Manganese (mmol L ⁻¹)	0.9	0.1	0.7	0.04	7.3	0.01 ^a
Copper (mg kg ⁻¹)	3.1	0.3	2.9	0.4	0.1	0.7
Iron (mg kg ⁻¹)	206.3	32.1	146.5	46.1	1.1	0.3
Zinc (mg kg ⁻¹)	2.4	0.2	2.8	0.3	1	0.3
Sodium (mg kg ⁻¹)	1	0.3	1.2	0.3	0.3	0.6
Electrical Conductivity (mS cm ⁻¹)	–	–	0.7	0.1	138.7	<0.0001**
Sand (%)	16	0.3	26	4.9	3.6	0.1
Clay (%)	71	1.7	62	4.9	3.2	0.1
Silt (%)	12	1.6	12	1.2	0.01	1

^a = P < 0.05, ** = P < 0.001.

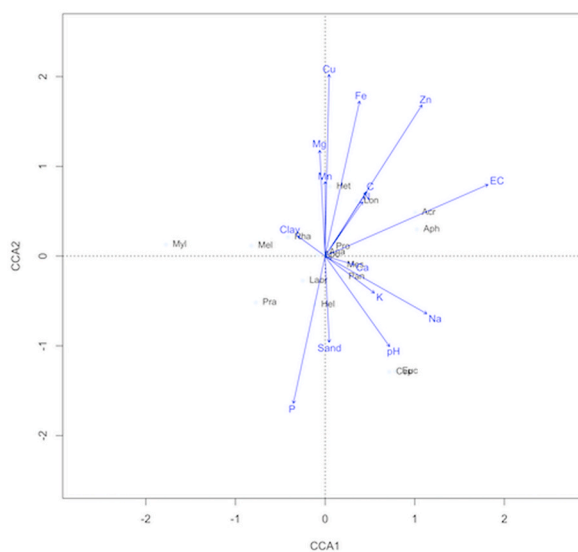


Fig. 6. Canonical correspondence analysis of nematode genera abundance and soil properties in Nyangati and Tebere, Kirinyaga, Kenya. First and second axis eigenvalues are 0.21 and 0.20, respectively. Acr-Acroboloides, Ana-Anaplectus, Aph-Aphelenchoides, Apo-Aporcelaimus, Cep-Cephalobus, Euc-Eucephalobus, Hel-Helicotylenchus, Het-Heterocephalobus, Labr-Labronema, Lon-Longidorus, Mel-Meloidogyne, Mes-Mesodorylaimus, Myl-Mylonchulus, Pan-Panagrellus, Pra-Pratylenchus, Pro-Prodorylaimus, Rha-Rhabditis.

into the role of various nematode groups in nutrient cycling [62]. Several other factors that were not assessed in the current study such as climatic variables and their interactions with nematodes, soil properties and other organisms may also affect nematode community dynamics in the rice fields. Changes in cropping practices and the type of rice cultivar may also increase PPN damage in rice [18].

2. Conclusion

Nematode diversity in Nyangati and Tebere was low with the highest contribution being from fields within a region but a few genera showed differences in abundance between regions. The soil food web structure in both regions was enriched due to the presence of enrichment opportunists and it was also structured with moderate disturbance. Integrated nematode management schemes should be put in place to control PPN genera that were identified in this study — some of which cause significant yield losses in rice. The baseline information on the status of nematode-based soil food web provided in this study can be used in the development of sustainable rice cropping systems.

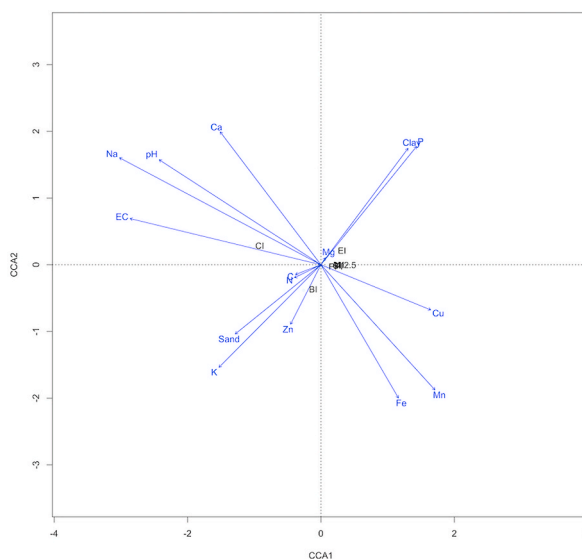


Fig. 7. Canonical correspondence analysis of soil properties, Structure index (SI), Plant-Parasitic Index (PPI), Maturity Index (MI), Maturity Index of nematodes in cp2-5 (MI2-5) (overlapping labels), Channel Index (CI), Basal Index (BI) and Enrichment index (EI) in Nyangati and Tebere, Kirinyaga, Kenya.

Author contribution statement

Dorcas Mokuah: Performed the experiments; Analyzed and interpreted the data; Wrote the paper.

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

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

Funding statement

This work was supported by the CIRCLE research uptake fund (grant no. 201871).

Data availability statement

Data will be made available on request.

Declaration of interest's statement

The authors declare no competing interests.

References

- [1] Y. Fukuta, M.J. Telebanco-Yanoria, N. Hayashi, S. Yanagihara, C.W. Machungo, D. Makihara, Pathogenicities of rice blast (*Pyricularia oryzae* cavara) isolates from Kenya, *Plant Dis.* 103 (2019) 3181–3188, <https://doi.org/10.1094/PDIS-04-19-0870-RE>.
- [2] A. Onyango, Rice production, Food security, New rice for Africa, Agricultural research and development, *World Environ.* 4 (2014) 172–179.
- [3] Ministry of Agriculture, National Rice Development Strategy (2008–2018), Government Printer, Nairobi, Kenya, 2008.
- [4] S.M. Njinju, H. Samejima, K. Katsura, M. Kikuta, J.P. Gweyi-Onyango, J.M. Kimani, et al., Grain yield responses of lowland rice varieties to increased amount of nitrogen fertilizer under tropical highland conditions in central Kenya, *Plant Prod. Sci.* 21 (2018) 59–70, <https://doi.org/10.1080/1343943X.2018.1436000>.
- [5] M.E. Abo, A.A. Sy, Rice virus diseases: epidemiology and management strategies, *J. Sustain. Agric.* 11 (1997) 113–134, https://doi.org/10.1300/J064v11n02_09.
- [6] W. Bakker, Rice yellow mottle, a mechanically transmissible virus disease of rice in Kenya, *Neth. J. Plant Pathol.* 76 (1970) 53–63, <https://doi.org/10.1007/BF01974433>.
- [7] J. Kihoro, N.J. Bosco, H. Murage, E. Ateka, D. Makihara, Investigating the impact of rice blast disease on the livelihood of the local farmers in greater Mwea region of Kenya, *SpringerPlus* 2 (2013) 308, <https://doi.org/10.1186/2193-1801-2-308>.
- [8] N.N. Pili, T. Kyndt, G. Gheysen, T. Janssen, M. Couvreur, W. Bert, et al., First report of *Pratylenchus zeae* on upland rice from Kwale County, Kenya, 1022, *Plant Dis.* 100 (2016) 1022.
- [9] S. Sánchez-Moreno, H. Ferris, A. Young-Mathews, S.W. Culman, L.E. Jackson, Abundance, diversity and connectance of soil food web channels along environmental gradients in an agricultural landscape, *Soil Biol. Biochem.* 43 (2011) 2374–2383, <https://doi.org/10.1016/j.soilbio.2011.07.016>.
- [10] L. Su, T. Bai, X. Qin, H. Yu, G. Wu, Q. Zhao, et al., Organic manure induced soil food web of microbes and nematodes drive soil organic matter under jackfruit planting, *Appl. Soil Ecol.* 166 (2021), 103994, <https://doi.org/10.1016/j.apsoil.2021.103994>.
- [11] K.-H. Wang, C.R.R. Hooks, S.P. Marahatta, Can using a strip-tilled cover cropping system followed by surface mulch practice enhance organisms higher up in the soil food web hierarchy? *Appl. Soil Ecol.* 49 (2011) 107–117, <https://doi.org/10.1016/j.apsoil.2011.06.008>.

- [12] J. Puissant, C. Villenave, C. Chauvin, C. Plassard, E. Blanchart, J. Trap, Quantification of the global impact of agricultural practices on soil nematodes: a meta-analysis, *Soil Biol. Biochem.* 161 (2021), 108383, <https://doi.org/10.1016/j.soilbio.2021.108383>.
- [13] T. Liu, X. Chen, F. Hu, W. Ran, Q. Shen, H. Li, et al., Carbon-rich organic fertilizers to increase soil biodiversity: evidence from a meta-analysis of nematode communities, *Agric. Ecosyst. Environ.* 232 (2016) 199–207, <https://doi.org/10.1016/j.agee.2016.07.015>.
- [14] N. Li, F. Pan, X.-Z. Han, B. Zhang, Development of soil food web of microbes and nematodes under different agricultural practices during the early stage of pedogenesis of a Mollisol, *Soil Biol. Biochem.* 98 (2016) 208–216, <https://doi.org/10.1016/j.soilbio.2016.04.011>.
- [15] S. Sánchez-Moreno, H. Ferris, Nematode ecology and soil health, Sikora R Coyne Hallmann J Timper PEds Plant-Parasit. Nematodes Subtrop. Trop. Agric. CAB Int. Wallingford (2018) 62–83.
- [16] D.L. Coyne, B. Thio, R.A. Plowright, D.J. Hunt, Observations on the community dynamics of plant parasitic nematodes of rice in Cote d'Ivoire, *Nematology* 1 (1999) 433–441, <https://doi.org/10.1163/156854199508324>.
- [17] T. Kyndt, D. Fernandez, G. Gheysen, Plant-parasitic nematode infections in rice: molecular and cellular insights, *Annu. Rev. Phytopathol.* 52 (2014) 135–153, <https://doi.org/10.1146/annurev-phyto-102313-050111>.
- [18] D. Peng, H.S. Gaur, J. Bridge, Nematode Parasites of Rice. Plant-Parasit Nematodes Subtrop Trop Agric, third ed., Sikora RA Coyne Hallmann J Timper P, 2018, pp. 120–162.
- [19] D. Makihara, J. Kimani, H. Samejima, M. Kikuta, D. Menge, Y. Inukai, et al., Development of Rice Breeding and Cultivation Technology Tailored for Kenya's Environment. *Crop Prod. Stress. Cond.*, Springer, 2018, pp. 27–47.
- [20] C.T. Gilces, D.N. Santillán, L.V. Velasco, Plant-parasitic nematodes associated with rice in Ecuador, *Nematropica* 46 (2016) 45–53.
- [21] P.P. Win, P.P. Kyi, D. De Waele, Effect of agro-ecosystem on the occurrence of the rice root-knot nematode *Meloidogyne graminicola* on rice in Myanmar, *Australas. Plant Pathol.* 40 (2011) 187–196, <https://doi.org/10.1007/s13313-011-0029-y>.
- [22] D. Coyne, M. Smith, R. Plowright, Plant parasitic nematode populations on upland and hydromorphic rice in Côte d'Ivoire: relationship with moisture availability and crop development on a valley slope, *Agric. Ecosyst. Environ.* 84 (2001) 31–43, [https://doi.org/10.1016/S0167-8809\(00\)00193-6](https://doi.org/10.1016/S0167-8809(00)00193-6).
- [23] Y. Lü, W. Bai, X. Wang, Q. Cai, W. Liang, Responses of soil micro-food web to land use change from upland to paddy fields with different years of rice cultivation, *Pedosphere* 27 (2017) 155–164, [https://doi.org/10.1016/S1002-0160\(15\)60102-3](https://doi.org/10.1016/S1002-0160(15)60102-3).
- [24] S. Sánchez-Moreno, H. Ferris, Suppressive service of the soil food web: effects of environmental management, *Agric. Ecosyst. Environ.* 119 (2007) 75–87, <https://doi.org/10.1016/j.agee.2006.06.012>.
- [25] D.I. Korobushkin, K.O. Butenko, K.B. Gongalsky, R.A. Saifutdinov, A.S. Zaitsev, Soil nematode communities in temperate rice-growing systems, *Eur. J. Soil Biol.* 93 (2019), 103099, <https://doi.org/10.1016/j.ejsobi.2019.103099>.
- [26] J. Wang, M. Li, X. Zhang, X. Liu, L. Li, X. Shi, et al., Changes in soil nematode abundance and composition under elevated [CO₂] and canopy warming in a rice paddy field, *Plant Soil* 445 (2019) 425–437, <https://doi.org/10.1007/s11104-019-04330-4>.
- [27] H. Okada, S. Niwa, S. Takemoto, M. Komatsuzaki, M. Hiroki, How different or similar are nematode communities between a paddy and an upland rice fields across a flooding–drainage cycle? *Soil Biol. Biochem.* (2011) <https://doi.org/10.1016/j.soilbio.2011.06.018>. S0038071711002471.
- [28] V.S. Nguyen, M.K. Chau, Q.M. Vo, V.K. Le, T.K.P. Nguyen, M. Araki, et al., Impacts of saltwater intrusion on soil nematodes community in alluvial and acid sulfate soils in paddy rice fields in the Vietnamese Mekong Delta, *Ecol. Indic.* 122 (2021), 107284, <https://doi.org/10.1016/j.ecolind.2020.107284>.
- [29] Iuss Working Group Wrk, World Reference Base for Soil Resources. International Soil Classification System for Naming Soils and Creating Legends for Soil Maps, fourth ed., International Union of Soil Sciences (IUSS), Vienna, Austria, 2022.
- [30] G. Akoko, T. Kato, L.H. Tu, Evaluation of irrigation water resources availability and climate change impacts—a case study of Mwea irrigation scheme, Kenya, *Water* 12 (2020) 2330, <https://doi.org/10.3390/w12092330>.
- [31] L. Wiesel, T.J. Daniell, D. King, R. Neilson, Determination of the optimal soil sample size to accurately characterise nematode communities in soil, *Soil Biol. Biochem.* 80 (2015) 89–91, <https://doi.org/10.1016/j.soilbio.2014.09.026>.
- [32] D.J. Hooper, Extraction of free-living stages from soil, in: J.F. Southey (Ed.), *Lab. Methods Work Plant Soil Nematodes*, Her Majesty's Stationary Office, London, 1986, pp. 5–30.
- [33] D.J. Hooper, Handling, Fixing, Staining and Mounting Nematodes, Technical Bulletin. Ministry of Agriculture, Fisheries and Food, 1970.
- [34] T. Bongers, De nematoden van Nederland: een identificatietabel voor de in Nederland aangetroffen zoetwater-en bodembewonende nematoden, Koninklijke Nederlandse Natuurhistorische Vereniging, Zeist, Netherlands, 1988.
- [35] W.F. Mai, P.G. Mullin, Plant-parasitic Nematodes: A Pictorial Key to Genera, Cornell University Press, Ithaca, NY, 1996.
- [36] A. Klute, Methods of soil analysis: Part 1 Physical and mineralogical methods, *Water Retent. Lab. Methods* 5 (1986) 635–662.
- [37] A. Mehlich, C. Pinkerton, W. Robertson, R. Kepton, Mass Analysis Methods for Soil Fertility Evaluation, National Agricultural Laboratories, Nairobi, 1962.
- [38] J. Bremner, C. Mulvaney, Nitrogen-total. Methods Soil Anal. Part 2 Chem. Microbiol. Prop, Am Soc Agron Inc Soil Sci Soc Am Inc, Madison, Wisconsin, USA, 1982, pp. 595–622, 2nd Edn Number 9 Part 2 Agron.
- [39] J. Anderson, J. Ingram, *Tropical Soil Biology and Fertility: A Handbook of Methods*, CAB International, Wallingford, Oxon, England, 1993.
- [40] B. Sieriebriennikov, H. Ferris, RGM de Goede, NINJA: an automated calculation system for nematode-based biological monitoring, *Eur. J. Soil Biol.* 61 (2014) 90–93, <https://doi.org/10.1016/j.ejsobi.2014.02.004>.
- [41] G. Du Preez, M. Daneel, R. De Goede, M.J. Du Toit, H. Ferris, H. Fourie, et al., Nematode-based indices in soil ecology: application, utility, and future directions, *Soil Biol. Biochem.* 169 (2022), 108640, <https://doi.org/10.1016/j.soilbio.2022.108640>.
- [42] B. Tóthmérész, Comparison of different methods for diversity ordering, *J. Veg. Sci.* 6 (1995) 283–290, <https://doi.org/10.2307/3236223>.
- [43] A. Rényi, On Measures of Entropy and Information. *Berkeley Symp Math Stat. Prob Proc Fourth Berkeley Symp PC Math Stat. Prob*, University of California Press, 1961, pp. 547–561.
- [44] B. Tóthmérész, On the characterization of scale- dependent diversity, *Abstr Botánica* 22 (1998) 149–156.
- [45] T.O. Crist, J.A. Veech, J.C. Gering, K.S. Summerville, Partitioning species diversity across landscapes and regions: a hierarchical analysis of α , β , and γ diversity, *Am. Nat.* 162 (2003) 734–743.
- [46] M.J. Anderson, Distance-based tests for homogeneity of multivariate dispersions, *Biometrics* 62 (2006) 245–253, <https://doi.org/10.1111/j.1541-0420.2005.00440.x>.
- [47] M.J. Anderson, A new method for non-parametric multivariate analysis of variance, *Austral Ecol.* 26 (2001) 32–46.
- [48] K.R. Clarke, Non-parametric multivariate analyses of changes in community structure, *Aust. J. Ecol.* 18 (1993) 117–143, <https://doi.org/10.1111/j.1442-9993.1993.tb00438.x>.
- [49] R Core Team, R, A Language and Environment for Statistical Computing, 2020.
- [50] V. Korenko, C. Schmidt, Effects of agricultural practices in the rice crop system on nematode communities in Uruguay, *Nematol. Mediterr.* 35 (2007) 109–121.
- [51] S.V. Nguyen, P.T.K. Nguyen, M. Araki, R.N. Perry, L. Ba Tran, K. Minh Chau, et al., Effects of cropping systems and soil amendments on nematode community and its relationship with soil physicochemical properties in a paddy rice field in the Vietnamese Mekong Delta, *Appl. Soil Ecol.* 156 (2020), 103683, <https://doi.org/10.1016/j.apsoil.2020.103683>.
- [52] A. Schmidt, K. John, G. Arida, H. Auge, R. Brandl, F.G. Horgan, et al., Effects of residue management on decomposition in irrigated rice fields are not related to changes in the decomposer community, *PLoS One* 10 (2015), e0134402, <https://doi.org/10.1371/journal.pone.0134402>.
- [53] M.L.D. Pascual, W. Decraemer, I.T.D. Ley, A. Vierstraete, H. Steel, W. Bert, Prevalence and characterization of plant-parasitic nematodes in lowland and upland rice agro-ecosystems in Luzon, Philippines 44 (2014) 15.
- [54] C.N.B. Bambaradeniya, J.P. Edirisinghe, D.N. De Silva, C.V.S. Gunatilleke, K.B. Ranawana, S. Wijekoon, Biodiversity associated with an irrigated rice agro-ecosystem in Sri Lanka, *Biodivers. Conserv.* 13 (2004) 1715–1753, <https://doi.org/10.1023/B:BIOC.0000029331.92656.de>.
- [55] D. Coyne, R.A. Plowright, Nematode threats to intensifying smallholder upland rice production in the Guinea savannah of Côte d'Ivoire, *Trop. Sci.* 40 (2000) 67–74.

- [56] M. Chinapen, F. Lamberti, A. Ciancio, P. Jokhun, Losses caused by concomitant infestations of *Criconebella onoensis* and *Helicotylenchus dihystra* on upland rice in Mauritius, *Nematol. Mediterr.* 16 (1988) 175–177.
- [57] H. Ferris, T. Bongers, R.G.M. de Goede, A framework for soil food web diagnostics: extension of the nematode faunal analysis concept, *Appl. Soil Ecol.* 18 (2001) 13–29, [https://doi.org/10.1016/S0929-1393\(01\)00152-4](https://doi.org/10.1016/S0929-1393(01)00152-4).
- [58] M. Watanabe, Y. Sumita, I. Azechi, K. Ito, K. Noda, Production costs and benefits of Japonica rice in Mwea, Kenya, *Agriculture* 11 (2021) 629, <https://doi.org/10.3390/agriculture11070629>.
- [59] N.V. Sinh, C.M. Khoi, N.T.K. Phuong, T.B. Linh, D.D. Minh, R.N. Perry, et al., Impacts of fallow conditions, compost and silicate fertilizer on soil nematode community in salt-affected paddy rice fields in acid sulfate and alluvial soils in the Mekong Delta, Vietnam, *Agronomy* 11 (2021) 425, <https://doi.org/10.3390/agronomy11030425>.
- [60] Y. Kouser, A.A. Shah, S. Rasmann, The functional role and diversity of soil nematodes are stronger at high elevation in the lesser Himalayan Mountain ranges, *Ecol. Evol.* 11 (2021) 13793–13804, <https://doi.org/10.1002/ece3.8061>.
- [61] A. Archidona-Yuste, T. Wiegand, N. Eisenhauer, C. Cantalapiedra-Navarrete, J.E. Palomares-Rius, P. Castillo, Agriculture causes homogenization of plant-feeding nematode communities at the regional scale, *J. Appl. Ecol.* 58 (2021) 2881–2891, <https://doi.org/10.1111/1365-2664.14025>.
- [62] K. Wang, R. McSorley, R. Gallaher, Relationship of soil management history and nutrient status to nematode community structure, *Nematropica* 34 (2004) 83–96.
- [63] S. Landi, R. Papini, G. d'Errico, G. Barzanti, P. Roversi, Nematode indicators as integrative measures of soil condition during conversion from conventional to organic rice production in Italy: a case study, *Biol. Agric. Hort.* 34 (2018) 141–153.