NEMATODE COMMUNITIES IN PINEAPPLE PLANTATIONS IN THE PLAINS OF THE REGIÓN HUETAR NORTE, COSTA RICA

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ABSTRACT

Varela-Benavides, I., J. P. Jiménez-Madrigal, F. Echeverría-Beirute, and. Z. Castro-Jiménez. Nematode communities in pineapple plantations in the plains of the Región Huetar Norte, Costa Rica. Nematropica 52:19-32.

Little is known about nematode communities related to Costa Rican crops, which limits the efforts to offer adequate responses to producers interested in soil conservation. The objective of this work was to describe nematode fauna of pineapple plantations in the northern plains of Costa Rica as an example of how agronomical management practices can influence nematode diversity. The abundance of families (or genera) of the nematode communities in soil samples of 15 pineapple plantations and 11 patches of forests or tree plantations near them was calculated. Forty-three families were identified, 39 families in forest, 36 in tree plantations, and 35 in pineapple plantations. *Helicotylenchus* was the most abundant genus in pineapple, while *Discocriconemella* dominated in forests and tree plantations. Non-metric multidimensional scaling and redundancy analysis showed few differences but revealed that forests and tree plantations correlated with organic matter, Ca, Mg, and with *Discocriconemella*. Meanwhile, pineapple plantations correlated with exchangeable acidity, K, and with abundance of *Mesocriconema*. Basal index was significantly lower in forest and tree plantations while the Structure index was higher. Other calculated indexes (Plant-parasitic index, Maturity index, Channel index, Enrichment index, and Metabolic Footprints) did not show any statistical differences among land uses. Most statistical differences were found at the nematode genus level.

Key words: Costa Rica, functional guilds, nematode communities, pineapple, tropical soils

RESUMEN

Varela-Benavides, I., J. P. Jiménez-Madrigal, F. Echeverría-Beirute, and. Z. Castro-Jiménez. Comunidades de nematodos en plantaciones de piña en las llanuras de la Región Huetar Norte, Costa Rica. Nematropica 52:19-32.

El poco conocimiento sobre las comunidades de nematodos asociadas a los cultivos de Costa Rica limita los esfuerzos para ofrecer respuestas acertadas a los productores interesados en la conservación del suelo, el cultivo de la piña es un ejemplo. El objetivo de este trabajo fue describir la nematofauna asociada a las plantaciones de piña en las llanuras de la de la Región Huetar Norte de Costa Rica. La abundancia de familias (o géneros), de las comunidades de nematodos en muestras de suelo de 15 plantaciones de piña y 11 zonas boscosas o plantaciones forestales cercanas a ellas, fue calculada. Cuarenta y tres familias fueron identificadas, 39 familias en bosque, 36 en plantaciones forestales, y 35 en plantaciones de piña. *Helicotylenchus* fue el género más abundante en piña, mientras que *Discocriconemella* dominó en bosque y plantaciones forestales. El Escalamiento multidimensional no métrico y el Análisis de redundancia, revelaron pocas diferencias, pero los bosques y plantaciones forestales se correlacionaron con: la materia orgánica, el Ca, el Mg y con el género *Discocriconemella*. Mientras que las plantaciones de piña se correlacionaron con la acidez intercambiable, el K y la abundancia de *Mesocriconema*. El índice basal fue significativamente más bajo en el bosque y en las plantaciones forestales, contrariamente al índice de estructura que fue más alto en estos. Otros índices calculados: Índice de madurez, el Índice de fitopatógenos, el Índice de canal, el Índice de enriquecimiento y las Huellas metabólicas, no mostraron ninguna diferencia significativa entre los diferentes usos del suelo. La mayor parte de las diferencias significativas se encontraron a nivel de género.

Palabras clave: Costa Rica, gremios funcionales, comunidades de nematodos, piña, suelos tropicales

INTRODUCTION

Soil organisms have been demonstrated to be important actors in maintaining soil health and productivity (Chaparro *et al.*, 2012; Ferris and Tuomisto, 2015). They play important roles in biogeochemical cycles, controlling pathogen populations, and degrading possible soil contaminants (Rousk and Bengtson, 2014; Javaid *et al.*, 2016; Durán *et al.*, 2018). Despite their importance, soil organisms are not well known when compared to aboveground biota (Powers *et al.*, 2009; Lehmann *et al.*, 2020).

Although different agricultural practices affect soil biological communities, the effects on the composition and inter-specific interactions of those communities are not completely understood, nor are they predictable (Thiele-Bruhn *et al.*, 2012; Lehmann *et al.*, 2020). This is particularly relevant in tropical soils where fewer research publications are available compared to temperate regions, high temperature and humidity accelerate decomposition processes, and soils are different in structure and management (Porazinska *et al.*, 2010; Cavaleri *et al.*, 2015; Franco *et al.*, 2019). Increased knowledge about biota in tropical soils will aid in establishing adequate conservation policies and offer correct responses to producers interested in soil conservation practices. Proper management will result in reduced pesticide and fertilizer usage.

Among soil biota, nematodes are known to be useful bioindicators of the structure and function of underground ecosystems (Neher, 2001; Wilson and Kakouli-Duarte, 2009; Ferris, 2010; Chaparro *et al.*, 2012; Ferris *et al.*, 2012; Gingold *et al.*, 2013; Zhang *et al.*, 2017).Their study in tropical soils could be used in programs that intend to assess the sustainability of agricultural practices in farming. Despite previous studies demonstrating that agricultural practices change nematode communities (Zhao and Neher, 2013; Ilieva-Makulec *et al.*, 2016; Shaw *et al.*, 2019), more information is needed if the objective is to use nematodes as useful indicators of agricultural management for specific environments and crops.

In Costa Rica, pineapple plantations have been identified as detrimental for the environment (Echeverría-Sáenz *et al.*, 2012; Sherman and Brye, 2019). However, some producers try to implement agricultural practices for better soil conservation. For example, adding different preparations of organic matter and using no tillage or minimum tillage have been proposed as a beneficial practice for soil conservation (Fonseca-Vargas *et al.*, 2019; Mahmud *et al.*, 2020; Vega-Rodríguez and Hernández-Chaverri, 2020). According to pineapple producers, these practices improve plant health, but little is known about their effect on edaphic biota, including soil nematodes.

Even if some studies on plant-parasitic nematodes in pineapple plantations have been conducted (Guzmán-Hernández *et al.*, 2014; Araya, 2019), only one study (Varela Benavides, 2018) has explored the non-plant feeding groups of nematodes in Costa Rican pineapple plantations. The objective of this research was to describe nematode fauna of pineapple plantations in the northern plains of Costa Rica, as an initial approach to establish parameters related to soil health in these ecosystems. At the same time, forest patches and tree plantations near the cultivated pineapple fields were sampled in order to assess differences in nematode communities due to pineapple cultivation and the impact of different soil preparation practices.

MATERIALS AND METHODS

Study site

The lowland plains of the Region Huetar Norte (RHN) is a territory of about 6,000 km² located in the northern part of Costa Rica. The region is economically important due to its high agricultural productivity, including food crops such as pineapple, citrus, cassava, sweet potato, banana, and taro (Ministerio de Agricultura y Ganadería de Costa Rica, 2020). The region´s landscape represents a complex matrix of crop fields, urban, rural, industrial, and protected areas without clear boundaries between them. Tropical rainforest is the predominant life zone in the area (Holdridge, 1967), with annual precipitation range between 2,000-4,000 mm and mean annual temperature above 24°C (Tapia, 2014). In the plains the soils are classified as ultisols (Mata *et al.*, 2013).

Sampling and data collection

The total pineapple plantations in the plains of RHN cover about 44,200 ha distributed over approximately 600 fields (70 ha per field) (Vargas-Bolaños *et al.*, 2020). Thus, the sampling fields were selected from this area (Fig. 1), and from those that met following criteria: permission from owner to sample, production of pineapple for exportation, and also maintained with a minimum standard of soil management.

A total of 26 sites were selected across the plains. Of these, 15 were pineapple plantations (2.5% of the plantations), and the remaining were adjacent areas of low anthropogenic disturbance: natural forest patches (FO) and mature timber plantations (TP). Most of the pineapple plantations

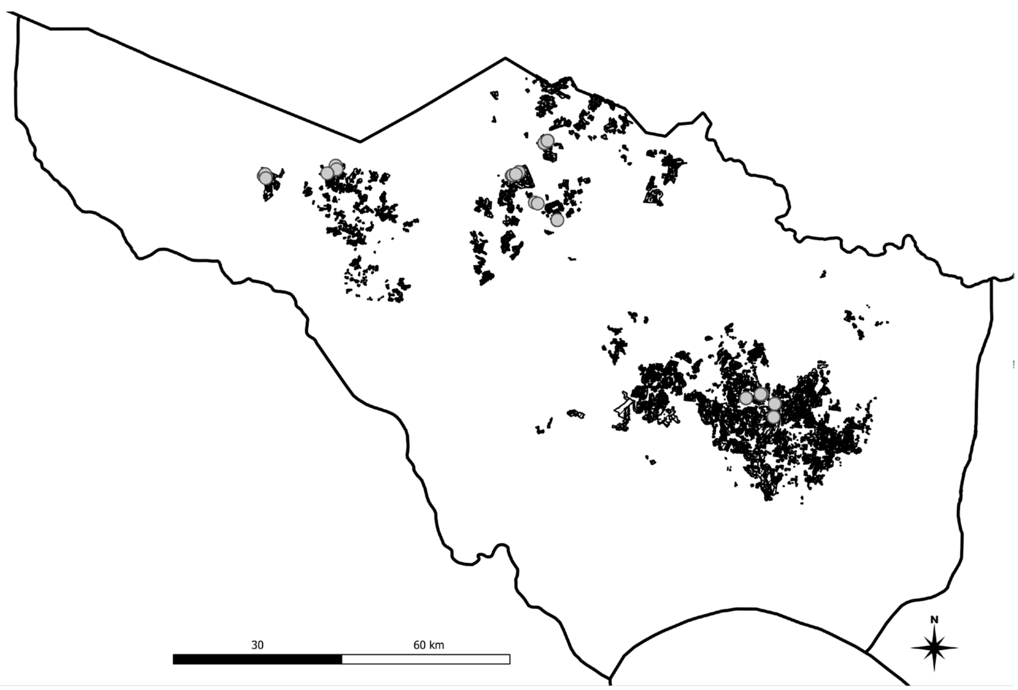

Figure 1. Map of the Región Huetar Norte, Costa Rica showing the areas with pineapple plantations (black patches) and the sampling sites in these areas (grey circles enlarged for easy visualization). The map was drawn in QGIS ver 3.16.3 using layers from SNIT prepared by the MOCUPP piña project (Instituto Geográfico Nacional de Costa Rica, n.d.; Vargas-Bolaños *et al.*, 2020).

were conventionally managed (CPP), three were under minimum tillage (MT), and four had received applications of organic matter (OM).

Within each field, samples were taken from three linear 50 m transects, which were located in the center of the field to avoid borders and were representative of the field. The transects were separated from each other by 25 m, and a composite sample was taken from each one. Three cores were taken for each composite sample. Cores were taken at a depth of 15 cm with a Dutch auger of 5 cm in diameter at the base of a plant in the case of pineapple plantations. In total, 78 composite samples were taken in this survey. The samples were transported to the laboratory in labeled plastic bags, where they were stored at 4°C until processed. A subsample of soil was processed for chemical analyses by the Laboratorio de Análisis Agronómicos at Instituto Tecnológico de Costa Rica. The concentrations of Ca, Mg, K, P, Zn, Mn, Cu, S, and Fe were determined with the modified Olsen method, exchangeable acidity was determined with KCl solution, and the percentage of organic matter was measured using the Walkley-Black method (Nelson and Sommers, 1996).

Extraction and mounting

Upon homogenization of each soil sample, nematodes were extracted from 200 g using an Oostenbrink elutriator (Oostenbrink, 1960) and thereafter the final separation of individuals from soil was made by the centrifugation flotation method (Coolen, 1979). The total number of nematodes per sample was counted under an inverted microscope (Olympus CKX 41, Tokyo, Japan), heat-killed, fixed in formaldehyde 4%, and processed to pure glycerin using the Seinhorst (1966) method. Once counted and fixed, at least 20% of the nematodes in each sample, the first in the counting chamber, were mounted and identified to family or genus under a compound microscope (Olympus BX51, Tokyo, Japan).

Analyses for the nematode communities

Abundance and frequency were calculated for each family or genus, while abundance diversity curves were made using the function "radfit" of *vegan* package in R (Oksanen *et al.*, 2019), and then plotting the resulting logarithmic abundances in decreasing order (Wilson, 1991). Composition of the nematode assemblages were explored using non-metric multidimensional scaling (NMDS) with the Bray Curtis similarity matrix in the vegan package in R. Adonis statistical analysis was used to evaluate the statistical significance among differences. Hellinger transformation of the data was used to reduce the stress of the analysis. The relationship between chemical characteristics of the soil and nematode assemblages was established with redundancy analysis (RDA) on Hellinger transformed abundance, only environmental variables that were statistically significant and not redundant (variance inflation factor <10) were used in the analysis.

Indexes and functional structure of the nematode communities

Each genus was assigned to a trophic group according to Yeates *et al.* (1993) and a *cp* (colonizer-persisters) group according to Bongers (1990) and Bongers and Bongers (1998). The *cp* groups represent different life history strategies for nematodes. Based on *cp* groups, Maturity index, and Plant-parasitic index (Bongers, 1990) were calculated as indicators of the state of the ecological succession of the soil ecosystem. Based on *cp* and trophic groups, Soil food web indexes were calculated according to Ferris *et al.* (2001), and included the Basal index, an indicator of environmental degradation; the Enrichment index, an indicator of conditions supporting fast-growing bacterivores; the Channel index, an indicator of fungal-mediated dominance of organic matter decomposition; and the Structure index, an indicator of more highly structured soil food webs with enhanced ecological functions due to a greater number of trophic links. Composite, enrichment, and structure metabolic footprints were calculated according to Ferris (2010). These indexes consider the biomass of the nematodes in the soil, which is estimated for each genus according to its body size (Andrassy, 1956) and is used to evaluate the mean carbon consumed by each nematode throughout its life cycle. According to Ferris (2010): composite footprint is calculated with all nematode assemblage regardless of trophic role or ecosystem function; enrichment footprint is calculated with nematodes most rapidly responsive to resource enrichment bacterial and fungal feeding nematodes with low *cp* values; and, structure footprint is calculated with higher trophic levels, predators and omnivores, indicators of a structured soil food web. All indexes were calculated using the NINJA tool: Nematode indicator joint analysis (Sieriebriennikov *et al.*, 2014).

Analysis of variance (ANOVA) and comparisons of means were tested using Tukey's studentized range (HSD) test. Data were previously transformed with Hellinger to satisfy the condition of normality and homogeneity of variance. All statistical procedures were performed using R Statistical software (4.1.1). Differences with $P < 0.05$ were considered significant.

RESULTS

Abundance, diversity, and distribution

Forty-three families and eight orders were identified in this study, 39 families were found in forests, 36 in tree plantations, and 35 in pineapple plantations. Mean abundance per sample was 970 nematodes/200 g of soil. High variability was frequent for all measured variables rendering it difficult to find significant differences. In the case of mean abundances, these ranged from 75 to 3,086 nematodes/200 g of soil. Forests tended to have higher abundance (ranges from 255 to 1,821 nematodes/200 g of soil) than pineapple plantations (ranges from 74 to 2,077 nematodes/200 g of soil), but no significant difference was found between them. Dominance diversity curves (Fig. 2) showed the most abundant genera for each land use. Dominance was highest in pineapple and tree plantations. In pineapple, *Helicotylenchus* was the most abundant genus and represented between 23 and 28% of the total of the individuals. Moreover, more than 80% of the individuals belonged to only five families: Hoplolaimidae (*Helicotylenchus*), Criconematidae (*Mesocriconema*), Cephalobidae, Tylenchidae and Anguinidae (*Ditylenchus*). In tree plantations and in forests, *Discocriconemella* was the most abundant genus. The curve for the forests was softer and 80% of the nematodes belong to seven families, suggesting less dominance.

Regarding abundance and frequency of taxa, six families and seven genera were only found in forests and tree plantations (marked with an "w" in Table 1), among these taxa, *Longidorus*, *Xiphinema*, *Coomansus,* and *Aphanolaimus* were the most frequent and abundant. Also, the genera *Diphtherophora* and *Discocriconemella*, and the family Belondiridae were more abundant in forests and tree plantations than in pineapple plantations (Table 1). Similarly, densities of *Aporcelinus* (Aporcelaimidae) were significantly different among land uses. Populations of this nematode were less abundant in conventionally managed pineapple plantations compared to other types of land use, indicating that minimum tillage and the addition of organic matter may favor their abundance. Conversely, the only family that was more abundant in pineapple plantations was Cephalobidae, with no significant difference between different soil management practices in fields under pineapple production.

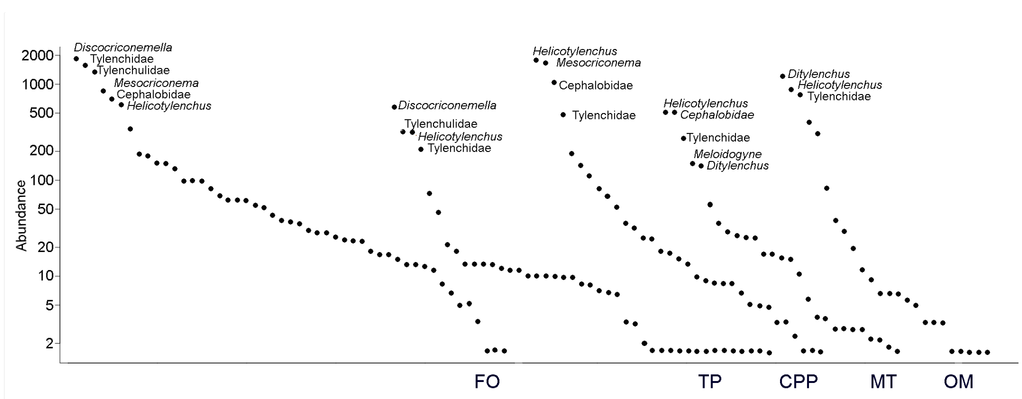

Figure 2. Dominance-diversity curves for soil nematodes associated with different land uses inside plains of the Región Huetar Norte, Costa Rica. FO: forest; TP: tree plantation; CPP conventional pineapple plantation; MT: pineapple under minimum tillage; OM: organic matter applied to pineapple.

Table 1. Abundance and frequency of nematode families and genera (if identified) for different land uses inside the plains of the Región Huetar Norte, Costa Rica.

Family/genus	FG[q]	FO[r] (n=8)	TP[s] (n=3)	CPP[t] (n=8)	MT[u] (n=3)	OM[v] (n=4)
Achromadoridae[w]	o3	3[x] (1)[y]	1 (1)	-	-	-
Actinolaimidae[w]	o4	1 (2)	1 (1)	-	-	-
Aporcelaimidae/*Aporcelaimellus*	o5	1 (5)	1 (1)	1 (1)	-	-
Aporcelaimidae/*Aporcelinus*	o5	8 (4)ab[z]	3 (2)ab	1 (1)a	8 (3)b	1 (3)b
Aporcelaimidae/*Makatinus*[w]	o5	2 (4)	1 (1)	-	-	-
Aporcelaimidae/*Metaporcelaimus*	o5	2 (4)	2 (2)	1 (3)	1 (1)	1 (1)
Aporcelaimidae/*Sectonema*[w]	o5	1 (2)	-	-	-	-
Belondiridae/*Metaxonchium*	h5	8 (5)	6 (1)	1 (1)	-	-
Belondiridae	h5	22 (7)a	24 (3)a	4 (2)b	1 (1)b	-
Discolaiminae[w]	p5	1 (2)	-	-	-	-
Dorylaimidae	o4	8 (7)	4 (2)	1 (4)	10 (2)	10 (3)
Leptonchidae	f4	-	-	-	-	2 (1)
Longidoridae/*Longidorus*[w]	h5	8 (4)	1 (1)	-	-	-
Longidoridae/*Xiphinema*[w]	h5	6 (2)	4 (1)	-	-	-
Nordiidae[w]	o4	1 (1)	-	-	-	-
Qudsianematinae	o4	5 (5)	1 (1)	-	7 (1)	2 (1)
Thornenematidae	o5	2 (3)	4 (1)	-	-	1 (1)
Tylencholaimellidae	f4	-	-	-	2 (1)	-
Tylencholaimidae	f4	2 (4)	3 (1)	1 (2)	-	1 (1)
Alaimidae	b4	19 (5)	7 (2)	3 (6)	1 (1)	2 (1)
Anatonchidae/*Iotonchus*	p4	5 (3)	3 (2)	2 (3)	1 (2)	1 (1)
Mononchidae/*Clarkus*	p4	4 (4)	2 (2)	1 (1)	-	-
Mononchidae/*Coomansus*[w]	p4	5 (3)	1 (1)	-	-	-
Mylonchulidae/*Mylonchulus*	p4	7 (3)	3 (2)	1 (2)	-	-
Aphanolaimidae/*Aphanolaimus*[w]	b3	4 (6)	4 (2)	-	-	-
Metateratocephalidae/*Euteratocephalus*	b3	4 (1)	-	1 (1)	1 (1)	-
Odontolaimidae[w]	b3	-	3 (1)	-	-	-
Plectidae/*Plectus*	b2	3 (5)	1 (1)	1 (2)	1 (1)	2 (2)
Plectidae/*Wilsonema*	b2	2 (3)	2 (1)	1 (2)	-	-
Bunonematidae	b1	1 (1)	1 (1)	2 (2)	-	-
Cephalobidae/*Acrobeles*	b2	1 (1)	1 (1)	2 (3)	5 (1)	1 (1)
Cephalobidae	b2	87 (8)a	69 (3)a	114 (9)b	147 (3)b	100 (4)ab
Diploscapteridae	b1	3 (2)	1 (1)	1 (1)	5 (1)	-
Mesorhabditidae	b1	2 (3)	1 (1)	1 (2)	1 (2)	1 (1)
Panagrolaimidae	b1	-	-	-	1 (1)	-
Protorhabditidae	b1	1 (2)	1 (2)	-	16 (1)	1 (1)
Rhabditidae	b1	12 (5)	4 (2)	1 (2)	7 (3)	1 (1)
Teratocephalidae/*Teratocephalus*[w]	b3	1 (1)	-	-	-	-
Diphtherophoridae/*Diphtherophora*	f3	12 (7)ab	15 (3)a	3 (6)b	-	1 (1)b
Prismatolaimidae/*Prismatolaimus*	b3	12 (6)	1 (1)	3 (2)	-	-
Tobrilidae[w]	p3	-	1 (1)	-	-	
Trichodoridae	h4	4 (4)	3 (2)	1 (2)	-	-
Tripylidae	p3	2 (5)	1 (2)	1 (2)	-	-
Anguinidae/*Ditylenchus*	f2	10 (5)	3 (2)	21 (7)	41 (2)	305 (4)
Aphelenchidae/*Aphelenchus*	f2	16 (5)	1 (1)	16 (6)	8 (2)	5 (1)
Aphelenchoididae/*Aphelenchoides*	f2	23 (7)	4 (2)	6 (7)	5 (3)	21 (4)
Criconematidae/*Mesocriconema*	h3	105 (6)	-	184 (9)	3 (2)	76 (3)
Criconematidae/*Discocriconemella*	h3	230 (6)a	1070 (2)a	1 (2)b	-	1 (1)b
Heteroderidae/*Meloidogyne*	h3	42 (8)a	3 (3)b	7 (5)b	43 (3)ab	3 (3)ab
Hoplolaimidae/*Helicotylenchus*	h3	76 (8)	106 (3)	194 (9)	147 (3)	222 (4)
Pratylenchidae/*Pratylenchus*	h3	18 (7)	4 (1)	12 (7)	4 (2)	7 (4)
Telotylenchidae	h3	3 (2)	-	-	1 (1)	-

Table 1. Continued.

Family/genus	FG[q]	FO[r] (n=8)	TP[s] (n=3)	CPP[t] (n=8)	MT[u] (n=3)	OM[v] (n=4)
Tylenchidae	h2	193 (8)	104 (3)	53 (9)	79 (3)	195 (4)
Tylenchulidae	h3	165 (8)	191 (3)	9 (7)	1 (1)	1 (2)

[q]Functional guilds (FG): b = bacterivore; f = fungivore; o = omnivore; p = predator; and h = plant-feeding. The numbers from 1 to 5 represented the cp value.
[r]FO: forest
[s]TP: tree plantation
[t]CPP conventional pineapple plantation
[u]MT: pineapple under minimum tillage
[v]OM: organic matter applied to pineapple
[w]Indicates families and genera that were not present in pineapple plantations.
xAbundance is expressed as mean number of nematodes/200 g of soil
[y]Frequency is given in parenthesis and expressed as the number of sites in which the family is present.
[z]Significant differences ($P \leq 0.05$), if any, are indicated with different letters to the right side of the column.

Finally, *Helicotylenchus* was prevalent in forests and plantations, which is in agreement with other reports of the high abundance of this genus in other tropical environments (Cardoso *et al.*, 2015; Franco-Navarro and Godinez-Vidal, 2017). However, little continues to be known about the species within this genus and their distribution.

Regarding the ordination based on distance matrix, few differences were observed within the NMDS analysis (Fig. 3). The biplot showed forests and tree plantations arranged in the left-side quadrants, while pineapple plantations under

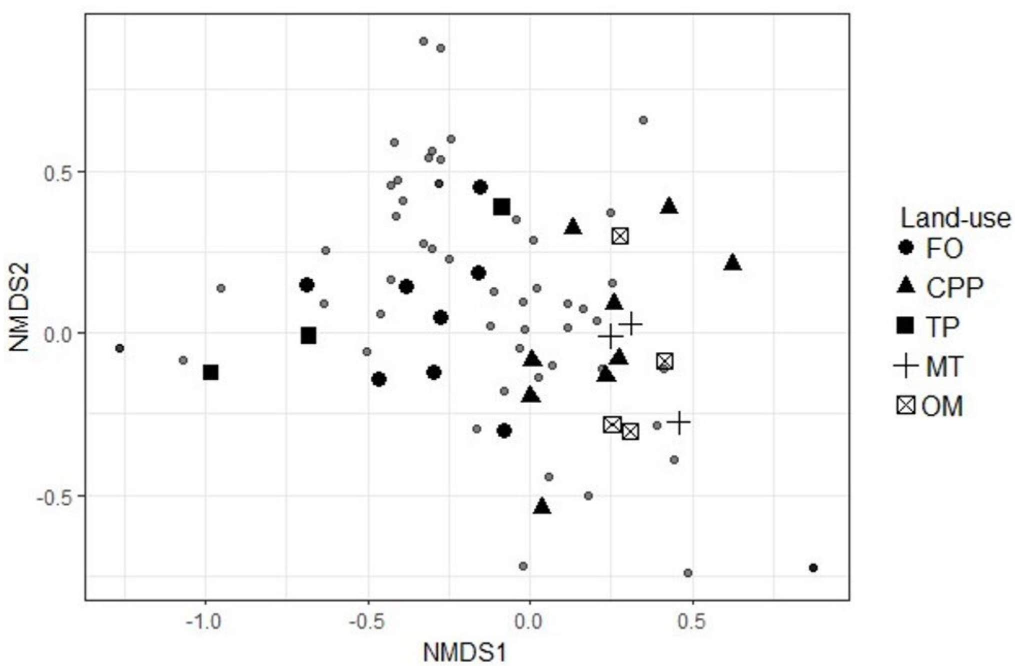

Figure 3. Non-metric multidimensional scaling (NMDS) biplot for abundance of families of nematodes associated with different land uses inside the plains of the Región Huetar Norte, Costa Rica. FO: forest; TP: tree plantation, CPP conventional pineapple plantation, MT: pineapple under minimum tillage, OM: organic matter applied to pineapple. Points in the biplot indicate the abundance of the species. Stress of the analysis is 0.16.

different management types arranged in the right-side quadrants. However, no clear clustering pattern occurred based on land use alone.

Similarly, RDA (Fig. 4) showed forests and tree plantations in the left side of the plot, correlated with: organic matter, Ca and Mg in the soil, with *Discocriconemella,* and to some extent, but less so, with Tylenchulidae, Belondiridae, and Tylenchidae. Pineapple plantations were arranged in the right side of the plot, correlated with exchangeable acidity and K in the soil, with *Mesocriconema* and, to a lesser extent, with Cephalobidae, *Ditylenchus*, and *Helicotylenchus.*

Indexes for the community

Some of the indices for nematode communities (Fig. 5, 6 and 7) differed between plantations and forest, while others, like the Maturity index and Plant-parasitic index (Fig. 7), did not significantly differ among land uses. The Basal index, an indicator of environment degradation (Ferris *et al.*, 2001), was lower in forests and tree plantations (p = 0.004) compared to pineapple plantations, while the Structure index, an indicator of more structured soil food webs, was higher in forests, but particularly in tree plantations (p = 0.02) (Fig. 5). There were no statistical differences for these indexes among pineapple plantations, despite the distinct soil management treatments. However, there was a tendency that deserves attention, minimum tillage could favor a more structured soil.

The metabolic footprints (Fig. 6) take into account the functional guilds in addition to the nematode biomass. Only composite footprints for conventional management in pineapple plantations and forests significantly differed (p = 0.005). Yet again, there was a tendency that deserves attention. The use of minimum tillage and organic matter in pineapple plantations may favor soil nematode communities with metabolic footprints resembling those of forests.

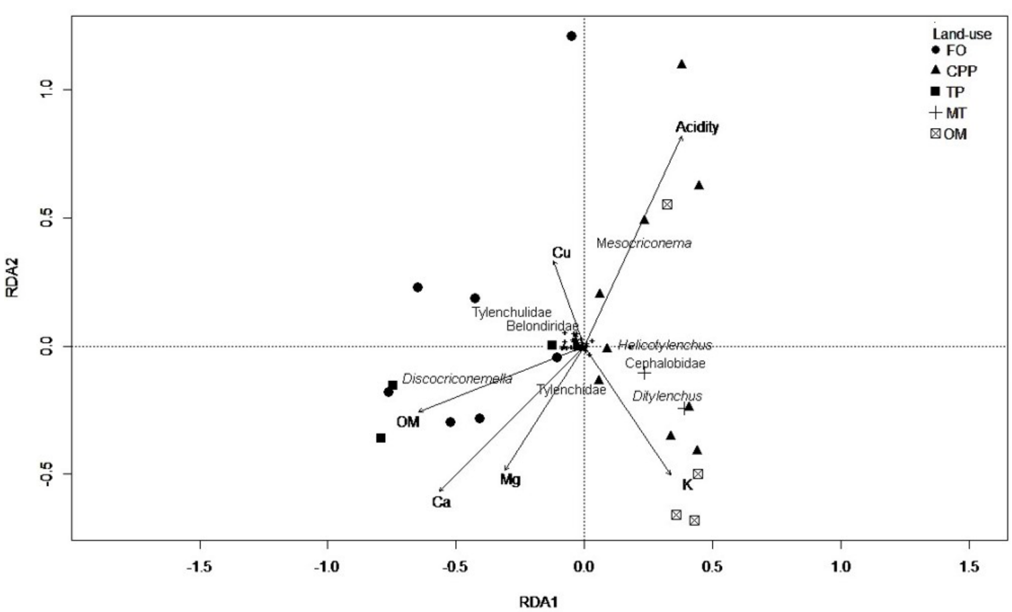

Figure 4. Plot of the redundancy analysis (RDA) between soil chemical properties and abundance of nematode families associated with different land uses inside the plains of the Región Huetar Norte, Costa Rica. Land uses are represented by geometric forms, families (or genera) by small crosses, or their name was annotated if high correlated. The length and position of an explanatory variable's arrow illustrate its significance on the canonical axes. Only environmental variables that were statistically significant and no redundant were used in the analysis. Adjusted R = 0.20, permutation test for RDA P = 0.002, Inertia Proportion Rank for constrained fraction 0.4. FO: forest; TP: tree plantation, CPP conventional pineapple plantation, MT: pineapple under minimum tillage, OM: organic matter applied to pineapple.

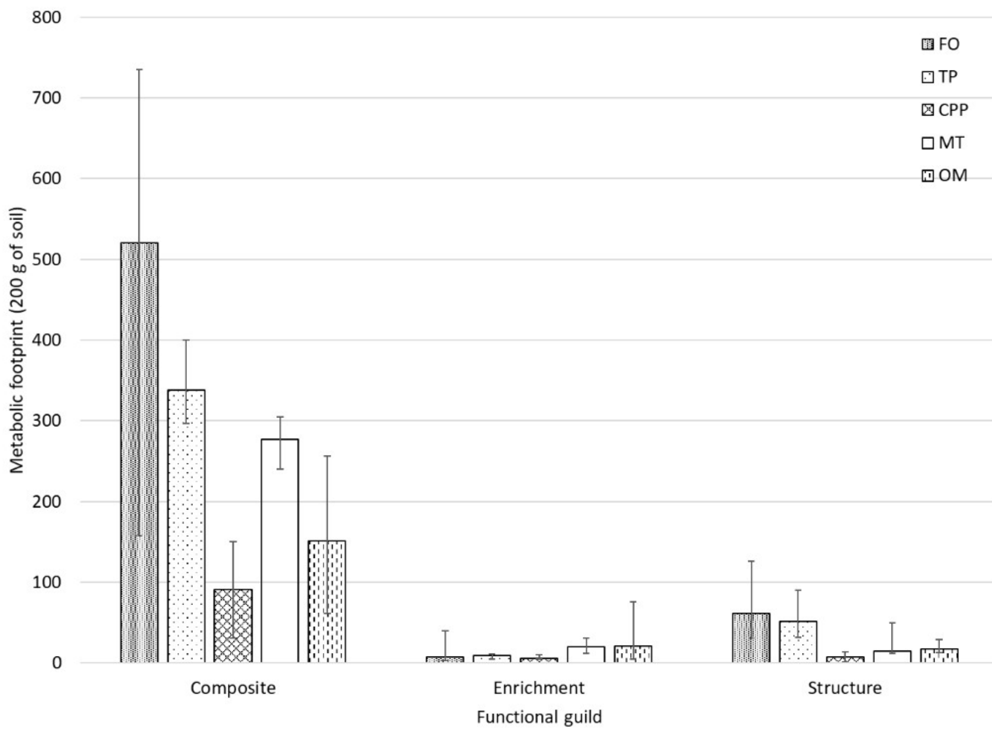

Figure 5. Distribution of the values of the soil food web indexes calculated for different land uses inside the plains of the Región Huetar Norte, Costa Rica. The boxes represent the values of the median and the whiskers the 25th and 75th percentiles. FO: forest; TP: tree plantation; CPP conventional pineapple plantation; MT: pineapple under minimum tillage; OM: organic matter applied to pineapple.

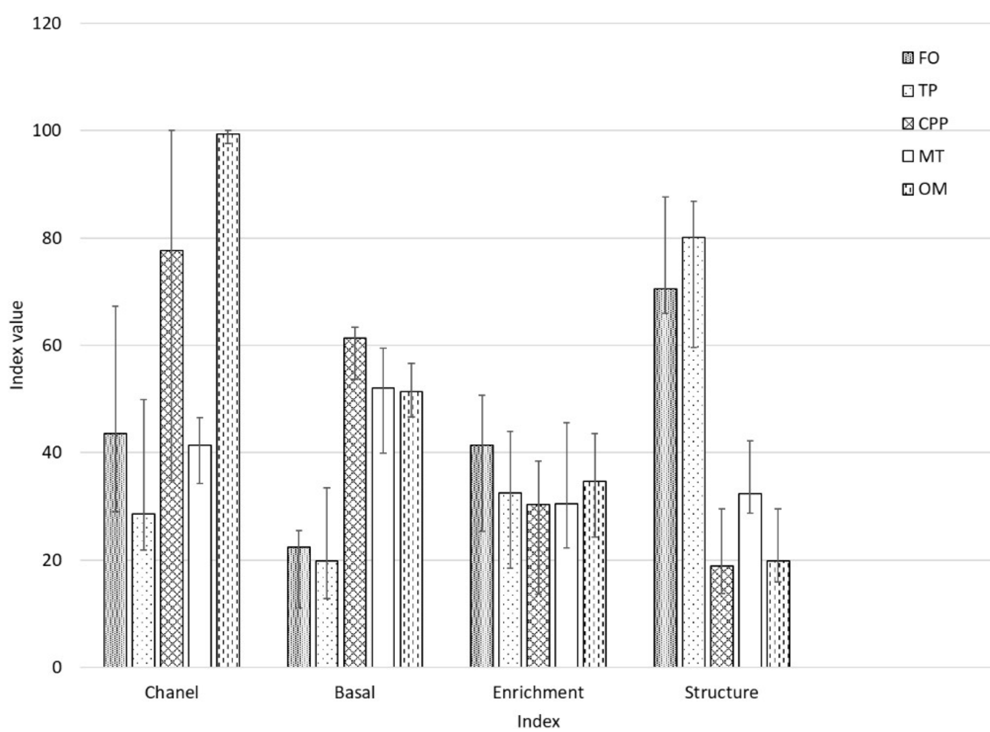

Figure 6. Distribution of the values of the composite, enrichment and structure footprints calculated for different land uses inside the plains of the Región Huetar Norte, Costa Rica. The boxes represent the values of the median and the whiskers the 25th and 75th percentiles. FO: forest; TP: tree plantation; CPP conventional pineapple plantation; MT: pineapple under minimum tillage; OM: organic matter applied to pineapple.

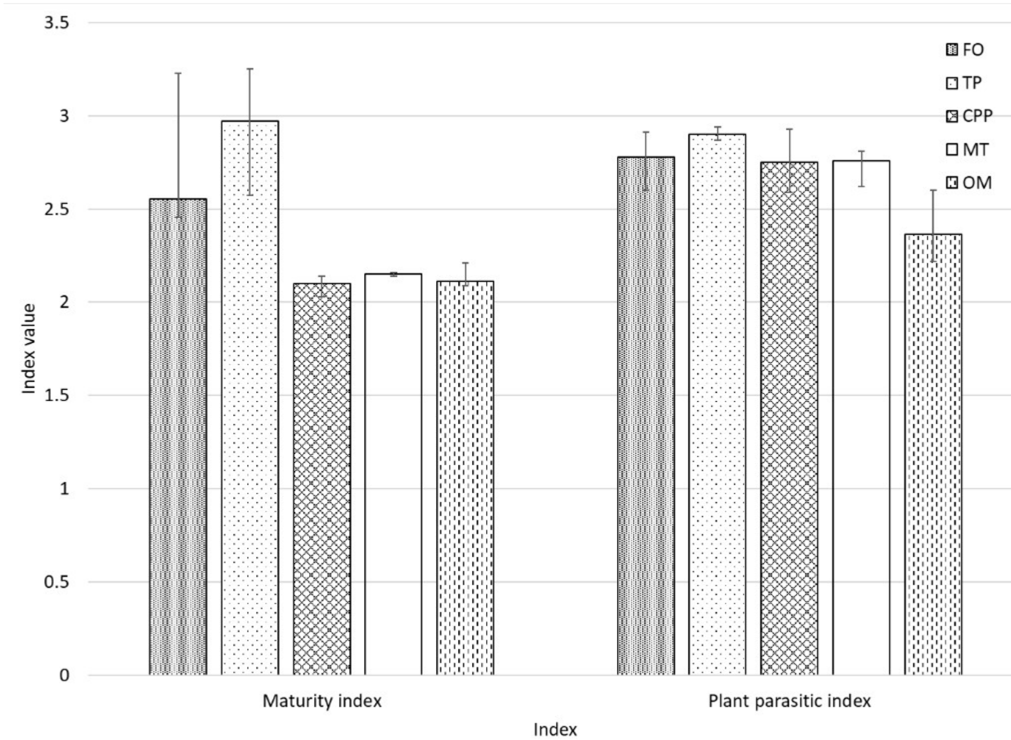

Figure 7. Distribution of the values of the Maturity index and Plant-parasitic index calculated for different land uses inside the plains of the Región Huetar Norte, Costa Rica. The boxes represent the values of the median and the whiskers the 25th and 75th percentiles. FO: forest; TP: tree plantation; CPP conventional pineapple plantation; MT: pineapple under minimum tillage; OM: organic matter applied to pineapple.

DISCUSSION

This initial approach to nematode fauna in pineapple plantations at the plains of the RHN in Costa Rica provided findings that deserve attention. The variability in the abundance, the changes in dominance of taxonomic groups due to pineapple cultivation, the occurrence of some genera that could be used as indicators of soil perturbations, and the insights given by indexes of the nematode community, are criteria that deserve further attention.

Variability in nematode communities is not unusual and has been studied (Lins *et al.*, 2017; Tsiafouli *et al.*, 2017; da Silva *et al.*, 2020). Variability suggests heterogeneous characteristics of the soil, mostly organic matter, but also other properties such as soil water content and pH, which can influence nematode communities (Simon *et al.*, 2018; Quist *et al.*, 2019; Liu *et al.*, 2019). RDA analysis in this study supports this statement. Studies of nematode communities should consider soil properties of the places nematodes inhabit, especially in tropical areas, where microhabitats are frequent due to heterogeneity and particularities of environment.

Apart from what is particular to tropical soils, most of the differences were found between perennials (forests and tree plantations) and pineapple plantations, with only one exception: the abundance of *Aporcelinus*, which differed between conventional pineapple and pineapple under minimum tillage or organic matter addition. However, some trends deserve further study. In some instances or combined with another practices, minimum tillage and addition of organic matter could promote a more structured and less degraded soil. Both practices, and especially non-tillage, have been demonstrated to influence nematode communities (Bongiorno *et al.*, 2019; Neher *et al.*, 2019; Su *et al.*, 2021).

Regarding abundance, diversity, and distribution, most statistical differences were found at the genus level, revealing the importance of increased knowledge about the genera and species present in tropical regions to determine which ones could be used as indicators or may be associated with certain environments, crops, or agricultural practices. Although, the indexes for nematode communities use the abundance of families for their calculation, some genera could be used as indicators of specific conditions and should be studied (Zhao and Neher, 2013; Franco *et al.*, 2019).

Further studies into the genera *Discocriconemella*, *Aporcelinus*, *Longidorus*, *Xiphinema*, *Coomansus*, *Aphanolaimus*, and *Diphtherophora* should be conducted to assess their potential as environmental indicators. Moreover, an in-depth analysis of the species of *Helicotylenchus*, common in tropical environments (Powers *et al.*, 2009; Peraza-Padilla, 2010; Cardoso *et al.*, 2015; Franco-Navarro and Godinez-Vidal, 2017), should be conducted to ascertain the species diversity and ecological functions studied to the species level.

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