



Cover crops alter the soil nematode food web in banana agroecosystems

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ABSTRACT

Cover crops are increasingly being used in agriculture, primarily for weed or erosion management. The addition of cover crops increases the primary productivity of the system and diversifies basal resources for higher trophic levels. How increases in the quality and quantity of basal resources affect bottom-up and top-down control remains a key question in soil food web ecology. We evaluated the response of the nematode community to the introduction of cover crops between rows of a banana plantation. We measured changes in nematode food web structure and inferred the prevalence of bottom-up and top-down effects on the abundance of phytophagous nematodes (i.e., plant-feeding and root-hair-feeding species) 1.5 years after plots with cover crops (Poaceae or Fabaceae species) or bare soil were established. The addition of a cover crop greatly affected the structure and the abundance of the soil nematode community 1.5 years after planting. The abundance of all trophic groups except for plant-feeding nematodes tended to increase with the addition of cover crops. The Shannon–Weaver diversity index and the enrichment index increased with the addition of cover crops, indicating that opportunistic, bacterivorous and fungivorous nematodes benefited from the added resources. Plant-feeding nematodes were least abundant in plots with Poaceae cover crops, while bacterivorous, omnivorous, and root-hair-feeding nematodes were more abundant with Fabaceae cover crops than with bare soil, indicating that cover crop identity or quality greatly affected soil food web structure. Bottom-up effects on all trophic groups other than plant-feeding nematodes were evident with Poaceae cover crops, suggesting a top-down control of plant-feeding nematodes by omnivorous nematodes. Conversely, plant-feeding nematodes were evidently not suppressed in Fabaceae cover crops, perhaps because bottom-up effects on omnivorous nematodes were weaker (hence, top-down control by omnivorous nematodes was weaker), and because Fabaceae cover crops probably served as good hosts for some plant-feeding nematodes.

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1. Introduction

The enhancement of biodiversity in agricultural systems is receiving increasing attention because increased biodiversity is associated with pest suppression, reduced chemical inputs, and the closing of biogeochemical cycles (Altieri, 1999; Tilman et al., 2002). One practical way to enhance biodiversity is by the planting of cover crops (Teasdale, 1996), which are also frequently used for weed management (Moonen and Barberi, 2008). While cover crops directly provide several services, e.g., they reduce soil erosion (Derpsch et al., 1986), increase soil carbon and nitrogen content, and increase microbial activity (Ramos et al., 2010), they also have the potential to decrease the use of chemical pesticides by

promoting natural enemies. Adding a cover crop typically increases the quantity of primary resource for herbivorous species and therefore for the predators that consume herbivores. One risk of adding cover plants in agroecosystems is that this new resource may increase the numbers of one or more herbivorous pest species to damaging levels. However, when the entire community, including predators and other species that suppress herbivorous populations, benefits from this new resource and their numbers are increased, peaks in pest populations may be controlled by top-down effects (Chen and Wise, 1999). Cover crops can also directly affect pests through chemical components; exudates from *Tagetes* spp., for example, suppress plant-parasitic nematodes (Hooks et al., 2010). Cover crops should be selected that do not aggressively compete with the cultivated plant for resources (Tixier et al., 2011) and that do not increase populations of the pests including those of plant-feeding nematodes.

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As noted, the addition of cover crops typically increases primary productivity of the system and diversifies the basal resources used by higher trophic levels. Theoretical approaches predict that ecosystems with high primary productivity should have food webs with greater structure and longer food chains than ecosystems with low productivity (Lindeman, 1942; Post, 2002). From a functional point of view, increasing the quantity and diversity of basal resources alters trophic links. A key question in food web ecology is whether food webs are bottom-up controlled, top-down controlled, or both (Bardgett and Wardle, 2010; Neher, 2010). Bottom-up effects are relatively straightforward; when a new resource is added, it can modify consumer populations at various levels of the food web (Birkhofer et al., 2008; Scherber et al., 2010; Aguilar-Fenollosa et al., 2011). In contrast, responses of top-down effects to basal resources can be complex. Addition of a basal resource may enhance top-down effects by supporting longer food chains, e.g., by supporting an increased abundance of predators that can control plant-feeding species (including plant-parasitic and root-hair-feeders), or by modifying food web structure, e.g., by providing alternative prey that increase predator abundance (Wise et al., 2006; Barberi et al., 2010). In this paper, we investigated how bottom-up and top-down effects on herbivores (plant-parasitic nematodes) are altered by addition of a basal resource (a cover crop) to an ecosystem.

Because of their relatively simple food webs, agroecosystems, including banana plantations, can be useful biological models for studying how the addition of a new basal food source affects top-down suppression of herbivores. Until now, most of the dessert bananas (*Musa* spp., AAA group, cv. Cavendish Grande Naine) grown for export, whether from Martinique or other countries, have been intensively cultivated in monocultures on bare soil. Several candidate species, which belong to the Fabaceae and Poaceae (legumes and true grasses, respectively), are being studied as cover crops in bananas (Blazy et al., 2009). The selection of the most appropriate species depends on their agronomical compatibility, e.g., how they compete with banana for resources and how well they control weeds (Tixier et al., 2011), and on their effect on pest populations. In most tropical countries including the entire Caribbean region, the most damaging pests in banana ecosystems are plant-parasitic nematodes (Quénéhervé, 2009). In Martinique, the nematode community parasitizing bananas comprises migratory endoparasites and sedentary endoparasites. The migratory endoparasites include the burrowing nematode *Radopholus similis* (Cobb, 1893) Thorne, 1949; the lesion nematode *Pratylenchus coffeae* Goodey, 1951; the spiral nematode *Helicotylenchus multicinctus* (Cobb, 1893) Sher, 1961; and the lance nematode *Hoplolaimus seinhorsti* Luc, 1958. The sedentary endoparasites include the root-knot nematodes *Meloidogyne* spp. and the reniform nematode *Rotylenchulus reniformis* Linford & Oliviera, 1940. By attacking primary and lateral roots, these plant-parasitic nematodes reduce plant nutrition, root anchorage, plantation life, and yield (Quénéhervé, 1993).

Although Duyck et al. (2011a) showed that the addition of a cover crop (signal grass, *Brachiaria decumbens*, Poaceae) alters the food web of macrofauna in soil litter and may help control the banana weevil, *Cosmopolites sordidus*, the impact of cover crops on the nematode community in banana plantations remains unclear. Cover crops can affect plant-parasitic nematodes by acting as a food resource (a bottom-up effect) and by enhancing predators of nematodes (a top-down effect). In addition to abiotic factors that structure the nematode community (Duyck et al., 2011b), the quality of the cover crop (species identity) can affect the entire soil food web. For example, the composition of the plant community affected the structure of a plant-feeding nematode community (Duyck et al., 2009), and complementarity in resource quality and

the identity of plants explained the diversity of primary consumers and higher trophic groups (De Deyn et al., 2004).

Soil nematodes are important components of soil systems, and they have been widely used as indicators of soil food web structure and soil health (Bongers and Bongers, 1998; Ferris and Bongers, 2006). Soil nematodes include the following trophic groups: phytophages (plant-feeding and root-hair-feeding nematodes), bacterivores, fungivores, omnivores, and predators. Nematodes may be particularly relevant for the study of resource-driven effects on trophic composition because they are involved in an array of ecosystem functions: i) consumption of plants (by phytophagous nematodes), ii) decomposition and nutrient mineralization (by bacterivorous and fungivorous nematodes) (Djigal et al., 2010), and iii) control of plant-feeding nematodes (by predacious and omnivorous nematodes) (Yeates and Wardle, 1996). The relative proportions of nematode trophic groups have been used to generate enrichment and structure indices, which are indicators of soil health (Ferris et al., 2001; Pattison et al., 2008), and a maturity index, which is an indicator of system resilience (Bongers, 1990).

The objective of this study was to evaluate the response of the nematode community to the introduction of cover crops in banana plantations. We attempted to answer two questions: Is nematode food web structure differentially altered by the addition of different cover crops? Is the abundance of phytophagous nematodes more affected by bottom-up effects than top-down effects when a cover crop is added to the ecosystem?

2. Materials and methods

2.1. Site, experimental design, and treatments

The experiment was conducted in a banana plantation at the Rivière Lézarde CIRAD Research station in the center of Martinique (14°40'21.38"N; 60°59'50.07"W). The experimental site was a former banana plantation; after 1 year of fallow, a duration that is sufficient to considerably reduce the abundance of root-feeding nematodes (Chabrier et al., 2010), banana and cover crops were planted. The soil was a nitisol derived from volcanic ash (andesitic basalt) with 73% clay. This type of soil is characteristic of the lowlands in central Martinique. Before the start of the experiment, herbicides had been applied every 3 months during the fallow period but no nematicide or insecticide had been applied for at least 5 years. The experiment had six cover crop treatments. These included a control without cover crop, which was maintained by herbicide application every 2 months; a "spontaneous" cover crop (composed exclusively of Poaceae species that were not planted); and four cover crop that were planted. The cover crops planted were *Paspalum notatum* cv. Common, *Neonotonia wightii*, *Pueraria phaseoloides*, and *Stylosanthes guyanensis*. *P. notatum* is a perennial grass in the Poaceae, and the latter three cover crop species are legumes (Fabaceae). The experimental design included three replicates of the six treatments, giving 18 plots that were randomly distributed over the experimental field. Each plot occupied 75 m² and was separated from adjacent plots by a 2 m-wide alley.

2.2. Soil and root sampling

Soil samples were collected in October 2010 and February 2011 (16 and 20 months after the plots were established), corresponding to the rainy and dry season, respectively. From each of the 18 plots, four monoliths of soil (25 × 25 × 15 cm) were collected in the banana inter-row and mixed thoroughly to form a composite sample; banana roots were removed from soil and were analyzed separately. Thirty-six composite soil samples (two sampling dates) and 18 banana root samples (first sampling date) were collected.

Very little nonliving organic matter (litter) was observed on the soil surface because crop residues decompose rapidly under tropical conditions. If present, the small quantity of litter was removed from the samples before they were processed. The contents of NH_4^+ and NO_3^- in the soil samples, as determined with a dry combustion analyzer (Flash2000, Thermo Scientific), did not differ among cover crop treatments (mean values: 10.8 and 27.1 ppm in dry soil, respectively), it was lower in the bare soil treatment (mean values: 1.7 and 26.7 ppm in dry soil, respectively).

2.3. Extraction, counting, and identification of nematodes

Nematodes were extracted from 250 g soil samples (fresh weight) by elutriation (Seinhorst, 1950) and were counted with a stereomicroscope ($\times 40$). Nematodes were fixed in a 4% formaldehyde solution. Then, 200 specimens per sample were randomly selected on mass slides (containing about 250 nematodes per slide) and identified to genus or family with a compound microscope ($\times 400$). Nematodes taxa were then assigned to six trophic groups as described by Yeates et al. (1993): plant-feeders (Pf), root-hair-feeders (Rhf), bacterivores (Ba), fungivores (Fu), omnivores (Om), and carnivores (Ca). Nematodes were extracted from banana roots by centrifugation–flotation (Coolen and D'Herde, 1972), and the specimens obtained, which were mostly plant-feeders, were identified to the species level and counted with a compound microscope.

2.4. Ecological indices

The effects of cover crops on the nematode community were evaluated by the determination of ecological indices. The maturity index (MI) as defined by Bongers (1990) was calculated as the weighted average of colonizer–persister (c–p) values for each non-plant-feeding taxon according to the 1–5 c–p scale defined by Bongers and Bongers (1998). The plant-parasitic index (PPI) was calculated in the same manner as the MI but using only herbivorous nematode data (plant-feeders and root-hair-feeders). Nematodes were also assigned to functional guilds according to trophic groups and colonizer–persister classes (Bongers and Bongers, 1998). For example, bacterivores with a c–p value of 2 were classified in functional guild Ba_2 and fungivores with a c–p value of 3 were classified in functional guild Fu_3 . The enrichment index, the structure index, the nematode channel ratio, and the Shannon–Weaver index were also calculated. The enrichment index, or EI, and the structure index, or SI, were developed by Ferris et al. (2001) and are calculated as:

$$\text{EI} = 100 \times (e/(e + b))$$

$$\text{SI} = 100 \times (s/(b + s))$$

where e , b , and s were the abundance of individuals in guilds representing enrichment (e), basal (b), and structure (s) food web components. These components are calculated based on the weighted abundance of guilds Ba_1 and Fu_2 (e), Ba_2 and Fu_2 (b), and Ba_{3-5} , Fu_{3-5} , Om_{4-5} , and Ca_{2-5} (s). The EI assesses food web response to availability of resources (Ferris et al., 2001) while the SI indicates whether the soil community is basal (typical of disturbed systems) or structured (typical of more stable systems) (Ferris et al., 2001). The nematode channel ratio (NCR) was calculated according to Yeates (2003):

$$\text{NCR} = B/(B + F)$$

where B and F are, respectively, the relative contributions of bacterivorous and fungivorous nematodes to total nematode abundance.

This NCR indicates the relative importance of fungal-fed and bacterial-fed trophic channels in the soil decomposer food web. Finally, the Shannon–Weaver index (H') as described by Shannon (1948) was used to calculate the taxonomic diversity of the nematode community:

$$H' = - \sum p_i (\ln(p_i))$$

where p_i is the proportion of individuals in the i -th taxon.

2.5. Statistical analyses

A Poisson log-linear model (analysis of deviance with Poisson error) was used to analyze nematode abundance (numbers of individuals per 100 g of dry soil or 100 g of roots) as a function of trophic group, cover crop treatment, root taxa, year, and interactions. We used standard simplification procedures to eliminate non-significant terms in the model; the significance of each term was assessed based on the change in deviance between models with and without that term. Overdispersion, when present, was accounted for by using a quasi-Poisson instead of Poisson error (O'Hara and Kotze, 2010). Nematode ecological indices were subjected to analysis of variance (ANOVA) as a function of cover crop treatment; an arcsin(\sqrt{X}) transformation was performed when necessary to normalize residuals. All statistical analyses were performed with R software (R Development Core Team, 2009).

3. Results

A total of 82,780 nematodes from 40 taxa were counted and identified in the 36 soil samples (Table 1). Bacterivores and omnivores were the most diverse trophic groups, with 11 and 9 taxa, respectively. The plant-feeding nematode *R. reniformis* Linford & Oliveira, 1940 numerically dominated the soil nematode community, representing 45% of all nematodes extracted. Other main genera (i.e., with densities greater than 20 individuals per 100 g of dry soil) were *Meloidogyne*, *Itonchus*, *Hoplolaimus*, *Helicotylenchus*, *Mesodorylaimus*, *Filenchus*, *Prodorylaimus*, *Cephalenchus*, *Rhabditis*, *Mononchus*, and *Eucephalobus*.

Table 1
Nematode taxa identified at the experimental site.

Taxa	cp class	Trophic group	Taxa	cp class	Trophic group
<i>Rhabditis</i>	1	Ba	<i>Radopholus</i>	3	Pf
<i>Cephalobus</i>	2	Ba	<i>Hoplolaimus</i>	3	Pf
<i>Eucephalobus</i>	2	Ba	<i>Helicotylenchus</i>	3	Pf
<i>Heterocephalobus</i>	2	Ba	<i>Rotylenchulus</i>	3	Pf
<i>Pseudacrobeles</i>	2	Ba	<i>Meloidogyne</i>	3	Pf
<i>Acrobeloides</i>	2	Ba			
<i>Cervidellus</i>	2	Ba	<i>Pungentus</i>	4	Om
<i>Macrolaimus</i>	3	Ba	<i>Thonus</i>	4	Om
<i>Desmodora</i>	3	Ba	<i>Oxydirus</i>	4	Om
<i>Achromodoridae</i>	3	Ba	<i>Aporcelaimellus</i>	5	Om
<i>Alaimus</i>	4	Ba	<i>Prodorylaimus</i>	5	Om
			<i>Mesodorylaimus</i>	5	Om
<i>Aphelenchus</i>	2	Fu	<i>Oxybelondira</i>	5	Om
<i>Aphelenchoides</i>	2	Fu	<i>Belondira</i>	5	Om
<i>Ditylenchus</i>	2	Fu	<i>Axonchium</i>	5	Om
<i>Tylencholaimus</i>	4	Fu			
			<i>Tobrilus</i>	3	Ca
<i>Tylenchus</i>	2	Rhf	<i>Mononchus</i>	4	Ca
<i>Filenchus</i>	2	Rhf	<i>Itonchus</i>	4	Ca
<i>Cephalenchus</i>	2	Rhf	<i>Paractinolaimus</i>	5	Ca
<i>Ultramella</i>	2	Rhf	<i>Westindicus</i>	5	Ca
<i>Basiria</i>	2	Rhf			
<i>Neopsilenchus</i>	2	Rhf			

Ba: bacterivores; Ca: carnivores; Fu: fungivores; Pf: plant-feeders; Rhf: root-hair-feeders; Om: omnivores.

The analysis of deviance with Poisson error indicated that the abundance of soil nematodes differed among trophic groups and was affected by cover crop treatment (Table 2a). The interaction between trophic groups and cover crop treatments was also significant but sampling date was not.

The effects of treatments on each trophic group are presented in Table 2b. All trophic groups were significantly affected by cover crop treatments except the fungivore group (which had a nearly significant P -value of 0.06). Other than plant-feeding nematodes, nematodes were more abundant in plots with cover crops than in plots with bare soil (Fig. 1). Numbers of plant-feeding nematodes were similar with bare soil or with Fabaceae (*N. wightii*, *P. phaseoloides*, and *S. guyanensis*). However, plant-feeder abundance was lower with Poaceae (spontaneous cover and *P. notatum*) than with bare soil. *P. notatum* was particularly favorable to most trophic groups, except for plant-feeding nematodes. Fabaceae cover crops (*N. wightii*, *P. phaseoloides*, and *S. guyanensis*) tended to support high numbers of carnivores and plant-feeders. In contrast, Poaceae cover crops (spontaneous cover and *P. notatum*) tended to support high numbers of bacterivores, omnivores, and root-hair-feeders. Carnivorous nematodes were more abundant with cover crops than with bare soil and tended to be most abundant with all three Fabaceae cover crops. Carnivore numbers were highest with *P. phaseoloides*. The numbers of bacterivores, carnivores, or plant-feeders did not differ among plots with Fabaceae cover crops (*N. wightii*, *P. phaseoloides*, *S. guyanensis*) but numbers of omnivores and root-hair-feeders were higher with *S. guyanensis* than with *P. phaseoloides* and *N. wightii*.

The Shannon–Weaver index was significantly affected by treatment ($F = 11.7$; d.f. = 5, 29; $P < 0.0001$). Nematode diversity was higher with cover crops than with bare soil and was highest

with Poaceae cover crops (Fig. 2). The enrichment index (EI) was higher with cover crops than with bare soil ($F = 3.9$; d.f. = 5, 29; $P = 0.0075$), while the structure index (SI) did not significantly differ among the cover crop treatments ($F = 1.9$, d.f. = 5, 29; $P = 0.1161$) (Fig. 2). EI was highest with *P. phaseoloides*. The maturity index (MI) did not significantly differ among the cover crop treatments ($F = 2.4$; d.f. = 5, 29; $P = 0.0571$) but tended to be higher with Poaceae cover crops than with bare soil or Fabaceae cover crops. Conversely, the plant-parasitic index (PPI) was significantly lower with Poaceae cover crops ($F = 5.2$; d.f. = 5, 29; $P = 0.0015$). The nematode channel ratio (NCR) ranged from 0.81 to 0.93 and was not affected by cover crop treatment ($F = 0.527$; d.f. = 5, 29; $P = 0.7539$).

Six species of plant-feeding nematodes were identified in the banana roots: *R. similis*, *P. coffeae*, *Meloidogyne arenaria*, *M. incognita*, *H. multincinctus*, and *H. seinhorsti*. *R. similis* and *P. coffeae* were present in low numbers (fewer than 300 individuals 100 g^{-1} of root). The abundance of plant-feeding nematodes in banana roots (i.e., numbers 100 g^{-1} of root) significantly differed among nematode species and among cover crop treatments, and the interaction between species and cover crop treatment was also significant (Table 2c). *H. multincinctus* was more abundant in banana roots in the *P. phaseoloides* plots than in the plots of the other treatments (Fig. 3). *M. arenaria* and *M. incognita* were more abundant in banana roots in the bare soil plots than in the *P. notatum* plots. *H. seinhorsti* abundance in banana roots was greater in plots with bare soil than in plots with cover crops and was greater in the spontaneous and *S. guyanensis* plots than in the *N. wightii* and *P. phaseoloides* plots (Fig. 3).

4. Discussion

4.1. Food web modification by cover crops

The addition of cover crops to a banana plantation greatly affected the soil nematode community, both in terms of structure and abundance. The abundance of all trophic groups except for plant-feeding nematodes tended to increase with the addition of cover crops, and the effect of cover crops on the abundance of different trophic groups depended on the cover crop species. Nematode abundance was relatively homogeneous inside each cover crop group (Poaceae and Fabaceae). Poaceae cover crops had the lowest abundance of plant-feeding nematodes but supported higher numbers of bacterivores, omnivores, and root-hair-feeders than Fabaceae cover crops or bare soil. Fabaceae cover crops supported food chains with more carnivores than the other treatments. These results are in line with Blanchart et al. (2006), who reported an increase in the abundance of bacterivorous, predaceous, and facultatively phytophagous nematodes but a decrease in the abundance of obligatory phytophagous nematodes in maize intercropped with a Fabaceae cover crop (*Mucuna pruriens*). The higher abundance of omnivores and carnivores in both studies indicates that the addition of cover crops enhances resource availability for higher trophic groups and consequently the stability of soil food webs. Differences in the effects of Poaceae and Fabaceae cover crops on nematode trophic groups suggest that the identity of the cover crop also plays an important role in the structuring of soil food webs. The higher abundance of bacterivores with cover crops indicates an increase in bacterial activity and microbial biomass, and a faster turnover of nutrients in soil (Ferris et al., 1998; DuPont et al., 2009). This result was confirmed by the greater soil microbial biomass and NH_4^+ content with cover crop treatments than with bare soil in the current study (data not shown).

Table 2

Results of the analysis of deviance on the abundance of nematodes (a) for the complete community, (b) for each trophic group, and (c) for taxa within banana roots. All the effects retained in the final model (see Methods) are given, and their significance is indicated (chi-square tests and corresponding P -values). Δ dev corresponds to changes in deviance due to the suppression of the 'effect' term from the reference model (indicated in the second column). The residual deviance and d.f. relate to the reference P -value of the chi-square test that was used to determine the significance of the model effect. Codes for effects: S = sampling period, T = cover crop treatment, G = trophic group, Sp = root taxa. Interactions are indicated by colons.

(a)						
Effect in reference model	Terms included	Δ dev	Δ d.f.	Residual dev	Residual d.f.	P -value
S	G + T + S	186	1	14387	198	0.181
T	G + T + S	1360	5	15747	203	0.003
G	G + T + S	47979	5	62366	203	<0.0001
T:G	G + T + G:T	9027	25	5545	174	<0.0001
(b)						
Trophic group	Δ dev	Δ d.f.	Residual dev	Residual d.f.	P -value	
Bacterivores	892	5	477	29	0.0033	
Fungivores	212	5	544	29	0.060	
Omnivores	3211	5	1768	29	<0.0001	
Carnivores	633	5	884	29	0.0007	
Plant-feeders	1498	5	4028	29	0.0481	
Root-hair-feeders	912	5	911	29	<0.0001	
(c)						
Effect in reference model	Terms included	Δ dev	Δ d.f.	Residual dev	Residual d.f.	P -value
T	T + Sp	15,322	5	161,350	84	0.004
Sp	T + Sp	59,946	4	101,404	80	<0.0001
T:Sp	T + Sp + T: Sp	40,734	20	60,670	60	0.0008

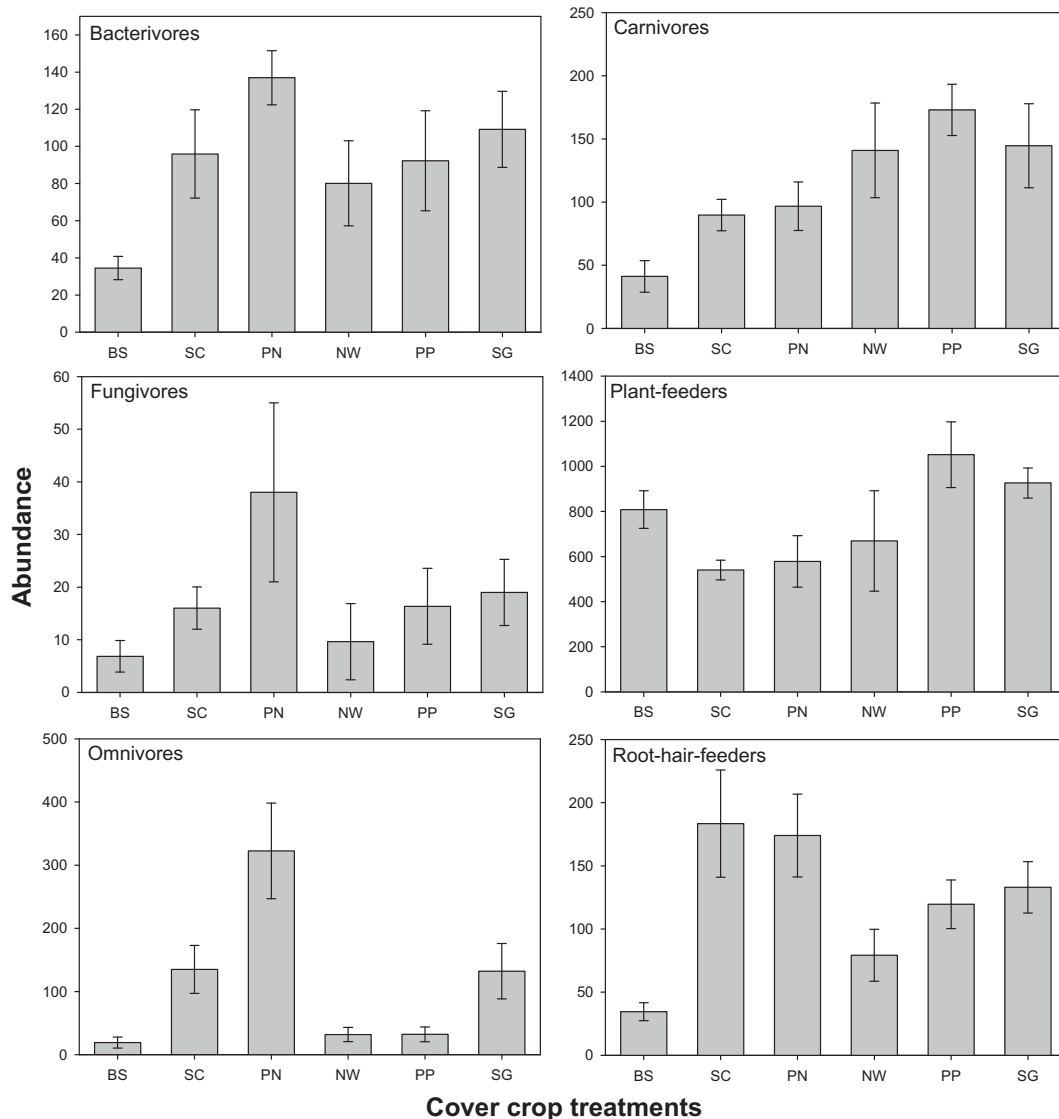


Fig. 1. Abundance (number of individuals 100 g⁻¹ dry soil, mean \pm SE) of nematode trophic groups in plots with and without cover crops in a banana plantation. Data were combined for samples from the two sampling dates (16 and 20 months after the plots were established). BS: bare soil; SC: spontaneous cover; PN: *Paspalum notatum*; NW: *Neonotonia wightii*; PP: *Pueraria phaseoloides*; SG: *Stylosanthes guyanensis*. SC and PN are Poaceae species, while NW, PP, and SG are Fabaceae species.

Dominance of the plant-feeding trophic group by the reniform nematode *R. reniformis* is commonly observed in the Caribbean (Ayala and Roman, 1963). This species generally feeds on secondary or tertiary banana roots (Edmunds, 1968). However, the most damaging species for banana plants are the burrowing nematode *R. similis* and the lesion nematode *Pratylenchus spp.*, which feed on primary roots and are usually found inside the roots (Quénéhervé, 2009).

The Shannon–Weaver index, which indicates taxa diversity, was higher in all cover crop treatments than in the bare soil treatment. The Shannon–Weaver index also was higher with Poaceae cover crops than with Fabaceae cover crops. These results confirm those of De Deyn et al. (2004) and Wardle et al. (2006), who showed that plant identity affects the diversity and abundance of nematodes in the soil food web. Viketoft et al. (2009) also suggested that plant identity has stronger effects than plant diversity on nematode community composition. These authors attributed the effect of plant species diversity to the complementarity in resource quality of the component plant species rather than to an increase in total

resource quantity. In our case, banana and cover crop resources complement each other in providing diverse resources.

The addition of cover crops increased the enrichment index (EI). A similar finding was reported by DuPont et al. (2009), who showed that opportunistic non-herbivorous guilds (bacterivore guild Ba₁ and fungivore guild Fu₂) benefit from the added resource. However, the absence of a cover crop effect on fungivorous nematodes and their low abundance suggest that enrichment opportunists (Ba₁; *Rhabditidis*) benefit more from the added resource than fungivores (Fu₂; *Aphelenchus*, *Aphelenchoides*, and *Ditylenchus*) in banana plantations. Moreover, the tendency for EI to be higher for Fabaceae cover crops than for the Poaceae cover crops showed that the food resource provided by Fabaceae crops, which are nitrogen-fixing plants, was more favorable to the Ba₁ guild than the food resource provided by Poaceae crops. Indeed, the cp1 group of bacterivores were more abundant in the Fabaceae plots (42 individuals 100 g⁻¹ dry soil) than in the Poaceae plots (25 individuals 100 g⁻¹ dry soil). This was probably linked to the quality of the Fabaceae litter, which contains relatively low levels of lignin and

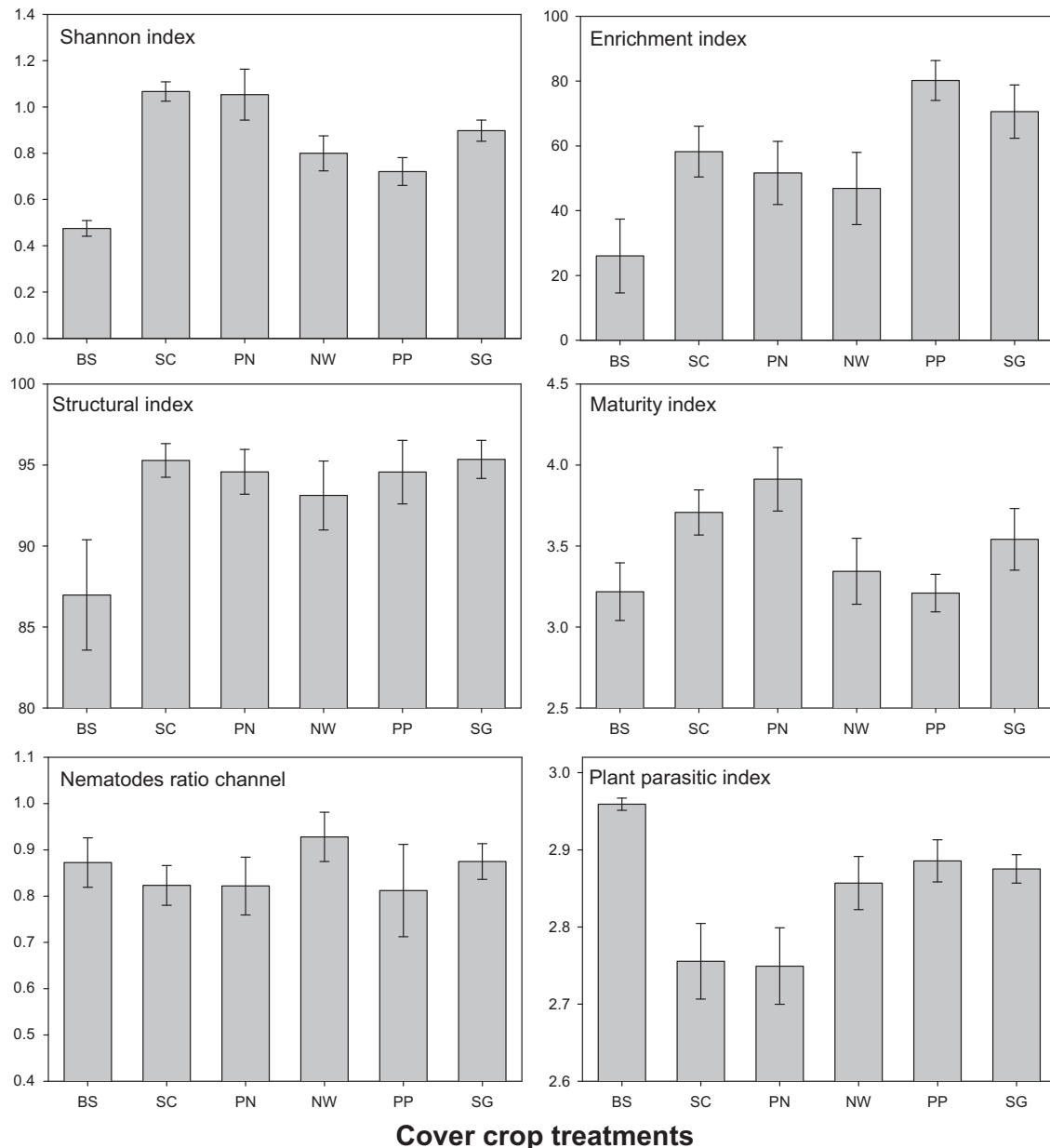


Fig. 2. Indices (mean \pm SE) of the soil nematode community for the six cover crop treatments. Data were combined for the two sampling dates (16 and 20 months after the plots were established). BS: bare soil; SC: spontaneous cover; PN: *Paspalum notatum*; NW: *Neonotonia wightii*; PP: *Pueraria phaseoloides*; SG: *Stylosanthes guyanensis*. SC and PN are Poaceae species, while NW, PP, and SG are Fabaceae species.

cellulose, and is therefore easily degraded by bacteria (Nakhone and Tabatabai, 2008); this would promote bacterial numbers and consequently promote the enrichment opportunist guild Ba₁. That bacterivores were more abundant in the Poaceae plots (Fig. 1) was due to the dominance of cp2 taxa in those plots: cp2 taxa were represented by 90 individuals 100 g⁻¹ dry soil in the Poaceae plots vs. 32 individuals 100 g⁻¹ dry soil in the Fabaceae plots. The structure index (SI) was equally increased by the addition of any of the cover crops, and an increase in SI indicates that the length of food chains was increased to include more carnivores and omnivores. This finding is consistent with the productivity hypothesis, which predicts that food webs sustained by high primary productivity are more structured and have longer food chains than food webs sustained by low primary productivity. The maturity index (MI) was increased only by Poaceae cover crops, suggesting that the food web was more resilient with Poaceae cover crops than with

Fabaceae cover crops or bare soil. This trend was confirmed by the plant-parasitic index (PPI), which was lower for Poaceae cover crops than for the other treatments. The nematode ratio channel (NRC) was not affected by cover crop, but the high NRC values (above 0.8) indicated that bacterial decomposition pathways dominated the fungal pathways and confirm that bacterivores were more favored than fungivores in these banana cropping systems.

4.2. Bottom-up vs. top-down regulation

Soil food webs are often considered to be regulated by resources (bottom-up controlled), especially in the case of nematode food webs (Neher, 2010), and recent studies confirm the importance of plant species in the structuring of the nematode community (Duyck et al., 2009). Nevertheless, regulation by predators (top-down control) is supported by data in the current study and should not be

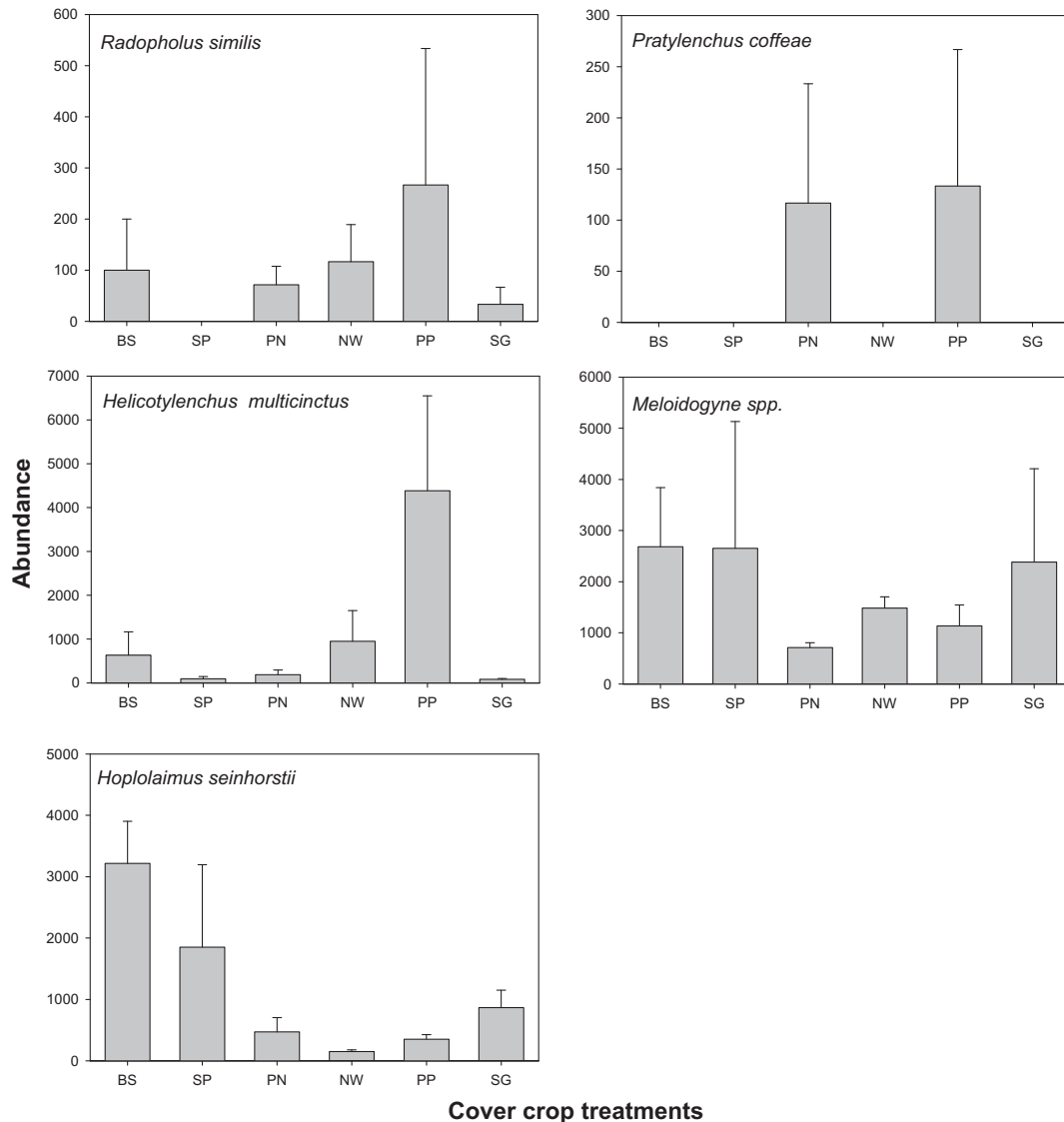


Fig. 3. Abundance (number of individuals 100 g⁻¹ of root, mean ± SE) of plant-feeding nematode taxa in banana roots sampled between banana rows where cover crops had or had not been planted. Data were combined for the two sampling dates (16 and 20 months after the plots were established), BS: bare soil; SC: spontaneous cover; PN: *Paspalum notatum*; NW: *Neonotonia wightii*; PP: *Pueraria phaseoloides*; SG: *Stylosanthes guyanensis*. SC and PN are Poaceae species, while NW, PP, and SG are Fabaceae species.

ignored. The dichotomy as to whether food webs are bottom-up vs. top-down controlled is reconciled by the theoretical approach of de Ruiter et al. (1998), who suggested that food web control is both bottom-up and top-down. In our case, we clearly identified the bottom-up effect of the new resource on the abundance of root-hair-feeding, bacterivorous, omnivorous, and carnivorous trophic groups. Our data also suggest a possible top-down control on plant-feeding nematodes when higher trophic groups are enhanced. The moderate use of pesticides on the field before planting the experiment (no nematicide or insecticide had been applied during the 5 years before planting) probably contributed to the establishment of the top-down control because it allowed for the persistence of higher trophic levels. Fig. 4 summarizes the possible bottom-up and top-down effects of Poaceae and Fabaceae cover crops on the nematode food web and on the regulation of plant-feeding nematodes. As indicated in Fig. 4, Poaceae cover crops increased the abundance of lower trophic groups, except plant-feeding nematodes. This increase in lower trophic groups supported an increase in the abundance of higher trophic groups, and the increase in the

higher trophic groups evidently resulted in top-down control of plant-feeding nematodes. The top-down control appeared to be stronger for *H. multincinctus* and *Meloidogyne* spp., especially when *P. notatum* was the cover crop. Enhancement of the abundance of lower trophic groups was less with Fabaceae cover crops than with Poaceae cover crops, and this apparently resulted in less top-down control of plant-feeding nematodes in the Fabaceae plots. In addition, Fabaceae cover crops were probably good hosts for some of the plant-feeding nematodes (*P. phaseoloides* for *H. multincinctus* and *S. guyanensis* for *Meloidogyne* spp.), which would explain the greater abundance of plant-feeding nematodes with Fabaceae cover crops than with bare soil. Omnivorous nematodes may have been involved in the top-down control of plant-feeding nematodes because the omnivore families Belondoriidae and Aporcelaimidae were relatively abundant in Poaceae plots but were rare in Fabaceae and bare soil plots (data not shown).

From an applied perspective, cover crops i) should enhance the abundance of higher trophic levels but ii) should not provide additional resource for plant-feeding nematodes. With regard to

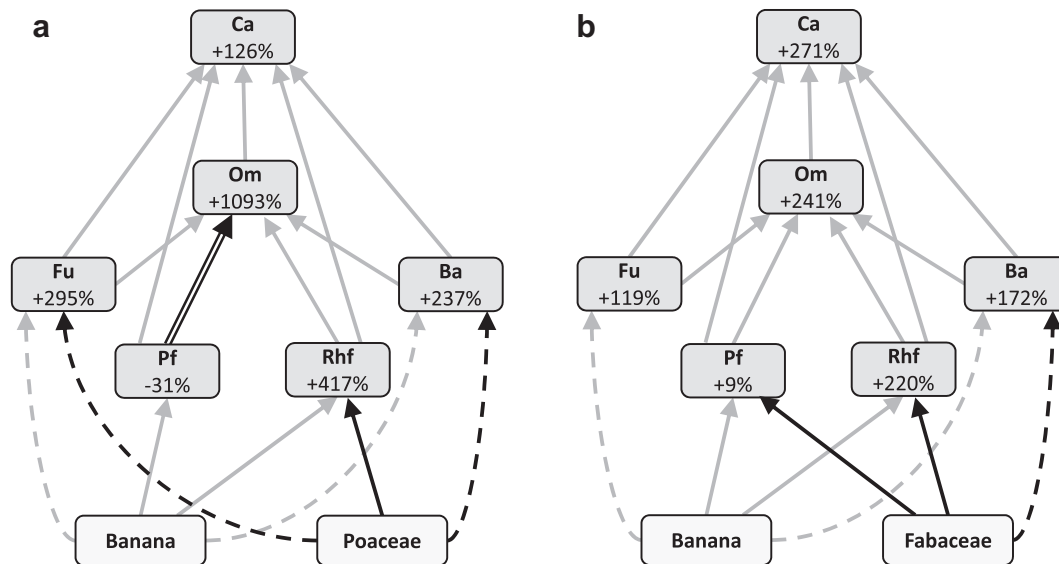


Fig. 4. Summary of possible bottom-up and top-down effects in plots with Poaceae (a) and Fabaceae (b) cover crops. Percentages in trophic group boxes indicate the mean change in abundance compared to bare soil. Gray arrows indicate possible trophic links based on banana, dashed arrows indicate indirect trophic links, black arrows indicate direct bottom-up trophic links enhanced by the cover crop, and the double-line plus arrow indicates a top-down trophic link on plant-feeding nematodes enhanced by the cover crop. Ba: bacterivores; Ca: carnivores; Fu: fungivores; Pf: plant-feeders; Rhf: root-hair-feeders; Om: omnivores.

the second point, the host status of cover crops should be checked against the main pests (*R. similis* and *P. coffeae* in the case of banana) before their introduction in the cropping system.

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