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# EFEITO DO USO DO SOLO, PRORIEDADES DO SOLO E VARIÁVEIS CLIMÁTICAS SOBRE A ESTRUTURA DA COMUNIDADE E FUNÇÕES ECOSSISTÊMICAS DOS NEMATOIDES NA CAATINGA

Recife
2020

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Tese apresentada ao Programa de Pós-Graduação em Biologia Animal da Universidade Federal de Pernambuco, como requisito parcial para a obtenção do título de Doutora em Biologia Animal

**Área de concentração**: Ecologia

**Orientador**: Profº. Dr. André Morgado Esteves

**Coorientador**: Profº. Dr. Juvenil Enrique Cares

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Aprovada em: 28/02/2020

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## RESUMO

A biodiversidade do solo enfrenta pressões crescentes das ações humanas, incluindo a conversão, degradação e fragmentação de habitats. O efeito desses fatores somado às mudanças climáticas não reduz apenas a diversidade e abundância da biota do solo, mas também suas funções e serviços ecossistêmicos. Nesta tese, investigamos como diferentes tipos de uso da terra, propriedades do solo e variáveis climáticas afetam a estrutura da comunidade e função ecossistêmica dos nematoides na Caatinga. O estudo foi conduzido em parcelas com diferentes tipos de uso da terra no Parque Nacional do Catimbau, o qual cobre uma área de 607 $km^2$ de vegetação da Caatinga. Embora o local de estudo seja uma unidade de conservação, ele ainda está sujeito a diferentes interferências dos habitantes cujas atividades principais são criação de caprinos e bovinos e agricultura de subsistência. Além disso, o local de estudo cobre uma área com diferentes regimes de precipitação variando de 480 a 1.100 mm. Diante disso, o Catimbau fornece uma excelente oportunidade para avaliar os efeitos dos distúrbios antrópicos e mudanças climáticas sobre a comunidade de nematoides na Caatinga. No primeiro capítulo, nós investigamos o efeito das propriedades do solo, precipitação e temperatura sobre a estrutura das comunidades de nematoides em áreas com diferentes tipos de uso da terra. Para isso, coletamos amostras de solo em áreas de floresta natural, áreas agrícolas e floresta secundária para a extração dos nematoides e realização de análises físico-químicas do solo. Nós verificamos que a conversão da vegetação nativa da Caatinga em sistemas de cultivo afetou negativamente a comunidade de nematoides, reduzindo a abundância total dos nematoides, dos bacteriófagos e dos onívoro-predadores. Além disso, a composição taxonômica dos nematoides em diferentes tipos de uso da terra foi fortemente afetada pelas propriedades do solo e variáveis climáticas. No segundo capítulo, nós investigamos os efeitos do tipo de uso da terra e efeito sazonal (estação seca e chuvosa) sobre a estrutura e função da cadeia alimentar dos nematoides. Para isso, nós calculamos a abundância, biomassa de carbono e *metabolic footprint* de cada guilda funcional, para estimar a contribuição dos nematoides para funções relacionadas ao carbono e à ciclagem de nutrientes. Nós verificamos que a conversão da vegetação nativa da Caatinga em sistemas de cultivo diminuiu a fertilidade do solo, como também a biomassa de carbono, *metabolic footprint* e a função do ecossistema dos nematoides. Além disso, a *metabolic footprint* de todas as guildas funcionais dos nematoides foram maiores durante o período de precipitação elevada (estação chuvosa). Entretanto, encontramos poucas evidências do efeito interativo do uso da terra e efeito sazonal sobre a atividade metabólica dos nematoides. No geral, nosso estudo indicou que o conhecimento sobre a estrutura da comunidade e função

ecossistêmica dos nematoides solo na Caatinga fornece informações referentes aos efeitos de distúrbios antrópicos e mudanças climáticas sobre a saúde do solo nas florestas tropicais sazonalmente secas

Palavras-chave: Agricultura. Cadeia alimentar do solo. Estrutura de comunidade. Florestas tropicais sazonalmente secas.

## ABSTRACT

Soil biodiversity faces increasing pressures from human actions, including habitat conversion, degradation and fragmentation. The effect of these factors added to climate change not only reduces the diversity and abundance of soil biota, but also its ecosystem functions and services. In this thesis, we investigated how different types of land use, soil properties and climatic variables affect the community structure and ecosystem function of nematodes in the Caatinga. The study was conducted in plots with different types of land use in the Catimbau National Park, which covers an area of 607 $km^2$ of Caatinga vegetation. Although the study site is a conservation unit, it is still subject to different interferences from the inhabitants whose main activities are livestock pressure (herbivory by goats and cattle) and subsistence agriculture. In addition, the study site covers an area with different rainfall regimes ranging from 480 to 1100 mm. Thus, Catimbau provides an excellent opportunity to assess the effects of anthropogenic disturbance and climate change on the nematode community in the Caatinga. In the first chapter, we investigated the effect of soil properties, rainfall and temperature on the structure of nematode communities in areas with different types of land use. We collected soil samples in areas of natural forest, agricultural areas and secondary forest for the extraction of nematodes and analysis of soil properties. We found that conversion of native Caatinga vegetation to crop systems negatively affected the nematode community, reducing the total abundance of the nematodes, bacterivores and omnivore-predators. In addition, the taxonomic composition of the nematodes in different types of land use was strongly affected by soil properties and climate variables. In the second chapter, we investigated the effects of land use and seasonal effect (dry and rainy season) on the structure and function of nematode food web. We calculated the abundance, biomass carbon and metabolic footprint of each functional guild to estimate the contribution of nematodes to functions related of the carbon and nutrient cycling. We found that the change of land use from undisturbed Caatinga for agricultural production decreased soil fertility, biomass carbon, metabolic footprint and ecosystem function of the nematodes. Furthermore, the metabolic footprint of all functional guilds was higher during the period of high rainfall (rainy season). However, we found little evidence of the interactive effect of land use and seasonal effect on the metabolic activity of the nematodes. Overall, our study indicated that knowledge about the community structure and ecosystem function of the nematodes in the Caatinga provides information regarding the effects of anthropogenic disturbance and climate changes on soil health in the seasonally dry tropical forests.

Keywords: Agriculture. Community structure. Seasonally dry tropical forests. Soil food web.

**SUMÁRIO**

# 1 INTRODUÇÃO

A biota do solo é um componente essencial para o funcionamento dos ecossistemas, mediando processos de decomposição de matéria orgânica, ciclagem de nutrientes e fluxo de energia que garantem a produção primária (DE VRIES et al., 2013; FERRIS, 2010; FERRIS; TUOMISTO, 2015). Entre as ameaças à biodiversidade do solo, mudança no uso da terra e mudanças climáticas são consideradas os principais fatores que afetam a estabilidade dos processos e serviços do ecossistema (BARNES et al., 2017; SCHWARZ et al., 2017).

Sob forte influência de distúrbio antrópico, como a criação de caprinos e bovinos, práticas agrícolas de subsistência, extração de madeira e exploração de recursos florestais variados, a biodiversidade da Caatinga tem sido fortemente afetada (ARNAN et al., 2018; BELLARD et al., 2012; OLIVEIRA et al., 2019; RITO et al., 2017). Além disso, as mudanças climáticas, como por exemplo aumento da temperatura e redução da precipitação (MAGRIN et al., 2004), também ameaçam a Caatinga (DIRZO et al., 2011) e podem até agravar os efeitos de distúrbios antrópicos (BANDA et al., 2016; BURKETT et al., 2014), limitando a persistência da biodiversidade e suas respectivas funções ecossistêmicas.

Os nematoides constituem um importante modelo de biota para compreender as respostas da biodiversidade do solo aos efeitos dos distúrbios antrópicos (SÁNCHEZ-MORENO et al., 2018; ZHANG et al., 2017) e mudanças climáticas (SCHWARZ et al., 2017). Eles ocupam uma posição central na cadeia alimentar e compreendem uma gama de grupos funcionais ou tróficos (BONGERS; BONGERS, 1998; YEATES et al., 1993). Por isso, os nematoides são amplamente utilizados como indicadores da estrutura e funcionamento das cadeias alimentares do solo e das condições gerais do ecossistema. A contribuição dos nematoides do solo para os processos e funções do ecossistema varia de acordo com a abundância, diversidade e magnitude da atividade metabólica da comunidade de nematoides (BRENNAN, 2012; FERRIS; SÁNCHEZ-MORENO; ZHANG et al., 2017).

As funções e serviços ecossistêmicos fornecidos pelos nematoides em florestas tropicais são afetados principalmente por alterações ou distúrbios ambientais, como a conversão da vegetação nativa em usos agrícolas, fatores edáficos (propriedades químicas e físicas do solo), temperatura e precipitação (NIELSEN et al., 2014; SONG et al., 2017).

## 1.1 OBJETIVOS

### 1.1.1 Objetivo geral

Avaliar como diferentes tipos de uso da terra, propriedades do solo e variáveis climáticas afetam a estrutura de comunidade e função ecossistêmica dos nematoides na Caatinga, uma das maiores e mais diversificadas florestas tropicais sazonalmente secas do mundo.

### 1.1.2 Objetivos específicos

- Avaliar o efeito das propriedades do solo, precipitação e temperatura sobre a estrutura das comunidades de nematoides em áreas com diferentes tipos de uso da terra.
- Investigar os efeitos do tipo de uso da terra e efeito sazonal (estação seca e chuvosa) sobre a estrutura e função da cadeia alimentar dos nematoides.

# 2 REFERENCIAL TEÓRICO

*Efeito do distúrbio antrópico e mudanças climáticas sobre a biodiversidade do solo*

O solo apresenta uma importância central para a prestação de serviços ecossistêmicos que beneficiam ao homem. Eles não apenas fornecem nutrientes para o crescimento das plantas, mas também armazenam quantidades significativas de carbono (C) e nitrogênio (N) no solo, o que contribui para o equilíbrio do clima e a produção sustentável de alimentos (EISENHAUER et al., 2012; DE VRIES et al., 2013, WAGG et al., 2018). Contudo, o resultado de um bom funcionamento do ecossistema depende da magnitude do serviço ecossistêmico fornecido não apenas por um organismo, mas sim por toda a biota que compõe a cadeia alimentar do solo (FERRIS; TUOMISTO, 2015; HAYGARTH; RITZ, 2009). Por exemplo, as minhocas e os fungos podem atuar como engenheiros do ecossistema, reestruturando o material do solo, o que afeta a erosão, a qualidade da água e o suprimento de água (serviços do ecossistema) (PULLEMAN et al., 2012). Os microorganismos e seus consumidores também são importantes decompositores de nutrientes, e as mudanças na comunidade microbiana podem reduzir as taxas de ciclagem e decomposição, afetando o fornecimento de alimentos, fibras e água, bem como a capacidade do solo de reduzir as concentrações de poluentes (BARDGETT; VAN DER PUTTEN, 2014). As taxas e magnitudes dessas funções e serviços ecossistêmicos são determinadas, portanto, pela abundância, biomassa corporal e diversidade da biota (DE VRIES et al., 2013; FERRIS; TUOMISTO, 2015; VAZQUEZ et al., 2019).

Entre as ameaças à biodiversidade do solo e à sua contribuição ao ecossistema, a mudança no uso da terra devido à intensificação agrícola e subsequente perda de matéria orgânica, como também mudanças climáticas estão entre os principais fatores (LI et al., 2016). De fato, nas últimas décadas, vêm crescendo estudos mostrando que perturbações antrópicas e mudanças climáticas são capazes de alterar não apenas a população de um grupo funcional, mas também a comunidade do solo como um todo, reduzindo assim a magnitude do serviço ecossistêmico coordenado por eles (BARNES et al., 2017; HOOGEN et al., 2019; NEWBOLD et al., 2015).

A transformação de um ecossistema natural para o uso intensivo do solo (atividade agrícola) resulta em uma redução da biomassa (atividade metabólica), abundância e diversidade da microbiota (bactérias, fungos e seus consumidores) em função das ações diretas sobre as propriedades físico-químicas do solo (ADAMCZYK; KITUNEN; SMOLANDER, 2013; LIU et al., 2016). Por exemplo, a remoção da vegetação nativa e em seguida atividade agrícola

reduzem a disponibilidade de recursos (matéria orgânica) que são necessários para o sucesso da atividade e desenvolvimento da microbiota do solo (BARNES et al., 2017; MBUTHIA et al., 2015). Como consequência disso, o acúmulo de carbono orgânico e nitrogênio do solo diminuem, afetando negativamente a ciclagem de nutrientes (ITO et al., 2013; MANN et al., 2019).

Por sua vez, as mudanças climáticas, tais como a redução da precipitação e aumento da temperatura, afetam a biodiversidade do solo (DARBY et al., 2011; FREY; ELLIOTT; PAUSTIAN, 1999), agindo, principalmente a interação consumidor-recurso, com consequências na estrutura da rede alimentar e o fluxo de energia e matéria através dos ecossistemas (EISENHAUER et al., 2012; PAPATHEODOROU; ARGYROPOULOU; STAMOU, 2004; SCHWARZ et al., 2017). A precipitação, por exemplo, interfere enormemente no crescimento das plantas, no teor de matéria orgânica e nitrogênio do solo, na mineralização, bem como, na atividade microbiana (SONG et al., 2017; STRICKLAND; ROUSK, 2010). Quanto à temperatura, esta desempenha um fator importante na regulação do ciclo biogeoquímico nos ecossistemas terrestres. A decomposição da serapilheira, a respiração do solo e as atividades metabólicas dos organismos do solo são alguns dos exemplos de processos regulados pela temperatura ambiental (BAI et al., 2010).

*Diversidade de nematoides e seu potencial como bioindicadores ambientais*

Os nematoides são os animais mais abundantes e diversificados do planeta e estão amplamente distribuídos por todos os biomas terrestres e aquáticos (HOOGEN et al., 2019). São invertebrados pertencentes ao filo Nematoda o qual compreende as classes Chromadorea e Enoplea (DE LEY; BLAXTER, 2004). Os nematoides pertencentes à classe Chromadorea são quase exclusivamente terrestres, raramente sendo de água doce ou marinha. Já os nematoides pertencentes à classe Enoplea ocupam nichos nos três habitats (BONGERS; FERRIS, 1999). Estimam-se a existência de 200 mil a 1 milhão de espécies de nematoides, das quais menos de 35 mil já foram descritas (DE LEY; BLAXTER, 2004).

Os nematoides são seres, em geral, microscópicos e que apresentam uma diversidade de formas corporais e hábitos alimentares, além de possuírem a capacidade de se adaptarem a variadas condições ambientais de todas as latitudes do planeta onde haja carbono orgânico (BOAG; YEATES, 1998; BONGERS; BONGERS, 1998; HOOGEN et al., 2019; SONG et al., 2017). Como consequência da flexibilidade evolutiva, os mesmos desempenham uma variedade de funções o que permite estabelecerem interações entre si, com a biota e com o ambiente

(HOOGEN et al., 2019).

Quanto aos nematoides do solo, as adaptações corporais, principalmente as do aparato alimentar, permitiram ocuparem posições-chave nas redes alimentares do solo e explorar as diversas fontes de alimentos, por meio do parasitismo de vegetais e de animais, da ingestão de microoganismos (bactérias e fungos) e da predação de nematoides e outros microinvertebrados (YEATES et al.,1993). Por isso, os nematoides são classificados em cinco grupos tróficos: bacteriófagos, fungívoros, parasitas de plantas, onívoros e predadores (BONGERS; BONGERS, 1998; YEATES et al.,1993).

Além disso, os nematoides são classificados quanto a suas estratégias de vida. Bongers (1990) classificou os mesmos em: em colonizadores (c) e persistentes (p), sendo os colonizadores, equivalentes aos estrategistas “r” e os persistentes aos estrategistas “K”. Os colonizadores (c) produzem muitos ovos pequenos, apresentam ciclo de vida curto e exploram rapidamente hábitats ricos em nutrientes. Em contraste, os persistentes (p) produzem poucos ovos, apresentam longo ciclo de vida e dificilmente reagem positivamente a condições de alta disponibilidade de nutrientes. Nesse sistema de classificação, os nematoides são alocados em uma escala colonizador-persistente (c-p), que varia de 1 (c) a 5 (p). Nematoides com valores c-p 1 e 2 são considerados colonizadores e possuem tolerância a diversos distúrbios ocorridos no ambiente e nematoides com valor c-p 4 e 5 são as classes consideradas persistentes, tendo como característica sensibilidade à distúrbios. Nematoides com valor c-p 3, possuem características entre os grupos 2 e 4, sendo relativamente sensíveis a distúrbios (BONGERS, 1990; BONGERS; BONGERS, 1998).

Sendo assim, o fato de viverem em comunidades multiespecíficas, em que cada espécie desempenha uma função e apresenta sensibilidade diferenciada aos estímulos do ambiente (BONGERS; BONGERS, 1998; HOOGEN et al., 2019; NEHER, 2001), além de exercerem importantes papéis no funcionamento do ecossistema, incluindo decomposição de material orgânico, rotatividade de nutrientes e transferência de energia ao longo da cadeia alimentar (FERRIS, 2010a; FERRIS, 2010b; FERRIS; SÁNCHEZ-MORENO; BRENNAN, 2012; FERRIS: TUOMISTO, 2015; ZHANG et al., 2017) confere aos nematoides a qualidade de excelentes indicadores de distúrbios ambientais (BONGERS; BONGERS, 1998; BONGERS; FERRIS, 1999; NEHER, 2001; YEATES, 2003), tais como mudanças climáticas, impactos provocados por práticas agrícolas, por poluentes químicos e por outras atividades antropogênicas em ambientes terrestres e aquáticos (ws).

Entre os nematoides do solo, os bacteríofagos e fungívoros são intermediários-chave nos processos de decomposição e ciclagem de nutrientes; eles aumentam a renovação

bacteriana e aceleram a decomposição da matéria orgânica do solo (BARDGETT; CHAN, 1999; NEHER, 2001; YEATES, 2003). Além disso, esses nematoides transportam bactérias ao longo da área para novos recursos, acelerando ainda mais as taxas e a magnitude da atividade de decomposição e ciclagem de nutrientes (BROWN et al., 2004; FU et al., 2005; ZHANG et al. 2017). Além disso, como os nematoides microbianos ingerem mais nutrientes do que o necessário, os excessos são excretados de forma mineral ou facilmente mineralizável e, portanto, podem aumentar o crescimento das plantas (FERRIS; VENETTE; LAU, 1997; NEHER; WEICHT; BARBERCHECK, 2012). Já os nematoides onívoros e predadores, também estão envolvidos na ciclagem de nutrientes através de um processo mais indireto que envolve a atividade de predação (FERRIS, 2010b; FERRIS; SÁNCHEZ-MORENO; BRENNAN, 2012).

Os nematoides também são bioindicadores úteis da abundância e atividade de outros organismos do solo que fornecem serviços similares (FERRIS, 2010a; FERRIS; SÁNCHEZ-MORENO; BRENNAN, 2012). Com base nas taxas de abundância e rotatividade, os nematoides do solo podem ser responsáveis por até 25% da mineralização de nitrogênio no solo (FERRIS, 2010a; FERRIS; SÁNCHEZ-MORENO; BRENNAN, 2012; FERRIS; VENETTE; SCOW, 2014).

Diante disso, índices sobre a atividade metabólica de cada guilda funcional dos nematoides para a avaliação quantitativa da magnitude das funções do ecossistema no solo foram desenvolvidos. Ferris (2010b) elaborou o índice *metabolic footprint*, que é baseado na utilização de carbono no crescimento corporal e na respiração, fornecendo informações sobre as respostas da teia alimentar do solo aos recursos e sua contribuição para as funções e serviços do ecossistema (FERRIS; SÁNCHEZ-MORENO; BRENNAN, 2012; ZHANG et al., 2017). O *metabolic footprint* é dividido em: pegada de enriquecimento, representando a atividade metabólica dos nematoides que respondem rapidamente à entrada de recurso no solo (nematoides cp 1-2); pegada estrutural, representando a atividade metabólica dos nematoides onivoros-predadores (cp 3-5) que têm uma função reguladora na cadeia alimentar e são indicativos da abundância de organismos de funções semelhantes em não nematoides; e atividade metabólica dos bacteriófagos, fungivoros e parasitas de plantas, que são os indicadores de carbono e energia que entram na cadeia alimentar do solo através de seus respectivos canais de decomposição (FERRIS, 2010b).

Dada tais características apresentadas, o índice *metabolic footprint* é uma ferramenta sensível para indicar as respostas das cadeias alimentares do solo ao status dos nutrientes do solo e aos distúrbios ambientais (BHUSAL; TSIAFOULI; SGARDELIS, 2015; FERRIS,

2010b; FERRIS et al., 2001; FERRIS; SÁNCHEZ-MORENO; BRENNAN, 2012; ZHANG et al., 2015; ZHANG et al., 2017; ZHANG et al., 2019).

*O cenário da Caatinga e suas implicações sobre a estrutura da comunidade de nematoides e a saúde do solo*

A Caatinga é uma região ecológica bem reconhecida que fica localizada no interior do semiárido do Nordeste do Brasil, compreendendo uma área total de 912.529 km$^2$ (SILVA et al., 2018). A Caatinga é considerada um mosaico da floresta tropical sazonalmente seca (PENNINGTON et al., 2009) que exibe pelo menos 13 fitofisionomias diferentes, abrangendo uma ampla gama de densidades e diversidades de plantas lenhosas (PRADO, 2003). A temperatura média é constante ao longo do ano, variando de 25 a 30 °C. No entanto, a precipitação média anual não é constante, variando no ano em entre regiões. A maior parte da região (68,8%) recebe entre 600 e 1.000 mm de chuva por ano, com apenas 0,6% recebendo menos de 400 mm e 1,6%, mais de 1.200 mm (SILVA et al., 2018). A maior parte da chuva está concentrada em três meses consecutivos, embora sejam frequentes grandes variações anuais e secas recorrentes (SILVA et al., 2018). A vegetação da Caatinga varia de mata aberta a florestas altas e secas (SILVA et al., 2018). No total, a flora da Caatinga é muito rica e diversificada com uma proporção relativamente alta de espécies endêmicas em comparação com outras florestas tropicais sazonalmente secas (SILVA et al., 2018).

Embora seja um ecossistema de extrema importância, a Caatinga é o terceiro ecossistema brasileiro mais ameaçado e ainda é o mais mal estudado e compreendido (SILVA et al., 2018). Os 27 milhões de pessoas que vivem na Caatinga são altamente dependentes de seus recursos naturais para sua subsistência, como por exemplo, extração de madeira, criação de caprinos e bovinos e agricultura, o que tem resultado em uma crescente degradação (LEAL et al., 2005; RIBEIRO et al., 2015; RITO et al., 2017). Além disso, a Caatinga é um dos seis ecossistemas com maior vulnerabilidade intrínseca à variabilidade climática (BURKETT et al., 2014; SEDDON et al., 2016). Modelos climáticos preveem consistentemente uma redução nos níveis de precipitação (22%) e um aumento na temperatura nos próximos anos (MAGRIN et al., 2014).

Apesar dos achados recentes sobre os impactos negativos dos fatores climáticos e antrópicos para a composição taxonômica e filogenética de comunidades de plantas (RIBEIRO et al., 2015; RIBEIRO-NETO et al., 2016; RITO et al., 2017), bem como para as comunidades animais (RIBEIRO-NETO et al., 2016; OLIVEIRA et al., 2017; OLIVEIRA et al., 2019),

algumas questões permanecem em aberto, principalmente no que diz respeito à resposta do solo à ação individual e interativa desses fatores. Diante desse contexto, os nematoides se apresentam como um modelo de biota do solo útil para compreender as respostas da biodiversidade do solo e seu funcionamento frente aos diferentes tipos de distúrbios antrópicos e às condições climáticas na Caatinga.

Quaisquer alterações ou distúrbios ambientais que afetem a composição ou fisiologia da vegetação e / ou textura do solo, como a conversão da vegetação primária em usos agrícolas ou redução da umidade, podem alterar a composição taxonômica e a diversidade de grupos funcionais de nematoides (HOOGEN et al., 2019 SONG et al., 2017; ZHAO et al., 2011). Por exemplo, a redução da matéria orgânica do solo por meio da remoção da vegetação nativa diminui significativamente a atividade microbiana e a abundância de nematoides, especialmente algumas bactérias e bacteriofagos r-estrategistas (TREONIS et al., 2010; TREONIS et al., 2019). Por sua vez, o efeito do preparo do solo para a prática agrícola leva à redução da biomassa fúngica (DE VRIES et al., 2012; FREY; ELLIOTT; PAUSTIAN, 1999; WAGG et al., 2018) e, em seguida, dos nemátodos de alimentação fúngica k-estrategistas (TREONIS et al., 2010; TREONIS et al., 2019).

Já a temperatura e a precipitação são importantes fatores ambientais para a sobrevivência e reprodução de nematoides (NIELSEN et al., 2014; SONG et al., 2017; THAKUR et al., 2019). As mudanças climáticas podem ter impactos significativos no número e na composição da comunidade e atividades metabólica dos nematoides do solo (SIEBERT et al., 2019; THAKUR et al., 2017), uma vez que são essencialmente animais aquáticos que dependem do filme de água ao redor das partículas do solo para seu desenvolvimento e movimento através do solo (GRIFFITHS; CAUL, 1993).

Análises mais abrangentes, entretanto, dos fatores que governam a estrutura da comunidade de nematoides na Caatinga se faz necessária para o entendimento completo da transferência de energia e nutrientes nesses microhabitats.

# 3 LAND USE, SOIL PROPERTIES AND CLIMATE VARIABLES INFLUENCE THE NEMATODE COMMUNITIES IN THE CAATINGA DRY FOREST

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**Abstract**: 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.

**Keywords**: agriculture; anthropogenic disturbance; Nematoda; semi-arid ecosystem.

## 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 less than 1800 mm, and some forests have dry season lasting 3 to 6 months, receiving less than 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. Material 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 x 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 1,000 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 one minute. 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).

151 *2.4 Data Analyses*

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

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

165 To assess changes in genus diversity among the types of land use, we used Hill numbers (Hill,
166 1973) for each plot, of order 0 ($^0D$, species richness), 1 ($^1D$, exponential of Shannon entropy)
167 and 2 ($^2D$, Inverse Simpson concentration) (Jost, 2006, 2007), calculated with the "*entropart"*
168 package for R (Marcon et al., 2014). $^0D$ is not sensitive to species abundances and thus gives
169 a disproportionate weight to rare species (Jost, 2006). $^1D$ weights each species according to its
170 abundance in the community, interpreted as the number of 'common' or 'typical' species in
171 the community (Jost, 2006). Finally, $^2D$ favors abundant species, and is interpreted as the
172 number of 'very abundant' or 'dominant' species in the community. Then, a one-way
173 ANOVA was used to assess the differences in each level of diversity among the types of land
174 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.

## 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

200 the more acidic soils, with a high Al saturation (m%). The second axis described a soil
201 gradient also related to fertility, from soils with higher residual moisture to soils with a higher
202 sum of exchangeable bases, high cation-exchange capacity (CEC) and high concentrations of
203 Ca, Na, K and H (Table 1).

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

209 Only two variables (silt% and P) differed among the types of land use ($P < 0.02$). The AA
210 plots were characterized as basic soil, with more than twice the phosphorus content as that
211 found in the SF forest and NF plots. The SF and NF plots had acidic soils with lower silt
212 contents. The monthly rainfall ($P < 0.001$) and temperature ($P < 0.05$) differed among the types
213 of land use; in the NF, the rainfall was lowest and the temperature was highest (Table 1).
214

215 *3.2 Effects of land use on nematode community structure*

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

221 Total abundance of nematodes was significantly affected by types of land use $\chi^2 = 7.69$, P
222 <0.01; Fig. 2a). Abundance was highest in SF and lowest in AA. Among the nematode
223 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 $^{q}D$ (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).

## 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., 2008; 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,

348 soil moisture levels and living space. Together, these factors positively influence the
349 movement and reproduction of soil nematodes (Yeates, 1999; Cardoso et al., 2015).

350 The nematode composition and the low abundance in some of the NF plots were associated
351 with higher monthly mean temperatures. High temperatures result in a decrease in nematode
352 abundance, since plant cover decreases, allowing the soil to become overexposed and
353 consequently reducing the soil water content and limiting microbial growth and reproduction
354 (Song et al., 2017).
355

356 **5. Conclusions**

357 The history and types of land use affect the composition and structure of the nematode
358 community in the Caatinga. In this study, conversion of native Caatinga vegetation to crop
359 systems negatively affected the nematode community, once reduced the total abundance of
360 nematodes, bacterivores and omnivore-predators. However, these changes are reversible
361 through regeneration of secondary forest after the fields are abandoned. The nematode
362 community composition is strongly related to soil properties and climate variables in the
363 Caatinga, which suggests that these factors may be acting as important environmental filters
364 in structuring nematode communities in the SDTFs. It is important to note that these factors
365 cannot be analyzed separately in terms of their effects on the nematode community. These
366 must be analyzed in terms of their integrative effect, since land use, temperature and rainfall
367 affect the soil structure and consequently the nematode community structure. In general, our
368 study demonstrated that knowledge of the nematode community structure on a landscape
369 scale, and of the effect of climate and ecosystem properties on community structure, can be
370 used to predict the effect of changes in soil use, in climate, and other disturbances on soil
371 health in the Caatinga.
372

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**Figure legends**

**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).

**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.

**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.

**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

**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 |

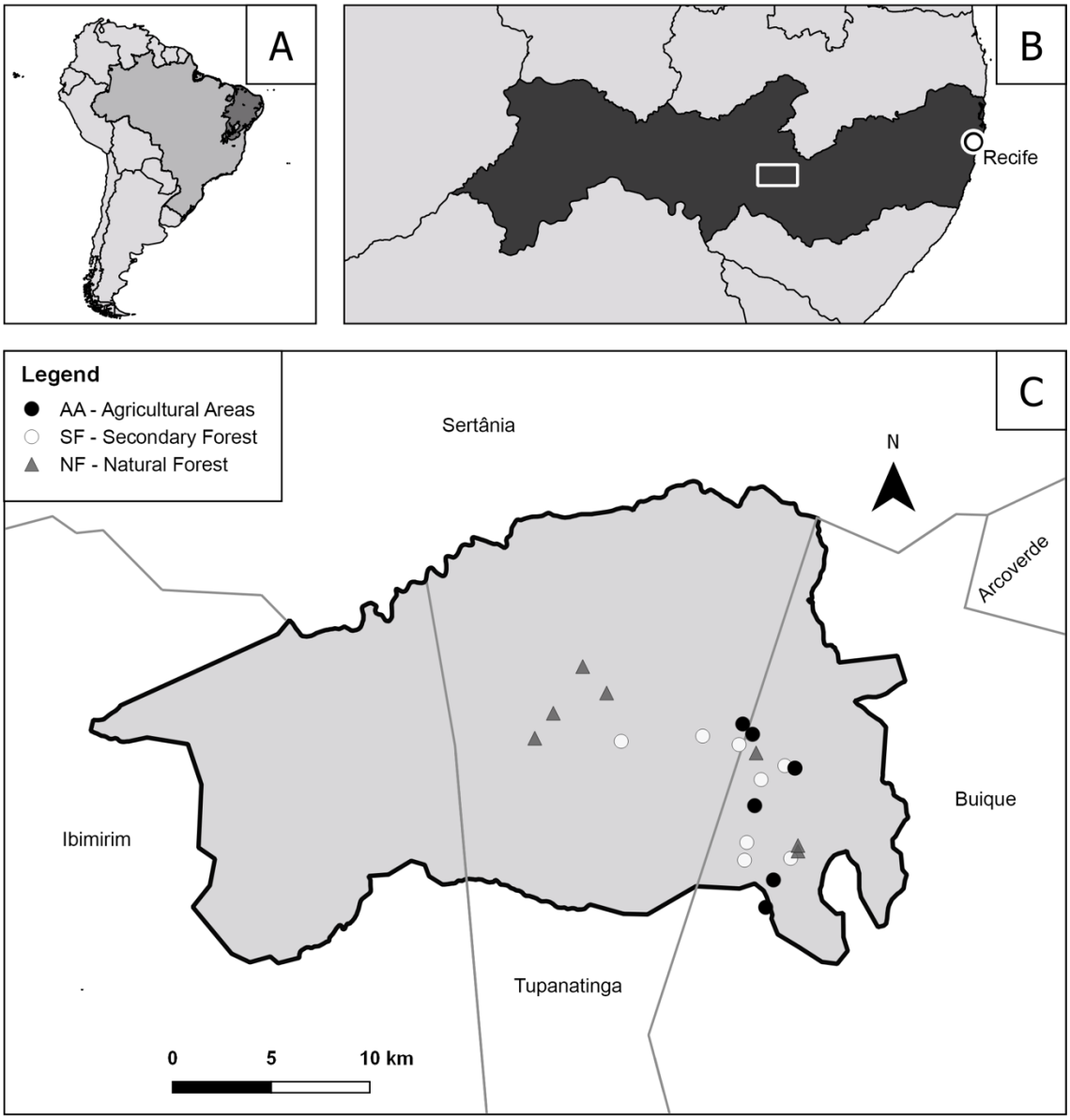

A
B
Recife
C
Legend
AA - Agricultural Areas
SF - Secondary Forest
NF - Natural Forest
Sertânia
N
Arcoverde
Buique
Ibimirim
Tupanatinga
0
5
10 km

Figure 1.

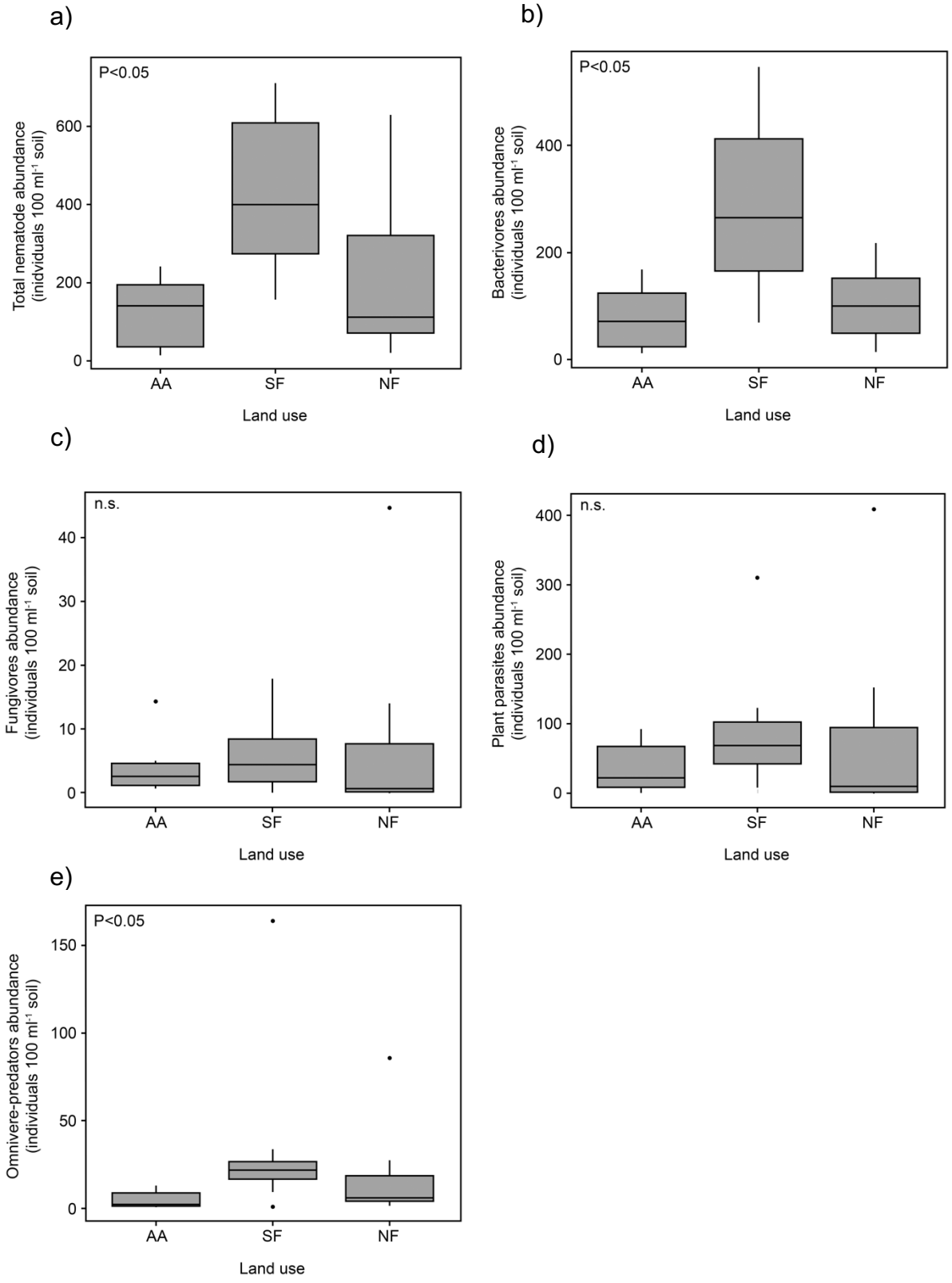

a)
P<0.05
Total nematode abundance (inidviduals 100 ml-1 soil)
0
200
400
600
AA
SF
NF
Land use
b)
P<0.05
Bacterivores abundance (individuals 100 ml-1 soil)
0
200
400
AA
SF
NF
Land use
c)
n.s.
Fungivores abundance (individuals 100 ml-1 soil)
0
10
20
30
40
AA
SF
NF
Land use
d)
n.s.
Plant parasites abundance (individuals 100 ml-1 soil)
0
100
200
300
400
AA
SF
NF
Land use
e)
P<0.05
Omnivere-predators abundance (individuals 100 ml-1 soil)
0
50
100
150
AA
SF
NF
Land use

Figure 2.

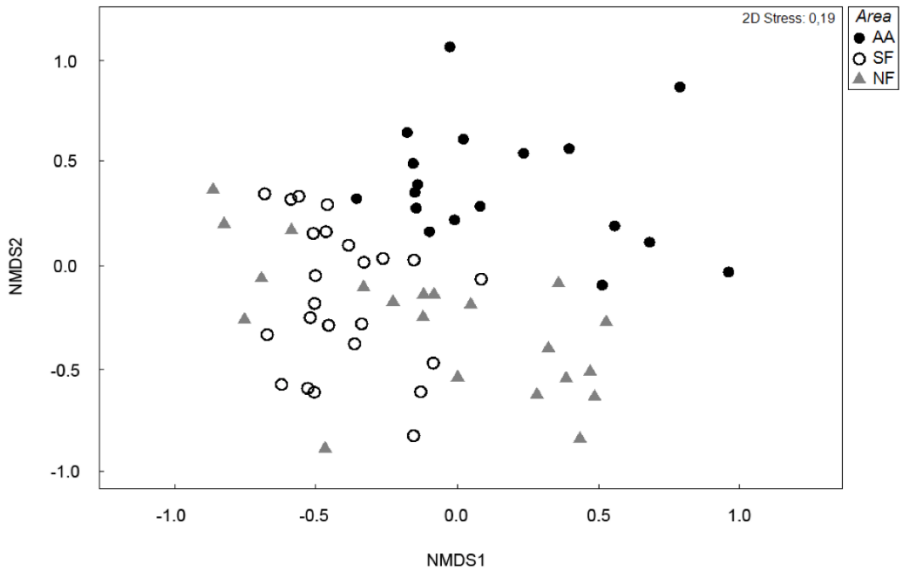

2D Stress: 0,19
Area
AA
SF
NF
1.0
0.5
0.0
-0.5
-1.0
NMDS2
-1.0
-0.5
0.0
0.5
1.0
NMDS1

Figure 3.

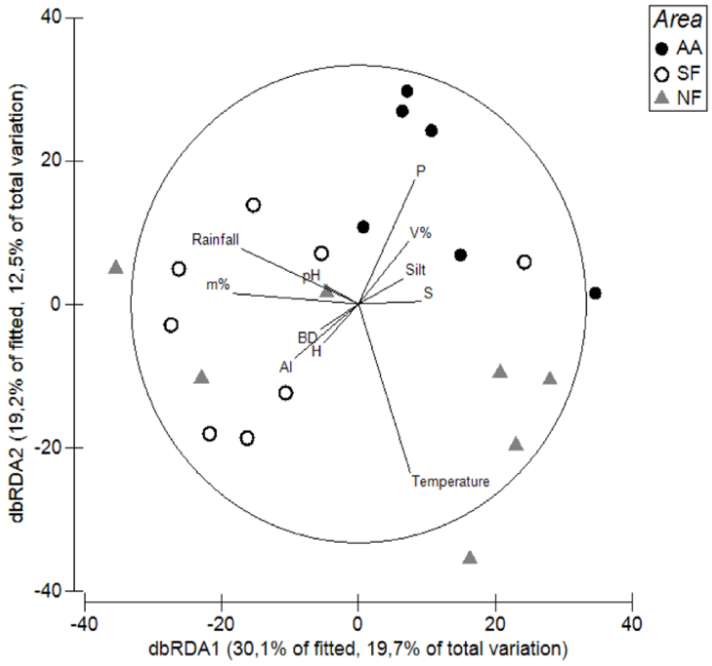

Area
AA
SF
NF
P
V%
Silt
S
Rainfall
pH
m%
BD
H
Al
Temperature
40
20
0
-20
-40
-40
-20
0
20
40
dbRDA2 (19,2% of fitted, 12,5% of total variation)
dbRDA1 (30,1% of fitted, 19,7% of total variation)

Figure 4.

## Supplementary materials

**Supplemental Table 1.** Description of the plots in agricultural areas (AA) and secondary forest (SF). The information was obtained from semi-structured interviews with local residents in 2015, in Catimbau National Park, Buíque, Pernambuco, Brazil.

| Plot | Period of abandonment (years) | Crop | Time of use |
|---|---|---|---|
| AA1 | N.A. | Cactus (*Opuntia* sp.), corn (maize) and bean | >20 years |
| AA2 | N.A. | Corn, manioc, bean, coconut, mango and cashew | >50 years |
| AA3 | N.A. | Manioc | 48 years |
| AA4 | N.A. | Manioc | 30 years |
| AA5 | N.A. | Corn and manioc | >35 years |
| AA6 | N.A. | Corn, manioc, bean, potato, tomato and coriander | 47 years |
| SF1 | 4 | Pasture | >30 years |
| SF2 | 6 | Corn | Crop failed |
| SF3 | 7 | Corn, watermelon and squash | >30 years |
| SF4 | 17 | Manioc | No information |
| SF5 | 18 | Manioc, corn and bean | Two plantings followed by abandonment |
| SF6 | 23 | Corn, bean, manioc, cactus and watermelon | Two plantings followed by abandonment |
| SF7 | 40 | Corn, bean and watermelon | No information |
| SF8 | 45 | Manioc and cactus | No information |

**Supplemental Table 2.** Relative abundance (%) of nematodes in the agricultural areas (AA), secondary forest (SF) and natural forest (NF), Catimbau National Park, Buíque, Pernambuco, Brazil. "–" not presented.

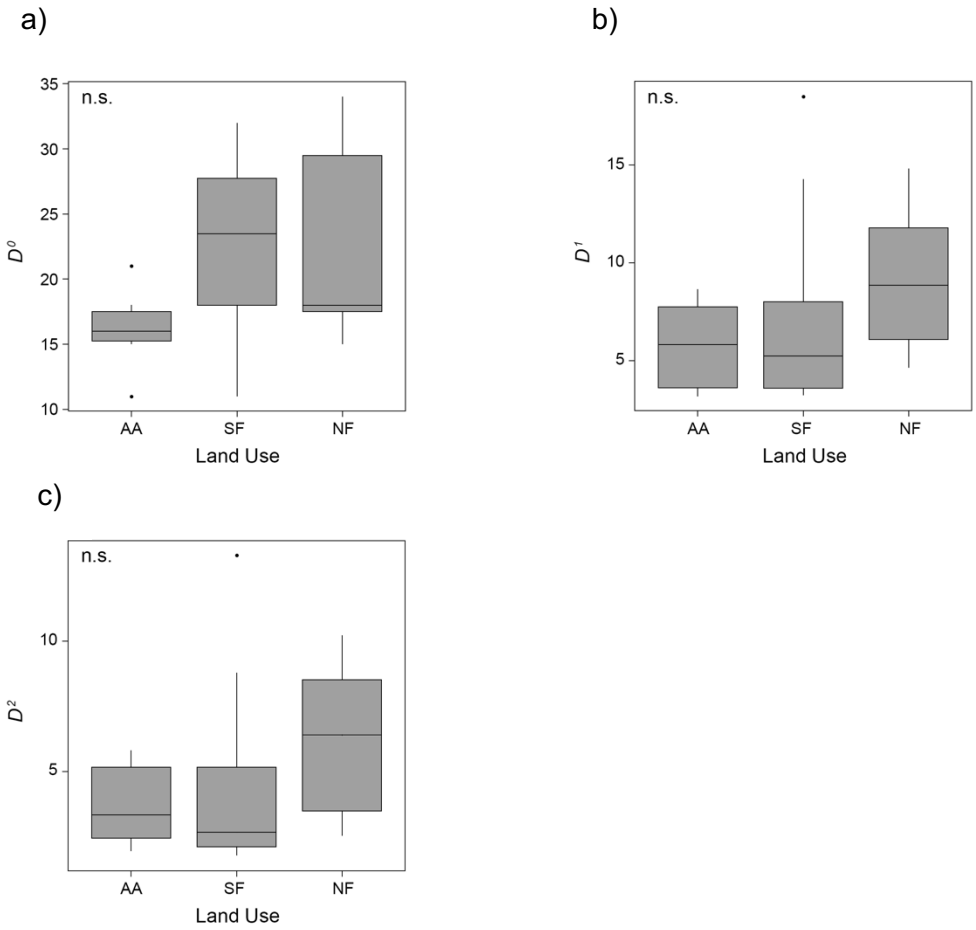
| Family | *Genus* | AA | SF | NF |
|---|---|---|---|---|
| Actnolaimidae | *Afractionobimis* | - | 0.06 | - |
| Anatonchidae | *Miconchus* | - | 0.26 | - |
| Anguinidae | *Ditylenchus* | 1.20 | - | 0.85 |
| Aphelenchidae | *Aphelenchus* | 2.24 | 1.09 | 1.96 |
| Aphelenchoididae | *Aphelenchoides* | - | 0.38 | 1.15 |
| | *Akrotonus* | 0.70 | 0.49 | 0.25 |
| | *Aporcelaimium* | - | 0.06 | 0.04 |
| | *Aporcelaimus* | 0.74 | 2.54 | 2.55 |
| Aporcelaimidae | *Makatinus* | - | 0.11 | - |
| | *Torumanawa* | - | 0.68 | 0.58 |
| | *Tubixaba* | - | 0.44 | 0.15 |
| | *Takamangi* | - | 0.08 | 0.13 |
| Brevibuccidae | *Plectonchus* | - | 0.06 | - |
| | *Acrobeles* | 44.20 | 53.64 | 29.96 |
| | *Acrobeloides* | 0.15 | 2.11 | 1.89 |
| | *Acrolobus* | - | - | 0.04 |
| | *Cephalobus* | 1.88 | 0.13 | 1.45 |
| | *Cervidellus* | 0.89 | 0.11 | 0.09 |
| | *Chiloplacoides* | - | - | 0.25 |
| | *Chiloplacus* | 0.10 | 0.08 | - |
| | *Cribronema* | - | - | 0.02 |
| | *Eucephalobus* | 1.21 | 0.41 | 0.30 |
| Cephalobidae | *Heterocephalobellus* | 0.33 | 1.29 | 0.90 |
| | *Macrolaimellus* | 0.06 | - | 0.13 |
| | *Medibulla* | - | 0.16 | - |
| | *Metacrobeles* | 8.95 | 3.76 | 1.94 |
| | *Nothacrobeles* | - | - | 0.13 |
| | *Paracrobeles* | - | - | 0.02 |
| | *Placodira* | - | 0.02 | 0.26 |
| | *Pseudacrobeles* | 0.06 | 0.91 | 0.40 |
| | *Scottnema* | 0.09 | 0.47 | 0.64 |
| | *Stegelletina* | - | 0.04 | 0.44 |

| | | | | |
|---|---|---|---|---|
| | *Teratolobus* | 0.04 | - | - |
| Chambersiellidae | *Zeldia* | 0.13 | 1.90 | 0.98 |
| | *Carcharolaimus* | 0.43 | 0.09 | 0.60 |
| | *Cornilaimus* | - | 0.06 | 0.28 |
| Criconematidae | *Criconema* | - | 0.74 | 2.92 |
| | *Criconemoides* | - | 1.11 | 3.27 |
| | *Hemicriconemoides* | - | - | 0.69 |
| | *Mesocriconema* | - | 2.88 | 5.13 |
| Diplogasteridae | *Diplogasteriana* | - | - | 0.09 |
| | *Diplogasteroides* | - | - | 0.14 |
| Diplogasteroididae | *Monobutlerius* | - | 0.07 | - |
| | *Fuchsnema* | 0.04 | - | - |
| Dolichodoridae | *Amplimerlinius* | - | 0.08 | - |
| | *Trophurus* | - | 0.04 | - |
| Dorylaimellidae | *Tylenchorhynchus* | - | 3.72 | 5.01 |
| | *Dorylaimellus* | - | 0.08 | - |
| Dorylaimidae | *Mesodorylaimus* | - | 0.08 | - |
| | *Mylodiscus* | - | - | 0.04 |
| | *Rhinodorylaimus* | - | 0.08 | - |
| | *Timminema* | - | 0.03 | - |
| Hoplolaimidae | *Helicotylenchus* | 9.56 | 12.09 | 7.78 |
| | *Hoplolaimus* | 1.10 | 0.74 | 5.26 |
| | *Peltamigratus* | - | - | 0.19 |
| | *Rotylenchulus* | 18.68 | - | 8.99 |
| Leptonchidae | *Capilonchus* | - | 0.09 | 0.21 |
| | *Gymnotyleptus* | - | - | 0.86 |
| | *Tylencholaimellus* | - | - | 0.06 |
| Longidoridae | *Longidorus* | - | 0.11 | - |
| Monhysteridae | *Monhystera* | - | 0.16 | - |
| Mononchidae | *Mononchus* | 0.24 | 0.82 | 0.36 |
| | *Mylonchulus* | 0.36 | - | - |
| | *Paramononchus* | - | - | 0.05 |
| Mydonomidae | *Prionchulus* | - | 0.18 | 0.08 |
| | *Dorylaimoides* | - | 0.05 | 0.08 |
| | *Mydonomus* | - | - | 0.08 |
| Mylonchulidae | *Sporonchulus* | 0.04 | - | - |

| | | | | |
|---|---|---|---|---|
| Nordiidae | *Oriverutus* | 0.50 | - | 0.09 |
| | *Longidorella* | - | - | 0.19 |
| Nygolaimidae | *Clavicaudoides* | - | - | 0.68 |
| | *Nygolaimellus* | - | 0.01 | - |
| Osstellidae | *Deficephalobus* | 0.04 | 0.06 | 0.02 |
| | *Drilocephalobus* | 0.68 | 1.71 | 3.73 |
| Panagrolaimidae | *Brevistoma* | - | - | 0.06 |
| | *Panagrellus* | 0.66 | - | 0.13 |
| | *Panagrobelus* | 0.06 | 0.49 | 1.88 |
| | *Panagrolaimus* | - | 0.03 | 0.23 |
| | *Panagrolobus* | 0.09 | - | - |
| | *Procephalobus* | 0.14 | - | - |
| Paraxonchidae | *Paraxonchium* | - | - | 0.30 |
| Plectidae | *Ereptonema* | 0.13 | 0.45 | 0.29 |
| | *Plectus* | - | 0.04 | 0.23 |
| Pratylenchidae | *Tylocephalus* | - | 0.03 | - |
| | *Pratylenchus* | 0.35 | 0.03 | 0.10 |
| Qudsianematidae | *Crassolabium* | - | 0.06 | 0.10 |
| | *Discolaimoides* | - | 0.22 | - |
| | *Ecumenicus* | - | 0.08 | - |
| | *Eudorylaimus* | - | 0.03 | - |
| | *Indokochinema* | - | 0.01 | - |
| | *Labronema* | 1.47 | 0.22 | 0.25 |
| | *Oonaguntus* | - | 0.01 | - |
| | *Thonus* | - | 1.56 | 1.77 |
| Rhabditidae | *Crustorhabditis* | 0.13 | - | - |
| | *Mesorhabditis* | 1.92 | - | - |
| | *Pelodera* | 0.13 | - | - |
| | *Rhabditoides* | - | - | 0.04 |
| | *Rhabditonema* | 0.09 | - | - |
| | *Rhabpanus* | 0.16 | - | - |
| Swangeriidae | *Paractinolaimus* | - | 0.07 | - |
| Tripylidae | *Trypitoides* | - | - | 0.08 |
| Tylencholaimellidae | *Agmodorus* | - | 0.02 | - |
| | *Goferus* | - | - | 0.08 |
| | *Tantunema* | - | 0.23 | 0.08 |

**Supplemental Table 3.** Hill number in each plot in the agricultural areas (AA), secondary forest (SF) and natural forest (NF), in the order: 0 ($^0D$, species richness), 1 ($^1D$, exponential entropy of Shannon) and 2 ($^2D$, inverse Simpson concentration), Catimbau National Park, Buíque, Pernambuco, Brazil.

| Plots | $^0D$ | $^1D$ | $^2D$ |
|---|---|---|---|
| AA1 | 16 | 4.3 | 2.9 |
| AA2 | 21 | 7.9 | 5.6 |
| AA3 | 16 | 8.7 | 5.8 |
| AA4 | 15 | 7.3 | 3.8 |
| AA5 | 11 | 3.2 | 2.3 |
| AA6 | 18 | 3.4 | 1.9 |
| SF1 | 32 | 14.3 | 8.8 |
| SF2 | 25 | 3.7 | 1.8 |
| SF3 | 27 | 5.8 | 2.8 |
| SF4 | 30 | 18.5 | 13.3 |
| SF5 | 11 | 3.3 | 2.6 |
| SF6 | 19 | 3.2 | 1.9 |
| SF7 | 22 | 4.7 | 2.2 |
| SF8 | 15 | 5.9 | 4.0 |
| NF1 | 17 | 6.3 | 4.3 |
| NF2 | 15 | 8.9 | 6.4 |
| NF3 | 18 | 12.7 | 10.2 |
| NF4 | 18 | 4.7 | 2.6 |
| NF5 | 27 | 5.9 | 2.5 |
| NF6 | 34 | 10.9 | 7.1 |
| NF7 | 32 | 14.8 | 10.0 |




**Supplemental Figure 1.** Hill's diversity associated with three categories of land use. Hill diversity indices represent the mean diversity per area and are weighted to the order of q, which reflects the sensitivity of the indices to the relative abundance of species: (a) $D^0$= is sensitive to rare species; (b) $D^1$= is sensitive to common species; and (c) $D^2$= is sensitive to highly abundant species. AA: Agricultural Areas; SF: Secondary Forest; NF: Natural Forest. n.s.= not significant.

# 4 EFFECT OF LAND USE AND RAINFALL ON THE STRUCTURE AND FUNCTION OF NEMATODE COMPONENTS OF THE SOIL FOOD WEB IN THE CAATINGA DRY FOREST

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**Abstract:** The anthropogenic disturbance and climate change alter the activity and functional composition of soil communities that are responsible for crucial ecosystem functions and services. However, effects of interaction of these factors on soil nematodes, which are bioindicators of soil quality and soil health, remain poorly understood. We investigated the effects of land use and seasonal effect on the structure and function of nematode components of the soil food web in Caatinga, north-eastern Brazil. The study was conducted in Catimbau

National Park, Pernambuco State, which covers 607 km$^2$ of Caatinga vegetation. Soil samples were collected in dry and rainy seasons in three types of land use: natural forest (NF), agricultural areas (AA), and secondary forest (SF). 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 seasons, respectively across different types of land use. The biomass carbon of total nematode, bacterivores, fungivores and omnivores-predators were affected by types of land use and seasonal effect. The enrichment and structure footprint were also affected by the type of land use and seasonal effect. The metabolic footprints of nematodes were higher in SF than in NF and AA, and higher in 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, representing the ecosystem service of nutrient mineralization, was related to the level of soil organic carbon. We found little evidence of interactive effects of land use and season effect on the metabolic footprint of soil nematode guilds. Our study indicates that change of land use, soil C and rainfall act independently on the structure and metabolic footprints of soil nematode food web in Caatinga. The vulnerability of metabolic footprints of nematodes in the soil food web to these factors impacts the functional magnitude of ecosystem services performed by each functional guild in Caatinga.

**Keywords:** anthropogenic disturbance; Caatinga; ecosystem function; metabolic footprints; Nematoda; semi-arid ecosystem.

## 1. Introduction

The soil biota is an essential component of soil ecosystems, mediating nutrient cycling and energy flow processes that ensures primary production, regulating climate change and sustaining biodiversity (Ferris, 2010a; de Vries et al., 2012; de Vries et al., 2013). However, anthropogenic disturbances (Barnes et al., 2017) and climatic changes (Schwarz et al., 2017) may affect processes they govern, and the ecosystem services that these processes underpin (Ferris, 2010a; de Vries et al., 2013; Zhao and Neher, 2013; Barnes et al., 2017). Intensive land use, for example, negatively affects organisms of the soil microfaunal food web and their participation in carbon (C) and nitrogen (N) cycling (de Vries et al., 2012). Climate change, on the other hand, affects the structure of the soil food chain, modifying predator-prey interactions, thus altering the flow of energy and matter through ecosystems (de Vries et al., 2012; Schwarz et al., 2017).

The biodiversity of Seasonally Dry Tropical Forests (SDTFs) has been impacted by exploitation and management, including grazing and agricultural practices, wood extraction and utilization of various forest resources (Bellard et al., 2012). In addition, it is projected that SDTFs will be subjected to increases in evaporation and temperature during the current century (Burkett et al., 2014), resulting in longer and more severe droughts that may affect the maintenance of their biodiversity and ecosystem services. Recent studies in SDTFs have shown the negative impacts of anthropogenic disturbance and rainfall variation on plant communities (Rito et al., 2017) and on ecosystem services provided by ants (Ribeiro-Neto et al., 2016; Oliveira et al., 2017; Oliveira et al., 2019). However, the combined effects on soil biodiversity of anthropogenic disturbance and climate change remain poorly understood and their consequences for ecosystem function are unknown.

Soil nematodes, are a major mesofauna component of soil food webs; they participate at many trophic linkages and are useful bioindicators of food web decomposition pathways, soil

nutrient status, environmental quality, contaminant effects and climate change (Bongers, 1990; Ferris et al., 2001; Siebert et al., 2019; Thakur et al., 2019). 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 (Yeates, 2003; Ferris and Bongers, 2006; Ferris, 2010b). Soil nematodes are involved in soil carbon (C) cycling in two contrasting ways: i) conserving C in body structure to sustain growth and generating products that can be sequestrated and ii) releasing C as $CO_2$ through respiration (Ferris, 2010b; Liang et al., 2017; Zhang et al., 2019).

Based on these two components (growth and respiration), Ferris (2010b) introduced the nematode metabolic footprint (NMF) concept of, which allows a functional quantification of biomass, metabolic activity and magnitude of carbon and energy flow in the soil food web (Ferris et al., 2012; Zhang et al., 2017). The metabolic footprints of nematodes, based on carbon utilization in production and respiration, can provide information on the responses of soil food web to resources and their contribution to ecosystem functions and services (Ferris et al., 2012). In addition, it is a sensitive tool for illustrating the responses of soil food webs to soil nutrient status and environmental stresses (Ferris et al., 2001; Zhang et al., 2017).

The Caatinga, a mosaic of SDTFs and scrub vegetation (Pennington et al., 2009; Silva et al., 2018) that covers 912,529 $km^2$ of north-eastern Brazil (Silva et al., 2018), is considered one of the most endangered ecosystems in Brazil (Banda et al., 2016). The extensive ranching, wood extraction and conversion to agriculture, have deforested 45% of Caatinga´s area (Silva et al., 2018). Under future climate change, the Caatinga is projected to receive a 22% reduction in rainfall (Magrin et al., 2014). Consequently, the Caatinga represents an excellent opportunity for examining how conversion to agriculture, soil nutrition condition and variation of rainfall in the SDTFs affects soil nematode assemblages and their magnitudes of ecosystem functions.

Therefore, we investigated the effect of land use and season effect (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 forests (Banda et al., 2016; Rito et al., 2017). It has been previously shown that conversion of native Caatinga vegetation to crop systems negatively affected the nematode community, once reduced the total abundance of nematodes, bacterivores and omnivore-predators (da Silva et al., 2019). However, it is unclear how representative this is on magnitudes of ecosystem functions provided by component organisms of the soil food web, since nematode abundance data do not account for respiratory attributes, body size or longevity of nematodes with different functional characteristics (Ferris, 2010b; Ferris et al., 2012). 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, metabolic activity and ecosystem function; (ii) natural regeneration of Caatinga after agriculture increases the soil fertility, and subsequently increases nematode biomass, metabolic activity and ecosystem function; (iii) reduced rainfall decreases the soil fertility (here represented by soil organic carbon), and subsequently decreases nematode biomass, metabolic activity and ecosystem function; (iv) the interactive effect of change of land use and change of rainfall levels will affect conditions for nematode biomass, metabolic activity and ecosystem function.

## 2. 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 (Sociedade Nordestina de Ecologia, 2002). The climate is hot. Mean

125 annual temperature ranges from 21 °C to 24 °C and mean annual rainfall ranges from 1100
126 mm in the southeast to 480 mm in the northwest (Sociedade Nordestina de Ecologia, 2002;
127 Rito et al., 2017). Most of the park has quartzolic sandy soils (70%), but planosols (15%) and
128 lithosols (15%) are also present (Sociedade Nordestina de Ecologia, 2002). The dominant
129 families of woody plants are Fabaceae, Euphorbiaceae, and Boraginaceae; on the surface of
130 the forest floor, species of Cactaceae, Bromeliaceae, Malvaceae, Asteraceae, and Fabaceae
131 dominate (Rito et al., 2017). The park was established in 2002 (Sociedade Nordestina de
132 Ecologia, 2002), but its original human inhabitants remain; they continue to hunt, graze
133 livestock, extract timber, collect firewood, practice subsistence agriculture, and harvest other
134 plant resources (Rito et al., 2017). Their historical presence has resulted in an extensive
135 mosaic of differential land use and anthropogenic pressure on the biota.

136

137 *2.2. Experimental design and sampling*

138 Soil samples were collected in two periods: in the dry season in November, 2015 and in the
139 rainy season in May, 2016. The monthly mean rainfall data for each plot in and different
140 sampling season (dry and rainy season) were obtained from the global data repository for
141 climate, WorldClim (Hijmans et al., 2005), with a special resolution of 30-arc seconds or
142 approximately 1 km along the equator (www.worldclim.org), using the software QGIS 2.18
143 with the complement “Point sampling tool”
144 (https://github.com/borysiasty/pointsamplingtool). The monthly mean rainfall in the dry
145 season ranged from 21 to 23 mm and in the rainy season, 47 mm to 98 mm (Hijmans et al.,
146 2005).

147 Soil samples were collected on 21 plots (each 50 x 20 m, separated from each other by at least
148 2 km) with different types and history of land use: (i) seven plots in areas with old-growth
149 vegetation that had not experienced slash-and-burn agriculture for at least 50 years (Natural

150 forest – NF); (i) six plots with active *slash-and-burn* agriculture (Agricultural Areas – AA);
151 and (ii) eight plots of secondary forest regenerating after abandonment of *slash-and-burn*
152 agriculture (Secondary Forest – SF), with successional ages from 4 to 45 years.

153 In each plot, three soil samples (for fauna analysis) and one sample (for analysis of soil
154 properties) were collected, each a composite sample from five randomly located sampling
155 points. The distance between each sample was 10 m. Each subsample was collected with a
156 cylindrical collector, at a depth of 0-30 cm. The subsamples were mixed and a 1,000 ml
157 aliquot was packed in a polyethylene bag labeled with the sample information. The samples
158 were collected at points close to shrub areas, in the crown projection line, where younger and
159 more active roots can be found (Barker, 1985).

160

161 *2.3. Nematode community analysis*

162 The nematodes were extracted from 300 ml of fresh soil from each sample by combination of
163 *flotation, sedimentation and sieving* technique (Flegg and Hooper, 1970) and centrifugal
164 sucrose flotation (Jenkins, 1964). Nematode abundance was expressed as the number of
165 individuals per 100 ml of dry soil, and at least 100 nematodes from each sample were
166 identified to genus using an inverted microscope at x400 and x1000 magnification.

167 The nematodes were assigned to a functional guild matrix of trophic group: bacterivores,
168 fungivores, plant parasites and omnivore-predators and colonizer-persister (cp) scale value of
169 life-course strategies (1-5) (Bongers, 1990; Yeates et al., 1993; Bongers and Bongers, 1998).
170 Nematodes in cp 1-2 have short generation duration, high fecundity, and are regarded as
171 “enrichment opportunists” and tolerant to disturbance and can be ascribed to r-strategists. In
172 contrast, nematodes of cp 3-5 have long life cycles, large bodies, low reproduction rates and

173 which are very sensitive to environmental disturbances resembling K-strategists (Bongers,
174 1990; Bongers and Bongers, 1998).

175 After identification, the length (L) and maximum body diameter of all identified adult
176 nematodes in each soil sample were determined using an ocular micrometer. Nematode fresh
177 weight was calculated using the formula:

178 $$W = \frac{(L\,3/a2)}{(1.6\,x\,10^{6})}$$

179 where *W* is the fresh weight (µg) of a nematode individual, and *L* and *a* are its body length
180 (µm) and greatest body diameter (µm), respectively. Assuming dry weight of a nematode as
181 20% of the fresh weight, and carbon (C) in the body as 52% of the dry weight (Ferris, 2010b),
182 total nematode biomass C was calculated as 52 % × 20 % $W_t$/100 (µg ml $^{-1}$), where $W_t$ is the
183 fresh body weight (Ferris, 2010b).

184 To assess the magnitudes of ecosystem functions provided by nematode components of the
185 soil food web on each plot of the different types of land use, the nematode metabolic footprint
186 (NMF) was calculated using the formula:

187 $$NMF = \Sigma\left(Nt\left(0.1\frac{Wt}{mt} + 0.273\,(W^{0.75})\right)\right),$$

188 where *Nt* is the number of taxa in each trophic group of interest, $W_t$ represents the body
189 weight and *mt* is the cp values of genus *t*, respectively (Ferris, 2010b; Ferris et al., 2012). The
190 weight of life-time C mineralized by each taxon is derived from the molecular weights of C
191 and $O_2$, as 12/44 or 0.273 of the mass of $CO_2$ evolved (Ferris, 2010b). The NMF has a
192 production component (the lifetime amount of C partitioned into growth and egg production)
193 and a respiration component (the C utilized in metabolic activity) (Ferris, 2010b).

194 The NMF was divided into: enrichment footprint (efootprint), representing the metabolic
195 footprint of those nematodes most rapidly responsive to resource enrichment (cp 1-2);
196 structure footprint (sfootprint), representing the metabolic footprint of higher trophic (cp 3–5)
197 levels which have a regulatory function in the food web and which are indicative of the
198 abundance of organisms of similar functions in non-nematode; and bacterial footprints (BF
199 fooprint), fungal footprints (FF fooprint), and plant parasites footprints (PP fooprint), which
200 are the indicators of C and energy entering the soil food web through their respective channels
201 (Ferris, 2010b; Ferris et al., 2012).

202

203 *2.4. Soil chemical and physical properties*

204 The soil chemical and physical properties were performed at Instituto Agronômico de
205 Pernambuco (IPA), using methods detailed in EMBRAPA (2011). Bulk density was measured
206 by the compliant cavity method. The different texture classes were determined by the
207 densimeter method (EMPRAPA, 2011). Soil moisture was determined gravimetrically by
208 drying samples at 105°C for 24 h. Soil pH was measured in a soil–water suspension (water,
209 KCl or $CaCl^2$), 1:2.5, using the combined electrode potentiometer. The Cation-exchange
210 capacity (CEC) was determined by the KCl 1 mol $L^{-1}$ method. The soil organic carbon (soil
211 C) of each sample was determined using the $K_2Cr_2O_7$ oxidation–titration method
212 (EMBRAPA, 2011).

213

214 *2.5. Statistical analyses*

215 We performed a two-way ANOVA to evaluate the effect of type of land use (NF, SF and AA)
216 and seasonal effect (dry and rainy season) on the soil physical (bulk density and silt) and
217 chemical properties (pH, organic matter, soil C and CEC), using R version 3.4.2. Where

218 necessary and appropriate, the data were ln (x + 1) transformed to achieve normality prior to
219 statistical analysis.

220 To test the effect type of land use and seasonal effect on biomass C (μg $ml^{-1}$) and metabolic
221 footprints of soil nematode functional guilds we used general linear models (GLMs) with a
222 Gaussian error distribution and "identity" link. Model selection was conducted with the '*glm*'
223 function of the '*MuMIn*' package in R. We used a separate model for biomass C (μg $ml^{-1}$)
224 total nematode and each trophic group, and each category of metabolic footprint: efootprint:
225 enrichment metabolic footprints; sfootprint: structure metabolic footprints; BF footprint:
226 bacterivores metabolic footprints; FF footprint: fungivores metabolic footprints; PP footprint:
227 plant parasites metabolic footprint. We checked residuals for normality and homoscedasticity
228 in all models. We also checked for overdispersion in all models. The interactions between
229 type of land use and seasonal effect were also included in the models.

230 Finally, to verify the effect of soil C on enrichment metabolic footprint, irrespective of type of
231 land use that resulted in the carbon, a simple linear regression was performed using R. We
232 examined the relationships between soil C and enrichment metabolic footprint in dry and
233 rainy season, separately.

234

235 **3. Results**

236 *3.1. Effect of type of land use and seasonal effect on soil physical and chemical properties*

237 The soil bulk density, sand and pH did not differ among the types of land use or between the
238 dry and rainy season ($P > 0.05$). The silt was higher in AA and NF than in SF ($P < 0.05$). The
239 silt, clay and soil moisture were higher in rainy season than in dry season ($P < 0.01$). The
240 values of organic matter and soil C were affected by the types of land use, seasonal effect and
241 their interaction ($P < 0.01$). The highest values of soil organic matter and soil C were found in

SF, followed by NF and AA ($P < 0.001$), and higher in the rainy season ($P < 0.01$). The values of CEC were higher in the dry season ($P < 0.05$; Table 1).

*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 S1). Among these genera, in the dry season the predominant trophic group in relative abundance was the 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 rainy season the predominant trophic group also was bacterivores (54.8%), followed by plant parasites (22.7%), omnivore-predators (18.5%) and fungivores (4.0%). The bacterivore, *Acrobeles* (Cephalobidae), was dominant in all types of land use in both seasons (Table S1).

*3.3. Effect of type of land use and seasonal effect on nematode biomass carbon and metabolic footprints*

The biomass C of total nematodes, bacterivores, fungivores and omnivores-predators were affected by types of land use and seasonal effect (Table 2; Table S2). The biomass C of total nematode, bacterivores and omnivores-predators were higher in SF followed by NF and AA; and of fungivores was higher in NF followed by SF and AA in both seasons (Fig. 1). The biomass C of plant parasites was affected by the seasonal effect (Table 2; Fig. 1d; Table S2). There was an interactive effect of types of land use and seasonal effect only on biomass C of omnivores-predators (Table 2; Table S2). Specifically, the difference verified in biomass C of omnivore-predator among types of land use was greater in the rainy season than in the dry

265 season (Fig. 1e). The biomass C of total nematode and all trophic groups were higher in the
266 rainy season than dry season (Fig. 1).

267 The efootprint, based on the abundance and metabolic activity of the bacterivores (cp 1-2) and
268 fungivores (cp 2) functional guilds, was clearly affected by types of land use and seasonal
269 effect (Table 2; Table S3). The sfootprint, based on the abundance and metabolic activity of
270 higher trophic level predation (omnivores-predators), was also affected by types of land use
271 and seasonal effect (Table 2; Table S3). No effect of interactions between predictors variables
272 on efootprint and sfootprint was observed (Table 2) The sfootprint and efootprint were lower
273 in AA than in SF and NF, and higher in the rainy season. (Fig. 2a,b).

274 In analyzing the BF, FF and PP footprint, in all type of land use and in both seasons, we
275 verified that most resource assimilation into the soil food web was via the bacterial channel;
276 fungivore and plant parasites channels were less active (Fig. 2).

277 Analyzing each channel separately, we verified that BF and FF footprint were affected by
278 types of land use and seasonal effect (Table 2; Table S3). The BF footprint was higher in SF,
279 followed by NF and AA (Fig. 2c). However, FF footprint was higher in NF, followed by SF
280 and AA (Fig. 2d). There was an interactive effect of types of land use and seasonal effect on
281 FF footprint (Table 2). This result indicates that increase in FF footprint in the rainy season is
282 much higher in NF areas (Fig. 2d). The PP footprint was not affected by types of land use
283 (Table 2). However, the PP footprint was higher in rainy season (Fig. 2e). No effect of
284 interactions between predictors variables on BF and PP footprint were observed (Table 2).

285

286

287

288

289 *3.4. The relationship between nematodes microvores and total soil organic carbon*

290 In both, the dry and rainy seasons, efootprint increased with increasing levels of total soil C
291 (Fig. 3). However, the effect of soil C on efootprint was more significant in the rainy season
292 ($R^2 = 0.54$, $P < 0.001$; Fig.3a) than in the dry season ($R^2 = 0.21$, $P < 0.05$; Fig. 3b).

293

294 **4. Discussion**

295 Our results addressed how soil fertility, trophic structure and ecosystem function of soil
296 nematodes changed in function of the type of land use and seasonal effect in the Caatinga. In
297 the 21st Century, the increase in anthropogenic disturbance, reduced soil fertility and climate
298 change are the main threats faced by soil biota in dry tropical regions (Dirzo et al., 2011). The
299 study of these effects on the magnitude of the ecosystem function provided by the different
300 functional guilds of the soil nematodes, which are bioindicators of soil quality and soil health,
301 constitutes an important means for the assessment of the sequestration and redistribution of
302 minerals, carbon and energy in the soil (Ferris et al., 2012; Zhang et al., 2017) of the
303 Caatinga.

304

305 *4.1. Effect of type of land use and seasonal effect on microbial food web metabolic activities*

306 In our study, we found that soil C, biomass C and metabolic activity of nematode functional
307 guilds were negatively affected by the change of land use from undisturbed Caatinga to
308 agricultural production, confirming our first hypothesis. We found that the biomass carbon
309 and metabolic footprint of enrichment indicator nematodes were significantly lower in AA
310 than in NF and SF. Similarly, the levels soil C verified were significantly lower in the AA
311 plots compared to the other land uses. Among the functional groups of nematodes,
312 bacterivores and fungivores are always the first to respond to the removal of native vegetation
313 for agricultural use (Bongers and Bongers, 1998) due to the bottom-up effect resulting from a

314 change in food resources (Zhao et al., 2011; Ferris et al., 2012; Li et al. 2016; Zhang et al.,
315 2017). For example, agricultural practice reduces the amount of organic matter in the soil due
316 to the reduction of plant residues, implying a decrease in the abundance and metabolic
317 activities of microorganisms (bacteria and fungi), the food supply of bacterivores and
318 fungivores (Li et al., 2016; Luo et al., 2019). Thus, since the agricultural soil management
319 system is inadequate in the Caatinga, where cutting and burning agricultural practices are
320 adopted and there is a lack of an irrigation system and soil fertilization (Rito et al., 2017; da
321 Silva., 2019), soil C, which is mainly derived from plant residues, as well as microbial
322 residues and root exudates (Luo et al.,2019), is negatively affected. Therefore, we can infer
323 that the decrease in soil C availability due to intensive land use in the Caatinga provided little
324 resources for soil biota and consequently for nematode microbivores and this was reflected in
325 a lower amount of C flowing through food web decomposition channels and nutrient cycling
326 (Ferris et al., 2012; Zhang et al., 2017) in these areas.

327 Biomass C and metabolic footprint of structure indicator nematodes were also lower in AA
328 than in NF and SF. Two causes may have led to low values of the metabolic activity of
329 generalist and specialized predators (cp 3-5) with the change of land use from undisturbed
330 systems to agricultural production. First, omnivore-predators, which represent a high trophic
331 level in the soil food web (Yeates et al., 1993), are strongly affected by physical soil
332 disturbance, such as agricultural practices (Ferris et al., 2001; Zhang et al., 2017). Then,
333 reduced prey productivity and metabolic activity (efootprint) in AA become insufficient to
334 meet the needs of omnivore-predators and to maintain the metabolic balance of the soil food
335 web (Ferris, 2010b; Ferris et al., 2012; Zhang et al., 2019). As a consequence of this, the AA
336 areas present not only a lower magnitude of conservation of body C from the initial level to
337 the upper level of the soil food web through the reduction of prey-predator connections (Ferris
338 et al., 2012; Zhang et al., 2017), but also a reduction of the nutrient cycling through of the

339 indirect process of predation on microbial grazers and herbivore species (Ferris et al., 2012;
340 Sánchez-Moreno et al., 2018).

341 In line with our expectations on the second hypothesis, the abandonment of agricultural
342 practices and the natural regeneration of the Caatinga increased the supply of resources below
343 ground (organic matter and soil C) as well as the metabolic activity of nematodes and
344 ecosystem function. The response capacity of the structure and function of nematode
345 components of the soil food web to the increased availability of nutrients in the soil caused by
346 the reorganization of the plant community over time is in line with similar studies (Li et al.,
347 2015; Zhang et al., 2015; Hu et al., 2016). Our results suggest that the abandonment of
348 agricultural practices and the natural regeneration of Caatinga increased availability of C in
349 those plots, providing resources for soil biota (Hu et al., 2016), and this was reflected in the
350 magnitude of functional guilds of the nematode assemblages. In addition, our results suggest
351 that secondary regeneration can recover the ecosystem function of soil food web to a level
352 close to the areas that had not experienced agricultural practice in the Caatinga.

353 We also verified a strong influence of rainfall, here represented by the seasonal effect (dry
354 and rainy season) in the Caatinga, on the levels of soil C, biomass C, efootprint and
355 sfootprint, thus confirming our third hypothesis. We found an expressive increase (almost
356 double) in these exploratory variables with the transition from the dry to the rainy season.
357 Rainfall is considered one of the environmental variables that most affect nematode
358 abundance and metabolic activity (Nielsen et al., 2014; Song et al., 2017; Siebert et al., 2019).
359 It has been shown that high rainfall can increase net primary productivity below ground (Bai
360 et al., 2010), stimulates soil microbial biomass and provides more resources for soil fauna (Li
361 et al., 2016; Song et al., 2016). In addition, changes in precipitation directly alter the
362 availability of water in the soil and subsequently affect soil nematodes (Darby et al., 2011),
363 since they are aquatic organisms that depend on water films around the soil particles to move

364 and capture food (Wallace and Doncaster, 1964). Thus, in the Caatinga, during the rainy
365 season, the greater availability of resources released in the soil added to the presence of water
366 that reactivated the anhydrobiotic state of the nematodes (Bongers and Bongers, 1998)
367 positively impacted the metabolic footprint of all functional groups. Therefore, the increase in
368 the nematode's metabolic footprint corresponds to that found in the literature (Cesarz et al.,
369 2015; Mueller et al., 2016; Hoogen et al, 2019) and indicates that seasonality is a strong
370 predictor for altering soil fertility.

371

372 *4.2. Effect of type of land use and seasonal effect on carbon and energy flow among soil*
373 *microbial food web*

374 The lower values of the FF footprint and PP footprint in relation to the BF footprint found
375 across different types of land use and in both seasons indicate that direct plant parasite and
376 fungivore activity were not expressive channels of resources into the soil food web; most
377 resource assimilation was via the bacterial channel. This predominance of the bacterial
378 channel in the Caatinga is associated with the lifestyle of the bacterivores group found. We
379 verified that nematodes of the family Cephalobidae (cp-2) was the predominant trophic group
380 in both season. Due to their life strategy of adapting to any environmental condition,
381 cephalobid nematodes in arid environments influence the decomposition, regulating the
382 population density and metabolic activity of bacteria (Bongers and Bongers, 1998; Ferris,
383 2010a; Nielsen et al., 2014). Therefore, it is reasonable that bacterivores of the family
384 Cephalobidae be dominant in C storage among different trophic groups (Zhang et al., 2019).

385 Although, the BF footprint was the predominant decomposition channel, we found that the
386 type of land use and seasonal effect not only affected soil C, as already noted, but also the
387 biomass C and metabolic footprint of the BF, FF and PP, indicating the effect of independent
388 variables on these decomposition channels and on their respective food resources (bacteria,

fungi and plant roots). This is due to the fact that the flow of resource and energy through the soil food web is mainly driven by the food interrelationship between soil biota communities (Butenko et al., 2017).

Our study revealed that both BF and FF footprint decreased with the change in land use from NF to AA, but increased with natural regeneration process (SF), and were higher in the rainy season than in the dry season. In this way, we also found support for our hypotheses regarding the decomposition channel. Our results showed that the physical disturbance and reduction of resources and nutrients available in the soil caused by agricultural activity were more evident on the biomass C of the fungivores and FF footprint than on the biomass C of the bacterivores and BF footprint. The varied behavior between BF and FF footprint in relation to agriculture may be associated with difference in the growth forms of fungi and bacteria (Hendrix et al., 1986; Strickland and Rousk, 2010; Geisen, 2016). For example, factors that physically disturb the soil cause direct damage to the fungus mycelia, since they present a form of hyphal growth (Hendrix et al., 1986). Bacteria, on the other hand, are little affected by physical disorder, since they are present as individual cells (Hendrix et al., 1986). However, the reduction in the BF footprint found with the change in land use from NF to AA can be attributed to the fact that bacterial biomass is strongly affected by the reduction of organic matter input (Strickland and Rousk, 2010; Pan et al., 2016). In general, the negative effect caused by the removal of native vegetation for agricultural activity, verified by the reduction of BF and FF footprint, nematode indicators of C and energy entering the soil food web through their respective channels, reflects the reduction of primary decomposers, decomposition of soil organic matter and mineralization rates of nutrients available for plant growth (Ferris, 2010b; Ferris et al., 2012; Zhang et al., 2017).

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 SF plots increased C and energy

414 flow into the soil food web. However, we found that biomass C of the bacterivores and BF
415 footprint recovered from the stress more quickly than biomass C of the fungivores and FF
416 footprint. Once again, the varied increase between BF and FF footprint in front of natural
417 regeneration of Caatinga after agriculture is associated with difference in the growth forms of
418 fungi and bacteria in the face of changing land use and nutrient availability (Hendrix et al.,
419 1986). Generally, fungal-based soil food webs recover slowly after related disturbances
420 because slow-growing organisms, including fungi and fungal feeding fauna, tend to be more
421 resistant (that is, they are more able to withstand a disturbance). In contrast, bacteria and
422 bacterivores, which are fast-growing organisms, tend to be more resilient (i.e., higher
423 recovery rate after a disturbance) (de Vries et al., 2012; Rivest et al., 2015; Wagg et al.,
424 2018).

425 There was no difference in the biomass C of plant parasites and PP footprint across different
426 types of land use, but between the dry and rainy seasons. The PP footprint was higher in the
427 rainy season. The strong influence of precipitation on the PP footprint is due to the fact that
428 plant parasitic nematodes are active in the moist rhizosphere, as they depend on the water
429 around the plant's root for their survival and reproduction (Song et al., 2017). Our results
430 indicate that the metabolic activity of plant parasites is more related to root activation, caused
431 by increased precipitation, than to anthropogenic disorders (Scharroba, 2016). In addition,
432 with the growth of vegetation, the release of organic matter increases (Pan et al., 2016). The
433 root growth may have increased under the influence of rainfall in these low humidity soils,
434 such as the Caatinga, allowing the proliferation of plant parasitic nematodes.

435 In our study, we found that there was little interactive effect of the type of land use and
436 precipitation on the metabolic activity of the different functional groups in the Caatinga.
437 Despite this, it is evident the vulnerability of these functional groups and their ecosystem
438 functions in face of anthropogenic disturbances and the climatic changes in these areas.

*4.3. The relationship between nematodes microvores and total soil organic carbon*

In our study, we found that 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 (Franzluebbers, 2010), the positive relationship of efootprint and soil C indicates that the greater the availability of C in the soil, the greater the abundance of soil microorganisms and, therefore, resources for microbivore nematodes (Ferris et al., 2001; Zhang et al., 2017). In addition, it also indicates the response of the opportunistic bacterivore and fungivore nematodes 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 (Zhang et al., 2019).

## 4. Conclusions

Our result showed that the type of land use and seasonal effect in the Caatinga affected the soil organic carbon levels, structure and function of nematode components of the soil food web. More specifically, we found that the conversion of native Caatinga vegetation to crop systems reduced soil organic carbon, as well as the biomass carbon and metabolic footprint of enrichment and structure indicator nematodes. Thus, agricultural land use has not only affected resource entry into the soil food web and ecosystem service of nutrient mineralization, but resources that are transferred to higher trophic links. On the other hand, regeneration of secondary forest after the agriculture disturbance increased the soil organic carbon, enrichment and structure metabolic footprint, indicating that the structure and function of the soil food web has the ability to recover after a disturbance. We also found that precipitation levels strongly affected the soil organic carbon, biomass carbon and metabolic footprint of the functional nematode guilds. Higher levels of precipitation increased the availability of soil organic carbon, thus providing resources for soil biota and this was

464 reflected in the magnitude of the ecosystem function of the functional guilds of the nematode
465 assemblages. Most resource assimilation and energy flow into the soil food web in Caatinga
466 was via the bacterial channel; plant parasitic and fungivore channels were less active. Finally,
467 the enrichment footprint was related with the level of total soil carbon. We found little
468 evidence of interactive effects of land use and season effect on the metabolic footprint of soil
469 nematode guilds. However, our findings of negative effects of agricultural land use and
470 reduced rainfall on the nematode components of the soil food web in Caatinga provide
471 important insights about the impact of anthropogenic disturbance and climate change on the
472 soil health in the SDTFs.
473

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483

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**Table 1.** Mean values (±SD) of soil physical and chemical properties in the natural forest (NF), agricultural areas (AA) and secondary forest (SF) in dry and rainy season in the Catimbau National Park, Pernambuco, Brazil.

| Soil properties | Dry season | | | Rainy season | | | Land use | Seasonal effect | Land use x seasonal effect |
|---|---|---|---|---|---|---|---|---|---|
| | NF | AA | SF | NF | AA | SF | | | |
| Bulk Density (kg/dm$^3$) | 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 ± 1.51a | 2.66 ± 1.00a | 0.88 ± 0.22b | 4.28 ± 1.96 | 5.83 ± 2.22 | 2.75 ± 1.5 | < 0.05 | < 0.01 | 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 | < 0.01 | 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 | < 0.01 | ns |
| Organic matter (g /kg) | 10.88 ± 1.60a | 9.90 ± 2.30a | 22.76 ± 2.28b | 14.90.18 ± 1.67 | 10.44 ± 1.22 | 29.96 ± 0.58 | < 0.001 | <0.01 | <0.01 |
| Organic Carbon (g/ kg) | 5.60 ± 3.73a | 6.43 ± 3.90a | 19.09 ± 8.43b | 17.90 ± 6.11 | 5.05 ± 2.71 | 18.61 ± 5.60 | < 0.001 | < 0.01 | <0.01 |
| Cation-exchange capacity (cmol$_c$ /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 2.** Chi-squared values ($X^2$) of the generalized linear models for the effects land use, seasonal effect (dry and rainy) and their interaction on soil nematode biomass carbon (µg $ml^{-1}$) and metabolic footprints (µg C $ml^{-1}$ soil) in the Catimbau National Park, Pernambuco, Brazil. *p < 0.05; ** p < 0.01; ***p < 0.001.

| Metabolic footprints | Land use | Seasonal effect | Land use x Seasonal effect |
|---|---|---|---|
| | $X^2$ | $X^2$ | $X^2$ |
| Nematode-C | 4.58** | 17.90*** | 0.05 |
| Bacterivores-C | 8.86*** | 11.20*** | 0.07 |
| Fungivores-C | 2.23* | 3.32* | 0.007 |
| Plant parasites-C | 0.005 | 4.08* | 0.42 |
| Omnivores-predators-C | 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 |

Nematode-C: biomass carbon of total nematode; bacterivores-C: biomass carbon of bacterivores; fungivores-C: biomass carbon of fungivores; plant parasites-C: biomass carbon of plant parasites; omnivores-predators-C: biomass carbon of omnivores-predators; efootprint: enrichment footprint; sfootprint: structure footprint; BF footprint: bacteriovores footprints; FF footprint: fungivores footprints; PP footprint: plant parasites footprints.

**Figure legends**

**Fig. 1.** Effect of land use and seasonal effect on biomass carbon of nematodes and on each trophic group (μg $ml^{-1}$ soil) in the natural forest (NF), agricultural areas (AA) and secondary forest (SF) in dry and rainy season in the Catimbau National Park, Pernambuco, Brazil. (a) Nematode-C: biomass carbon of total nematodes; (b) BF-C: biomass carbon of bacterivores; (c) FF-C: biomass carbon of fungivores; (d) PP-C: biomass carbon of plant parasites; and (e) OP-C: biomass carbon of omnivore-predators.

**Fig. 2.** Effect of land use and seasonal effect on metabolic footprints (μg C $ml^{-1}$ soil) of soil nematode functional guilds in soils in the natural forest (NF), agricultural areas (AA) and secondary forest (SF) in dry and rainy season in the Catimbau National Park, Pernambuco, Brazil. (a) efootprint: enrichment footprint; (b) sfootprint: structure footprint; (c) BF footprint: bacterial footprints; (d) FF footprint: fungal footprints; and (e) PP footprint: plant parasites footprints.

**Fig. 3.** Linear relationships between enrichment metabolic footprint and soil carbon (g/ $kg^{-1}$): (a) Enrichment footprint and soil carbon in dry season; (b) Enrichment footprint and soil carbon in rainy season.

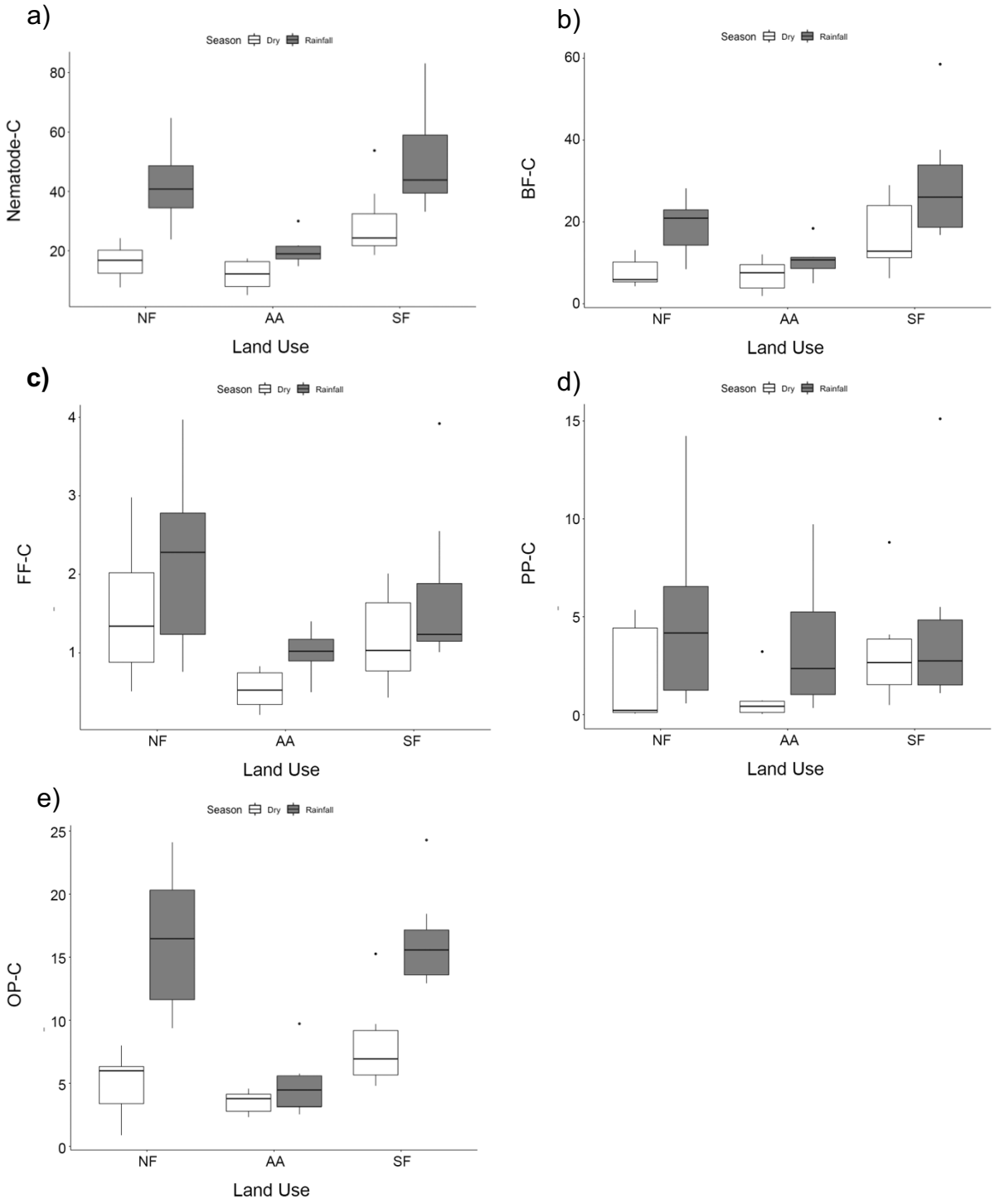
a)
Season Dry Rainfall
Nematode-C
80
60
40
20
NF
AA
SF
Land Use
b)
Season Dry Rainfall
BF-C
60
40
20
0
NF
AA
SF
Land Use
c)
Season Dry Rainfall
FF-C
4
3
2
1
NF
AA
SF
Land Use
d)
Season Dry Rainfall
PP-C
15
10
5
0
NF
AA
SF
Land Use
e)
Season Dry Rainfall
OP-C
25
20
15
10
5
0
NF
AA
SF
Land Use

Figure 1.

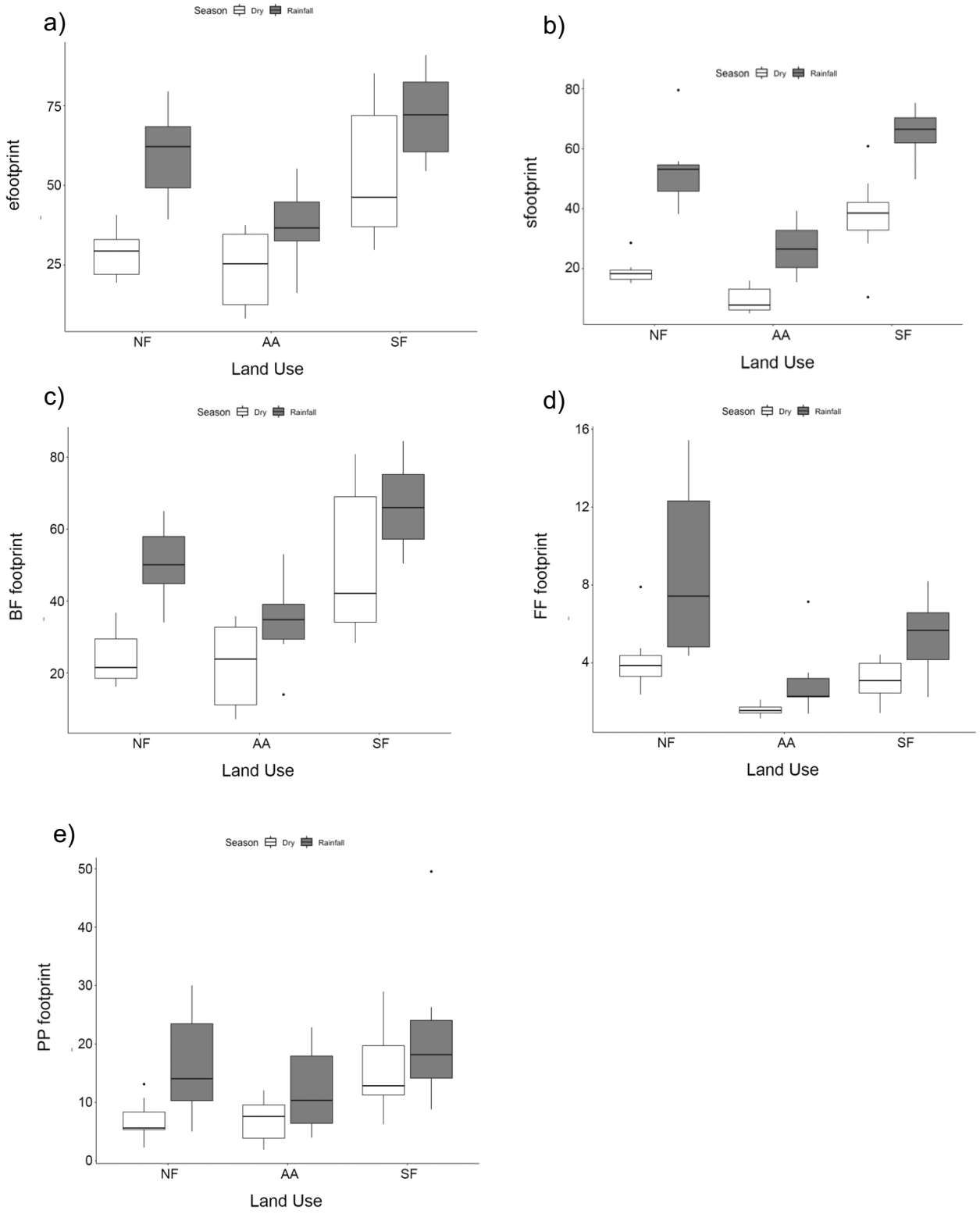
a)
Season Dry Rainfall
efootprint
75
50
25
NF
AA
SF
Land Use
b)
Season Dry Rainfall
sfootprint
80
60
40
20
NF
AA
SF
Land Use
c)
Season Dry Rainfall
BF footprint
80
60
40
20
NF
AA
SF
Land Use
d)
Season Dry Rainfall
FF footprint
16
12
8
4
NF
AA
SF
Land Use
e)
Season Dry Rainfall
PP footprint
50
40
30
20
10
0
NF
AA
SF
Land Use

Figure 2.

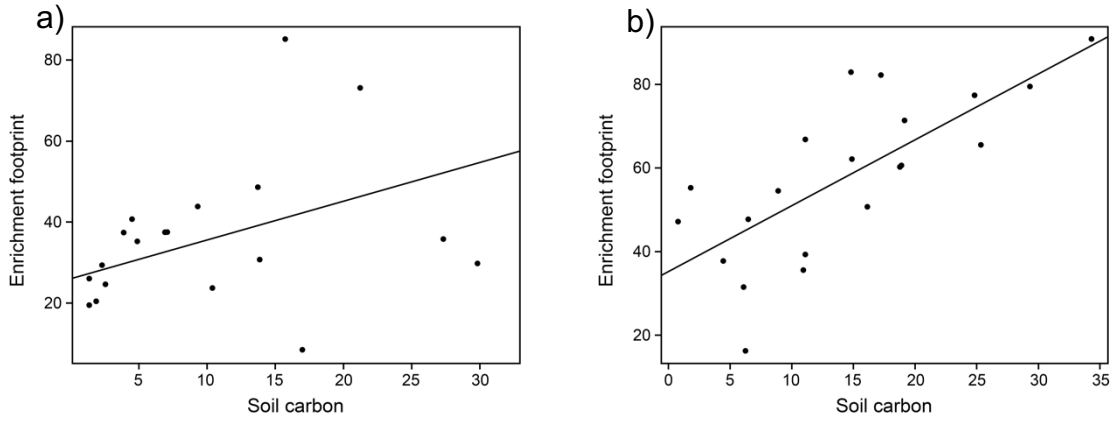
a)
Enrichment footprint
Soil carbon
b)
Enrichment footprint
Soil carbon

Figure 3.

**Supplementary material**

**Supplemental Table 1.** Relative abundance (%) of nematodes in the natural forest (NF), agricultural areas (AA) and secondary forest (SF) in dry and rainy season, Catimbau National Park, Buíque, Pernambuco, Brazil. "–" absent. c-p: colonizer-persister scale.

| Trophic groups | c-p | Family | Genus | Dry season | | |
|---|---|---|---|---|---|---|
| | | | | NF | AA | SF |
| Bacterivores | 2 | Cephalobidae | *Acrobeles* | 29,96 | 44,20 | 53,64 |
| | 2 | Cephalobidae | *Acrobeloides* | 1,89 | 0,15 | 2,11 |
| | 2 | Cephalobidae | *Acrolobus* | 0,04 | – | – |
| | 1 | Panagrolaimidae | *Brevistoma* | 0,06 | – | – |
| | 1 | Chambersiellidae | *Carcharolaimus* | 0,60 | 0,43 | 0,09 |
| | 2 | Cephalobidae | *Cephalobus* | 1,45 | 1,88 | 0,13 |
| | 2 | Cephalobidae | *Cervidellus* | 0,09 | 0,89 | 0,11 |
| | 2 | Cephalobidae | *Chiloplacoides* | 0,25 | – | – |
| | 2 | Cephalobidae | *Chiloplacus* | – | 0,10 | 0,08 |
| | 1 | Chambersiellidae | *Cornilaimus* | 0,28 | – | 0,06 |
| | 2 | Cephalobidae | *Cribronema* | 0,02 | – | – |
| | 1 | Rhabditidae | *Crustorhabditis* | – | 0,13 | – |
| | 2 | Osstellidae | *Deficephalobus* | 0,02 | 0,04 | 0,06 |
| | 1 | Diplogasteridae | *Diplogasteriana* | 0,09 | – | – |
| | 1 | Diplogasteridae | *Diplogasteroides* | 0,14 | – | – |
| | 2 | Osstellidae | *Drilocephalobus* | 3,73 | 0,68 | 1,71 |
| | 2 | Plectidae | *Ereptonema* | 0,29 | 0,13 | 0,45 |
| | 2 | Cephalobidae | *Eucephalobus* | 0,30 | 1,21 | 0,41 |
| | 1 | Diplogasteroididae | *Fuchsnema* | – | 0,04 | – |
| | 2 | Cephalobidae | *Heterocephalobellus* | 0,90 | 0,33 | 1,29 |
| | 2 | Cephalobidae | *Macrolaimellus* | 0,13 | 0,06 | – |
| | 2 | Cephalobidae | *Medibulla* | – | – | 0,16 |
| | 1 | Rhabditidae | *Mesorhabditis* | – | 1,92 | – |
| | 2 | Cephalobidae | *Metacrobeles* | 1,94 | 8,95 | 3,76 |
| | 1 | Monhysteridae | *Monhystera* | – | – | 0,16 |
| | 1 | Diplogasteridae | *Monobutlerius* | – | – | 0,07 |
| | 2 | Cephalobidae | *Nothacrobeles* | 0,13 | – | – |
| | 1 | Panagrolaimidae | *Panagrellus* | 0,13 | 0,66 | – |
| | 1 | Panagrolaimidae | *Panagrobelus* | 1,88 | 0,06 | 0,49 |
| | 1 | Panagrolaimidae | *Panagrolaimus* | 0,23 | – | 0,03 |

| | | | | | | |
|---|---|---|---|---|---|---|
| | 1 | Panagrolaimidae | *Panagrolobus* | – | 0,09 | – |
| | 2 | Cephalobidae | *Paracrobeles* | 0,02 | – | – |
| | 1 | Rhabditidae | *Pelodera* | – | 0,13 | – |
| | 2 | Cephalobidae | *Placodira* | 0,26 | – | 0,02 |
| | 1 | Brevibuccidae | *Plectonchus* | – | – | 0,06 |
| | 2 | Plectidae | *Plectus* | 0,23 | – | 0,04 |
| | 1 | Panagrolaimidae | *Procephalobus* | – | 0,14 | – |
| | 2 | Cephalobidae | *Pseudacrobeles* | 0,40 | 0,06 | 0,91 |
| | 1 | Rhabditidae | *Rhabditoides* | 0,04 | – | – |
| | 1 | Rhabditidae | *Rhabditonema* | – | 0,09 | – |
| | 1 | Rhabditidae | *Rhabpanus* | – | 0,16 | – |
| | 2 | Cephalobidae | *Scottnema* | 0,64 | 0,09 | 0,47 |
| | 2 | Cephalobidae | *Stegelletina* | 0,44 | – | 0,04 |
| | 2 | Cephalobidae | *Teratolobus* | – | 0,04 | – |
| | 2 | Plectidae | *Tylocephalus* | – | – | 0,03 |
| | 2 | Cephalobidae | *Zeldia* | 0,98 | 0,13 | 1,90 |
| Fungivores | 2 | Aphelenchoididae | *Aphelenchoides* | 1,15 | – | 0,38 |
| | 2 | Aphelenchidae | *Aphelenchus* | 1,96 | 2,24 | 1,09 |
| | 2 | Anguinidae | *Ditylenchus* | 0,85 | 1,20 | – |
| Plant parasites | 3 | Dolichodoridae | *Amplimerlinius* | – | – | 0,08 |
| | 3 | Criconematidae | *Criconema* | 2,92 | – | 0,74 |
| | 3 | Criconematidae | *Criconemoides* | 3,27 | – | 1,11 |
| | 5 | Dorylaimellidae | *Dorylaimellus* | – | – | 0,08 |
| | 3 | Hoplolaimidae | *Helicotylenchus* | 7,78 | 9,56 | 12,09 |
| | 3 | Criconematidae | *Hemicriconemoides* | 0,69 | – | – |
| | 3 | Hoplolaimidae | *Hoplolaimus* | 5,26 | 1,10 | 0,74 |
| | 4 | Nordiidae | *Longidorella* | 0,19 | – | – |
| | 5 | Longidoridae | *Longidorus* | – | – | 0,11 |
| | 3 | Criconematidae | *Mesocriconema* | 5,13 | – | 2,88 |
| | 3 | Hoplolaimidae | *Peltamigratus* | 0,19 | – | – |
| | 2 | Pratylenchidae | *Pratylenchus* | 0,10 | 0,35 | 0,03 |
| | 3 | Hoplolaimidae | *Rotylenchulus* | 8,99 | 18,68 | – |
| | 3 | Dolichodoridae | *Trophurus* | – | – | 0,04 |
| | 3 | Dolichodoridae | *Tylenchorhynchus* | 5,01 | – | 3,72 |
| Omnivores-predators | 5 | Actnolaimidae | *Afractionobimis* | – | – | 0,06 |
| | 4 | Tylencholaimellidae | *Agmodorus* | – | – | 0,02 |
| | 5 | Aporcelaimidae | *Akrotonus* | 0,25 | 0,70 | 0,49 |
| | 5 | Aporcelaimidae | *Aporcelaimium* | 0,04 | – | 0,06 |
| | 5 | Aporcelaimidae | *Aporcelaimus* | 2,55 | 0,74 | 2,54 |

| | | | | | |
|---|---|---|---|---|---|
| 4 | Leptonchidae | *Capilonchus* | 0,21 | – | 0,09 |
| 5 | Nygolaimidae | *Clavicaudoides* | 0,68 | – | – |
| 4 | Qudsianematidae | *Crassolabium* | 0,10 | – | 0,06 |
| 4 | Qudsianematidae | *Discolaimoides* | – | – | 0,22 |
| 4 | Mydonomidae | *Dorylaimoides* | 0,08 | – | 0,05 |
| 4 | Qudsianematidae | *Ecumenicus* | – | – | 0,08 |
| 4 | Qudsianematidae | *Eudorylaimus* | – | – | 0,03 |
| 4 | Tylencholaimellidae | *Goferus* | 0,08 | – | – |
| 4 | Leptonchidae | *Gymnotyleptus* | 0,86 | – | – |
| 4 | Qudsianematidae | *Indokochinema* | – | – | 0,01 |
| 4 | Qudsianematidae | *Labronema* | 0,25 | 1,47 | 0,22 |
| 5 | Aporcelaimidae | *Makatinus* | – | – | 0,11 |
| 4 | Dorylaimidae | *Mesodorylaimus* | – | – | 0,08 |
| 4 | Anatonchidae | *Miconchus* | – | – | 0,26 |
| 4 | Mononchidae | *Mononchus* | 0,36 | 0,24 | 0,82 |
| 4 | Mydonomidae | *Mydonomus* | 0,08 | – | – |
| 4 | Dorylaimidae | *Mylodiscus* | 0,04 | – | – |
| 4 | Mononchidae | *Mylonchulus* | – | 0,36 | – |
| 5 | Nygolaimidae | *Nygolaimellus* | – | – | 0,01 |
| 4 | Qudsianematidae | *Oonaguntus* | – | – | 0,01 |
| 4 | Nordiidae | *Oriverutus* | 0,09 | 0,50 | – |
| 5 | Swangeriidae | *Paractinolaimus* | – | – | 0,07 |
| 4 | Mononchidae | *Paramononchus* | 0,05 | – | – |
| 5 | Paraxonchidae | *Paraxonchium* | 0,30 | – | – |
| 4 | Mononchidae | *Prionchulus* | 0,08 | – | 0,18 |
| 4 | Dorylaimidae | *Rhinodorylaimus* | – | – | 0,08 |
| 4 | Mylonchulidae | *Sporonchulus* | – | 0,04 | – |
| 5 | Aporcelaimidae | *Takamangi* | 0,13 | – | 0,08 |
| 4 | Tylencholaimellidae | *Tantunema* | 0,08 | – | 0,23 |
| 4 | Qudsianematidae | *Thonus* | 1,77 | – | 1,56 |
| 4 | Dorylaimidae | *Timminema* | – | – | 0,03 |
| 5 | Aporcelaimidae | *Torumanawa* | 0,58 | – | 0,68 |
| 3 | Tripylidae | *Trypitoides* | 0,08 | – | – |
| 5 | Aporcelaimidae | *Tubixaba* | 0,15 | – | 0,44 |
| 4 | Leptonchidae | *Tylencholaimellus* | 0,06 | – | – |

| Trophic groups | c-p | Family | *Genus* | Rainy season | | |
|---|---|---|---|---|---|---|
| | | | | NF | AA | SF |

| | | | | | | |
|---|---|---|---|---|---|---|
| Bacterivores | 2 | Cephalobidae | *Acrobeles* | 19,46 | 23,02 | 18,1 |
| | 2 | Cephalobidae | *Acrobeloides* | 7,36 | 3,78 | 7,11 |
| | 2 | Cephalobidae | *Acrolobus* | 0,1 | 0,05 | 0,03 |
| | 1 | Panagrolaimidae | *Brevistoma* | 0,54 | 0,4 | 0,18 |
| | 1 | Rhabditidae | *Caudpilla* | – | 0,38 | – |
| | 2 | Cephalobidae | *Cephalobus* | 7,67 | 6,76 | 3,72 |
| | 2 | Cephalobidae | *Cervidellus* | 0,15 | – | 0,13 |
| | 2 | Cephalobidae | *Chiloplacoides* | – | 1,06 | – |
| | 2 | Cephalobidae | *Chiloplacus* | – | 0,14 | 0,35 |
| | 2 | Cephalobidae | *Cribronema* | 0,52 | – | 0,19 |
| | 2 | Osstellidae | *Deficephalobus* | 0,15 | 0,31 | – |
| | 1 | Chambersiellidae | *Diastolaimus* | 0,02 | – | – |
| | 1 | Diplogasteridae | *Diplogasteriana* | – | – | 0,17 |
| | 1 | Rhabditidae | *Diploscapter* | – | – | 0,05 |
| | 2 | Osstellidae | *Drilocephalobus* | – | 0,04 | – |
| | 1 | Rhabditidae | *Distolabrellus* | 5,8 | 5,78 | 1,27 |
| | 2 | Cephalobidae | *Elaphonema* | – | – | 0,04 |
| | 2 | Plectidae | *Ereptonema* | 0,02 | 0,40 | 0,6 |
| | 2 | Cephalobidae | *Eucephalobus* | 0,24 | 0,79 | 0,62 |
| | 1 | Panagrolaimidae | *Halicephalobus* | 0,14 | – | – |
| | 2 | Cephalobidae | *Heterocephalobellus* | 2,17 | 2,71 | 3,42 |
| | 2 | Cephalobidae | *Macrolaimellus* | 0,08 | – | – |
| | 1 | Chambersiellidae | *Macrolaimus* | 0,69 | – | – |
| | 2 | Cephalobidae | *Medibulla* | 3,84 | 0,34 | 0,01 |
| | 1 | Rhabditidae | *Mesorhabditis* | 0,97 | 0,93 | 3,02 |
| | 2 | Cephalobidae | *Metacrobeles* | 0,66 | 0,26 | – |
| | 1 | Monhysteridae | *Monhystera* | 0,2 | 0,09 | 0,19 |
| | 2 | Cephalobidae | *Nothacrobeles* | – | 0,05 | – |
| | 1 | Rhabditidae | *Oscheius* | 0,14 | 0,11 | – |
| | 1 | Panagrolaimidae | *Panagrellus* | – | – | 0,04 |
| | 1 | Panagrolaimidae | *Panagrocephalus* | 0 | 0,71 | – |
| | 1 | Panagrolaimidae | *Panagrolaimus* | 0,88 | 0,35 | 0,11 |
| | 1 | Panagrolaimidae | *Panagrolobus* | – | – | 0,36 |
| | 2 | Cephalobidae | *Paracrobeles* | 0,02 | – | – |
| | 1 | Rhabditidae | *Pellioditis* | 0,27 | 0,67 | 2,05 |
| | 1 | Rhabditidae | *Pelodera* | 0,64 | 0,68 | 0,05 |
| | 2 | Cephalobidae | *Placodira* | – | – | 0,19 |
| | 2 | Plectidae | *Plectus* | 0,29 | – | 0,05 |
| | 1 | Panagrolaimidae | *Panagrolaimus* | 0,34 | – | 1,07 |
| | 3 | Prismatolaimidae | *Prismatolaimus* | 0,69 | 0,19 | 0,09 |

| | | | | | | |
|---|---|---|---|---|---|---|
| | 2 | Cephalobidae | *Pseudacrobeles* | 0,05 | – | – |
| | 1 | Rhabditidae | *Rhabditoides* | – | – | 0,09 |
| | 1 | Rhabditidae | *Rhabditonema* | 0,09 | – | – |
| | 2 | Cephalobidae | *Scottnema* | 0,09 | – | 0,26 |
| | 2 | Cephalobidae | *Stegelleta* | – | – | 0,51 |
| | 2 | Cephalobidae | *Teratolobus* | 0,47 | 2 | 2,04 |
| | 2 | Bicirronematidae | *Tricirronema* | 1,08 | – | 0,05 |
| | 2 | Plectidae | *Tylocephalus* | 0,41 | 0,26 | 1,47 |
| | 2 | Plectidae | *Wilsonema* | 1,36 | 0,15 | 0,09 |
| | 2 | Cephalobidae | *Zeldia* | 2,15 | – | 1,40 |
| Fungivores | 2 | Aphelenchoididae | *Aphelenchoides* | 3,33 | 3,39 | 0,54 |
| | 2 | Aphelenchidae | *Aphelenchus* | 2,63 | 4,27 | 2,59 |
| | 2 | Anguinidae | *Ditylenchus* | 4,56 | 4,21 | 1,23 |
| Plant parasites | 3 | Hoplolaimidae | *Acontylus* | – | 0,54 | – |
| | 3 | Hoplolaimidae | *Aorolaimus* | 0,76 | 0,69 | – |
| | 3 | Criconematidae | *Criconemoides* | 0,13 | 2,67 | 0,12 |
| | 5 | Dorylaimellidae | *Dorylaimellus* | 0,46 | – | 0,22 |
| | 3 | Hoplolaimidae | *Helicotylenchus* | 0,62 | 2,42 | 3,49 |
| | 3 | Criconematidae | *Hemicycliophora* | 0,28 | – | 0,04 |
| | 3 | Heteroderidae | *Heterodera* | – | 0,15 | – |
| | 3 | Belonolaimidae | *Histotylenchus* | 0,14 | 0,07 | – |
| | 3 | Hoplolaimidae | *Hoplolaimus* | 0,72 | 2,07 | 0,78 |
| | 5 | Longidoridae | *Longidoroides* | – | – | 0,07 |
| | 5 | Longidoridae | *Longidorus* | 0,38 | 0,40 | 0,49 |
| | 3 | Dolichodoridae | *Merlinius* | 4,21 | 1,46 | 0,52 |
| | 3 | Criconematidae | *Mesocriconema* | 0,02 | 0,35 | – |
| | 3 | Hoplolaimidae | *Peltamigratus* | 0,02 | 0,04 | 0,29 |
| | 2 | Pratylenchidae | *Pratylenchus* | 0,38 | – | 0,02 |
| | 3 | Hoplolaimidae | *Rotylenchulus* | 3,47 | 5,49 | 2,68 |
| | 3 | Dolichodoridae | *Tylenchorhynchus* | 0,34 | 2,67 | 1,38 |
| | 3 | Tylenchidae | *Tylenchus* | 0,27 | 0,80 | 0,15 |
| | 5 | Longidoridae | *Xiphinema* | 0,83 | 4,59 | 1,22 |
| Omnivores-predators | 5 | Actinolaimidae | *Actinca* | 0,16 | – | – |
| | 4 | Leptonchidae | *Agmodorus* | 1,76 | – | 2,54 |
| | 5 | Aetholaimidae | *Aetholaimus* | – | – | 0,02 |
| | 5 | Nygolaimidae | *Afronygus* | – | – | 0,18 |
| | 5 | Aporcelaimidae | *Akrotonus* | 1,96 | – | 2,81 |
| | 5 | Aporcelaimidae | *Aporcelaimellus* | 0,40 | 0,44 | 0,62 |
| | 5 | Aporcelaimidae | *Aporcelaimium* | 0,79 | – | – |

| | | | | | |
|---|---|---|---|---|---|
| 5 | Aporcelaimidae | *Aporcelaimus* | 2,09 | 1,13 | 5,97 |
| 5 | Belondiridae | *Axonchium* | 0,11 | – | 0,05 |
| 5 | Tripyloididae | *Bathylaimus* | 0,19 | – | – |
| 5 | Belondiridae | *Belaxellus* | – | – | 0,05 |
| 4 | Leptonchidae | *Capilonchus* | 0,24 | – | – |
| 4 | Leptonchidae | *Caveonchus* | – | – | 1,13 |
| 5 | Nygolaimidae | *Clavicaudoides* | – | – | 0,46 |
| 4 | Qudsianematidae | *Discolaimus* | 1,05 | 3,26 | 1,66 |
| 4 | Mydonomidae | *Dorylaimoides* | 0,14 | 0,29 | – |
| 4 | Dorylaimidae | *Dorylaimus* | – | – | 0,18 |
| 5 | Belondiridae | *Durinema* | – | 0,20 | – |
| 4 | Qudsianematidae | *Ecumenicus* | – | – | 0,40 |
| 4 | Nordiidae | *Enchodelus* | 0,34 | – | – |
| 4 | Qudsianematidae | *Eudorylaimus* | 0,40 | – | 2,55 |
| 4 | Tylencholaimellidae | *Goferus* | – | – | 1,45 |
| 4 | Leptonchidae | *Gymnotyleptus* | 0,70 | – | 0,21 |
| 4 | Dorylaimidae | *Idorylaimus* | – | – | 0,42 |
| 4 | Ironidae | *Ironus* | 0,07 | – | – |
| 4 | Qudsianematidae | *Labronema* | 0,64 | 0,53 | 0,27 |
| 4 | Qudsianematidae | *Latocephalus* | – | – | 0,41 |
| 5 | Aporcelaimidae | *Makatinus* | 1,50 | – | 2,14 |
| 4 | Mononchidae | *Mononchus* | – | – | 0,03 |
| 5 | Actinolaimidae | *Paractinolaimus* | 0,07 | 0,16 | 0,35 |
| 5 | Paraxonchidae | *Paraxonchium* | 0,05 | – | 0,33 |
| 4 | Qudsianematidae | *Poronemella* | – | – | 0,75 |
| 4 | Nordiidae | *Oriverutus* | 0,32 | 2,13 | 2,89 |
| 4 | Mononchidae | *Prionchulus* | – | 0,39 | 0,26 |
| 4 | Lordellonematidae | *Poronemella* | 0,36 | – | – |
| 4 | Qudsianematidae | *Qudsianema* | 1,36 | 1,08 | 2,39 |
| 4 | Nordiidae | *Rhyssocolpus* | 0,06 | 1,03 | – |
| 5 | Aporcelaimidae | *Takamangi* | 0,03 | – | – |
| 4 | Qudsianematidae | *Thonus* | 0,61 | – | 0,79 |
| 5 | Aporcelaimidae | *Torumanawa* | – | – | 0,45 |
| 3 | Tripylidae | *Trypitoides* | 0,70 | 0,61 | 1,78 |
| 5 | Aporcelaimidae | *Tubixaba* | 0,02 | – | 0,83 |
| 4 | Leptonchidae | *Tylencholaimellus* | 0,61 | 0,08 | 0,64 |

**Supplemental Table 2.** Effects of land use, seasonal effect (dry and rainy), and their interaction on biomass carbon (μg $ml^{-1}$) of total nematodes and of each nematode trophic group at Catimbau National Park, Pernambuco, Brazil. $R^2$ represents the coefficient of determination of the whole model. Significant values are in bold.

| | **Biomass carbons** | | | | |
|---|---|---|---|---|---|
| | Variables | $R^2$ | DF | *t* | P |
| **Total nematodes** | Land use | 0.44 | 1.28 | 2.14 | **0.01** |
| | Seasonal effect | | 1.28 | 4.23 | **0.001** |
| | Land use x Seasonal effect | | 1.28 | 0.23 | 0.81 |
| **Bacterivores** | Land use | 0.56 | 1.28 | 2.98 | **0.001** |
| | Seasonal effect | | 1.28 | 3.34 | **0.001** |
| | Land use x Seeasonal effect | | 1.28 | 0.26 | 0.79 |
| **Fungivores** | Land use | 0.22 | 1.28 | 1.10 | **0.05** |
| | Seasonal effect | | 1.28 | 2.07 | **0.05** |
| | Land use x Seasonal effect | | 1.28 | 0.79 | 0.34 |
| **Plant parasites** | Land use | 0.10 | 1.28 | 0.21 | 0.83 |
| | Seasonal effect | | 1.28 | 2.02 | **0.05** |
| | Land use x Seasonal effect | | 1.28 | 0.65 | 0.52 |
| **Omnivores-predators** | Land use | 0.48 | 1.28 | 2.96 | **0.01** |
| | Seasonal effect | | 1.28 | 2.67 | **0.01** |
| | Land use x Seasonal effect | | 1.28 | 0.70 | 0.05 |

**Supplemental Table 3.** Effects of land use, seasonal effect (dry and rainy) and their interaction on metabolic footprint of functional guilds of soil nematodes at Catimbau National Park, Pernambuco, Brazil. $R^2$ represents the coefficient of determination of the whole model. Significant values are in bold.

| | Metabolic footprint | | | | |
|---|---|---|---|---|---|
| | Variables | $R^2$ | DF | *t* | P |
| **efootprint** | Land use | 0.68 | 1.28 | 2.97 | **0.01** |
| | Seasonal effect | | 1.28 | 3.86 | **0.001** |
| | Land use x Seasonal effect | | 1.28 | 0.88 | 0.38 |
| **sfootprint** | Land use | 0.65 | 1.28 | 8.78 | **0.001** |
| | Seasonal effect | | 1.28 | 5.49 | **0.01** |
| | Land use x Seasonal effect | | 1.28 | 0.52 | 0.60 |
| **BF footprint** | Land use | 0.50 | 1.28 | 3.62 | **0.001** |
| | Seasonal effect | | 1.28 | 3.68 | **0.001** |
| | Land use x Seasonal effect | | 1.28 | 0.79 | 0.43 |
| **FF footprint** | Land use | 0.38 | 1.28 | 2.06 | **0.001** |
| | Seasonal effect | | 1.28 | 3.32 | **0.001** |
| | Land use x seasonal effect | | 1.28 | 1.07 | **0.05** |
| **PP footprint** | Land use | 0.34 | 1.28 | 2.22 | **0.05** |
| | Seasonal effect | | 1.28 | 2.67 | **0.05** |
| | Land use x Seasonal effect | | 1.28 | 0.59 | 0.55 |

efootprint: enrichment footprint; sfootprint: structure footprint; BF: bacterivores; FF: fungivores; PP: plant parasites.

# 5 CONCLUSÃO

Nesta tese, investigamos como diferentes tipos de uso da terra, propriedades do solo e variáveis climáticas (precipitação e temperatura) afetam a estrutura da comunidade e função ecossistêmica dos nematoides na Caatinga. Nossos resultados podem ser considerados pontos iniciais para prever como a perturbação antrópica, a exemplo da atividade agrícola, e o aumento da temperatura e redução da precipitação nas florestas tropicais sazonalmente secas afetam a cadeia alimentar do solo e funções ecossistêmicas.

No primeiro capítulo, verificamos que a conversão da vegetação nativa da Caatinga para o uso agrícola afetou negativamente a comunidade de nematoides, reduzindo a abundância total de nematoides, dos bacteriófagos e dos onívoros-predadores. Por sua vez, a regeneração secundária das áreas após o abandono da prática agrícola foi responsável pela reversão de tais mudanças. Também verificamos que o gênero *Acrobeles*, bacteriófagos generalistas pertencentes à família Cephalobidae, são importantes na estruturação da comunidade de nematoides, pois sua abundância contribuiu para a dissimilaridade taxonômica entre as áreas agrícolas, floresta secundária e floresta natural. Por fim, constatamos que a composição taxonômica dos nematoides encontrada nos diferentes tipos de uso da terra está relacionada às propriedades físicas e químicas do solo e a variáveis climáticas na Caatinga, o que sugere que esses fatores podem estar atuando como importantes filtros ambientais na estruturação de comunidades de nematoides nas florestas tropicais sazonalmente secas.

Já no segundo capítulo, avaliamos o efeito do tipo de uso da terra e variação sazonal na Caatinga sobre a fertilidade do solo, a estrutura trófica e as funções ecossistêmicas de cada guilda funcional dos nematoides. Constatamos que a magnitude da função ecossistêmica desempenhada pelos bacteriófagos, fungívoros e onívoro-predadores foi reduzida diante da conversão da vegetação nativa da Caatinga em sistemas de cultivo. Possivelmente, a perda nos níveis de carbono orgânico do solo encontrados nas áreas agrícolas, devido a redução do sistema radicular e inadequado manejo agrícola do solo, forneceu pouco recurso para a atividade metabólica dos nematoides bacteriófagos e fungívoros, o que refletiu em uma menor quantidade de fluxo de carbono através dos canais de decomposição da cadeia alimentar e ciclagem de nutrientes. Além disso, a ciclagem de nutrientes através do processo indireto de predação pelos nematoides onívoro-predadores também foi reduzida. Por outro lado, a regeneração da floresta secundária após a perturbação da agricultura aumentou o carbono orgânico do solo, e a *metabolic footprints* dos nematoides indicadores de enriquecimento e estrutura da cadeia

alimentar, indicando a capacidade do solo de se recuperar após uma perturbação antrópica e física. Também verificamos que maiores níveis de carbono orgânico do solo e magnitude da função do ecossistema das guildas funcionais ocorreram durante a estação chuvosa e que a maior parte da assimilação de recursos e fluxo de energia na cadeia alimentar do solo na Caatinga foi via canal bacteriano. Entretanto, encontramos poucas evidências de efeitos interativos do uso da terra e do efeito sazonal sobre o *metabolic footprints* das guildas funcionais de nematoides.

Em síntese, nossos resultados mostram que a estrutura da comunidade de nematoides e atividades metabólicas dos nematoides na Caatinga são sensíveis a perturbação antrópica e a mudanças climáticas. Isso nos indica que tanto as perturbações antrópicas crescentes e redução da precipitação tem reduzido as funções ecossistêmicas fornecidas por cada grupo trófico dos nematoides, responsáveis por desempenharem um papel central na cadeia alimentar do solo.

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