Cacao agroforestry in Belize: Effects on soil nematode community structure

J. Parr McQueen · Amy M. Treonis

Abstract Cacao (*Theobroma cacao* L.) is a shade tolerant crop that can be grown beneath the rainforest canopy rather than in a conventional monoculture. Cacao agroforestry has been proposed as a more sustainable method of farming to mitigate climate change and protect above-ground biodiversity, yet impacts on soil biodiversity and function have rarely been investigated. Our goal was to study how the diversity and community structure of soil nematodes are impacted by planting the rainforest understory with cacao. At field sites in southern Belize and during two growing seasons, nematodes were extracted from soil from cacao agroforestry plots, undisturbed rainforests, and a banana plantation. Nematodes were enumerated and visually identified, and communities were analyzed using several community and diversity indices. In both the dry and wet seasons, soils from cacao plots contained similar nematode communities to the rainforest with respect to all measured variables, including the abundance of nematodes from each trophic group, the Bongers Maturity and Plant-Parasite indices, and the Shannon and Simpson's diversity indices. In contrast, the banana plantation soils were dominated by plant-parasitic nematodes with lower Shannon and Simpson's diversity indices. Overall, it appears that cacao agroforestry plots maintain nematode community structure relative to the undisturbed rainforest they were created from, suggesting that soil health is not compromised by this land-use strategy.

Keywords Biodiversity · Cocoa · Chocolate · Rainforest · Sustainable agriculture

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Introduction

Deforestation is a major threat to global biodiversity and a key contributor to climate change. In the tropics, old-growth rainforests have been converted to agriculture at higher rates than any other region (Giam 2017). The majority of this land is being converted into conventional monocultures using the slash and burn method, which reduces soil fertility and causes long-lasting reductions in biodiversity and ecosystem functioning, including within soil microbial communities (Rodrigues et al. 2013). Currently, Belize has a rate of deforestation twice as high as the rest of Central

America, making this region of great concern (Young 2008).

Cacao (*Theobroma cacao* L.) is an ancient Mayan crop from the family Malvaceae that is shade tolerant (Diemont et al. 2011). Instead of slash and burn clear-cutting, it is possible to plant cacao trees by merely thinning out the rainforest, removing only small bushes and the undergrowth while leaving larger trees and their established root systems. This form of agroforestry is predicted to protect ecosystem services and mitigate climate change (De Beenhouwer et al. 2013; Rice and Greenberg 2000), but its effects on biodiversity are unclear. Southern Belize currently hosts a large-scale commercial fruit industry (i.e., banana, oranges and pineapple), farming land that was once old growth forest. Banana is an important cash crop in Belize, making up 15% of all exports in 2017, and intensive commercial farming is the main driver of deforestation in this region (United Nations 2019). Shade-grown cacao is a valuable global commodity that could create competitive profits for farmers compared to conventional crops like banana (Waldron et al. 2012).

Some studies have shown that habitat in understory cacao systems can protect natural assemblages of avian (Harvey and González Villalobos 2007), ant (Roth et al. 1994), and macroinvertebrate species (Rousseau et al. 2012). Furthermore, cacao agro-forestry appears to promote natural disease control in cacao plants (Andres et al. 2018), possibly through soil microbiomes (Christian et al. 2017). However, other studies in cacao agroforestry have observed that soil microbial communities can shift in composition (Buyer et al. 2017), and some small vertebrate species can decline (Scales and Marsden 2008). Moreover, cacao plants in agroforestry systems may be more susceptible to mortality due to increases in tempera-ture from climate change compared to conventional full sun cacao (Abdulai et al. 2018). Finally, cacao agroforestry systems also play important roles in carbon sequestration, with understory cacao seques-tering less carbon than an undisturbed rainforest, but more than low-shade cacao (Middendorp et al. 2018; Leuschner et al. 2013; Somarriba et al. 2013). Overall, the environmental impact and sustainability of cacao agroforestry are not fully understood.

Nematodes are microscopic roundworms that play important roles in soil processes. They are very diverse, ubiquitous in soil, and their communities are sensitive to environmental change, making them an excellent organism to use as a measure of soil health (Neher 2001; Bongers and Ferris 1999). Nematode community analysis involves identifying the nema-todes present within soil and analyzing the structure of their communities (e.g., trophic diversity). Using this information, soil diversity and functioning can then be quantified using established nematode community indices (e.g., Maturity, Enrichment, and Structure indices; Bongers and Ferris 1999). Understanding nematode communities within cacao agroforestry systems will provide insights as to how this form of agriculture may be affecting soil diversity and health.

For this study, we investigated the impact of shade-grown cacao agroforestry on soil nematodes. We tested the hypothesis that nematode communities are similar in cacao agroforestry plots to adjacent, unfarmed rainforest. We also included an adjacent banana farm in our study to verify that our methods are able to discern differences in nematode communities, as it is well documented that intensive agriculture reduces soil fertility and biodiversity (Tsiafouli et al. 2015). We predicted that the banana farm soils would harbor depauperate nematode communities. In con-trast, we predicted that cacao agroforestry nematode communities would have similar abundance, diversity, and trophic structure to those from the old growth rainforest, reflecting the reduced impact this practice has on soil health.

Material and methods

Study systems and soil sampling

Soil was collected from three systems (cacao, rain-forest, and banana) from the Mayan Mountain region of southern Belize, in the Toledo District, near Trio Village and the Bladen Nature Reserve (16° 31′ 13.4″ N, 88° 38′ 20.5″ W). All seven sample sites were within a 3 km radius of each other to limit variation in edaphic factors. Rainforest plots (n = 2) are typified by Cohune Palm (*Attalea cohune* Mart.), a member of the Arecaceae family, receive annual rainfall between 3300 and 4160 mm per year, and have an average annual temperature around 25 °C (Internal Data, Belize Foundation for Research and Environmental Education). The cacao agroforestry plots (n = 4) were established in the rainforest understory 5–6 years

before the first sampling date and were planted with a mixture of Trinitario and Criollo cacao saplings (approximately 800 cacao trees ha^{-1}, planted ≈ 3.5 m apart). Each plot (about 4 ha each) received the same regime of maintenance. The trees were cleared of overgrowing vines and weeds twice a year. At harvest, pods were split open, pulp and seeds were collected, and the empty pods and leaf litter were retained on the ground to decompose. Cacao trees were pruned weekly and any visually diseased stems were removed. No pesticides or fertilizers were added. In order to verify that our methods are able to discern differences in nematode communities within this climate and ecosystem, we sampled from a nearby, conventionally-managed 4.7 ha banana farm (n = 1). Here nematicides (fluopyram as active ingredient) were applied as well as glyphosate- and diquat dibromide-based pesticides. Standard banana growing practices were followed (bagging, trimming, and cutting after harvesting), but we do not report specifics in order to protect the commercial interests of the farm. One rainforest plot and two of the cacao farms were located within private land managed by the Belize Foundation for Research and Environmental Education (BFREE). Two other cacao farms, the second rainforest plot, and the banana farm were also privately-owned. All field sites are within 10 km of the Bladen Nature Reserve, a 40,000 ha, undisturbed, contiguous area of Mesoamerican rainforest.

Soils were sampled in the dry season during early May 2017 and then during the wet season in late August 2018. Within each site, six 20 m transects were placed parallel to each other, 15 m apart. Along each transect six 2.5 cm diameter soil cores, spaced equally apart, were collected to a 20 cm depth, after sweeping away ground litter. These six cores were combined to create a single, composite soil sample. Each transect represents one composite sample, and six samples were taken from each plot. We were unable to access one of the private cacao farm sites to collect soils in 2018, and the banana farm was only sampled in 2018.

Nematode extraction and community analysis

Soils were refrigerated and hand-carried in coolers from Belize to the University of Richmond for further analysis. Nematodes were extracted from two replicate, 50 g subsamples from each sample using the

sugar flotation and centrifugation technique (Jenkins 1964). Nematodes from the two replicates were combined and preserved in 5% formalin for morphological analysis. Nematodes from each sample were counted, and 100 individuals were identified to the family level (genus, when possible) using a Zeiss Axiovert 40 CFL inverted microscope (Carl Zeiss MicroImaging, Inc., Thornwood, NY, USA). All nematodes were assigned to trophic groups according to Yeates et al. (1993). There is ambiguity with respect to the feeding behavior of genera from the root-associated Tylenchidae, species of which may be fungal-feeding, plant-parasitic or both (Treonis 2017). Species from this group were classified as fungal-feeders for this study.

Several diversity and ecological indices were calculated, including richness (i.e., the number of families represented), the Shannon diversity index (H′, Shannon and Weaver 1949), and Simpson's dominance index (λ, Simpson 1949). H′ gives more weight to rare taxa while λ gives more weight to abundant taxa. Several indices developed specifically for assessment of soil nematode communities were also calculated. The Bongers Maturity Index (MI) is based on the life history characteristics of each free-living nematode family (Bongers 1990; Bongers and Bongers 1998). It assigns all species within a family a c-p value from 1, indicating it is a r-selected "colonizer", to 5 for k-selected "persisters".

$$\text{MI} = \sum v_i f_i,$$

where v_i is the c-p value and f_i is the frequency of the ith family (free-living taxa only).

Lower MI values indicate that soils contain an abundance of nematodes that thrive in disturbed, enriched soils, while high scores reflect the presence of more nematode taxa associated with stable ecosystems. The Plant-Parasite Index (PPI) is a similar index, but includes only plant-parasitic nematodes that are excluded from the MI (Bongers and Bongers 1998).

$$\text{PPI} = \sum v_i f_i,,$$

where v_i is the c-p value and f_i is the frequency of the ith family (plant-parasite taxa only).

The Channel Index (CI), Enrichment Index (EI), and Structure Index (SI) use the Bongers c-p values to describe the food web structure and decomposition pathways and were calculated as described by Ferris

et al. (2001). Using these indices together provides a comprehensive assessment of nematode community diversity and structure and produces quantitative measures of belowground ecosystem functioning and soil health. Soils with higher nematode diversity, Maturity Index, and Structure Index and lower Plant-Parasite Index are considered to be the healthiest (Ferris et al. 2001).

Soil analyses

Soil moisture content was determined by exposing 25 g samples to 105 °C for 48 h, and organic content was measured by exposure of 10 g samples to 400 °C for 48 h. A subset of samples was selected for additional chemical analysis at the Penn State Agricultural Analytical Services Lab (Table 1). Soils were clay loams, as determined by the hydrometer method (Gee and Bauder 1986).

Statistical analyses

Statistics were performed in R Version 3.5.2 (https://www.r-project.org) (R Core Team 2018) using the *nlme* and *vegan* packages. Measured and calculated dependent variables (nematode abundance, abundance of trophic levels, and community indices) were compared among systems and seasons using linear mixed effects models in a factorial repeated measures design and fit by maximum likelihood tests. The system type (cacao, forest or banana) was a fixed effect, as we were interested in comparing these specific treatments to each other. Site and season (wet, dry) were random effects because we sampled only a limited number of

possible sites and dates. Due to low numbers for many families (Online Resource 1), statistical analyses of the nematode community were performed by trophic level only. Data were transformed prior to analysis to meet assumptions as needed (ln transformation for density of total nematodes, plant-parasites, and bacterial-feeders, $\ln(x + 1)$ for omnivore-predators) (Sokal and Rohlf 1995). Means were compared using orthogonal contrasts established a priori (Banana vs. Forest/Cacao, Cacao vs. Forest, and wet vs. dry season). Due to the unbalanced design of the experiment, it was not possible to test for interaction effects between plot type and season. A Bray–Curtis based nonmetric multidimensional scaling (NMDS) approach was used to explore the degree of similarity among seasons and plot types, using the abundance of each nematode family in each sample (Bray and Curtis 1957).

Results

Nematodes from 24 families were present across 72 soil samples (Table 2). Soils contained an average of 260 nematodes 100 g^{-1} dry soil. There was no difference in total nematode abundance between seasons or systems (Fig. 1a). Nematode abundance in soil from cacao was not significantly different from

Table 1 Physicochemical properties of soils sampled from 2017 dry season

	Forest (n = 2)	Cacao (n = 4)
pH	5.00 ± 0.20	5.09 ± 0.20
Nitrate-N (ppm)	43.03 ± 0.74	49.79 ± 3.38
Carbon (%)	2.32 ± 0.3	2.32 ± 0.13
Organic carbon (%, LOI)	5.70 ± 0.88	6.11 ± 1.00
Nitrogen (%)	0.25 ± 0.01	0.24 ± 0.01
Ammonium nitrogen (mg/kg)	10.41 ± 5.29	6.60 ± 1.47

Values are means ± s.e.m. (n = 2 for forest soils and n = 4 for cacao)

Table 2 Nematode families represented in Belize rainforest, cacao agroforestry, and banana plantation soils

| Bacterial-feeding	Plant-parasitic
Alaimidae	Criconematidae
Cephalobidae	Dolichodoridae
Plectidae	Hemicycliophoridae
Prismatolaimidae	Heteroderidae
Rhabditidae	Hoplolaimidae
Teratocephalidae	Meloidogynidae
Omnivore/predator	Trichodoridae
Actinolaimidae	Longidoridae
Anatonchidae	Fungal-feeding
Mononchidae	Aphelenchidae
Nygolaimidae	Psilenchidae
Onchulidae	Tylenchidae
Prodorylaimus	
Qudsianematidae	
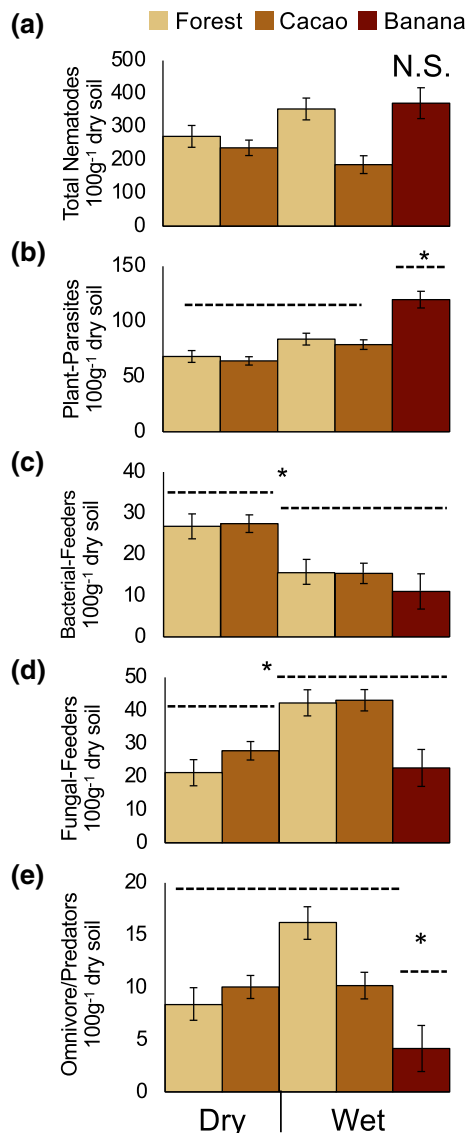
Fig. 1 Abundance of soil nematodes (0–20 cm) by system type and season. **a** Total nematodes, **b** plant-parasites, **c** bacterial-feeders, **d** fungal-feeders, and **e** omnivore/predators. In each graph, bars represent means ± s.e.m, and the placement of dashed horizontal lines indicate statistical differences among the systems or seasons. *NS* no significant differences

the forest soils ($b = -0.11$, $t(4) = -2.48$, $P = 0.068$, Fig. 1a), and the banana plantation soils had similar nematode abundance to the forest and cacao ($b = -0.077$, $t(4) = -1.00$, $P = 0.37$, Fig. 1a).

The nematode trophic groups that showed variation among the systems were the plant-parasites and omnivore/predators (Fig. 1). Banana plantation soils contained more plant-parasitic nematodes than the

forest or cacao soils ($b = -0.13$, $t(4) = -3.07$, $P = 0.037$, Fig. 1b) and lower numbers of omnivore/predators ($b = 0.38$, $t(4) = 3.38$, $P = 0.028$, Fig. 1e). The nematode trophic groups that showed seasonal variation were the bacterial- and fungal-feeders (Fig. 1). Bacterial-feeding nematodes decreased ($b = -0.55$, $t(4) = -5.05$, $P = 0.007$) and fungal-feeding nematodes ($b = 0.58$, $t(4) = 4.24$, $P = 0.013$) increased in the wet season versus the dry (Fig. 1c, d).

The Bongers Maturity Index (MI) and the Plant Parasite Index (PPI) did not differ among the systems ($P = 0.30$ and $P = 0.56$, respectively, Fig. 2a). The Enrichment Index did not vary among systems ($P = 0.24$, Fig. 4), but the Structural Index was lower in banana soils ($b = 8.83$, $t(4) = 3.93$, $P = 0.017$). This difference resulted in the banana soils plotting into a different quadrant of the Ferris Faunal Analysis (Fig. 2b). Nematode communities placed in Quadrant A of the Ferris Analysis (i.e., the banana soils) are associated with more stress and disturbance, while the
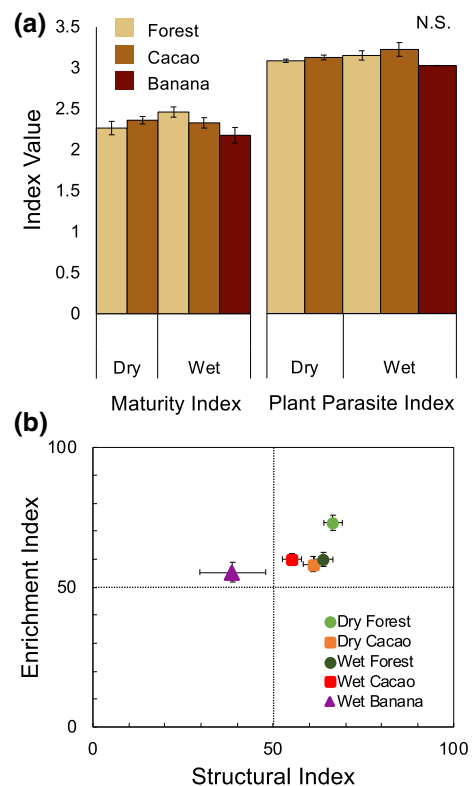
Fig. 2 **a** Bongers Maturity Index and Plant Parasite Index by system type and season. Bars represent means ± s.e.m. **b** Faunal analysis for nematode communities between different systems and seasons. Each point represents the mean ± s.e.m

placement of communities from the forest and cacao in Quadrant B is associated with more stability (Fig. 2b). The Channel Index was higher for nematode communities in the wet season ($b = 23.32$, $t(4) = 4.12$, $P = 0.014$), indicating increased importance of the fungal-mediated decomposition pathway (data not shown).

Richness (the number of families represented) did not vary among the systems or with season (range = 9–18, mean = 13.4, $P > 0.05$, data not shown). Nematode communities from banana soils had significantly lower Simpson's ($b = 0.041$, $t(4) = 3.86$, $P < 0.018$) and Shannon ($b = 0.16$, $t(4) = 4.21$, $P < 0.014$) diversity indices than cacao or forest (Fig. 3).

Integrating the abundance of nematodes from each family for all individual samples, nonmetric multidimensional scaling analysis (NMDS, Stress value = 0.18) shows a shift in the nematode communities in the dry (2017) and wet (2018) seasons, due to the seasonal differences in bacterial- and fungal-feeder abundance documented above (Fig. 4a). NMDS analysis also supports the similarity between nematode communities from the forest and cacao soils, which cluster together on the biplot, while banana soils show a degree of separation from the other types (Fig. 4b).

Banana soils contained significantly higher soil moisture content (0.37 ± 0.013 g 100 g^{-1}) compared to the forest and cacao (0.28 ± 0.01 g 100 g^{-1}, $b = -0.0015$, $t(4) = -0.073$, $P = 0.014$). Soil

organic matter content did not differ significantly between systems or seasons (Table 1, $P > 0.29$).

Discussion

To date, the amount of rainforest lost to deforestation in Belize has been smaller than for other countries in the region. Protected lands in Belize include the Bladen Nature Reserve, which is part of the largest stretch of intact rainforest remaining in Central America and is adjacent to our field sites (Rotenberg et al. 2012). This area is a biodiversity "hotspot", harboring charismatic megafauna such as harpy eagles, scarlet macaw, tapir, and jaguars (Dourson 2012). This region is threatened, however, by increasing demand for agricultural lands, and deforestation rates in Belize are accelerating (Young 2008). Organizations like the Belize Foundation for Research and Environmental Education, Ya'axché Conservation Trust, and others are working to promote cacao agroforestry and support farmers interested in adapting this historic Mayan practice to the modern commercial market. It is important to acknowledge that growing cacao within the rainforest may result in a lower crop yield compared to a conventional monoculture of cacao with intensive crop inputs (Waldron et al. 2012). However, this agroforestry approach represents a compromise that could allow for sustained economic benefits from the land without significant loss of biodiversity or carbon storage (Jose 2009). In addition, shade-grown cacao has the potential to be priced higher to compensate for lower yield (Waldron et al. 2012).

Our study is the first to examine the impact of cacao agroforestry on free-living soil nematodes. We found that this agricultural practice seems to conserve nematode abundance, diversity, and community structure, with cacao soils having similar richness, Maturity Index, Plant Parasite Index, and Simpson's and Shannon indices to the adjacent, undisturbed rainforest. Similar results were obtained by Deheuvels et al. (2014) in a study of litter/soil macroinvertebrates (i.e., arthropods, earthworms, and enchytraeids) when taxonomic richness was compared between cacao agroforestry and forest plots in Costa Rica. However, in this study, the actual composition of the assemblages did vary, with forest soils being more diverse when taxonomic dominance was considered (Deheuvels
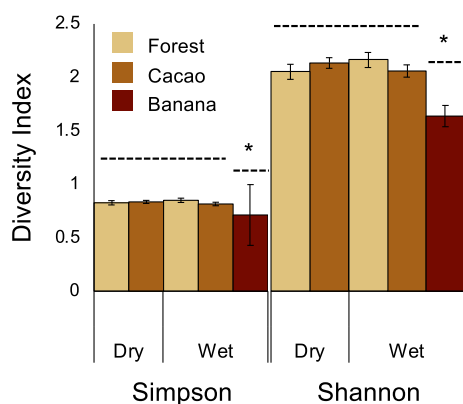
Fig. 3 Simpson and Shannon diversity indices by system type and season, based on abundance of nematodes at the family-level. Bars represent means ± s.e.m. For each index, the placement of dashed horizontal lines indicate statistical differences among the systems
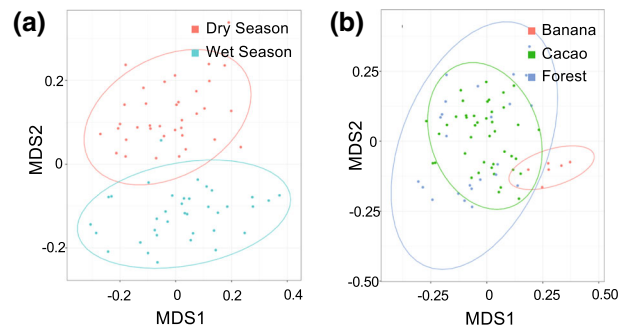
Fig. 4 Ordination biplot from nonmetric multidimensional scaling (NMDS) analysis of abundance for each represented family in soils from either the wet or dry season (**a**) or different systems (**b**). Points represent individual samples. Ellipses represent 95% confidence intervals around the centroid

et al. 2014). In a study of cacao agroforestry in Brazil, da Silva Moço et al. (2009) found that litter/soil macroinvertebrates actually increased in abundance and richness in cacao versus natural forest in Brazil, which they attributed to increased abundance of leaf litter. In a review of agroforestry: biodiversity studies conducted across the globe, Bhagwat et al. (2008) found that agroforestry systems of varying intensity conserved, on average, 25–60% of richness for taxa studied, including plants, insects, mammals, and birds. In another meta-analysis focusing specifically on coffee and cacao, De Beenhouwer et al. (2013) found that diversity of various taxa and ecosystem services (e.g., pollinators, carbon sequestration) declined in understory cacao and coffee systems as compared to undisturbed forest, but not nearly as much as when these crops were grown in monoculture plantations. The impact of cacao agroforestry on diversity and ecosystem functioning appears to be linked to the intensity of the system and amount of shade (Rice and Greenberg 2000; De Beenhouwer et al. 2013; Obeng and Aguilar 2015). Other studies support less of a connection between yield (as impacted by the level of farming intensity) and biodiversity (Clough et al. 2011). Our cacao plots were low-intensity/high-shade, and we detected no measurable effects on soil nematode communities. While soil biodiversity may be conserved in the cacao agroforestry systems we studied, more research is needed to establish the impacts of this practice on the ecosystem services provisioned by soils in this region, such as erosion prevention and nutrient cycling (Mortimer et al. 2018).

Nematodes are robust bioindicators due to their well-studied food web structure and ubiquitous distribution around the world. Analysis of soil nematode communities has proven to be a powerful approach to assessing the impacts of land use on soil biodiversity and functioning (Neher 2001). For example, nematode community analysis supports the benefits of organic practices (Treonis et al. 2018) and the linkages between above and below-ground biodiversity (Viketoft et al. 2009). Given the well-documented sensitivity of soil nematode communities to disturbance, land use change, and plant diversity (Bongers and Ferris 1999), it is probable that studies like ours are not failing to find differences among systems due to Type II error. Furthermore, we were able to quantify distinct, negative impacts of conventional banana farming on soil nematode communities, demonstrating the sensitivity of our specific sampling and extracting techniques for nematode community analysis in the same region as the rainforest and cacao plots. We also detected seasonal differences in the microbivorous components of the nematode communities, with bacterial-feeders showing more dominance in soils sampled during the dry season, while fungal-feeders dominated in the wet season soils. These changes are likely to reflect seasonal changes in soil biochemistry that influence bacterial and fungal communities. It is important to acknowledge that the coarse taxonomic resolution of our study (family or genus level) limits our sensitivity to changes in soil nematode assemblages that could be occurring at the species level. Molecular tools such as high throughput DNA sequencing can characterize nematode diversity at finer scales and hold great potential for future studies (Porazinska et al. 2012; Treonis et al. 2018).

Intensive agriculture causes declines in soil biodiversity and function (Tsiafouli et al. 2015). This includes negative effects on nematodes (Pothula et al.

2019), which is supported by our study. Unfortunately, we were unable to compare soil from understory cacao plots directly to conventional monocultures of cacao because these systems do not exist at a commercial scale within Belize. However, the banana plantation soils we sampled had higher densities of plant-parasitic nematodes than either the rainforest or cacao soils, as might be expected from a monoculture of a perennial plant. The banana soils seem to be a more stable environment for these plant pests, and high levels of plant-parasitic nematodes can be a strain for the farmer on top of the already low soil fertility that characterizes tropical soils. Application of nematicides can subtract from profits and are out of reach for many small scale farmers within Belize. Studies have shown that natural ecosystems are better at suppressing plant-parasitic nematodes than intensive systems (Cardoso et al. 2016). One mechanism of biological control of plant-parasitic nematodes is through consumption by omnivore/predator species, which are typically *k*-selected, sensitive species that have reduced abundance in disturbed soils (Oka 2010). The abundance of these omnivore/predators was lower in banana plantation soils in our study, and Ferris' Faunal Analysis confirms the less healthy status of banana soils compared to the rainforest and cacao. Banana soils also had lower Shannon and Simpson's Diversity indices than the rainforest and cacao soils, which reflects the increased dominance of these soils by plant-parasitic taxa. Interestingly, the Criconematidae stand out as a taxa under-represented in the banana soils (Online Resource 1). This family of nematodes is not a recognized pest of banana (Gowen et al. 2005), and it seems to be displaced by species from other plant-parasitic families in banana, as it was abundant in forest and cacao soils.

While much research has supported the value of nematode community analysis in temperate ecosystems, in general, nematode communities in tropical soils are understudied (Powers et al. 2009). Our work contributes to improving our understanding of a biome with a critical role in global climate change (Powers et al. 2009; Cardoso et al. 2016). Tropical soils are characterized by low nutrients and carbon storage due to high decomposition rates and high plant productivity and standing biomass. Soil nematode abundance is thought to be largely driven by soil organic matter content and quality in many ecosystems (Nielsen et al. 2014). We did not detect any effect of cacao agroforestry on soil organic matter, potentially due to the retention of cacao litter, which maintains nutrient levels in the soil (Pérez-Flores et al. 2017). The free-living component of the nematode communities we studied reflect the low quality of tropical soils, consisting mostly low cp-value nematodes from the Rhabditidae, Tylenchidae, and Aphelenchidae. Numerically, nematode communities were dominated by plant-parasites, instead of free-living taxa. In a study of soil nematode diversity and community structure across global biomes, Nielsen et al. (2014) found that plant-parasitic nematode taxa were the only trophic group to show an abundance: latitude relationship, being significantly more abundant at lower latitude sites, which was attributed to these systems having larger plant biomass. In tropical soils, nematodes, and the soil food web as a whole, seem to be more reliant on energy derived from living roots via parasitism or root exudates than on soil organic matter. It also has been shown that most tropical nematode diversity is actually associated with above-ground plant parts, not within the soil (Porazinska et al. 2012; Powers et al. 2009), and an exploration of how these microhabitats are impacted by cacao agroforestry would be beneficial.

Conclusions

Cacao agroforestry is a method of farming that has been proposed to mitigate climate change through the protection of biodiversity and ecosystem functioning as well as increasing carbon sequestration, but its effect on soil health is unclear. Our study shows that soil nematode community structure and diversity appear to be maintained when cacao agroforestry plots are established within old growth rainforest. In addition, when sampling a banana plantation in the same geographic area, we were able to discern distinct changes in nematode community structure that indicate less healthy soil, particularly an expansion of the abundances of plant-parasitic taxa. Our findings suggest that cacao agroforestry systems can preserve overall soil health, opening up the possibility to adopt this as a widespread sustainable farming method to help conserve biodiversity and mitigate climate change.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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