Land use, soil properties and climate variables influence the nematode communities in the Caatinga dry forest

Juliane Vanessa Carneiro de Lima da Silva[a,*], Maria Noel Clerici Hirschfeld[a], Juvenil Enrique Cares[b], André Morgado Esteves[c]

[a] *Programa de Pós-Graduação em Biologia Animal, Universidade Federal de Pernambuco, Av. Prof. Moraes Rego s/no, Recife, PE 50670-901, Brazil.*
[b] *Departamento de Fitopatologia, Universidade de Brasília, Campus Darcy Ribeiro, Brasília, DF 70910-900, Brazil.*
[c] *Departamento de Zoologia, Universidade Federal de Pernambuco, Av. Prof. Moraes Rego s/no, Recife, PE 50670-901, Brazil.*

A B S T R A C T

Seasonally dry tropical forests are strongly impacted by human activities such as agriculture and ranching, as well as variations in climate conditions. Soil nematodes are sensitive to these changes, given that soil and climate characteristics influence their survival and occurrence. We analyzed the changes in the structure of nematode communities in three different types of land use (agricultural areas, secondary forest and natural forest) in the Caatinga, at Catimbau National Park, Pernambuco, northeastern Brazil. We recorded a total of 17,177 nematode individuals belonging to 104 genera. Nematode abundance and richness were highest in the secondary forest and lowest in the agricultural areas. The total abundance of bacterivores and omnivore-predators was affected by types of land use. Different soil properties as well as monthly mean rainfall and temperature were strongly related to the differences in taxonomic composition among the agricultural areas, secondary forest and natural forest, accounting for 65.42% of the total variation. In general, our results indicate that agricultural activities in the Caatinga negatively affect the nematode communities, and that soil characteristics and climate variables also strongly affect the structure and composition of these communities.

1. Introduction

Global climate change and anthropogenic disturbances are the main threats to biodiversity, since they have strong impacts on biological populations and on community structures (Bellard et al., 2012). This is particularly true for Seasonally Dry Tropical Forests (SDTFs), which because of extensive deforestation have become one of the most threatened ecosystems in the world (Miles et al., 2006; Banda et al., 2016). SDTFs have a wide and fragmented distribution, whose vegetation is characterized by a closed canopy with distinct rainfall regimes, alternating the rainy and dry seasons (Pennington et al., 2009; Banda et al., 2016). The annual rainfall is < 1800 mm, and some forests have dry season lasting 3 to 6 months, receiving < 100 mm per month (Banda et al., 2016). The climates and fertile soils of SDTFs have led to higher human population densities, accelerating intensive cultivation of crops and conversion to pasture for cattle (Rito et al., 2017). It is estimated that SDTFs will face an increase in evaporation and temperature by 2100 (Burkett et al., 2014; Banda et al., 2016), resulting in longer and more severe droughts that may affect the maintenance of their biodiversity.

As with other SDTFs, the Caatinga, a mosaic of SDTFs with low woody vegetation that occurs only in northeastern Brazil, suffers strong anthropogenic pressure through ranching, wood extraction and subsistence agriculture (Pennington et al., 2009; Rito et al., 2017). Little effort has been made to understand the impacts of anthropogenic disturbance and climate change on the biodiversity of STDFs, specifically in the Caatinga. Some studies carried out in the Caatinga have described negative impacts for plant (Ribeiro et al., 2015; Rito et al., 2017) as well as animal communities (Oliveira et al., 2017). However, studies focusing on the soil biota, which forms a large portion of terrestrial biodiversity, have not yet been performed in the Caatinga.

Nematodes constitute a model of soil biota that is important for understanding the responses of soil biodiversity to climate conditions in this arid environment. Nematodes are found in almost all types of ecosystems, with a variety of life habits (Yeates et al., 1993). Their multi-specific assemblages, in which each species has its own function and shows different degrees of sensitivity to environmental stimuli, make nematodes excellent indicators of environmental disturbances, such as anthropogenic disturbance and climate change (Zhao and Neher, 2013; Thakur et al., 2017; Siebert et al., 2019; Thakur et al.,

---

2019). They play fundamental roles in ecosystem processes, such as improving soil physical properties, participating in carbon and nitrogen cycling, and maintaining ecosystem health by occupying key positions in the soil food web (Ferris, 2010; Zhang et al., 2017).

Nematode community structure, such as abundance and diversity, species distribution, and their related ecosystem services (Bongers and Bongers, 1998; Ferris, 2010) in tropical systems are affected mainly by vegetation, edaphic factors (moisture, chemical and physical soil properties) and climate (Neher et al., 2003; Nielsen et al., 2014; Song et al., 2017; Thakur et al., 2017; Thakur et al., 2019). Any environmental alterations or disturbances that affect the composition or physiology of the vegetation and/or soil texture, such as the conversion of primary vegetation to agricultural uses, can alter the taxonomic composition and diversity of functional groups of nematodes (Wall and Virginia, 1999; Song et al., 2017). With regard to climate, temperature and rainfall are important environmental factors for the survival and reproduction of nematodes (Song et al., 2017; Thakur et al., 2019). Climate change can have significant impacts on the number and community composition of soil nematodes (Thakur et al., 2017; Siebert et al., 2019), since they are essentially aquatic animals that depend on the water film around soil particles for their development and movement through their environment (Griffiths and Caul, 1993). Although the influence of temperature and rainfall on nematode diversity has been extensively reported (Nielsen et al., 2014; Song et al., 2017; Thakur et al., 2019), a comprehensive analysis of the factors that govern nematode community structure in the Caatinga is lacking, impeding the complete understanding of energy transfer and nutrients in these microhabitats.

Here, we evaluated the effect of soil properties, rainfall and temperature on the structure, i.e. abundance and diversity, of nematode communities in areas with different types of land use in the Caatinga. Specifically, we hypothesized that: (1) a change of land use from undisturbed systems to agricultural production will reduce the abundance and diversity of soil nematodes, and (2) nematode community taxonomic composition will be structured based on the soil properties, rainfall and temperature.

2. Materials and methods

2.1. Study site

The study was conducted in Catimbau National Park (8°24′00″ and 8°36′35″ S; 37°0′30″ and 37°1′40″ W, state of Pernambuco, northeastern Brazil), which covers an area of 607 km^2 of Caatinga vegetation (Rito et al., 2017). Mean annual temperature ranges from 21 °C to 24 °C and mean annual rainfall ranges from 1100 mm in the southeast to 480 mm in the northwest (Rito et al., 2017). Approximately 70% of Catimbau National Park is covered by quartzite sandy soils supporting low-stature Caatinga vegetation (Rito et al., 2017). The dominant families of woody plants are Fabaceae, Euphorbiaceae, and Boraginaceae; on the surface of the forest floor, species of Cactaceae, Bromeliaceae, Malvaceae, Asteraceae, and Fabaceae dominate (Rito et al., 2017).

The park was established in 2002, but its original human inhabitants remain; they continue to hunt, graze livestock, extract timber, collect firewood, practice subsistence agriculture, and harvest other plant resources (Rito et al., 2017). Their historical presence has resulted in an extensive mosaic of differential land use and anthropogenic pressure on the biota. Therefore, Catimbau provides an excellent opportunity to examine how anthropogenic disturbance (e.g., different types of land use) affects the soil nematodes of the Caatinga.

2.2. Sampling design and nematode inventory

Soil samples were collected in November 2015, in 21 plots (each 50 × 20 m, separated from each other by at least 2 km) (Fig. 1). The plots were selected based on different types and history of land use: (i)

six plots with active slash-and-burn agriculture (Agricultural Areas – AA); (ii) eight plots of secondary forest regenerating after abandonment of slash-and-burn agriculture (Secondary Forest – SF), with successional ages from 4 to 45 yr; and (iii) seven plots with no history of agriculture (Natural forest – NF). The characteristics of plots in the agricultural area and the secondary forest are described in Table S1.

In each plot, three soil samples (for fauna analysis) and one sample (for analysis of soil properties) were collected, each a composite sample from five randomly located sampling points. The distance between each sample was 10 m. Each sub-sample was collected with a cylindrical collector, at a depth of 0–30 cm. The subsamples were mixed and a 1000 ml aliquot was packed in a polyethylene bag labeled with the sample information. The samples were collected at points close to shrub areas, in the crown projection line, where younger and more active roots can be found (Barker, 1985).

The nematodes were extracted from 300 ml of fresh soil, using a combination of flotation, sedimentation and sieving technique (Flegg and Hooper, 1970) and centrifugal sucrose flotation (Jenkins, 1964). The nematodes were then killed in a water bath at 55 °C for 1 min. Nematode abundance was expressed as the number of individuals per 100 ml dry soil. The nematodes from each sample were fixed in formaldehyde (3%) and infiltrated with glycerin (Seinhorst, 1959), using method described by Cares and Huang (2008). For identification to the genus level and trophic groups, permanent slides were prepared. The first 100 nematodes per sample were identified, using an inverted microscope at x40 and x100 magnification. Nematodes were assigned to the following trophic groups (Yeates et al., 1993): bacterivores, fungivores, plant parasites and omnivore-predators.

2.3. Environmental variables

Soil samples were sent for laboratory testing for soil chemical and physical properties. The soil chemical analyses were based on the determination of the macro- and micronutrient contents and pH; all were performed according to the methodology recommended by EMBRAPA (2011). For soil physical analysis, soil particle density was determined by the volumetric flask method. Soil density was determined by the beaker method. Total porosity was calculated by the relationship between soil density and particle density. The different texture classes were determined by the densimeter method (EMBRAPA, 2011).

The monthly mean rainfall and temperature data for each plot were obtained from the global data repository for climate, WorldClim (Hijmans et al., 2005), with a special resolution of 30-arc seconds or approximately 1 km along the equator (www.worldclim.org), using the software QGIS 2.18 with the complement "Point sampling tool" (https://github.com/borysiasty/pointsamplingtool).

2.4. Data analyses

We performed a centered Pearson Principal Components Analysis (PCA) to reduce the soil chemical and physical variables dataset to two dimensions ('PC1' and 'PC2'), using PRIMER v6, for use as predictors in the analyses. Separate PCAs were performed for the soil chemical and physical properties. To determine if the monthly mean rainfall and temperature, soil fertility and soil granulometry, selected from the PCAs, differed among the types of land use, we performed a univariate analysis of variance (ANOVA), using R version 3.4.2. The prerequisites normality and homogeneity of the data were tested.

The total abundance of nematodes (individuals 100 ml^{-1} soil) and the abundance of each trophic group (individuals 100 ml^{-1} soil) were calculated for each plot. Then, we used generalized linear models (GLMs) with negative binomial error to assess the effects of types of land use (AA, SF and NF) on total abundance of nematodes and on each trophic group. No overdispersion was found in the data. GLMs were performed using the "*glm.nb*" package in R.

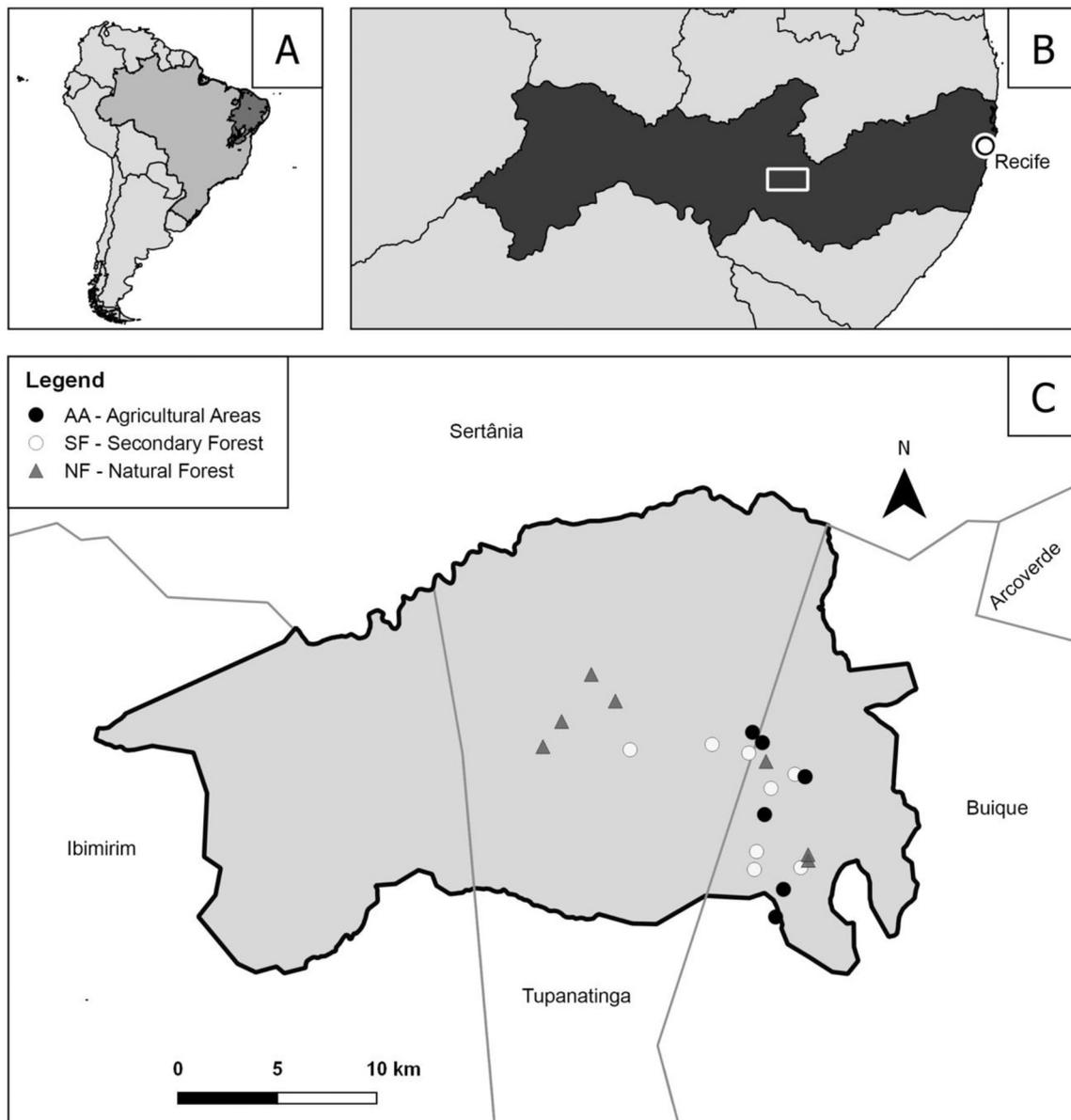To assess changes in genus diversity among the types of land use, we

Fig. 1. (A) Location of the study region in northeastern Brazil, and the study landscape (rectangle) in the state of Pernambuco (shaded area in B). Catimbau National Park and the locations of all plots (*n* = 21) are also indicated (C).

used Hill numbers (Hill, 1973) for each plot, of order 0 (^{0}D, species richness), 1 (^{1}D, exponential of Shannon entropy) and 2 (^{2}D, Inverse Simpson concentration) (Jost, 2006, 2007), calculated with the "*entropart*" package for R (Marcon et al., 2014). ^{0}D is not sensitive to species abundances and thus gives a disproportionate weight to rare species (Jost, 2006). ^{1}D weights each species according to its abundance in the community, interpreted as the number of 'common' or 'typical' species in the community (Jost, 2006). Finally, ^{2}D favors abundant species, and is interpreted as the number of 'very abundant' or 'dominant' species in the community. Then, a one-way ANOVA was used to assess the differences in each level of diversity among the types of land use, using R.

To determine if there is a difference in the nematode community taxonomic composition among the types of land use, we performed a Non-Metric Multidimensional Scaling analysis (NMDS) based on the Bray-Curtis similarity matrix (individuals 100 ml^{-1} soil) with 63 samples from 21 plots, followed by a PERMANOVA, using Primer v6. We used agricultural areas (AA), secondary forest (SF) and natural forest (NF) as factors. SIMPER analyses (Primer v6) were used to

determine the taxa that most account for the dissimilarities among the types of land use (cut-off of 50%).

To check for spatial independence of our sample units, we first applied Mantel tests to determine significant correlations between the geographical inter-plot distance matrix and the matrices of compositional similarity (Bray-Curtis index). This analysis was performed in the *vegan* package in R. The Mantel test did not reveal a significant spatial autocorrelation ($r = 0.17$; $P = 0.06$), indicating that our areas could be used as independent samples for the analyses.

Finally, to evaluate the relationship between the nematode community taxonomic composition and the environmental variables, i.e., the soil characteristics selected in the PCAs and the monthly mean rainfall and temperature data, we used a DistLM (distance-based linear model). The DistLM model was constructed using AICc as a selection criterion. Euclidean distance was used as a resemblance measure for DistLM procedures, and the results were displayed in dbRDA (distance-based redundancy analysis) plots, using Primer v6.

Table 1

Mean values (± SD) and loads of the variables on the first two axes of principal component analyses (PCA1 and PCA2) performed for soil physical and chemical properties in the agricultural areas (AA), secondary forest (SF) and natural forest (NF).

Soil properties	Variables	Mean values for each area			PCA values	
		AA	SF	NF	PC1	PC2
Physical	Bulk density (g/cm^3)	1.57 ± 0.06	1.58 ± 0.06	1.60 ± 0.12	0.067	−0.622
	Relative density (g/cm^3)	2.61 ± 0.02	2.60 ± 0.03	2.60 ± 0.02	0.358	−0.526
	Coarse sand (%)	60.50 ± 10.01	63.00 ± 10.25	59.00 ± 9.47	−0.624	−0.104
	Fine sand (%)	28.17 ± 9.00	29.13 ± 10.30	29.57 ± 7.70	0.588	−0.062
	Silt (%)	2.67 ± 1.25	0.88 ± 0.33	2.57 ± 1.68	0.328	0.453
	Clay (%)	8.67 ± 3.77	7.00 ± 2.00	8.86 ± 2.10	0.154	0.341
Chemical	Residual soil moisture (%)	1.17 ± 0.22	1.43 ± 0.30	1.61 ± 0.61	0.065	−0.2
	P (mg/dm^3)	14.67 ± 8.67	5.50 ± 2.18	6.57 ± 2.92	−0.288	0.006
	pH	5.73 ± 0.53	5.38 ± 0.39	5.41 ± 0.33	−0.315	−0.242
	Ca (cmolc/dm^3)	1.41 ± 0.72	1.14 ± 0.80	0.52 ± 0.29	−0.296	0.318
	Mg (cmolc/dm^3)	0.73 ± 0.07	0.64 ± 0.09	0.59 ± 0.10	−0.319	0.199
	Na (cmolc/dm^3)	0.04 ± 0.01	0.03 ± 0.01	0.02 ± 0.01	−0.204	0.29
	K (cmolc/dm^3)	0.15 ± 0.13	0.07 ± 0.03	0.06 ± 0.01	−0.146	0.293
	Al (cmolc/dm^3)	0.12 ± 0.12	0.26 ± 0.17	0.38 ± 0.39	0.334	0.223
	H (cmolc/dm^3)	3.19 ± 1.87	4.82 ± 2.51	4.19 ± 2.38	0.24	0.397
	Sum of exchangeable bases (cmolc/dm^3)	2.33 ± 0.81	1.90 ± 0.89	1.31 ± 0.37	−0.304	0.359
	Cation-exchange capacity (cmolc/dm^3)	5.63 ± 1.96	6.98 ± 2.94	5.90 ± 2.64	0.154	0.491
	Base saturation (%)	44.50 ± 17.25	28.88 ± 13.64	27.14 ± 12.18	−0.385	−0.084
	Al saturation (%)	5.17 ± 5.21	14.63 ± 11.18	20.57 ± 20.27	0.359	0.082

Note: Al saturation: the ratio of soluble aluminum to the exchangeable base and aluminum contents in CEC (cation-exchange capacity) of soil.

3. Results

3.1. Environmental variables

The first two axes of the PCA for soil chemical properties explained 68.3% of the variation. The first axis described the variation of the properties related to soil acidity and fertility, reflecting a basic soil gradient with higher base saturation (V%), Mg, pH and phosphorus, for the more acidic soils, with a high Al saturation (m%). The second axis described a soil gradient also related to fertility, from soils with higher residual moisture to soils with a higher sum of exchangeable bases, high cation-exchange capacity (CEC) and high concentrations of Ca, Na, K and H (Table 1).

The first two PCA axes for soil physical properties explained 68.1% of the variation. The first axis reflected a granulometric gradient from soils with a high coarse-sand content to soils with a high fine-sand content. The second axis indicated a gradient of soil water-retention capacity (high percentage of clay and silt) to soils with high bulk density (BD) and relative density (RD) (Table 1).

Only two variables (silt% and P) differed among the types of land use ($P < 0.02$). The AA plots were characterized as basic soil, with more than twice the phosphorus content as that found in the SF forest and NF plots. The SF and NF plots had acidic soils with lower silt contents. The monthly rainfall ($P < 0.001$) and temperature ($P < 0.05$) differed among the types of land use; in the NF, the rainfall was lowest and the temperature was highest (Table 1).

3.2. Effects of land use on nematode community structure

A total of 17,177 nematode individuals were recorded, representing 104 genera from 34 families (Table S2). The predominant families were Cephalobidae, with 23 genera, present in all study plots, and Qudsianematidae (8 genera), Aporcelaimidae (7 genera), Rhabditidae (6 genera) and Panagrolaimidae (6 genera). SF contained the most genera (70), followed by NF (69) and AA (40) (Table S2). Eleven genera were restricted to AA, 23 to SF and 21 to NF.

Total abundance of nematodes was significantly affected by types of land use $\chi^2 = 7.69$, $P < 0.01$; Fig. 2a). Abundance was highest in SF and lowest in AA. Among the nematode trophic groups, only bacterivores ($\chi^2 = 13.05$, $P < 0.001$; Fig. 2b) and omnivore-predators ($\chi^2 = 9.05$, $P < 0.01$; Fig. 2e) were significantly affected by type of

land use. Both trophic groups showed the highest abundance in the SF, followed by NF and AA.

Nematode diversity did not differ among types of land use, for all levels of ^qD ($P > 0.05$; Fig. S1. Table S3). The nematode community taxonomic composition was different among the types of land use (NMDS) (PERMANOVA: all $P = 0.001$) (Fig. 3).

The genus *Acrobeles* contributed most to the differences in nematode community taxonomic composition among the three study areas; its specimens were present in all study plots, although in different levels of abundance (Table 2). Specimens of *Acrobeles* were most abundant in SF and least in AA. After *Acrobeles*, the genera *Helicotylenchus*, *Rotylenchulus*, *Metacrobeles*, *Tylenchorhynchus*, *Drilocephalobus* and *Mesocriconema* also contributed to the dissimilarity among the different types of land use (Table 2). Nematodes of the genus *Rotylenchulus* were most abundant in AA and absent from SF; whereas the genera *Helicotylenchus*, *Metacrobeles*, *Tylenchorhynchus* and *Mesocriconema* were most abundant in SF, while *Tylenchorhynchus* was absent from AA. Finally, *Drilocephalobus* was most abundant in NF (Table 2).

3.3. Correlation between environmental variables and nematode community taxonomic composition in different types of land use

The results of the redundancy analysis (RDA) support the differences among the structures of the soil nematode community taxonomic composition among the types of land use, while also indicating how these changes relate to environmental characteristics (Fig. 4). In the RDA, the environmental variables accounted for 65.42% of the total variation of the nematode community taxonomic composition in the types of land use. The first two RDA axes accounted for 49.25% of the total variance (Fig. 4). The nematode community taxonomic composition in AA was associated with more basic soils, with a high sum of exchangeable bases (S), base saturation (V%), phosphorus (P) and silt. In contrast, the nematode community taxonomic composition in SF was associated with more acidic soils, with high Al (m%) saturation, H, pH, bulk density (BD) and rainfall (Fig. 4). In NF, part of the nematode community taxonomic composition was associated with acidic soils and the other part was associated with temperatures (Fig. 4).
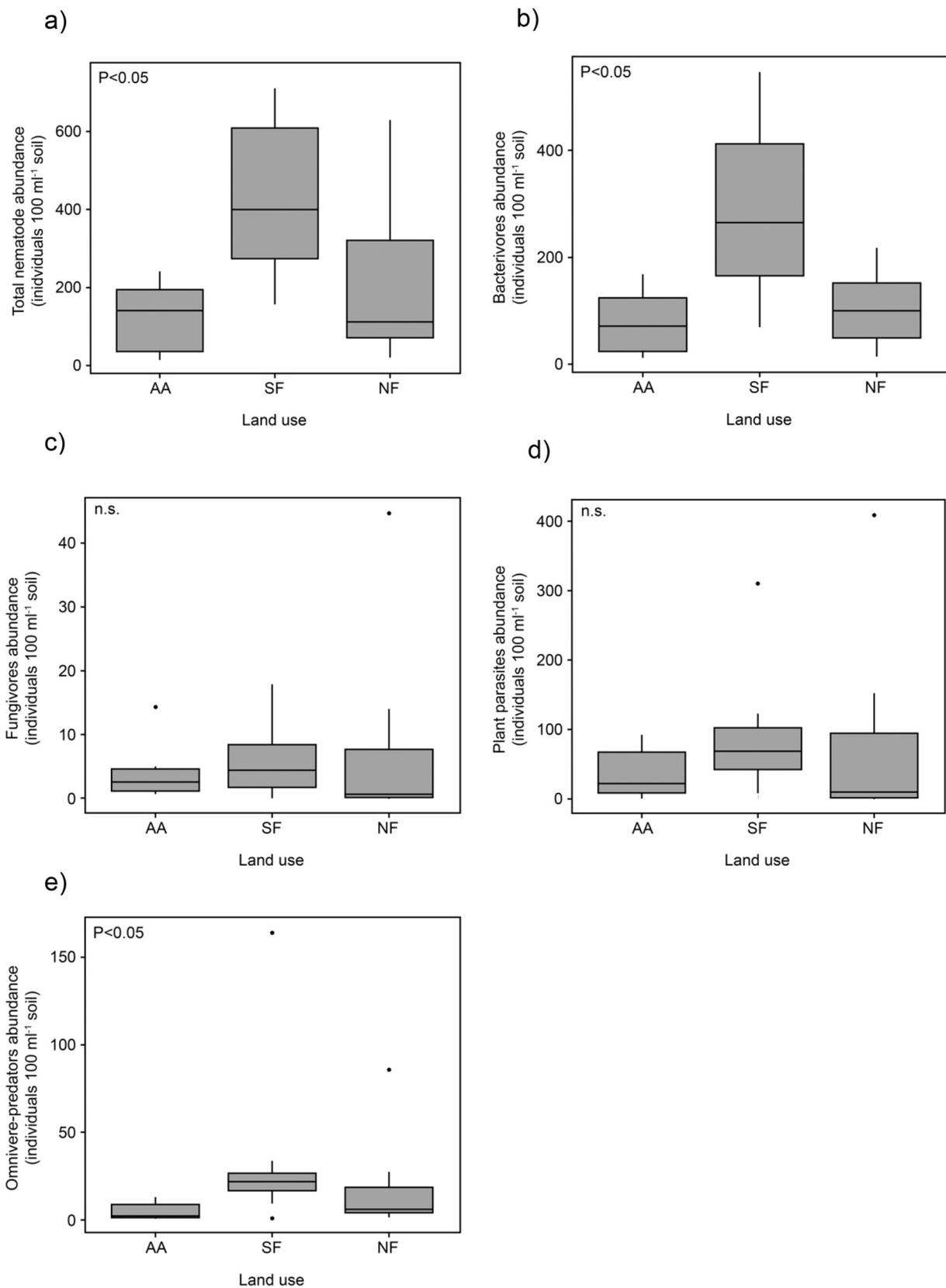
Fig. 2. Effect of land use on total abundance of nematodes and on each trophic group (individuals 100 ml^{-1} soil). (a) total nematode abundance; (b) bacterivores abundance; (c) fungivores abundance; (d) plant parasites abundance; and (e) omnivore-predators abundance. n.s. = not significant.
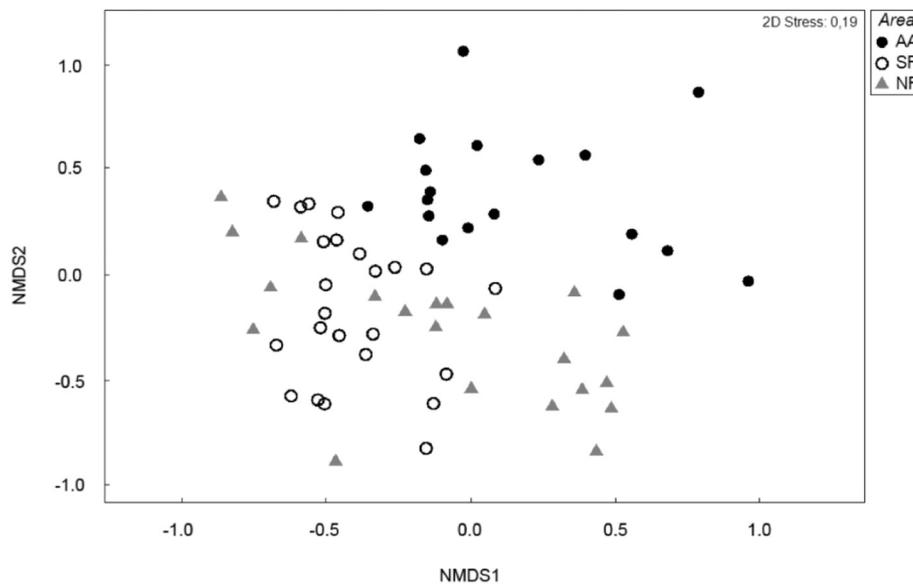
Fig. 3. Non-metric multidimensional scaling ordination (NMDS), based on the Bray-Curtis similarity index, showing the nematode community taxonomic composition under the influence of different types of land use. Area: AA = Agricultural Areas; SF = Secondary Forest; NF = Natural Forest.

Table 2
Results of SIMPER analysis showing five genera of nematodes that contributed most to the dissimilarity of nematode communities in areas with different types of land use. AA: Agricultural Areas; SF: Secondary Forest; NF: Natural Forest.

Genera	Mean abundance		Contribution%
Groups AA vs SF (Mean dissimilarity = 80.64%)			
Acrobeles	55.32	230.05	42.16
Helicotylenchus	11.96	51.85	9.17
Rotylenchulus	23.38	00.00	5.25
Metacrobeles	11.21	16.13	5.22
Tylenchorhynchus	00.00	15.96	4.18
Groups AA vs NF (mean dissimilarity = 80.54%)			
Acrobeles	55.32	66.07	28.60
Rotylenchulus	23.38	19.83	11.42
Helicotylenchus	11.96	17.16	8.41
Drilocephalobus	0.85	8.23	5.94
Metacrobeles	11.21	4.27	5.34
Groups SF vs NF (mean dissimilarity = 77.01%)			
Acrobeles	230.05	66.07	39.45
Helicotylenchus	51.85	17.16	9.20
Tylenchorhynchus	15.96	11.05	5.41
Mesocriconema	12.36	11.30	4.26
Metacrobeles	16.13	4.27	4.02

Fig. 4. Distance-based redundancy analysis (dbRDA) illustrating the DistLM model based on the relationship between the nematode community taxonomic composition and environmental variables. Symbols represent the plots. Area: AA = Agricultural Areas; SF = Secondary Forest; NF = Natural Forest. Environmental variables: BD = Bulk density; m% = Percentage aluminum saturation; Al = Aluminum; H = Hydrogen; pH = Potential of hydrogen; S = Sum of exchangeable bases; V% = Base saturation; P = Phosphorus.

4. Discussion

4.1. Effect of land use on the structure of nematode communities

The transformation of native vegetation to agricultural land use and its continued intensification have led to extensive losses in biodiversity (Barnes et al., 2017). In line with our expectations, the structure of nematode communities was affected by different types of land use in the Caatinga. The AA showed lower nematode abundance and diversity than SF and NF. Soils under native vegetation generally show higher diversity and abundance of nematodes compared to cultivated systems (Wall and Virginia, 1999; Cardoso et al., 2015; Vazquez et al., 2019). These findings can be explained by the changes in soil physical properties, reduced input of organic material, and reduced deposition of roots (Scharroba et al., 2016; Vazquez et al., 2019) in AA.

Arguably, the most interesting finding was that the highest abundance of nematodes in the Caatinga was not found in NF, but in SF. When agricultural areas are abandoned due to reduced productivity
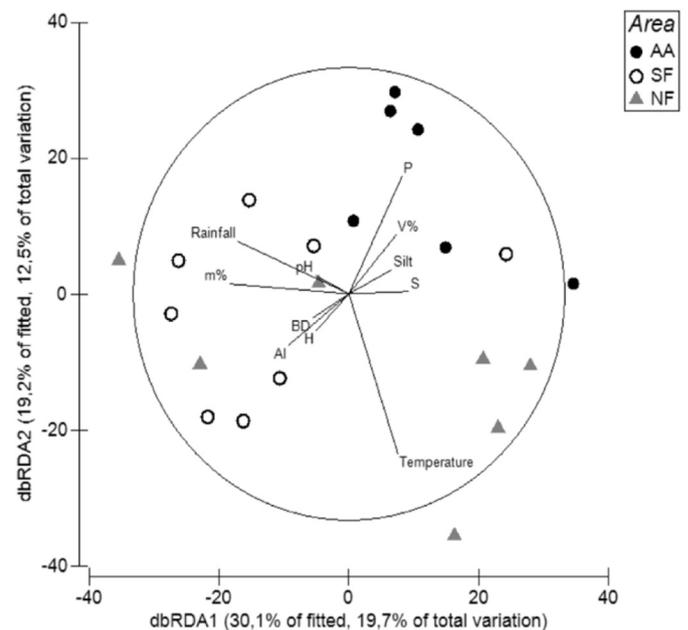
levels, for example, the natural regeneration process begins (Chazdon, 2008). Possibly, the reorganization of the plant community over time and the change in chemical and physical soil properties have led to an increase in the abundance of certain nematode groups, especially r-strategists (Bongers and Bongers, 1998). The increase in nematode abundance in SF areas compared to AA may be an important indicator of soil recovery.

The abundance of trophic groups, mainly bacterivores and predators-omnivores, was also affected by the type of land use. The total abundance of bacterivores was higher in SF and NF than in AA. Bacterivores tend to be predominant in areas where plant diversity and

biomass are higher (Tomazini et al., 2008), as is the case of SF and NF areas in the Caatinga. In these areas, more decomposing organic material accumulates on the soil surface layer, favoring soil microbiological activity (Tomazini et al., 2008; Li et al., 2015).

Regarding predators-omnivores, they also had the highest abundance in SF and NF and lowest in AA. Predators-omnivores often disappear with cultivation, since they are sensitive to soil disturbance (Bongers, 1990; Sánchez-Moreno et al., 2006; Zhao and Neher, 2013; Li et al., 2016). Although bacterivores and plant parasites were the most dominant trophic groups in the Caatinga, plant parasites were not affected by land-use types, nor were fungivores.

As expected, the communities in areas with different types of land use differed in their composition. Dissimilarity among the types of land use was due to variation in abundance or to the absence of some nematode genera, mainly the generalist bacterivores *Acrobeles*, *Drilocephalobus* and *Metacrobeles*, belonging to the family Cephalobidae; and the generalist plant parasites *Helicotylenchus*, *Rotylenchulus*, *Mesocriconema* and *Tylenchorhynchus* (Yeates et al., 1993; Bongers and Bongers, 1998). The family Cephalobidae is cosmopolitan, occurring in environments with both poor and abundant resources, in unfavorable temperature conditions and in extremely dry regions (Nielsen et al., 2014), some of them typical conditions in the Caatinga. A surprising finding was that *Acrobeles* contributed the most to the dissimilarity among the types of land use. Specimens of this genus were most abundant in SF and least abundant in AA. This finding allows us to speculate on the mechanisms that allow *Acrobeles* to predominate in Caatinga soils, such as their: (1) tolerance to hot, dry semi-arid environments; (2) dispersal/colonization ability; and (3) response to different types of land use through their reproductive rate (abundance) (Bongers and Bongers, 1998).

A secondary group that contributed to the differences among the areas was the plant parasites. Here, in the agricultural areas, *Rotylenchulus* was the most abundant plant parasite. Other studies have confirmed that nematodes of the genus *Rotylenchulus* are adapted to hot dry climates and parasitize specific crops such as corn, cassava and beans (Duyck et al., 2012). However, in this study *Rotylenchulus* was found associated with cactus (*Opuntia* sp.). Nematodes belonging to the genera *Helicotylenchus, Mesocriconema* and *Tylenchorhynchus* predominated in the SF and NF. The coexistence of these ectoparasitic nematodes is likely the result of weak interspecific competition (Duyck et al., 2012).

4.2. Changes in and nematode community taxonomic composition in response to environmental variables

Nematode community structures, on both landscape and global scales, have been found to be related to environmental variables (Nielsen et al., 2014; Song et al., 2017; Hoogen et al., 2019; Siebert et al., 2019; Thakur et al., 2019). Similarly, our results showed that the soil nematode community taxonomic composition in the Caatinga is related to soil properties as well as to rainfall and temperature.

The soil characteristics in the AA plots may have affected the nematode community in this study. The nematode community composition in AA was associated with basic soils, with a high concentration of phosphorus (P), sum of exchangeable bases (S), base saturation (V%), and silt. The supplementary use of compost, goat or bovine manure, plant biomass, and cow urine, as well as the practice of burning prior to a new planting in areas of the Caatinga are the main agricultural soil-management practices. These practices contribute to the increase in base contents (Ca, Mg, Na and K) and mainly phosphorus in the soils (Silva et al., 2015). Previous studies have shown that addition of large quantities of phosphorus has negative effects on nematode communities (Zhao et al., 2014). When the availability of phosphorus in an ecosystem is low, plants allocate resources to soil micro-organisms that decompose dead organic material and release phosphorus that can be used by plants. If the phosphorus content is high, plants can obtain it

directly from soil, which reduces the input of resources to soil organisms, including nematodes (Treseder and Vitousek, 2001; Zhao et al., 2014). Therefore, the decrease of soil nematode density might be due to the resource/food limitation after phosphorus addition. Another likely reason is that the additional mineral phosphorus input to soil leads to salt toxicity that harms soil nematodes (Zhao et al., 2014).

The composition of the nematode community in the SF and NF areas was associated with higher mean monthly rainfall and more-acidic soils. In these areas, abundance was higher than in AA. The population density of nematodes increases with increase in rainfall, because the rainfall positively affects the plant growth, soil nitrogen mineralization and nitrogen content, and soil microbial activity (Bai et al., 2010; Song et al., 2017), influencing nematode feeding, movement and reproduction (Kardol et al., 2011).

Regarding soil acidity in these areas and the relationship with nematodes, it is possible that factors leading to soil acidification have positively influenced the population growth of nematodes in SF and NF areas, such as higher values of mean monthly rainfall and organic-matter content. The action of rainfall causes leaching of Ca and Mg, which are replaced by Al, Mn and H in soil solution (Oliveira et al., 2002). As a result, aluminum saturation (m%) increases and the pH becomes more acidic. Organic matter lowers soil pH by releasing hydrogen ions associated with organic anions or nitrification in an open system (Ritchie and Dolling, 1985).

The nematode composition in the secondary forest was also associated with lower bulk density (BD). The bulk density reflects simultaneous changes in several soil properties. A decrease in bulk density is generally associated with an increase in organic-matter content, soil moisture levels and living space. Together, these factors positively influence the movement and reproduction of soil nematodes (Yeates, 1999; Cardoso et al., 2015).

The nematode composition and the low abundance in some of the NF plots were associated with higher monthly mean temperatures. High temperatures result in a decrease in nematode abundance, since plant cover decreases, allowing the soil to become overexposed and consequently reducing the soil water content and limiting microbial growth and reproduction (Song et al., 2017).

5. Conclusions

The history and types of land use affect the composition and structure of the nematode community in the Caatinga. In this study, conversion of native Caatinga vegetation to crop systems negatively affected the nematode community, once reduced the total abundance of nematodes, bacterivores and omnivore-predators. However, these changes are reversible through regeneration of secondary forest after the fields are abandoned. The nematode community composition is strongly related to soil properties and climate variables in the Caatinga, which suggests that these factors may be acting as important environmental filters in structuring nematode communities in the SDTFs. It is important to note that these factors cannot be analyzed separately in terms of their effects on the nematode community. These must be analyzed in terms of their integrative effect, since land use, temperature and rainfall affect the soil structure and consequently the nematode community structure. In general, our study demonstrated that knowledge of the nematode community structure on a landscape scale, and of the effect of climate and ecosystem properties on community structure, can be used to predict the effect of changes in soil use, in climate, and other disturbances on soil health in the Caatinga.

Acknowledgements

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.apsoil.2019.103474.

References

Bai, W., Wan, S., Niu, S., Liu, W., Chen, Q., Wang, Q., Zhang, W., Han, X., Li, L., 2010. Increased temperature and precipitation interact to affect root production mortality, and turnover in a temperate steppe: implications for ecosystem C cycling. Glob. Chang. Biol. 16, 1306–1316. https://doi.org/10.1111/j.1365-2486.2009.02019.x.

Banda, K., Delgado-Salinas, A., Dexter, K.G., Linares-Palomino, R., Oliveira-Filho, A., Prado, D., Pullan, M., Quintana, C., Riina, R., Rodríguez, M.G.M., Weintrit, J., Acevedo-Rodríguez, P., Adarve, J., Álvarez, E., Aranguren, B.A., Arteaga, J.C., Aymard, G., Castaño, A., Ceballos-Mago, N., Cogollo, A., Cuadros, H., Delgado, F., Devia, W., Dueñas, H., Fajardo, L., Fernández, A., Fernández, M.A., Franklin, J., Freid, E.H., Galetti, L.A., Gonto, R., González, M.R., Graveson, R., Helmer, E.H., Idárraga, A., López, R., Marcano-Vega, H., Martínez, O.G., Maturo, H.M., McDonald, M., McLaren, K., Melo, O., Mijares, F., Mogni, V., Molina, D., Moreno, N.P., Nassar, J.M., Neves, D.M., Oakley, L.J., Oatham, M., Olvera-Luna, A.R., Pezzini, F.F., Dominguez, O.J.R., Ríos, M.F., Rivera, O., Rodríguez, N., Rojas, A., Särkinen, T., Sánchez, R., Smith, M., Vargas, C., Villanueva, B., Pennington, R.T., 2016. Plant diversity patterns in neotropical dry forests and their conservation implications. Science 353, 1383–1387. https://doi.org/10.1126/science.aaf5080.

Barker, K.R., 1985. Sampling nematode communities. In: Barker, K.R., Carter, C.C., Sasser, J.N. (Eds.), An Advanced Treatise on *Meloidogyne*: Methodology. North Carolina State University/USAID, Raleigh, pp. 3–17.

Barnes, A.D., Allen, K., Kreft, H., Corre, M.D., Jochum, M., Veldkamp, E., Clough, Y., Daniel, R., Darras, K., Denmead, L.H., Haneda, N.F., Hertel, D., Knohl, A., Kotowska, M.M., Kurniawan, S., Meijide, A., Rembold, K., Prabowo, W.E., Schneider, D., Tscharntke, T., Brose, U., 2017. Direct and cascading impacts of tropical land-use change on multi-trophic biodiversity. Nat. Ecol. Evol. 10, 1511–1519. https://doi.org/10.1038/s41559-017-0275-7.

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., Courchamp, F., 2012. Impacts of climate change on the future of biodiversity. Ecol. Lett. 15, 365–377. https://doi.org/10.1111/j.1461-0248.2011.01736.x.

Bongers, T., 1990. The maturity index: an ecological measure of environmental disturbance based on nematode species composition. Oecologia 83, 14–19. https://doi.org/10.1007/BF00324627.

Bongers, T., Bongers, M., 1998. Functional diversity of nematodes. Appl. Soil Ecol. 10, 239–251. https://doi.org/10.1016/S0929-1393(98)00123-1.

Burkett, V.R., Suarez, A.G., Bindi, M., Conde, C., Mukerji, R., Prather, M.J., St. Clair, A.L., Yohe, G.W., 2014. Point of departure. In: Field, C.B., Barros, V.R., Dokken, D.J., Mach, K.J., Mastrandrea, M.D., Bilir, T.E., Chatterjee, M., Ebi, K.L., Estrada, Y.O., Genova, R.C., Girma, B., Kissel, E.S., Levy, A.N., MacCracken, S., Mastrandrea, P.R., White, L.L. (Eds.), Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part a: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, pp. 169–194.

Cardoso, M.O., Pedrosa, E.M.R., Ferris, H., Rolim, M.M., Vicente, T.F.S., David, M.F.L., 2015. Comparing sugarcane fields and forest plots: the effect of disturbance on soil physical properties and nematode assemblages. Soil Use Manag. 31, 397–407. https://doi.org/10.1111/sum.12190.

Cares, J.E., Huang, S.P., 2008. Comunidades de Nematoides de Solo sob Diferentes Sistemas na Amazônia e Cerrados Brasileiros. In: Moreira, F.M.S., Siqueira, J.O., Brussaard, L. (Eds.), Biodiversidade do solo em ecossistemas brasileiros. UFLA, Lavras, MG, pp. 409–444.

Chazdon, R.L., 2008. Beyond deforestation: restoring forests and ecosystem services on degraded lands. Science 320, 1458–1460. https://doi.org/10.1126/science.1155365.

Duyck, P.F., Dortel, E., Tixier, P., Vinatier, F., Loubana, P.M., Chabrier, C., Quénéhervé, P., 2012. Niche partitioning based on soil type and climate at the landscape scale in a community of plant-feeding nematodes. Soil Biol. Biochem. 44, 49–55. https://doi.org/10.1016/j.soilbio.2011.09.014.

EMBRAPA – Empresa Brasileira de Pesquisa Agropecuária, 2011. Centro Nacional de Pesquisas de Solos. Manual de métodos de análises de solos, 2.ed. Embrapa Solos, Rio de Janeiro.

Ferris, H., 2010. Contribution of nematodes to the structure and function of the soil food web. J. Nematol. 42, 63–67.

Flegg, J.J.M., Hooper, D.J., 1970. Extraction of free-living stages from soil. In: Southey, J.F. (Ed.), Laboratory Methods for Work with Plant and Soil Nematodes. Her Majesty's Stationery Office, London, pp. 5–22.

Griffiths, B.S., Caul, S., 1993. Migration of bacterial-feeding nematodes, but not protozoa, to decomposing grass residues. Biol. Fert. Soils 15, 201–207. https://doi.org/10.1007/BF00361612.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. Int. J. Climatol. 25, 1965–1978. https://doi.org/10.1002/joc.1276.

Hill, M., 1973. Diversity and evenness: a unifying notation and its consequences. Ecology 54, 427–432. https://doi.org/10.2307/1934352.

Hoogen, J., Geisen, S., Routh, D., Ferris, H., Traunspurger, W., Wardle, D.A., de Goede, R.G.M., Adams, B.J., Ahmad, W., Andriuzzi, W.S., Bardgett, R.D., Bonkowski, M., Campos-Herrera, R., Cares, J.E., Caruso, T., Caixeta, L.B., Chen, X., Costa, S.R., Creamer, R., Castro, J.M.C., Dam, M., Djigal, D., Escuer, M., Griffiths, B.S., Gutiérrez, C., Hohberg, K., Kalinkina, D., Kardol, P., Kergunteuil, A., Korthals, G., Krashevska, V., Kudrin, A.A., Li, Q., Liang, W., Magilton, M., Marais, M., Martín, J.A.R., Matveeva, E., Mayad, E.H., Mulder, C., Mullin, P., Neilson, R., Nguyen, T.A.D., Nielsen, U.N., Okada, H., Rius, J.E.P., Pan, K., Peneva, V., Pellissier, L., Silva, J.C.P., Pitteloud, C., Powers, T.O., Powers, K., Quist, C.W., Rasmann, S., Moreno, S.S., Scheu, S., Setälä, H., Sushchuk, A., Tiunov, A.V., Trap, J., Putten, W.V.D., Vestergård, M., Villenave, C., Waeyenberge, L., Wall, D.H., Wilschut, R., Wright, D.G., Yang, J., Crowther, T.W., 2019. Soil nematode abundance and functional group composition at a global scale. Nature 572, 194–198. https://doi.org/10.1038/s41586-019-1418-6.

Jenkins, W.R.A., 1964. Rapid centrifugal-flotation technique for separating nematodes from soil. Plant Dis. Rep. 4, 692.

Jost, L., 2006. Entropy and diversity. Oikos 113, 363–375. https://doi.org/10.1111/j.2006.0030-1299.14714.x.

Jost, L., 2007. Partitioning diversity into independent alpha and beta components. Ecology 88, 2427–2439. https://doi.org/10.1890/06-1736.1.

Kardol, P., Reynolds, N., Norby, R.J., Classen, A.T., 2011. Climate change effects on soil microarthropod abundance and community structure. Appl. Soil Ecol. 47, 37–44. https://doi.org/10.1016/j.apsoil.2010.11.001.

Li, N., Pan, F.J., Han, X.Z., Zhang, B., 2016. 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, 208–216. https://doi.org/10.1016/j.soilbio.2016.04.011.

Li, Y., Yang, G., Neher, D.A., Xu, C.Y., Wu, J., 2015. Status of soil nematode communities during natural regeneration of a subtropical forest in southwestern China. Nematology 17, 79–90. https://doi.org/10.1163/15685411-00002853.

Marcon, E., Zhang, Z., Herault, B., 2014. The decomposition of similarity-based diversity and its bias correction. Hal 00989454v3. https://hal-agroparistech.archives-ouvertes.fr/hal-00989454v3, Accessed date: 10 October 2018.

Miles, L., Newton, A.C., De Fries, R.S., Ravilious, C., May, I., Blyth, S., Kapos, V., Gordon, J.E., 2006. A global overview of the conservation status of tropical dry forests. J. Biogeogr. 33, 491–505. https://doi.org/10.1111/j.1365-2699.2005.01424.x.

Neher, D.A., Barbercheck, M.E., El-Allaf, S.M., Anas, O., 2003. Effects of disturbance and ecosystem on decomposition. Appl. Soil Ecol. 23, 165–179. https://doi.org/10.1016/S0929-1393(03)00043-X.

Nielsen, U.N., Ayres, E., Wall, D.H., Li, G., Bardgett, R.D., Wu, T., Garey, J.R., 2014. Global-scale patterns of assemblage structure of soil nematodes in relation to climate and ecosystem properties. Glob. Ecol. Biogeogr. 23, 968–978. https://doi.org/10.1111/geb.12177.

Oliveira, F.M.P., Ribeiro-Neto, J.D., Andersen, A.N., Leal, I.R., 2017. Chronic anthropogenic disturbance as secondary driver of ant community structure: interactions with soil type in Brazilian Caatinga. Environ. Conserv. 44, 115–123. https://doi.org/10.1017/S0376892916000291.

Oliveira, M.W., Trivelin, P.C.O., Boaretto, A.E., Muraoka, T., Moratti, J., 2002. Leaching of nitrogen, potassium, calcium and magnesium in a sandy soil cultivated with sugarcane. Pesq. Agropec. Bras. 37, 861–868. https://doi.org/10.1590/S0100-204X2002000600016.

Pennington, R.T., Lavin, M., Oliveira-Filho, A., 2009. Woody plant diversity, evolution, and ecology in the tropics: perspectives from seasonally dry tropical forests. Annu. Rev. Ecol. Evol. Syst. 40, 437–457. https://doi.org/10.1146/annurev.ecolsys.110308.120327.

Ribeiro, E.M.S., Arroyo-Rodríguez, V., Santos, B.A., Tabarelli, M., Leal, I.R., 2015. Chronic anthropogenic disturbance drives the biological impoverishment of the Brazilian Caatinga vegetation. J. Appl. Ecol. 52, 611–620. https://doi.org/10.1111/1365-2664.12420.

Ritchie, G., Dolling, P., 1985. The role of organic matter in soil acidification. Aust. J. Soil Res. 23, 569–576. https://doi.org/10.1071/SR9850569.

Rito, K.F., Arroyo-Rodríguez, V., Queiroz, R.T., Leal, I.R., Tabarelli, M., 2017. Precipitation mediates the effect of human disturbance on the Brazilian Caatinga vegetation. J. Ecol. 105, 828–838. https://doi.org/10.1111/1365-2745.12712.

Sánchez-Moreno, S., Minoshima, H., Ferris, H., Jackson, L.E., 2006. Linking soil properties and nematode community composition: effects of soil management on soil food webs. Nematology 8, 703–715. https://doi.org/10.1163/156854106778877857.

Scharroba, A., Kramer, S., Kandeler, E., Ruess, L., 2016. Spatial and temporal variation of resource allocation in an arable soil drives community structure and biomass of nematodes and their role in the micro-food web. Pedobiologia 59, 111–120. https://doi.org/10.1016/j.pedobi.2016.03.005.

Seinhorst, J.W., 1959. A rapid method for the transfer of nematodes from fixative to anhydrous glycerin. Nematologica 4, 67–69. https://doi.org/10.1163/187529259X00381.

Siebert, J., Sünnemann, M., Auge, H., Berger, S., Cesarz, S., Ciobanu, M., Guerrero-Ramírez, N.R., Eisenhauer, N., 2019. The effects of drought and nutrient addition on soil organisms vary across taxonomic groups, but are constant across seasons. Sci. Rep. 9, 639. https://doi.org/10.1038/s41598-018-36777-3.

Silva, G.F., Santos, D., Silva, A.P., Souza, J.M., 2015. Indicadores de qualidade do solo sob diferentes sistemas de uso na mesorregião do agreste paraibano. Rev. Caat. 28, 25–35. https://doi.org/10.1590/1983-21252015v28n303rc.

Song, D., Pan, K., Tariq, A., Sun, F., Li, Z., Sun, X., Zhang, L., Olusanya, O.A., Wu, X., 2017. Large-scale patterns of distribution and diversity of terrestrial nematodes. J. Appl. Ecol. 114, 161–169. https://doi.org/10.1016/j.apsoil.2017.02.013.

Thakur, M.P., Tilman, D., Purschke, O., Ciobanu, M., Cowles, J., Isbell, F., Wragg, P.D., Eisenhauer, N., 2017. Climate warming promotes species diversity, but with greater taxonomic redundancy, in complex environments. Sci. Adv. 3, e1700866. https://doi.org/10.1126/sciadv.1700866.

Thakur, M.P., Real, I.M.D., Cesarz, S., Steinauer, K., Reich, P.B., Hobbie, S., Ciobanu, M., Rich, R., Worm, K., Eisenhauer, N., 2019. Soil microbial, nematode, and enzymatic responses to elevated CO_2, N fertilization, warming, and reduced precipitation. Soil Biol. Biochem. 135, 184–193. https://doi.org/10.1016/j.soilbio.2019.04.020.

Tomazini, M.D., Ferraz, L.C.C.B., Monteiro, A.R., 2008. Abundância e diversidade de nematóides em áreas contíguas de vegetação natural e submetida a diferentes tipos de uso do solo. Nematol. Bras. 32, 185–193.

Treseder, K.K., Vitousek, P.M., 2001. Effects of soil nutrient availability on investment in acquisition of N and P in Hawaiian rain forests. Ecology 82, 946–954. https://doi.org/10.1890/0012-9658(2001)082[0946:EOSNAO]2.0.CO;2.

Vazquez, C., de Goede, R.G.M., Korthals, G.W., Rutgers, M., Schouten, A.J., Creamer, R., 2019. The effects of increasing land use intensity on soil nematodes: a turn towards specialism. Funct. Ecol. 33, 2003–2016. https://doi.org/10.1111/1365-2435.13417.

Wall, D.H., Virginia, R.A., 1999. Controls on soil biodiversity: Lessons from extreme environments. J. Appl. Ecol. 13, 127–150. https://doi.org/10.1016/S0929-1393(99)00029-3.

Yeates, G., 1999. Effects of plants on nematode community structure. Annu. Rev. Phytopathol. 37, 127–149. https://doi.org/10.1146/annurev.phyto.37.1.127.

Yeates, G.W., Bongers, T., De Goede, R.G.M., Freckman, D.W., Georgieva, S.S., 1993. Feeding habits in soil nematode families and genera - an outline for soil ecologists. J. Nematol. 25, 315–331.

Zhang, X., Ferris, H., Mitchell, J., Liang, W., 2017. Ecosystem services of the soil food web after long-term application of agricultural management practices. Soil Biol. Biochem. 111, 36–43. https://doi.org/10.1016/j.soilbio.2017.03.017.

Zhao, J., Neher, D.A., 2013. Soil nematode genera that predict specific types of disturbance. Appl. Soil Ecol. 64, 135–141. https://doi.org/10.1016/j.apsoil.2012.11.008.

Zhao, J., Wang, F., Li, J., Zou, B., Wang, X., Zhian, L., Fu, S., 2014. Effects of experimental nitrogen and/or phosphorus additions on soil nematode communities in a secondary tropical forest. Soil Biol. Biochem. 75, 1–10. https://doi.org/10.1016/j.soilbio.2014.03.019.