Effect of land use and seasonality on nematode faunal structure and ecosystem functions in the Caatinga dry forest

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ABSTRACT

Seasonally dry tropical forests are strongly affected by anthropogenic disturbance and climate changes, which represent the main threats to soil biodiversity, affecting the activity and functional composition of soil communities that provide crucial ecosystem functions and services. However, the effects of these factors and their interactions on soil nematodes, which are bioindicators of soil quality and health, remain poorly understood in the seasonally dry tropical forests. Thus, we investigated the effects of land use and seasonality on the structure and function of nematode components of the soil food web in Caatinga dry forest, north-eastern Brazil. The study was conducted in Catimbau National Park, Pernambuco State, which covers 607 km2 of Caatinga vegetation. Soil samples were collected in dry and rainy seasons in three types of land use: mature forest, agricultural areas, and secondary forest. We quantified the abundance, biomass carbon and metabolic footprint of each functional guild of nematodes. In this study, a total of 104 and 115 nematode genera were identified in the dry and rainy season, respectively. The biomass carbon and metabolic footprints of the total nematode assemblage, and of bacterivores, fungivores and omnivore-predators, were affected by types of land use and seasons. The soil organic carbon and metabolic footprints of nematodes were lower in agricultural areas than in mature forest and secondary forest, and lower in the dry season than in the rainy season. In all types of land use and in both seasons, we verified that most resource assimilation into the soil food web was via the bacterial channel. The enrichment footprint was positively related to the level of soil organic carbon and the structure footprint to the enrichment footprint. In turn, the interactive effect between types of land use and seasonality was observed only for soil organic carbon, biomass carbon of omnivore-predators and the fungal footprint. In general, the differences between types of land use became more significant during the rainy season. In general, our study indicates that change of land use and rainfall in the Caatinga affect the magnitudes of ecosystem functions of functional guilds of nematodes.

1. Introduction

The soil biota is an essential component of soil ecosystems, mediating nutrient cycling and energy flow processes that ensure primary production which, in turn, contribute to climate change mitigation and sustainable food production [1–3]. However, anthropogenic disturbances [4] and climatic changes [5] may affect the processes that underpin these ecosystem services [1]. Intensive land use, for example, negatively affects organisms of the soil microfaunal food web and their participation in carbon (C) and nitrogen (N) cycling [2]. At the same time, climate changes such as temperature increase and reduced precipitation affect the structure of the soil food web. The resultant alteration of predator-prey interactions change the flow of energy and matter through ecosystems [2,5]. Moreover, there is increasing concern that climate change might exacerbate the effects of anthropogenic disturbance by imposing an additional strong environmental filter in disturbed areas [2]. This is due to the fact that increased temperature and reduced precipitation in disturbed areas produced a major drop in the diversity of functions of soil biota [5].

The biodiversity of Seasonally Dry Tropical Forests (SDTFs) has been

impacted by exploitation and management, including grazing and slash-and-burn agriculture, wood extraction and utilization of various forest resources [6]. In addition, it is projected that SDTFs will be subjected to increases in evaporation and temperature during the current century, resulting in longer and more severe droughts that may affect the maintenance of their biodiversity and ecosystem services [7]. As a result, SDTFs are among the most threatened tropical forests in the world [7]. Recent studies in SDTFs have shown negative impacts of anthropogenic disturbance and rainfall variation on plant communities [8] and on ecosystem services provided by ants [9–11]. However, the combined effects on soil biodiversity remain poorly understood and their consequences for ecosystem function are unknown.

Soil nematodes are a major microfauna component of soil food webs [1]; they participate at many trophic linkages and are useful bio-indicators of food web decomposition pathways, soil nutrient status, environmental quality, contaminant effects and climate change [12,13]. Based on their abundance and turnover rates, soil nematodes can account for up to 25% of nitrogen mineralization in the soil [14]. In addition, soil nematodes are suitable for indicating the C metabolism of soil organisms in the food web as they occupy various trophic roles and perform various metabolic activities [15,16,18].

Due to the growing interest in the levels of metabolic activity in soil nematode communities [12,13], providing information on the magnitude of ecosystem functions [17], introduced the nematode metabolic footprint (NMF) concept. The NMF allows a functional quantification of biomass, metabolic activity and magnitude of carbon and energy flow in the soil food web [14,19,20]. In addition, it can provide information about the responses of soil food web to resources and the magnitude of their contribution to ecosystem functions and services [14,21]. In general, NMF is a sensitive tool for illustrating the responses of soil food webs to soil nutrient status and environmental stresses [12,22].

The Caatinga, a mosaic of SDTFs and scrub vegetation [23] that covers 912,529 km^2 of north-eastern Brazil, is considered one of the most endangered ecosystems in Brazil [24]. The extensive ranching, wood extraction and conversion to agriculture has deforested 45% of the area of Caatinga [8,24]. Moreover, the Caatinga is one of the six ecosystems with the greatest intrinsic vulnerability to climate variability [25]. Under future expected climate change, the Caatinga region is subject to receive a 22% reduction in rainfall and an increase in temperature of 3–6 °C [26]. Consequently, the Caatinga provides an excellent opportunity for examining how conversion to agriculture, changes in soil nutrient condition and variation of rainfall in the SDTFs affect soil nematode assemblages and the magnitude of their ecosystem functions.

Therefore, we investigated the effects of type of land use and seasonality (dry and rainy season) on the structure and function of nematode components of the soil food web in Caatinga, the largest and most diverse of the world's seasonally dry tropical forest. It has been previously shown that conversion of native Caatinga vegetation to crop systems negatively affected the nematode assemblages and reduced the total abundance of bacterivore and omnivore-predators nematodes [27]. However, the impact of such changes on the magnitude of ecosystem functions provided by component organisms of the soil food web is unclear since nematode abundance data do not account for respiratory attributes, body size or longevity of nematodes with different functional characteristics [14,17]. Thus, we hypothesize: (i) change of land use from undisturbed Caatinga to agricultural production decreases the soil fertility (here represented by soil organic carbon), and subsequently decreases nematode biomass and metabolic activity (here investigated by estimation of metabolic footprints); (ii) natural regeneration of Caatinga after agriculture increases the soil fertility, and subsequently increases nematode biomass and metabolic activity; (iii) reduced rainfall decreases the soil fertility, and subsequently decreases nematode biomass and metabolic activity; and (iv) the interactive effects of change of land use and change of rainfall levels will affect conditions for nematode biomass and metabolic activity. Specifically, change of land use will have a greater impact on the magnitude of nematode ecosystem functions in the rainy season, due to contribution of precipitation in increasing soil fertility.

2. Materials and method

2.1. Study site

We conducted this study in Catimbau National Park (8°24′00″ and 8°36′35″ S; 37°0′30″ and 37°1′40″ W, state of Pernambuco, north-eastern Brazil), which covers an area of 607 km^2 of Caatinga vegetation [8]. Mean annual rainfall varies markedly in Catimbau, from 1,100 mm in the south-east to 480 mm in the north-west; about 60–75% of the rains occur from March/April to June/July [8]. Mean annual temperature is 23 °C and the lowest temperature month is July, with values equivalent to 21 °C. December, with a mean temperature of 25 °C, is the hottest month [8]. Approximately 70% of its 607 km^2 is covered by quartzite sandy soils supporting low-stature Caatinga vegetation [8]. The dominant families of woody plants are Fabaceae, Euphorbiaceae, Boraginaceae and Burseraceae [8]. The park was created in 2002, and is still inhabited by low-income rural populations who use the land for grazing by livestock, collection of living and dead wood, subsistence agriculture, harvesting of non-timber forest products and hunting [8]. Thus, the park is characterized by a complex mosaic of types of land use (agricultural areas, secondary forests in different degrees of regeneration and mature forests) and by different degrees of anthropogenic pressures in the biota.

2.2. Experimental design and sampling

Soil samples were collected in two seasons: the dry season in November 2015 and the rainy season in May 2016. The monthly mean rainfall data for each plot during different sampling seasons was obtained from the global data repository for climate, WorldClim [28], 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 "Point sampling tool" (https://github.com/borysiasty/pointsamplingtool). The monthly mean rainfall in the dry season ranged from 21 to 23 mm and from 47 mm to 98 mm in the rainy season [28].

Soil was sampled in 21 plots (each 50 × 20 m, separated from each other by at least 1 km) in three different types of land use, viz.: (i) seven plots in areas with old-growth vegetation that had not experienced slash-and-burn agriculture for at least 50 years (Mature Forest); (ii) six plots with active slash-and-burn agriculture (Agricultural Areas); and (iii) eight plots of secondary forest regenerating after abandonment of slash-and-burn agriculture (Secondary Forest), with successional ages from 4 to 45 years (Fig. 1; Table S1).

In both seasons, three soil samples were collected in each plot (for nematodes community analysis) as well as one sample for analysis of soil properties. Each soil sample was selected from an area of 9 × 5 m, with a minimum distance of 10 m between them and arranged in order to explore the maximum of the collection area. In addition, each sample was composed of five subsamples (four located at the ends and one in the center) with a minimum distance of 5 m between them. The subsamples were collected with a cylindrical corer to a depth of 30 cm and then mixed and a 1,000 ml aliquot was put into individual plastic bag labeled with the sample information.

2.3. Nematode community analysis

Nematodes were extracted from 300 ml of soil from each sample by combination of flotation, sedimentation and sieving techniques [29] and centrifugal sucrose flotation [30]. Nematode abundance was expressed as the number of individuals per 100 ml of soil. Then, the nematodes from each sample were fixed in formaldehyde (3%) and infiltrated with glycerin. Taxonomic identification was made up to the genus level. To identification, at least 100 nematodes from each sample were
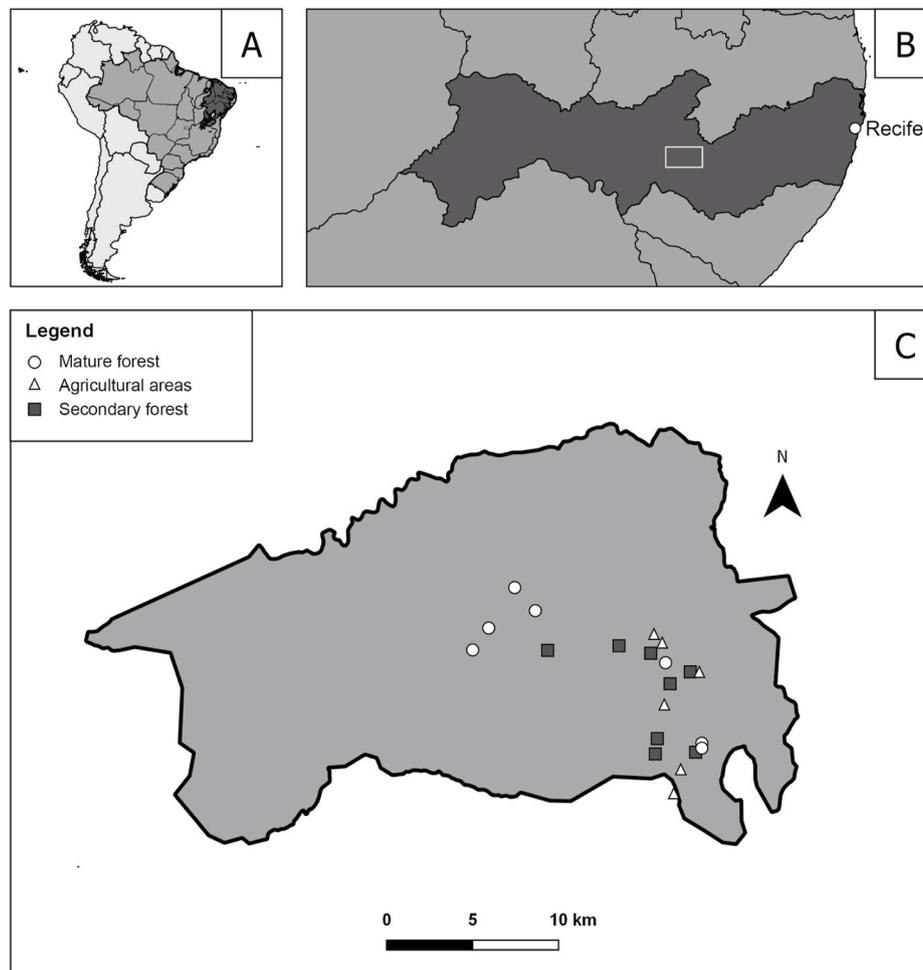
Fig. 1. Location of the study region (in dark gray; within northeastern Brazil) (A), Catimbau National Park (white box; within Pernambuco) (B), and the study plots (n = 21; each 50 × 20 m) within Catimbau (C).

transferred to permanent slide mounts and examined under a light microscope at ×40 and ×100 magnification.

Then, nematodes were assigned to a functional guild matrix of trophic group: bacterivores (BF), fungivores (FF), plant parasites (PP) and omnivore-predators (OP) and colonizer-persister scale (cp) value of life-course strategies (1–5) [31–33]. Nematodes in cp 1–2 have short generation duration, high fecundity, and are regarded as "enrichment opportunists" and tolerant to disturbance and can be considered as r-strategists. In contrast, nematodes of cp 3–5, with longer life cycles, large bodies, lower reproduction rates and greater sensitivity to environmental perturbations, resemble K-strategists [31,33].

After identification, the length (L) and maximum body diameter of all identified adult nematodes in each soil sample were determined using an ocular micrometer. Nematode fresh weight was calculated using the formula: $W = (L^3/a^2)/(1.6 \times 10^6)$, where W is the fresh weight (μg) of a nematode individual, and L and a are its body length (μm) and greatest body diameter (μm), respectively [34]. Assuming dry weight of a nematode as 20% of the fresh weight, and carbon (C) in the body as 52% of the dry weight, total nematode biomass C was calculated as 52% × 20 % Wt/100 (μg ml^{-1}), where Wt is the fresh body weight [17].

To assess the magnitude of ecosystem functions provided by nematode components of the soil food web on each plot of the different types of land use, the nematode metabolic footprint (NMF) was calculated using the formula: $NMF = (Nt(0.1(Wt/mt) + 0.273(Wt^{0.75})))$, where Nt is the number of taxa in each trophic group of interest and mt is the cp values of genus t, respectively [17]. The weight of life-time C mineralized by each taxon is derived from the molecular weights of C and O_2, as

12/44 or 0.273 of the mass of CO_2 evolved. The NMF has a production component (the lifetime amount of C partitioned into growth and egg production) and a respiration component (the C utilized in metabolic activity) [17].

The NMF was divided into: enrichment footprint (efootprint), representing the metabolic footprint of those microbivore (bacterivores plus fungivores) nematodes most rapidly responsive to resource enrichment (cp 1–2); structure footprint (sfootprint), representing the metabolic footprint of higher trophic (cp 3–5) levels which have a regulatory function in the food web and which are indicative of the abundance of organisms of similar functions in non-nematode prey organisms; and bacterial footprint (BF footprint), fungal footprint (FF footprint), and plant parasites footprint (PP footprint), which are the indicators of C and energy entering the soil food web through their respective channels [14,17].

2.4. Soil chemical and physical properties

The soil chemical and physical properties were analysed at Instituto Agronômico de Pernambuco (IPA), using methods detailed in Ref. [35]. Bulk density was measured by the compliant cavity method. The different texture classes were determined by the densimeter method [35]. Soil moisture was determined gravimetrically by drying samples at 105 °C for 24 h. Soil pH was measured in a soil–water suspension (water, KCl ou CaCl^2), 1:2.5, using the combined electrode potentiometer. The Cation-exchange capacity (CEC) was determined by the KCl 1 mol L^{-1} method. The soil organic carbon (soil C) of each sample was determined

using the $K_2Cr_2O_7$ oxidation–titration method [35].

2.5. Statistical analyses

We used general linear models (GLMs) to evaluate the effect of the type of land use, seasonality and their interaction on the: (i) soil physical (bulk density and silt) and chemical (pH, organic matter, soil C and CEC) properties; (ii) biomass C ($\mu g\ ml^{-1}$) total nematode and each trophic group; and (iii) each category of metabolic footprint ($\mu g\ C\ ml^{-1}$): efootprint; sfootprint; BF footprint; FF footprint; PP footprint. We used a separate model for each response variable. For all models, a Gaussian error distribution and "identity" link was used. Model selection was conducted with the '*glm*' function of the '*MuMIn*' package. Analyses were performed in R version 3.4.2. We checked residuals for normality and homoscedasticity in all models. We also checked overdispersion in all models. Once a significant factorial effect and their interaction was detected by those models, a Tukey post hoc test was performed using the '*glht*' function of the '*multcomp*' package.

Finally, to verify the effect of soil C on efootprint, regardless of the type of land use, a simple linear regression was performed using R. In addition, a simple linear regression was also used to verify the relationship between sfootprint and efootprint. We examined the relationships in dry and rainy season, separately.

3. Results

3.1. Effect of type of land use and seasonality on soil physical and chemical properties

The soil bulk density, sand and pH did not differ among the types of land use, between the dry and rainy season or their interaction (P > 0.05) (Table 1; Table S2). The silt was higher in agricultural areas and mature forest than secondary forest, and higher in the rainy season (P < 0.05). The clay and soil moisture were higher in rainy season than dry season (P < 0.001). The values of organic matter and soil C were affected by the types of land use, season and their interaction (P < 0.05). The highest values of soil organic matter and soil C were found in secondary forest, followed by mature forest and agricultural areas (P < 0.001), and higher in the rainy season (P < 0.01). The values of CEC were higher in the dry season (P < 0.05) (Table 1; Table S2).

3.2. Structure of nematode components of the soil food web

In this study, a total of 104 and 115 nematode genera were identified in the dry and rainy season across different types of land use, respectively (Table S3). Among these genera, the predominant trophic group in

total abundance was bacterivores, representing 62.0% of the total nematode population, followed by plant parasites (27.6%), omnivore-predators (8.1%) and fungivores (2.3%) in the dry season. In the rainy season, the predominant trophic group was also bacterivores (54.8%), followed by plant parasites (22.7%), omnivore-predators (18.5%) and fungivores (4.0%). The genus *Acrobeles* (Cephalobidae), a bacterivore, was dominant in all types of land use in both seasons (Table S3).

3.3. Effect of type of land use and seasonality on nematode biomass carbon and metabolic footprints

The biomass C of total nematode, bacterivores, fungivores were affected by types of land use and season, but was not affected by the interaction between land use and season (Table 2; Table S4). The biomass C of plant parasites was only affected by the season (Table 2; Table S4). The biomass C of the total nematode assemblage was higher in secondary forest, followed by mature forest and agricultural areas (P < 0.01; Table 3; Fig. 2a). The biomass C of bacterivores was higher in secondary forest than in mature forest and agricultural areas (P < 0.01; Table 3; Fig. 2b). However, the biomass C of fungivores was higher in mature forest, followed by secondary forest and agricultural areas (P < 0.01; Table 3; Fig. 2c). The biomass C of omnivore-predators was affected by types of land use, season and their interaction (Table 2; Table S4). Specifically, the difference in biomass C of omnivore-

Table 2

Chi-squared values (X^2) of the generalized linear models for the effects land use, seasonality (dry and rainy season) and their interaction on soil nematode biomass carbon ($\mu g\ ml^{-1}$) and metabolic footprints ($\mu g\ C\ ml^{-1}$ soil) in the Catimbau National Park, Pernambuco, Brazil. *P < 0.05; **P < 0.01; ***P < 0.001.

Biomass carbon and metabolic footprints	Land use	Season	Land use x season
		X^2	
Biomass C of total nematode	4.58**	17.90***	0.05
Biomass C of bacterivores	8.86***	11.20***	0.07
Biomass C of fungivores	2.23*	3.32*	0.007
Biomass C of plant parasites	0.005	4.08*	0.42
Biomass C of omnivore-predators	2.92**	5.47***	5.91*
efootprint	8.83**	14.91***	14.91
sfootprint	15.19***	18.78**	0.27
BF footprint	13.12***	13.55***	0.63
FF footprint	14.27***	11.05***	2.55*
PP footprint	4.94	7.14*	0.35

Biomass C: biomass carbon; efootprint: enrichment footprint; sfootprint: structure footprint; BF footprint: bacterivores footprint; FF footprint: fungivores footprint; PP footprint: plant parasites footprint.

Table 1

Mean values ($\pm$SD) of soil physical and chemical properties in the mature forest (MF), agricultural areas (AA) and secondary forest (SF) in dry and rainy season in the Catimbau National Park, Pernambuco, Brazil. Different letters denote significant differences between seasons within each land use (p < 0.05); different numbers denote significant differences between land use (p < 0.05); ns indicated no significant differences.

Soil properties	Dry season			Rainy season			Land use	Season	Land use x season
	MF	AA	SF	MF	AA	SF			
Bulk Density (kg/dm³)	1.60 ± 0.11	1.50 ± 0.06	1.58 ± 0.05	1.50 ± 0.06	1.61 ± 0.02	1.61 ± 0.02	ns	Ns	ns
Sand (g/kg)	59.00 ± 8.29	60.50 ± 8.16	63.00 ± 8.50	59.42 ± 11.51	59.50 ± 6.83	59.00 ± 10.75	ns	Ns	ns
Silt (g/kg)	2.57 ± 1.51¹	2.66 ± 1.00¹	0.88 ± 0.22²	4.28 ± 1.96¹	5.83 ± 2.22¹	2.75 ± 1.5²	<0.05	<0.001	ns
Clay (g/kg)	4.57 ± 0.81	5.00 ± 1.33	4.00 ± 0.01	8.85 ± 1.87	8.66 ± 3.55	7.00 ± 1.50	ns	<0.001	ns
pH	5.41 ± 0.33	5.73 ± 0.53	5.38 ± 0.39	5.00 ± 0.24	6.00 ± 0.48	6.00 ± 0.34	ns	Ns	ns
Soil moisture (g/100 g)	0.68 ± 0.15	1.08 ± 0.21	0.66 ± 0.66	1.61 ± 0.44	1.17 ± 0.20	1.43 ± 0.28	ns	<0.001	ns
Organic matter (g/kg)	10.88 ± 1.60a¹	9.90 ± 2.30b¹	22.76 ± 2.28c²	14.90 ± 1.67d¹	10.44 ± 1.22b²	29.96 ± 0.58c¹	<0.001	<0.01	<0.05
Organic Carbon (g/kg)	5.60 ± 3.73a¹	6.43 ± 3.90b¹	19.09 ± 8.43c²	17.90 ± 6.11d¹	5.05 ± 2.71b²	18.61 ± 5.60c¹	<0.001	<0.01	<0.05
Cation-exchange capacity (cmolc_c/kg)	5.90 ± 2.64	5.63 ± 1.96	6.98 ± 2.94	5.00 ± 2.11	4.93 ± 0.44	4.83 ± 1.29	ns	<0.05	ns

Table 3

Mean values (±SD) of soil nematode biomass carbon (µg ml^{-1}) and metabolic footprints (µg C ml^{-1} soil) in the mature forest (MF), agricultural areas (AA) and secondary forest (SF) in dry and rainy season in the Catimbau National Park, Pernambuco, Brazil.

Biomass carbon and metabolic footprints	Dry season			Rainy season			Land use	Season	Land use x Season
	MF	AA	SF	MF	AA	SF			
Biomass C of total nematode	16.29 ± 5.71[1]	11.87 ± 4.71[2]	28.99 ± 11.27[3]	42.23 ± 12.87[1]	20.31 ± 4.90[2]	51.73 ± 18.20[3]	<0.01	<0.001	ns
Biomass C of bacterivores	7.77 ± 3.13[1]	7.00 ± 3.65[1]	16.75 ± 8.20[2]	18.88 ± 6.40[1]	10.73 ± 4.06[1]	29.36 ± 13.14[2]	<0.001	<0.001	ns
Biomass C of fungivores	1.52 ± 0.84[1]	0.53 ± 0.24[2]	1.16 ± 0.53[2]	2.15 ± 1.07[1]	1.01 ± 0.28[2]	1.73 ± 0.95[2]	<0.05	<0.05	ns
Biomass C of plant parasites	2.10 ± 2.23	0.81 ± 1.10	3.15 ± 2.45	4.94 ± 4.54	3.60 ± 3.33	4.33 ± 4.35	ns	<0.05	ns
Biomass C of omnivore-predators	4.90 ± 2.28 ab[1]	3.53 ± 0.85a[2]	7.94 ± 3.23b[1]	16.26 ± 5.20c[1]	4.98 ± 2.40 ab[2]	16.32 ± 3.50c[1]	<0.01	<0.001	<0.05
efootprint	28.56 ± 7.27[1]	23.77 ± 11.95[2]	53.17 ± 19.24[3]	59.46 ± 13.12[1]	37.25 ± 12.23[2]	71.97 ± 12.29[3]	<0.01	<0.001	ns
sfootprint	19.12 ± 4.17[1]	9.58 ± 4.21[2]	37.44 ± 13.70[3]	53.14 ± 12.13[1]	26.81 ± 8.23[2]	64.90 ± 8.01[3]	<0.001	<0.01	ns
BF footprint	24.34 ± 7.36[1]	22.18 ± 11.68[2]	50.04 ± 18.84[3]	50.67 ± 9.86[1]	34.11 ± 11.82[2]	66.53 ± 11.41[3]	<0.001	<0.001	ns
FF footprint	4.30 ± 1.64a[1]	1.60 ± 0.30b[2]	3.13 ± 0.97 ab[3]	8.80 ± 4.33c[1]	3.14 ± 1.88 ab[2]	5.45 ± 1.78a[3]	<0.001	<0.001	<0.05
PP footprint	6.92 ± 3.44	7.00 ± 3.65	15.5 ± 6.93	16.66 ± 8.62	12.20 ± 7.00	21.43 ± 11.88	ns	<0.05	ns

Different letters denote significant differences between seasons within each land use (p < 0.05); different numbers denote significant differences between land use (p < 0.05); ns indicated no significant differences.

predators among types of land use was greater in the rainy season (P < 0.05; Table 3; Fig. 2e). The biomass C of omnivore-predators was higher in mature forest and secondary forest than agricultural areas (P < 0.05; Table 3; Fig. 2e). The biomass C of total nematodes and all trophic groups were higher in the rainy season (P < 0.05; Table 3; Fig. 2).

The efootprint, based on the abundance and metabolic activity of the BF (cp 1–2) and FF (cp 2) functional guilds, was clearly affected by types of land use and season (Table 2; Table S5). The sfootprint, based on the abundance and metabolic activity of higher trophic level predation (omnivore-predators), was also affected by types of land use and season (Table 2; Table S5). No interaction effects were observed between predictor variables on efootprint and sfootprint (Table 2). The efootprint and sfootprint were higher in secondary forest, followed by mature forest and agricultural areas, and higher in the rainy season. (P < 0.01; Table 3; Fig. 3a and b).

Magnitudes of BF, FF and PP footprint in all types of land use and in both seasons indicated that most resource assimilation into the soil food web was via the bacterial channel; fungivore and plant parasites channels were less active (Table 3; Fig. 3c,d,e).

Analyzing each channel separately, we verified that BF footprint was affected by different types of land use and season (Table 2; Table S5). No interaction effect was observed between predictor variables on BF footprint (Table 2; Table S5). The BF footprint was higher in secondary forest, followed by mature forest and agricultural areas, and higher in the rainy season (P < 0.05; Table 3; Fig. 3c). The FF footprint was affected by types of land use, season and their interaction (Table 2; Table S5). This result indicates that FF footprint was higher in mature forest, followed by secondary forest and agricultural areas (P < 0.01; Table 3; Fig. 3d). However, the increase in FF footprint in the rainy season is much higher in mature forest areas (P < 0.01; Table 3; Fig. 3d). The PP footprint was not affected by types of land use (Table 2). However, the PP footprint was higher in rainy season (Table 3; Fig. 3e). No effect of interactions between predictors variables on PP footprint was observed (Table 2; Table S5).

3.4. The relationship between microbivore nematodes and soil organic carbon, and predator-prey relationships

In both the dry and rainy seasons, the efootprint increased with increasing level of total soil C (Fig. 4). However, the effect of soil C on efootprint was more significant in the rainy season (R^2 = 0.54, P < 0.001; Fig. 4a) than in the dry season (R^2 = 0.21, P < 0.05; Fig. 4b). A

significant regression relationship was also found between sfootprint and efootprint both in the dry season (R^2 = 0.67, P < 0.001; Fig. 5a) and in the rainy season (R^2 = 0.61, P < 0.001; Fig. 5b).

4. Discussion

4.1. Effect of type of land use and seasonality on soil fertility and microbial food web metabolic activities

In our study, we found that soil C, biomass C and metabolic activity of nematode functional guilds, except for plant parasites, were negatively affected by the change of land use from undisturbed Caatinga to agricultural production, confirming our first hypothesis. The biomass C and metabolic footprint of enrichment indicator nematodes were significantly lower in agricultural areas than in mature forest and secondary forest. Similarly, the levels of soil C were significantly lower in the agricultural plots when compared to the other land uses. Among the functional groups, bacterivore and fungivore nematodes are always the first to respond to the removal of native vegetation for agricultural use due to the bottom-up effect resulting from a change in food resources [36]. For example, destructive agricultural practices reduces the amount of organic matter in the soil due to the reduction of plant residues and elevated respiration of soil organisms, which results in a decrease of the abundance and metabolic activities of microorganisms (bacteria and fungi), the food supply of bacterivores and fungivores [37,38]. The existing socio-ecological framework for the 26 million people who inhabit the Caatinga is based on extraction of resources [24]. The high dependence on natural resources has led to a continuous loss of nutrients from soil and vegetation through agricultural practices such as slash-and-burn. In addition, agricultural management techniques for the reintroduction of nutrients in soil and vegetation are rarely used in this ecosystem [24,27]. Thus, soil C, which is mainly derived from plant residues, microbial residues and root exudates [39], is negatively affected in the Caatinga. We can infer that the decrease in available soil C due to land-use changes in the Caatinga provide reduced resources for soil biota and consequently for microbivore nematodes, Consequently, there is a lower amount of C flowing through food web decomposition channels and reduced nutrient cycling [40].

Biomass C and metabolic footprint of structure indicator nematodes were also lower in agricultural areas than in mature forest and secondary forest. Two dynamics may have led to low values of the metabolic activity of generalist and specialist predators (cp 3–5) with the
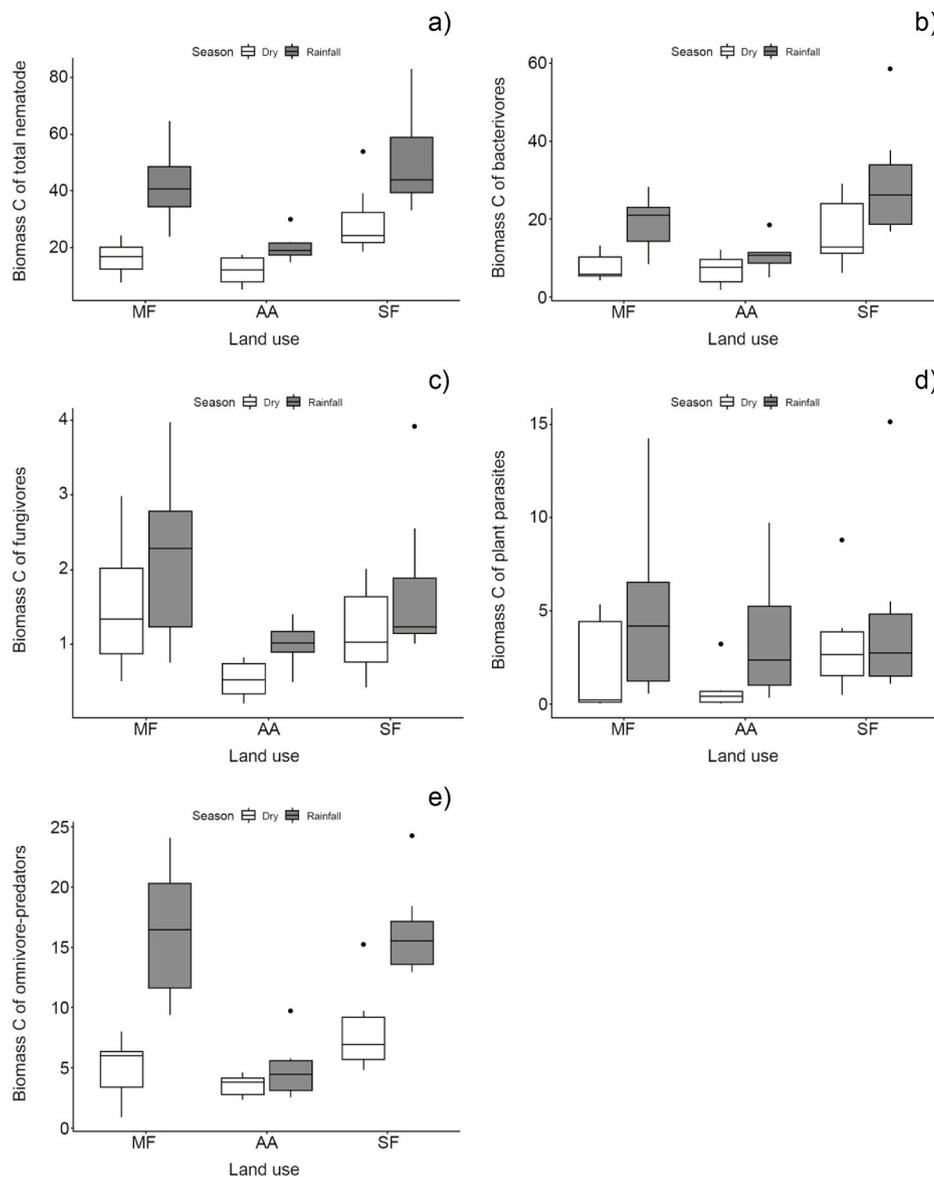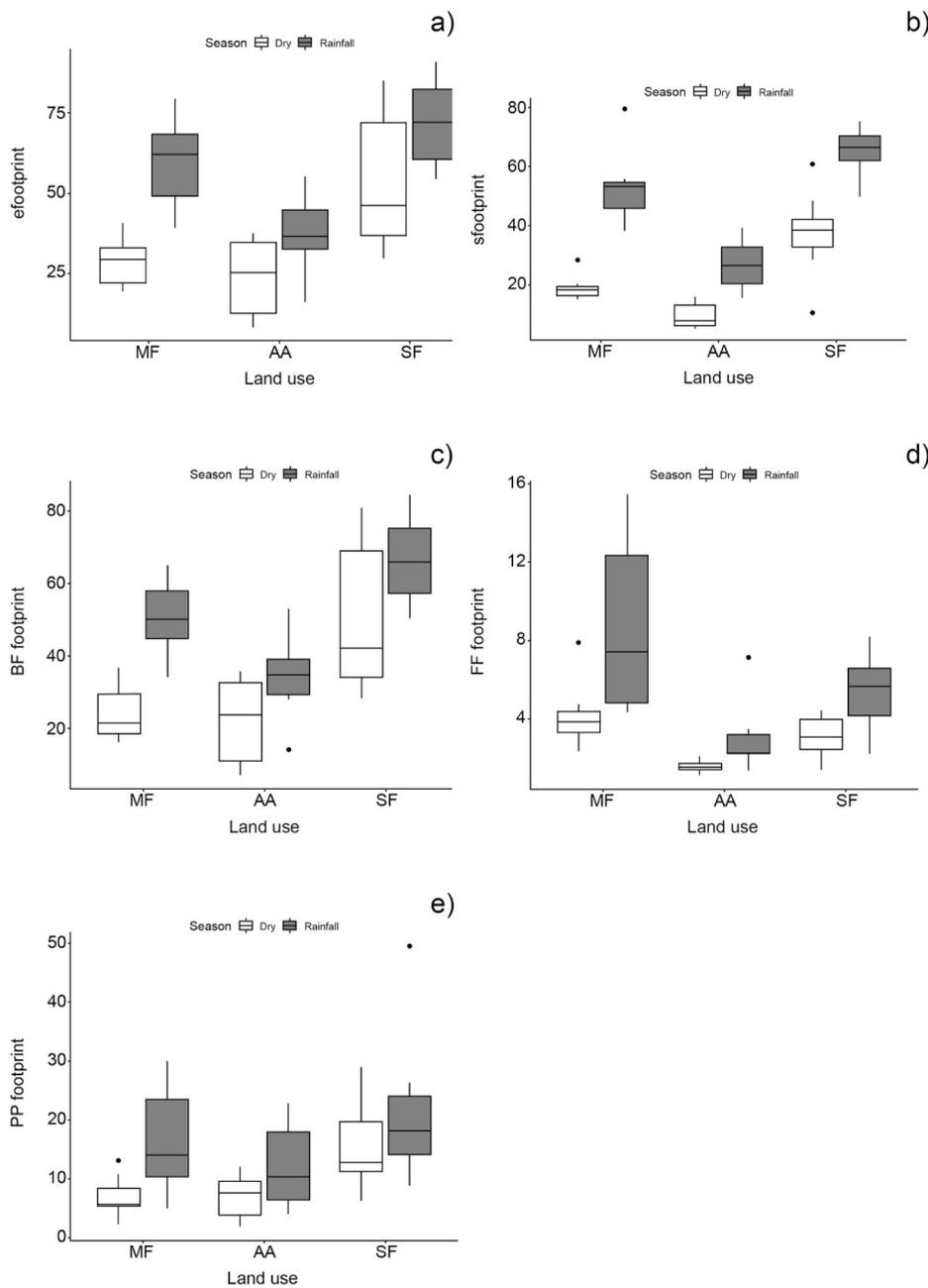
Fig. 2. Effect of land use and seasonality (dry and rainy season) on biomass carbon of nematodes and on each trophic group (µg ml^{-1} soil) in the mature forest (MF), agricultural areas (AA) and secondary forest (SF) in dry and rainy season in the Catimbau National Park, Pernambuco, Brazil.

conversion to agriculture. First, omnivore-predators are strongly affected by physical soil disturbance, such as soil tillage [12,22]. Then, reduced prey availability and metabolic activity (efootprint) in agricultural areas become insufficient to meet the needs of omnivore-predator nematodes and to maintain the metabolic balance of the soil food web [14,17,41]. As a consequence, the agricultural areas have not only a lower magnitude of conservation of biomass C from the entry level to higher trophic levels level of the soil food web through the reduction of prey-predator connections [41], but also a reduction of the nutrient cycling through of the indirect process of predation on microbial grazers and herbivore species [14,42].

In line with our second hypothesis, the abandonment of agricultural practices and the natural regeneration of the Caatinga increased the supply of resources below ground (organic matter and soil C) as well as the metabolic activity of nematodes and ecosystem function. The response of the structure and function of nematode components of the soil food web to the increased availability of nutrients in the soil during regeneration of forests is in line with similar studies [20,37,43]. Our results suggest that the abandonment of agricultural practices and the natural regeneration of Caatinga increased availability of carbon in

those plots due to greater vegetational heterogeneity over large areas, providing resources for soil biota [20,27,37]. In addition, our results suggest that secondary regeneration can recover the ecosystem function of soil food web to a level close to the areas that had not experienced agricultural practice (mature forest) in the Caatinga.

We also verified a strong influence of rainfall, here represented by seasonality, on the levels of soil C, efootprint, biomass C and sfootprint, consequently, confirming our third hypothesis. When comparing the values of these variables between the dry and rainy seasons, we found a substantial reduction (almost double) in these variables with the reduction of rainfall in the Caatinga. Rainfall is considered one of the environmental variables that most affect nematode abundance and metabolic activity [43–46]. It has been shown that low rainfall can reduce net primary productivity below the ground [47], reduce soil microbial biomass and provide less resources for soil fauna [45,48]. In addition, changes in precipitation directly alter the availability of water in the soil and subsequently affect community structure and ecosystem functions of nematodes [49]. The high sensitivity of nematodes to precipitation is due to the fact that nematodes are aquatic organisms that depend on water films around the soil particles to move and capture

Fig. 3. Effect of land use and seasonality (dry and rainy season) on metabolic footprints (μg C ml^{-1} soil) of soil nematode functional guilds in soils in the mature forest (MF), agricultural areas (AA) and secondary forest (SF) in dry and rainy season in the Catimbau National Park, Pernambuco, Brazil. (a) efootprint: enrichment metabolic footprint; (b) sfootprint: structure metabolic footprint; (c) BF footprint: bacterial metabolic footprint; (d) FF footprint: fungal metabolic footprint; and (e) PP footprint: plant parasites metabolic footprint.
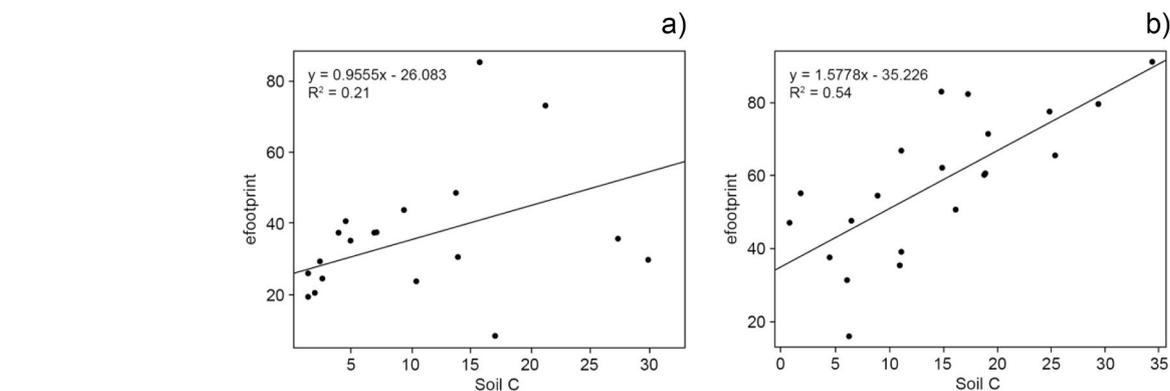
Fig. 4. Linear relationships between enrichment metabolic footprint (efootprint) (μg C ml^{-1} soil) and soil C (g/kg^{-1}): (a) The relationship between efootprint and soil C in dry season; (b) The relationship between efootprint and soil C in rainy season.
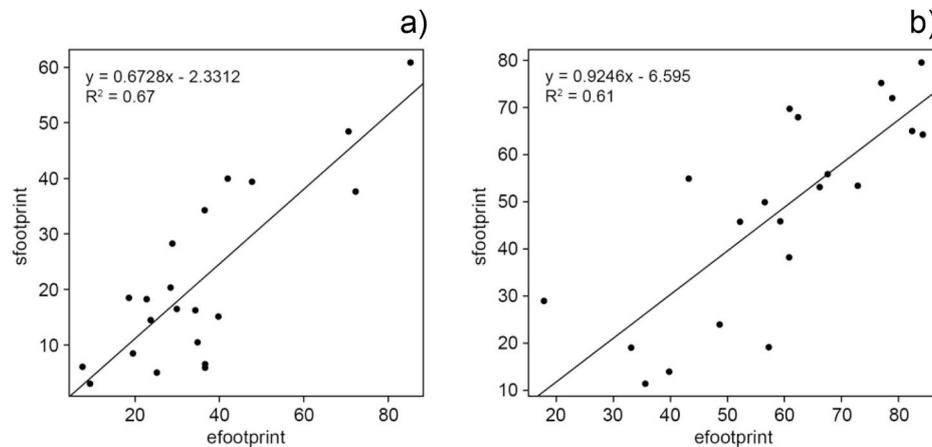
Fig. 5. Linear relationships between structure metabolic footprint (sfootprint) and enrichment metabolic footprint (efootprint) (µg C ml^{-1} soil): (a) The relationship between sfootprint and efootprint in dry season; (b) The relationship between sfootprint and efootprint in rainy season.

food [50,51]. Thus, in the Caatinga, during the period with the lowest levels of precipitation, the lower availability of resources released in the soil plus the reduction of soil humidity increases the nematode's anhydrobiotic state [33], negatively impacting the metabolic footprint of all functional groups.

4.2. Effect of type of land use and seasonality on carbon flow through soil microbial food web

The lower values of FF footprint and PP footprint in relation to the BF footprint found across different types of land use in both seasons indicate that direct plant parasite and fungivore activity were not major resource channels into the soil food web; most resource assimilation was via the bacterial channel. The predominance of the bacterial channel in the Caatinga is associated with the life strategies among the bacterivores group found. We verified that nematodes of the family Cephalobidae (cp-2) was the predominant trophic group in both seasons. Due to their life strategy of adapting to any environmental condition, cephalobid nematodes in arid environments influence the decomposition, regulating the population density and metabolic activity of bacteria [17]. Therefore, it is reasonable that bacterivores of the family Cephalobidae are dominant in C storage among different trophic groups [20].

Although the most resource assimilation into the soil food web was via the bacterial channel, we found that the type of land use and the season not only affected soil C, but also the biomass C and metabolic footprint of the BF, FF and PP and on their respective food resources (bacteria, fungi and plant roots).

Our study revealed that both BF and FF footprint decreased with the change in land use from mature forest to agricultural areas, but increased with natural regeneration processes and were higher in the rainy season. That supported our first three hypotheses regarding the decomposition channels. We also verified that the physical disturbance and reduction of resources and nutrients available in the soil caused by agricultural activity were more evident on the C biomass of fungivore nematodes and FF footprint than on the biomass C of the bacterivore nematodes and BF footprint. The differences between BF and FF footprint in relation to agriculture may be associated to difference in the growth forms of fungi and bacteria [52]. For instance, factors that physically disturb the soil cause direct damage to hyphal growth of fungi [52]. Bacteria, on the other hand, are little affected by physical disorder, since they are present as individual cells and disturbance may expose them to new resources [52]. However, the reduction in the BF footprint found with the change in land use from mature forest to agricultural areas can be attributed to the fact that bacterial biomass is strongly affected by the reduction of organic matter input [53,54]. In general, the negative effect caused by the removal of native vegetation for

agricultural activity, verified by the reduction of BF and FF footprint, reflects the reduction of primary decomposers, decomposition of soil organic matter and mineralization rates of nutrients available for plant growth [14,22].

The BF and FF biomass C and metabolic footprint also increased with natural forest regeneration. The increase in organic matter and soil C in the secondary forest plots increased C and energy flow into the soil food web. However, we found that biomass C and metabolic footprint of BF was higher in the secondary forest plots than biomass C and metabolic footprint of FF. Possibly, the varied increase between BF and FF footprint observed in the natural regeneration of Caatinga after agriculture is associated with difference in the growth forms of fungi and bacteria in the face of changing land use and nutrient availability [52]. Generally, fungal-based soil food webs recover slowly after related disturbances because slow-growing organisms, including fungi and fungal fauna, tend to be more resilient (that is, they are more able to withstand a disturbance). In contrast, bacteria and bacterivore nematodes, which are fast-growing organisms, tend to be more resilient (i.e., higher recovery rate after a disturbance) [2,55].

There was no difference in the biomass C and metabolic footprint of plant parasites (PP footprint) across different types of land use. Rainfall, however, positively influenced the PP footprint and this can be explained because during the highest levels of precipitation, plants grow more vigorously, providing more C to the roots [54]. In addition, the strong influence of precipitation on the PP footprint is due to the fact that plant parasitic nematodes are active in the moist rhizosphere, as they depend on the water around the plant's root for their survival and reproduction [45].

The types of land use and rainfall play strong and consistent roles in soil fertility and nematode metabolic activity as evidenced in the discussion above. In addition, the results showed that these factors also acted interactively on soil C, biomass C of omnivore-predators and FF footprint. More specifically, during the rainy season, the values of these variables differed even more among the types of land use than during the dry season, corroborating our fourth hypothesis. The reason for this is that during the dry season, the soil temperature is so high, and the soil moisture and fertility are so low that the change in land use produces weak, but significant, effects on these variables. In turn, with the increase in rainfall, humidity and soil fertility, the management and type of land use have a greater effect on soil properties. During the rainy season in the Caatinga, the difference between the levels of organic matter and soil C between the different types of land use become greater due, mainly to intensive agricultural practice. In order to increase production, local producers end up increasing the erosion process, contributing to soil loss and low productivity. Thus, it is evident that the inappropriate agricultural practices presents much lower values of soil C

and trophic groups sensitive to anthropic disturbances, such as fungivores and omnivores-predators, especially in situations of less precipitation. Together, these findings present new evidence that anthropogenic disturbances and climate change, acting jointly, can have complex effects on soil fauna in dry forests [27].

4.3. The relationship between microbivore nematodes and total soil organic carbon

The efootprint was positively related to soil C, irrespective of type of land use, both in the dry and rainy seasons. Since soil C is the main source of energy for soil microorganisms [56], the positive relationship of efootprint and soil C indicates that the greater the availability of soil C in the soil, the greater the abundance of soil microorganisms and, therefore, resources for microbivore nematodes [12,22]. In addition, it also indicates the response of the opportunistic bacterivore and fungivore nematode to organic enrichment in the Caatinga, as well as the participation of these nematodes in the carbon cycling in the soil through the use of soil carbon for body growth and respiration [22,41].

5. Conclusion

The change of land use and rainfall in the Caatinga dry forest affected the soil organic carbon levels, structure and functions of the soil food web. More specifically, we found that the conversion of native vegetation to crop systems reduced soil C, as well as biomass carbon and metabolic footprint of enrichment and structure indicator nematodes. On the other hand, regeneration of secondary forest after the agriculture disturbance increased the soil C, enrichment and structure metabolic footprint. We also found that rainfall levels strongly affected the soil carbon, biomass carbon and metabolic footprint of the functional nematode guilds. Lower levels of rainfall decreased the availability of soil C, thus providing less resources for soil biota and this was reflected in the magnitude of the ecosystem function of the functional guilds of the nematode assemblages. Most resource assimilation and energy flow into the soil food web in Caatinga was via the bacterial channel; plant parasitic and fungivore channels were less active. Finally, there was a strong positive relationship between enrichment footprint and level of total soil carbon, and structure footprint and enrichment footprint. We found evidence of interactive effects of land use and season effect on the soil C, biomass C of omnivore-predators and FF footprint. Our study reinforces the importance of using nematode biomass carbon and metabolic footprints in functional approaches to investigate the impact of anthropogenic disturbance and climate changes on the soil health in the SDTFs.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Silva).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ejsobi.2021.103296.

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