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Comparing sugarcane fields and forest fragments: the effect of disturbance on soil physical properties and nematode assemblages

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Abstract

Comparisons of agricultural and natural ecosystems reveal the magnitude of the effects of agricultural practices on the diversity and abundance of soil nematodes. Consequently, there is the need for testing ecological hypotheses, specifically with regard to nematode ecology, in natural and agricultural soils to seek strategies for biological control and environmental monitoring. We studied soil nematode assemblages and soil physical attributes of five soil layers (0–10, 10–20, 20–30, 30–40 and 40–50 cm) from sugarcane plantations and forest remnants in the sugarcane zone of Pernambuco State, Brazil. Structure and composition of the nematode assemblage and soil properties differed between forest and sugarcane soils, even in the same locality. The soil bulk density and the abundance of all nematodes and the diversity of plant-parasitic nematodes were greater whereas soil porosity, soil respiration and abundance of predator nematodes were smaller in sugarcane than in forest areas. We suggest that sugarcane management practices result in changes in the soil properties and concomitantly alter the composition and structure of the nematode assemblages. Co-inertia analysis indicated that others environmental factors also might be affecting the nematofauna.

Keywords: Atlantic Forest, co-inertia analysis, bulk density, total porosity

Introduction

The Atlantic Forest of Brazil is considered one of the world's biological diversity hotspots (Myers *et al.*, 2000; Mittermeier *et al.*, 2004). However, vast areas of Atlantic Forest have been converted to agricultural production so that it is now one of the earth's most threatened tropical biomes with only 11.73% of its original area remaining (Ribeiro *et al.*, 2009). In the northeast of Brazil, government economic incentives during the 1980s led to expansion of sugarcane farming and concomitant reduction of native vegetation. However, the sugarcane crop plays important agronomic, economic and societal roles. During 2013, in Pernambuco State, 14 400 tonnes of sugarcane were harvested from 284 600 ha with production of 50 600 kg/ha (CONAB, 2013).

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Under conventional high-yielding production systems, agricultural soils are commonly subjected to long-term monoculture, uncontrolled traffic of heavy machinery and excessive tillage. Such practices eventually contribute to yield decline due to their effects on the biological, physical or chemical characteristics of the soil (Garside *et al.*, 2005; Briar *et al.*, 2007, 2011). Biological effects of farming system practices are observed on the soil fauna, including nematode communities, with important implications for the functioning and stability of soil food webs (Powell, 2007; Ferris, 2010; Briar *et al.*, 2011; Sánchez-Moreno *et al.*, 2011). Moreover, forest conversion to conventional agriculture impacts soil quality, reduces biodiversity and alters the soil physical properties and increases compaction (Gajić, 2013; Rousseau *et al.*, 2013).

Comparisons of agricultural and natural ecosystems reveal the magnitude of the effects of agricultural practices on the diversity and abundance of soil nematodes (Sánchez-Moreno & Ferris, 2007; Pattison *et al.*, 2008; Stirling *et al.*, 2010). Consequently, Neher (2010) emphasized the need for testing ecological hypotheses, specifically with regard to nematode

ecology, in natural and agricultural soils to seek strategies for biological control and environmental monitoring.

There have been some studies on the effects of soil physical properties on nematode assemblages in Brazil; however, there is a need for better understanding of their roles and relevance in both natural and agricultural ecosystems. The challenge and opportunity are to develop management systems that sustain and improve sugarcane yields while minimizing environmental impact. For example, soil compaction (Cardoso *et al*., 2012) that results from agricultural practices affect the structure of soil nematode assemblages.

In considering previous studies, we hypothesized that (i) abundance and diversity of plant-parasitic nematodes differs in forest and sugarcane fields, (ii) soil physical properties are affected by management practices, and (iii) changes in soil physical properties affect the abundance and diversity of plant-parasitic and predator nematodes. Therefore, we aimed to (i) describe the nematode diversity of native forest fragments and sugarcane fields and (ii) evaluate the relationships between soil attributes (bulk density, total porosity and soil respiration) and nematode assemblages.

Materials and methods

Study sites

This research was carried out in ten sugarcane plantations and eight forest fragments. Each forest fragment was entirely surrounded by one of the sugarcane plantations (Table 1). Soil samples were collected between 2010 and 2012 from four farms (Estreliana, União e Indústria, Trapiche and Salgado) located in Zona da Mata Sul of Pernambuco. The local climate is humid tropical type 'Am', according to the Köppen Climate Classification (Köppen, 1948), with precipitation in autumn and winter and average annual rainfall between 1000 and 2200 mm.

Soil sampling

At each site, soil samples were collected at five 10-cm depth increments from the four corners of a 10 × 10 m square. Soil samples were taken by a modified TORSOL® sampler for assessment of bulk density, water content and soil respiration and stored in parafilm-sealed plastic containers. About 600 g of soil was collected at each depth for nematode and texture analyses. The samples were packaged in labelled plastic bags and immediately transported to the Phytonematology Laboratory, Agronomy Department, University of Pernambuco, Dois Irmãos, Recife (UFRPE).

Nematodes extraction

Nematodes were extracted by the sucrose centrifugation method (Jenkins, 1964). The suspensions were stored in a refrigerator for no more than 3 days before counting and identification. Nematodes were counted at ×20 magnification in two replicate aliquots on Peters glass counting slides (1 mL of capacity). All nematodes counted were identified to

Table 1 Location and soil characteristics of ten sugarcane fields and eight forest fragments at Zona da Mata Sul of Pernambuco

Label	Coordinates	Farm	Municipality	Date sampling	Soil texture	Soil type
Sugarcane						
ST1	8°33′52.4″S; 35°08′36.2″ W	Trapiche	Sirinhaém	Jun 2010	Sandy clay loam	Yellow Ultisol
ST2	8°34′57.3″S; 35°07′01.7″ W	Trapiche	Sirinhaém	Jun 2010	Sandy clay loam	Yellow Ultisol
SE1	8°43′12.7″S; 35°07′17.7″ W	Estreliana	Ribeirão	Nov 2010	Loamy sand	Yellow Oxisol
SE2	8°42′46.3″S; 35°07′38.1″ W	Estreliana	Ribeirão	Nov 2010	Sandy loam	Yellow Oxisol
SE3	8°42′25.3″S; 35°07′14.4″ W	Estreliana	Ribeirão	Jan 2011	Sandy clay loam	Yellow Oxisol
SE4	8°43′49.3″S; 35°07′13.9″ W	Estreliana	Ribeirão	Jan 2011	Sandy clay loam	Yellow Oxisol
SU1	8°19′57.1″S; 35°18′11.9″ W	União e Indústria	Primavera	Jun 2010	Clay	Yellow Ultisol
SU2	8°18′49.3″S; 35°19′39.6″ W	União e Indústria	Primavera	Jun 2010	Sandy clay loam	Yellow Ultisol
SS1	8°26′50.1″S; 35°06′21.9″ W	Salgado	Ipojuca	Jun 2010	Sandy	Yellow Oxisol
SS2	8°26′53.3″S; 35°06′02.0″ W	Salgado	Ipojuca	Jun 2010	Sandy	Yellow Oxisol
Forest						
FA	8°34′07.4″S; 35°08′33.4″ W	Trapiche	Sirinhaém	Mar 2012	Sandy loam	Yellow Ultisol
FB	8°33′57.4″S; 35°07′44.6″ W	Trapiche	Sirinhaém	Mar 2012	Sandy	Yellow Ultisol
FC	8°34′59.5″S; 35°22′00.5″ W	Estreliana	Ribeirão	Nov 2011	Loamy sand	Yellow Oxisol
FD	8°35′28.1″S; 35°20′30.7″ W	Estreliana	Ribeirão	Nov 2011	Loamy sand	Yellow Oxisol
FE	8°33′05.4″S; 35°08′48.4″ W	Trapiche	Sirinhaém	Set 2012	Sandy clay	Yellow Ultisol
FF	8°33′30.8″S; 35°09′31.2″ W	Trapiche	Sirinhaém	Set 2012	Sandy clay loam	Yellow Ultisol
FG	8°40′33.4″S; 35°25′06.9″ W	Estreliana	Ribeirão	Set 2012	Sandy clay loam	Yellow Oxisol
FH	8°39′20.7″S; 35°25′12.3″ W	Estreliana	Ribeirão	Set 2012	Sandy clay loam	Yellow Oxisol

genus/family level at ×40 and ×100 magnification. For identification to the genus level, temporary slides were prepared. Nematode abundance was expressed per 300 cm^3 of soil.

Trophic and functional structure of the nematode assemblages

Nematodes were assigned to five trophic groups according to feeding habits: plant-parasitic (root feeders), bacterivores (bacteria feeders), fungivores (feed on fungal spores), predators (feed on other nematodes) and omnivores (feed on a variety of food sources, including algae, fungi, bacteria, small rotifers, enchytraeids and small nematodes). This trophic classification was based on the morphology of the stoma and oesophagus according to Yeates *et al.* (1993). Even though the trophic habits of the Tylenchidae are uncertain, all individuals in this family were considered plant-parasitic nematodes. Nematodes also were classified in functional guilds based on feeding habits and five colonizer–persister (c-p) groups which represent life history characteristics and sensitivity to environmental perturbation (Bongers, 1990; Bongers & Bongers, 1998). Plant-parasitic nematodes were identified to genus level using keys and descriptions of Mai *et al.* (1996) and free-living nematodes to the family level according to keys of Tarjan *et al.* (1977).

The nematode assemblage structure and composition, and taxa dominance were also determined in this study. The structure refers to composition of the assemblage, and the abundance of nematode taxa and dominance is the predominance of one or a few taxa within an ecosystem.

Soil respiration

Microbial activity was estimated from soil respiration as indicated by the C-CO_2 evolution rate (Grisi, 1978). Soil samples (100 g) and a container with 10 mL 0.5N KOH were placed into sealed glass chambers and incubated at 25 ± 2 °C for 15 days. The CO_2 absorbed by the KOH was determined by titration with HCL 0.1 N, using phenolphthalein and methyl orange as indicators.

Soil physical properties

Soil physical analyses were performed at the Laboratory of Soil Mechanics and Waste Utilization, Department of Agricultural Engineering, UFRPE, using methods detailed in EMBRAPA (1997):

1. Soil texture by the hydrometer method using sodium hydroxide as dispersant.
2. Soil bulk density (BD) was determined for intact soil cores 5 cm in diameter, 2.5 cm in length and 50 cm^3 in volume. To determine gravimetric water content (WC), soil samples were dried at 105–110 °C for 24 h and weighed before and after to determine their weight loss. BD was estimated by division between dry weight (DW) and core volume (BD = DW/50 cm^3).
3. Soil particle density (PD) was determined in a 50-mL volumetric flask using 20 g of air-dried soil and alcohol as fluid to determine the volume occupied by the particles (PD = 20 g of soil/ (50 mL – alcohol volume)).
4. Total porosity (Po) calculated according to formula: Po = (1 – (BD/ PD))*100.

Data analyses

Descriptive statistics were calculated to determine the distribution of the data from nematode and soil analyses. Nematode data were log-transformed log(x + 1), prior to analysis to comply with assumptions of normality. Relevant data from each study area were graphed to allow visualization. In addition, two-way ANOVA was performed and the Scott-Knott test to assess significant differences among areas and depths ($P < 0.05$). ANOVA, descriptive statistics and Pearson's correlation were carried out by software Statistica 8.0 (StatSoft Inc, 2008).

Data matrices of nematode abundance and soil properties were separately analysed using principal component analysis (PCA1 and PCA2, respectively). Covariance between the nematode abundance and soil properties were revealed using co-inertia analysis (Dolédec & Chessel, 1994; Dray *et al.*, 2003). Co-inertia analysis (CoIA) is a multivariate method that identifies covariances between two data matrices and is often used for the analysis of covariances between species lists and environmental variables in ecological studies. The RV coefficient was used to measure the relationship between two sets of variables. RV (R = correlation and V = vectorial) coefficient is a multidimensional correlation coefficient equivalent to the Pearson correlation coefficient (Robert & Escoufier, 1976). PCA, CoIA and RV coefficient were performed with ade4 package in R environment version 3.1.1 (Dray & Dufour, 2007; R Core Team, 2014).

Differences in nematode community composition from forest and agricultural soils were analysed by nonmetric multidimensional scaling (NMDS) and analysis of similarity (ANOSIM) based on Dice-Sorensen distance measure. The 'stress' value from NMDS should be small, at least less than 0.20 and ideally less than 0.10, showing that the reduction to two dimensions implies very little loss of information (Legendre & Legendre, 1998). NMDS and ANOSIM were performed by PAST version 2.15 (Hammer *et al.*, 2001).

Results and discussion

Structure and composition of nematode assemblages

Twenty-one nematode taxa were identified at either genus or family levels; twelve (indicated by *) were common to all

areas (Table 2). Alaimidae, Prismatolaimidae, Anguina, *Discocriconemella, Paratylenchus, Rotylenchus* and Tylenchidae were detected only in forest fragments. In contrast, *Trichodorus* and *Paratrichodorus* were found, exclusively, in sugarcane fields.

Plant-parasitic nematodes were the most abundant functional group in sugarcane, comprising 76% of the total dominance. *Pratylenchus* and *Helicotylenchus* were genera dominant in sugarcane, 41 and 23% of the total dominance, respectively. *Pratylenchus* was absent from only one of the 10 sugarcane fields.

Free-living nematodes comprised 69% of the nematode dominance in forest fragments and the order Dorylaimida (Qudsianematidae, Thornematidae, Dorylaimidae and Nordiidae) predominated with 49%. There was also a substantial presence in forest soils of the root associates and root feeders: Tylenchidae and *Helicotylenchus*, 6.7 and 6.4%, respectively.

The abundance of predator nematodes was significantly lower in sugarcane areas ($P < 0.05$); conversely, the plant-parasitic nematodes predominated. Total nematode abundance was significantly greater ($P < 0.05$) in sugarcane than in forest soils. Therefore, the structure and composition of nematode assemblages in sugarcane and forest soils were quite different.

Effects of management practices on soil biological and physical properties

Compared to forest fragments, the soil bulk density (BD) tended to be higher ($P < 0.05$) in sugarcane areas and in two forest fragments (FC and FD). Consequently, total porosity and C-CO_2 evolution rates were smaller at those sites ($P < 0.05$).

BD did not vary with depth, but differed significantly between areas with a smaller mean value being present in

Table 2 Abundance, means, standard deviations and dominance of the nematode assemblages associated with ten sugarcane fields and eight Atlantic Forest fragments in Zona da Mata Sul of Pernambuco

Nematodes		Sugarcane fields			Forest fragments		
Trophic groups	F	A	Means ± SD	D (%)	A	Means ± SD	D (%)
Bacterivores							
Alaimidae	b4	0	0.00 ± 0.00	0	74	0.46 ± 4.19	0.17
Cephalobidae*	b2	1300	6.50 ± 23.85	1.74	313	1.95 ± 8.21	0.71
Prismatolaimidae	b3	0	0.00 ± 0.00	0	727	4.54 ± 18.86	1.65
Rhabditidae*	b1	3467	17.33 ± 33.43	4.63	2862	17.88 ± 36.43	6.49
Fungivores							
Aphelenchidae*	f2	1884	9.42 ± 18.42	2.52	355	2.21 ± 11.78	0.80
Anguinidae	f2	0	0.00 ± 0.00	0	1598	9.98 ± 43.63	3.62
Omnivores							
Dorylamida*	o4	10 726	53.63 ± 75.07	14.33	21 682	135.51 ± 165.79	49.15
Predators							
Mononchida*	p4	669	3.34 ± 11.12	0.89	2853	17.83 ± 48.46	6.47
Plant-parasitic							
*Criconemella**	h3	4179	20.89 ± 56.37	5.58	1319	8.24 ± 43.17	2.99
Discocriconemella	h3	0	0.00 ± 0.00	0	1245	7.78 ± 42.73	2.82
*Helicotylenchus**	h3	17 516	87.58 ± 160.35	23.41	2834	17.71 ± 43.09	6.42
*Hemicycliophora**	h3	11	0.05 ± 0.77	0.01	16	0.10 ± 1.26	0.04
*Hoplolaimus**	h3	2270	11.35 ± 41.29	3.03	178	1.11 ± 6.31	0.40
*Meloidogyne**	h3	936	4.68 ± 14.66	1.25	1647	10.29 ± 38.63	3.73
*Pratylenchus**	h3	30 776	153.88 ± 236.94	41.13	2279	14.24 ± 43.09	5.17
Paratrichodorus	h4	18	0.09 ± 0.95	0.02	0	0.00 ± 0.00	0
Paratylenchus	h2	0	0.00 ± 0.00	0	47	0.29 ± 2.15	0.11
Rotylenchus	h3	0	0.00 ± 0.00	0	29	0.18 ± 2.29	0.07
Tylenchidae	h2	0	0.00 ± 0.00	0	2973	18.58 ± 57.45	6.74
Trichodorus	h4	452	2.26 ± 6.00	0.60	0	0.00 ± 0.00	0
*Xiphinema**	h5	629	3.14 ± 12.67	0.84	1.078	6.73 ± 22.77	2.44
Nematodes Total		74 833			44 109		

F = functional guilds; A (abundance) = sum of nematodes number in 200 samples from ten sugarcane areas and 160 samples from eight forest fragments (300 cm3 of soil in each sample), Means ± SD = Means number and standard deviation of nematodes per 300 cm3 of soil in each area, D (%) = Dominance of each taxa expressed as a percentage; *taxa common to all areas.

forest fragments (1.19 Mg/m^3) and a larger mean value for sugarcane areas (1.42 Mg/m^3) ($P < 0.05$; Standard Error: 0.01; Data not shown). Similarly, Araújo *et al.* (2011) found BD values: 1.22 Mg/m^3 in forest soil and in pasture soil 1.34 Mg/m^3, in the same soil type as for this study. Soil total porosity (Po) also did not vary with depth, and mean values were higher in forest fragments than in sugarcane areas, 57 and 46%, respectively ($P < 0.05$; Standard Error: 0.05).

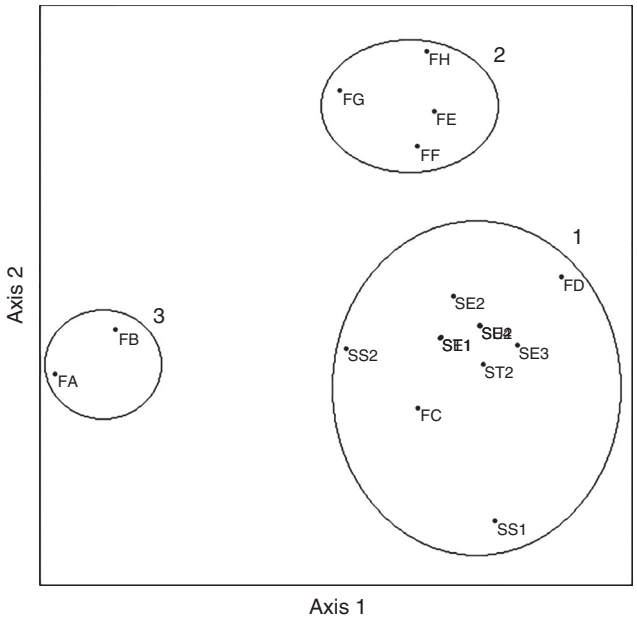

Figure 1 Non-metric multidimensional scaling (NMDS) illustrating the divergence in community composition of soil nematodes between sugarcane soils (S) and in Atlantic Forest soils (F) in Pernambuco, Brazil. The plot was produced using Dice-Sorensen as a distance measure (Stress: 0.11).

Thus, we corroborated the inverse relationship between BD and pore size reported by Dörner *et al.* (2010).

A one-way analysis of similarity (ANOSIM) revealed significant differences between the nematode assemblages of the 18 study sites (Global $R = 0.94$; $P = 0.0001$). A nonmetric multidimensional scaling (NMDS) highlighted three distinct groups (the sampling groupings were based on Sorensen clustering: (i) FC, FD, SU1, SU2, SE1, SE2, SE3, SE4, ST1, ST2, SS1 and SS2; (ii) FE, FF, FG and FH; and (iii) FA and FB (Figure 1)). These groupings were also confirmed by the generally significant differences detected with the pair-wise of the ANOSIM test, which showed significant difference in community composition in both group 2 and 3 compared to the group 1 (group 1 vs. group 2, $P < 0.0006$; group 1 vs. group 3, $P < 0.01$), whereas the community composition of group 2 and 3 did not differ.

The differences among sampling sites illustrated the effects of conversion of forest to agriculture on the structure and composition of nematode assemblages. Sugarcane areas were characterized by greater bulk density, smaller Po and larger *Pratylenchus* and *Helicotylenchus* abundance. The grouping of the two forest fragments (FC and FD) with the sugarcane plantations was attributed to the large abundance of these nematodes genera. Moreover, these fragments were characterized by a large bulk density, which may be the result of natural compaction, and may have favoured the establishment these plant-parasitic nematodes.

Graphical representations reveal differences in the means and standard deviations of soil respiration in forest fragments and sugarcane areas, indicating differences in biological activity of the soils (Figure 2).

In forest soils, the C-CO_2 evolution rate decreased with depth ($P < 0.05$). However, the mean C-CO_2 rate was 42.01 mg in forest soils and 8.45 mg in sugarcane soils

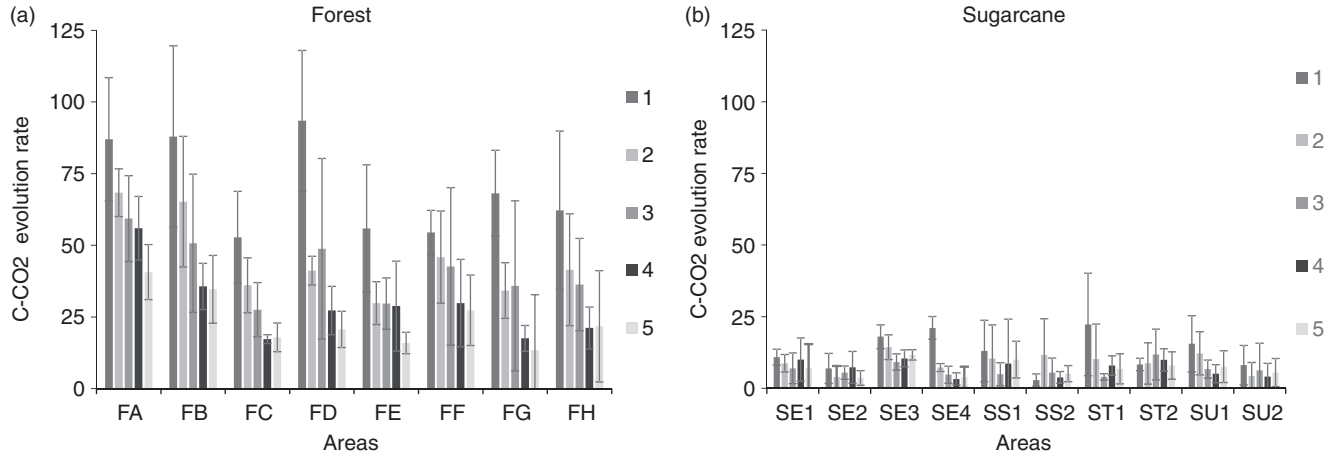

Figure 2 Soil respiration in forest fragments (a) and sugarcane areas (b). Bars represent the standard deviation. Depths: (1) 0–10 cm; (2) 10–20 cm; (3) 20–30 cm; (4) 30–40 cm; (5) 40–50 cm.

Table 3 Main characteristics of co-inertia analysis

Co-inertia axes	Covariance	Variance 1	Variance 2	Correlation	Inertia 1	Inertia 2
Sugarcane soils						
1	1.37538	1.836539	1.258013	0.5953	3.616213	2.054286
2	0.40246	1.349348	0.754429	0.3953	5.254425	2.824327
Forest soils						
1	1.357389	1.923066	0.955673	0.7385	3.710425	1.147181
2	0.603342	1.363997	0.868468	0.5093	5.632676	2.101665

Covariance: covariance between both systems of coordinates of co-inertia analysis (maximized by the analysis). Variance 1: inertia of the soil properties data projected onto co-inertia axes. Variance 2: inertia of the nematode abundance data projected onto co-inertia axes. Correlation: correlation between both systems of coordinates of co-inertia analysis. Inertia 1: maximum inertia projected onto axes of the simple analysis of soil properties data (eigenvalues of PCA). Inertia 2: maximum inertia projected onto axes of the simple analysis of nematode abundance data (eigenvalues of PCA).

($P < 0.05$; Standard Error: 1.04). In others words, the biological activity was greater in forest fragment soils than in sugarcane soils, corroborating observations of Stirling *et al.* (2010) in comparisons of pasture soils and sugarcane soils under conventional and nonconventional management.

The total porosity may be influencing this result. According to Grant & Rochette (1994), optimum biological activity occurs at between 60 and 70% of Po, which corresponded to bulk densities between 1.06 and 0.8 Mg/m^3. In this study, these porosity levels occurred in the forest soils, which also had greater availability of decomposable organic substrates, with both factors supporting greater soil respiration.

We concur with other researchers that sugarcane management practices result in changes in bulk density and porosity, biological activity and nematode assemblages in sugarcane plantations compared with those in native forest (Bell *et al.*, 2007; Stirling *et al.*, 2010; Baquero *et al.*, 2012).

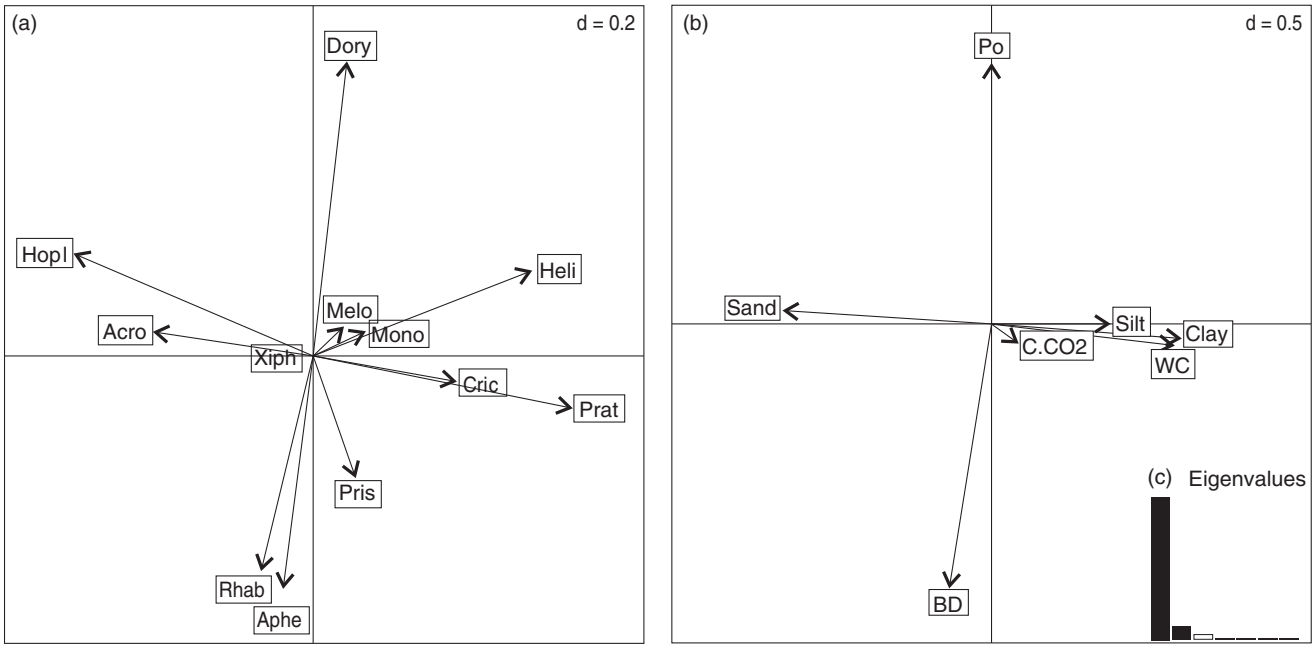

Figure 3 Co-inertia analysis between nematode assemblages composition and soil properties in sugarcane soils. (a) Factor map of nematode abundance. (b) Factor map of soil properties. Variables located in a common direction are positively associated whereas those located in the opposite direction are considered as negatively associated. Variables located close to the centre do not structure the data and are not labelled to improve clarity. (c) Eigenvalue diagram of the co-inertia analysis in sugarcane. Acro, *Acrobeles*; Aphe, Aphelenchidae; Cric, *Criconemella*; Dory, Dorylaimida; Heli, *Helicotylenchus*; Hoplo, *Hoplolaimus*; Melo, *Meloidogyne*; Mono, Mononchida; Prat, *Pratylenchus*; Rhab, Rhabditidae; Tric, *Trichodorus*; Xi, *Xiphinema*; BD, bulk density; Po, total porosity; WC, water content; C-CO2, soil respiration, clay, sand, silt.

Moreover, conversion of forest soils to agricultural usage negatively impacts diverse soil quality parameters, reduces biodiversity and increases soil compaction (Gajić, 2013; Rousseau *et al*., 2013).

Relationships among soil physical properties, soil respiration and composition of nematode assemblages

Co-inertia analysis is a multivariate method well adapted to identifying species–environment relationships; the main characteristics of this analysis are in the Table 3. The co-inertia factor maps pointed to associations of certain nematode taxa with the soil physical properties in sugarcane and forest soils (Figures 3 and 4).

Co-inertia analysis in sugarcane soils demonstrated a co-structure between the nematode abundance (Figure 3a) with the soil physical properties (Figure 3b) (RV coefficient = 0.21). The permutation test confirmed that this co-structure was significant ($P = 0.001$). The first two axes accounted for 88.8% (F1) and 7.6% (F2) of the total covariance. The eigenvalue diagram of the co-inertia analysis (Figure 3c) clearly indicates the importance of F1 axis.

On the F1 axis data were discriminated mainly by water, clay and sand content of the soils. Water content and clay content were located in the opposite direction to sand. C-CO_2 evolution rate had no influence on discrimination of the data. *Hoplolaimus* (plant-parasitic) and *Acrobeles* (bacterivore) were associated with sand content. By contrast, *Pratylenchus* and *Criconemella* (plant-parasitic) ordered in an opposite position due to their negative relationship with sand content and showed strong association with water and clay content. Specifically, Po and bulk density structured the data along the F2 axis and were located opposite to each other. Dorylaimida (omnivore), which are generally larger-bodied nematodes, were related to total porosity. Aphelenchidae (fungivore) and Rhabditidae (bacterivore) showed strong association with soil bulk density and smaller Po.

Co-inertia analysis in forest soils also demonstrated a co-structure between the nematode abundance (Figure 4a) and soil physical properties (Figure 4b) (RV coefficient = 0.28). The permutation test confirmed that this co-structure was significant ($P = 0.001$). The eigenvalue diagram of the co-inertia analysis (Figure 4c) indicates the importance of F1 axis (81.4% F1, 16.1% F2).

Clay content was located in the opposite direction to sand. Likewise, soil Po and BD were opposites. *Pratylenchus*, *Meloidogyne* and *Hoplolaimus* (plant-parasitic nematodes) were associated with BD; Dorylaimida (omnivore) and Mononchida (predator) were related to Po and water content; *Criconemella* and *Discocriconemella* were related to

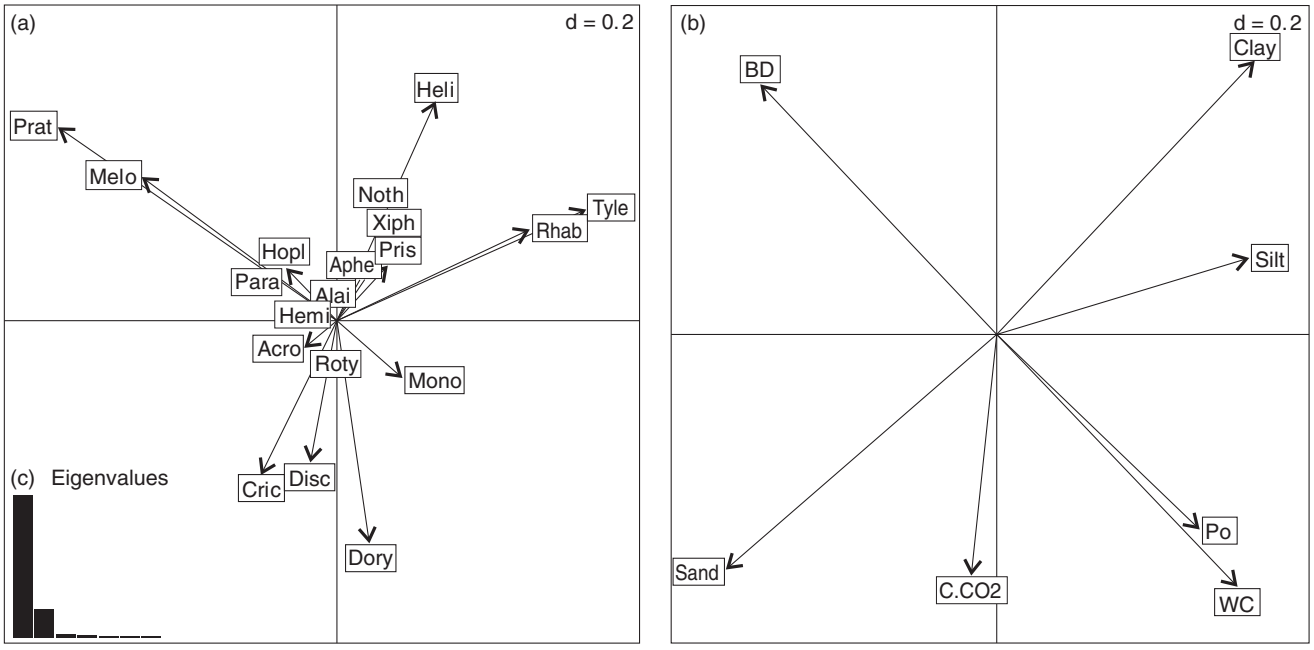

Figure 4 Co-inertia analysis between nematode assemblages composition and soil properties in forest soils. (a) Factor map of nematode abundance. (b) Factor map of soil properties. Variables located in a common direction are positively associated whereas those located in the opposite direction are considered as negatively associated. Variables located close to the centre do not structure the data and are not labelled to improve clarity. (c) Eigenvalue diagram of the co-inertia analysis in forest. Acro, *Acrobeles*; Alai, Alaimidae; Aphe, Aphelenchidae; Cric, *Criconemella*; Disc, *Discocriconemella*; Dory, Dorylaimida; Heli, *Helicotylenchus*; Hemi, Hemicycliophora; Hoplo, *Hoplolaimus*; Melo, *Meloidogyne*; Mono, Mononchida; Prat, *Pratylenchus*; Pris, Primatolaimus; Rhab, Rhabditidae; Roty, Rotylenchulus; Tric, *Trichodorus*; Tyle, Tylenchidae; Xiph, *Xiphinema*; BD, bulk density; Po, total porosity; WC, water content; C-CO2, soil respiration, clay, sand, silt.

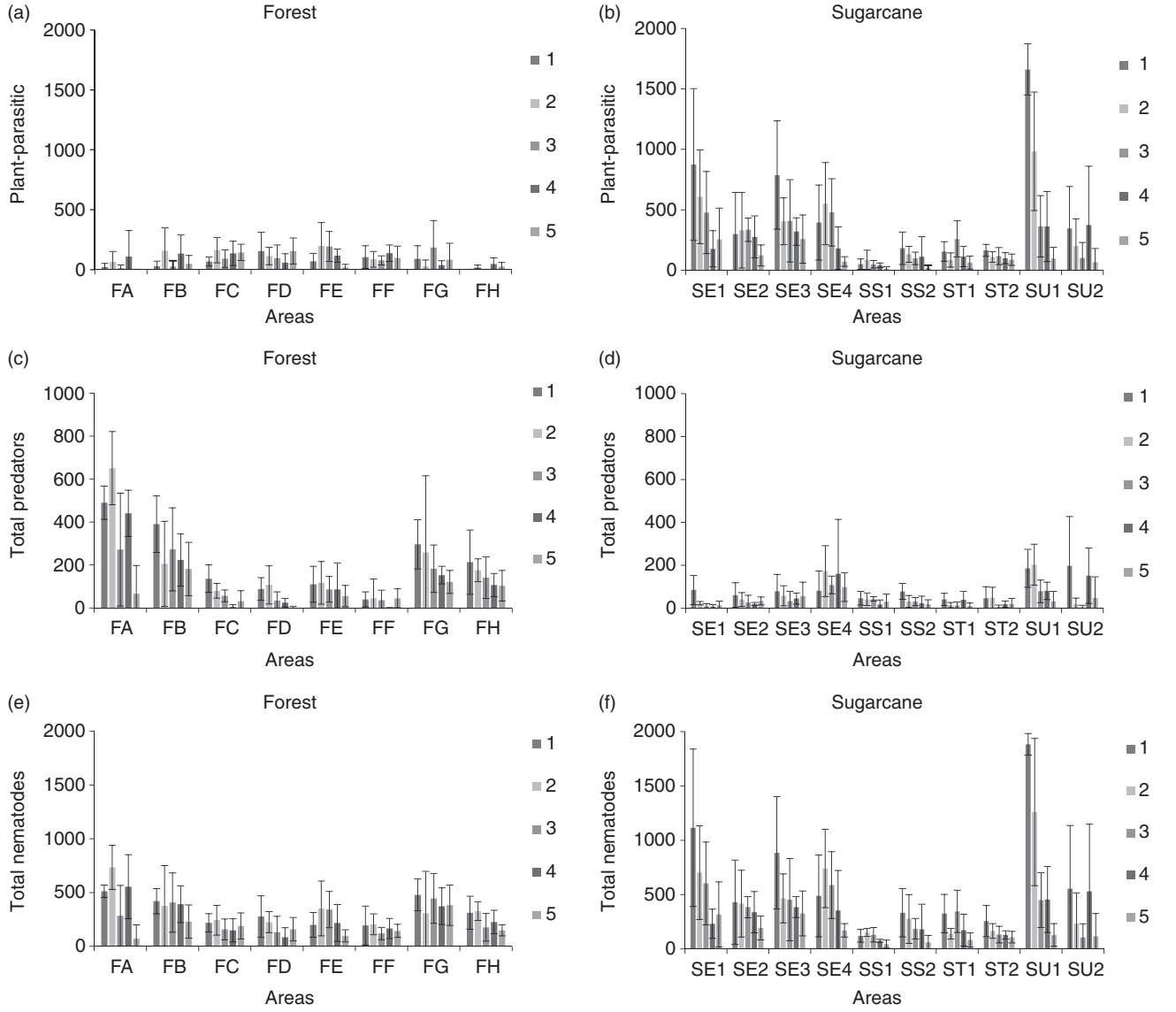

Figure 5 (a) plant-parasitic in forest; (b) plant-parasitic in sugarcane; (c) predator forest; (d) predator sugarcane; (e) total nematodes forest; (f) total nematodes sugarcane. Depths: (1) 0–10 cm; (2) 10–20 cm; (3) 20–30 cm; (4) 30–40 cm; (5) 40–50 cm.

soil respiration; *Acrobeles* (bacterivore) was related to soil sand content; Rhabditidae (bacterivore) and Tylenchidae (plant-parasitic) were associated with silt content; and *Helicotylenchus* (plant-parasitic) was associated with soil clay content.

Nematode in the order Dorylaimida were associated with greater Po in both sugarcane areas and forest fragments. Similarly, Pattison *et al.* (2008) found that abundance of omnivore nematodes (e.g. Dorylaimida) was negatively correlated with increasing soil bulk density which suggests that in our study, unfavourable habitats may have occurred in soil with high soil bulk density. Activity and survival of large nematodes (e.g. Qudsianematidae, Dorylaimidae, Aporcelaimidae, etc.) may be restricted by smaller pores spaces, which renders them sensitive to the changes in soil properties that are associated with intensive management (Cardoso *et al.*, 2012).

In forest areas *Pratylenchus*, *Meloidogyne* and *Hoplolaimus* (plant-parasitic nematodes) were more abundant with at greater BD. In sugarcane areas, abundance of Aphelenchidae (fungivore) and Rhabditidae (bacterivore) was also related to greater BD corroborating results of Sánchez-Moreno *et al.* (2006). These nematode families are basal and enrichment indicators, respectively. In addition, they are indicators for stress tolerant and disturbed conditions.

The co-inertia analysis also revealed that in forest soils, the nematode assemblages were more strongly affected by environmental variables than in sugarcane fields. We

conclude that the constant and continuous soil management practices employed in sugarcane fields create an environment more unstructured and unstable than that in forest soils.

In this study, we have demonstrated that edaphic factors significantly influence the patterns of the community structures of nematodes in both sugarcane and forest soils. Among the studied variables, soil bulk density, water content and texture were main factors that influencing plant-parasitic abundance, corroborating Godefroid *et al.* (2013) and Nielsen *et al.* (2014). However, the small correlation coefficient between data sets suggests that others factors are influencing the assemblage composition and structure of nematodes.

Effects of the depth in nematode assemblages

Relative abundances of plant-parasitic nematode decreased in depth in sugarcane soils ($P < 0.05$; Figure 5b), corroborating Caixeta *et al.* (2011) who investigated farming systems in the same geographic region as this study. Total nematode abundance also decreased with depth ($P < 0.05$; Figure 5f), similar to the observations of Biederman & Boutton (2010) that total nematode and family richness decreased with depth in forest clusters and grasslands. All these observations reflect are probably associated with the decrease of important soil resources (organic carbon, microbial biomass and root biomass) with increasing soil depth (Griffiths *et al.*, 2003; Agnelli *et al.*, 2004; Potthoff *et al.*, 2006).

In forest soils, plant-parasitic nematodes were distributed almost uniformly across depths (Figure 5a,e). This difference was probably associated with differences in root morphology and distribution; 65% the sugarcane root system is concentrated in the layer above 20-cm depth while in forest, the root systems extend from the surface to 4 m (Sternberg *et al.*, 1998; Otto *et al.*, 2009; Stirling *et al.*, 2011). Total predator nematodes, specialists (e.g. Mononchida) and generalists (e.g. Dorylaimida), were more abundant in the root zones and decreased in the deeper layers (Figure 5c), and in parallel with soil respiration (Figure 3a) and presumably with the presence of other organisms associated with the microbial biomass. Likewise, Cardoso *et al.* (2012) observed a negative correlation between depth and predator nematodes in forest soil.

Conclusion

Forest and sugarcane soils differed with regard to soil properties and the structure and composition of the nematode assemblages. Soil bulk density and abundances of all nematodes and of plant-parasitic nematodes tended to be greater in sugarcane soils. In contrast, porosity, soil respiration and abundance of predator nematodes were smaller in sugarcane than in forest soils. We conclude that sugarcane management practices result in changes in soil properties and concomitantly alter the composition and structure of the nematode assemblages. Nonmetric multidimensional scaling and co-inertia analyses not only revealed differences in the nematode assemblage composition of study sites in relation to some of the measured parameters but also indicated that other environmental factors probably also affected the nematofauna.

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