

## Associations of soil type and previous crop with plant-feeding nematode communities in plantain agrosystems



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### ABSTRACT

Understanding the influence of soil properties and cultural practices on the communities of plant-feeding nematodes (PFNs) in agrosystems is a prerequisite for cost-efficient and environment-friendly pest control. Although plantain is a staple food crop in the Caribbean, the relationships between PFN communities and environmental factors are poorly understood in plantain agrosystems. In this study, which was conducted in Martinique (French West Indies), we quantified the PFNs in 301 root samples taken from 53 plantain fields that differed in climate, edaphic conditions, and cultural practices. The physico-chemical properties were also determined for the soil in each field. Coinertia analysis (CI) and General Linear Mixed Models (GLMMS) were used to investigate the relationships between the PFN communities, soil properties, and cultural practices. Four nematode taxa were found in plantain roots: *Radopholus similis*, *Pratylenchus coffeae*, *Helicotylenchus multicinctus*, and *Meloidogyne* spp. The lesion nematode *P. coffeae* was the most prominent PFN species, followed by the burrowing nematode *R. similis*, root-knot nematodes *Meloidogyne* spp., and the spiral nematode *H. multicinctus*. *P. coffeae* was significantly more abundant in ferralsols and nitisols (which have a low organic matter content and a high exchangeable cation content) than in andosols (which have a high organic matter content). Nematode abundances were apparently affected by the previous crops e.g., *P. coffeae* was slightly more abundant in fields where tuber plants such as sweet potato, yam, or dasheen were the previous crop; *R. similis* was particularly abundant in fields where banana or plantain was the previous crop; and *Meloidogyne* spp. were abundant in fields where a market garden was the previous crop. The results of this study will be useful for the design of PFN control methods in plantain.

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### 1. Introduction

There is an increasing need to understand the biotic and abiotic drivers that shape the structure of plant-feeding nematode (PFN) communities in tropical agrosystems because such information is central to the design of cost-efficient and environment-friendly control methods. The structure of nematode communities in agrosystems depends on many factors including climate (Bakonyi et al., 2007; Duyck et al., 2012; Papatheodorou et al., 2004; Ruess

et al., 1999), soil properties (Avendano et al., 2004; Ettema and Wardle, 2002; Godefroid et al., 2013; Goodell and Ferris, 1980; Ortiz et al., 2010; Quénéhervé, 1988), plant composition (Yeates, 1999), interspecific interactions such as competition or trophic interactions (Djigal et al., 2012; Ferris et al., 2012; Wardle et al., 2004), and cultural practices or past disturbance (Bongers, 1990; Chabrier and Quénéhervé, 2003; Neher, 2010; Verschoor et al., 2001).

Plantain is a major fruit crop in tropical and subtropical areas and is important for food security in many developing areas, including the Caribbean region (Lescot, 2004). In the Caribbean, plantains are often cultivated by smallholder farmers and sold in local markets. Unlike dessert bananas, which are primarily grown for export, plantains are generally managed with low chemical

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input and have a very short lifespan, i.e., 2–3 years for plantains vs. 7 years or more years for intensively managed dessert bananas (Quénéhervé, 2009). Because nematological research has mainly focused on dessert bananas, insufficient information is available regarding the composition of PFN communities in plantain agrosystems in the Americas and especially in the Caribbean. Previous research, however, has established that PFNs may cause severe damage to plantain roots (Brentu et al., 2004; Coyne et al., 2013, 2005) and may consequently cause substantial yield losses (Fogain, 2000; Jacobsen, 2009). A better understanding of the PFN communities associated with plantains is required to design efficient pest control methods (Coyne, 2007).

Bananas infected with PFNs are less able to take up water and nutrients, which results in stunting, delayed maturation, reduced bunch size, and finally in significant yield loss (Quénéhervé, 2009). In banana and plantain fields of the Caribbean, the burrowing nematode *Radopholus similis* Cobb and the lesion nematode *Pratylenchus coffeae* Zimmerman are particularly prevalent (Roman, 1978; Stover, 1972) and feed in root cells (Gowen et al., 2005). These migratory endoparasites cause necrosis and lesions on which other opportunistic pathogens can develop, reduce root biomass, and most importantly increase the susceptibility to toppling (Chabrier et al., 2005, 2002). *R. similis* is a native of the Pacific region but over the last several hundred years has invaded most of the banana-growing regions, including Latin America and the Caribbean, following the transport of infested *Musa* plants between countries (Marin et al., 1998). This species is now found in both dessert (Cavendish cultivars) and plantain bananas. *P. coffeae* is a widespread pantropical species associated with most tropical crops (Bridge et al., 2005; CABI, 2016). In Caribbean banana plantations, other harmful PFNs include the spiral nematode, *Helicotylenchus multicinctus* Cobb, and root-knot nematodes, *Meloidogyne* spp. (Cofewicz et al., 2005; Roman, 1978).

The objective of the current study was to increase our basic understanding of PFN communities in plantain agrosystems in the Caribbean. To achieve this goal, we performed a large-scale survey in Martinique and used multivariate analyses and statistical models to explore the relationships between PFN communities, soil type, and cultural practices.

## 2. Materials and methods

### 2.1. Data collection

Between January and July 2011, a total of 301 root samples were collected from 53 plantain fields (*Musa* AAB, cv. Crème Blanche) located throughout Martinique island in the Caribbean. The fields ranged from 0.1–15 ha, and 90% were  $\leq 3$  ha. Field age ranged from 1 to 5 years. In each field, 5–10 root samples (about 500 g of fresh roots per sample) were independently collected from 0 to 30 cm depth at the base of randomly selected flowering plantains (one sample per plantain mat). Each root sample was washed with water and cut into small pieces (from 0.5 to 2 cm). For each root sample, a 50-g quantity was used for nematode extraction.

Nematodes were extracted in a mist chamber for 10 days (Seinhorst, 1950) and were then identified and counted with the aid of a stereomicroscope. Nematode densities were expressed as numbers of individuals per 100 g of fresh roots. We thus obtained 5–10 measures of nematode densities in roots for each field. We calculated the geometric mean of the abundance of each PFN species in each plantation.

Four soil samples from 0 to 30 cm depth were also collected from each field. The soil samples were collected near the roots of randomly selected flowering plantains. These samples were mixed to yield one composite sample per field. This composite soil sample was then subjected to physical and chemical analyses. Total carbon (C; mg g<sup>-1</sup> soil) and nitrogen (N; mg g<sup>-1</sup> soil) contents were quantified after dry combustion using a CNS elemental analyzer (Carlo Erba). Soil pH values were measured in 1:2.5 (w:v) soil: water suspensions, and total phosphorus (P; µg g<sup>-1</sup> soil) was determined by colorimetry (Petard, 1993). The cation-exchange capacity (CEC) was measured with ammonium acetate at pH 7. The contents of the main exchangeable cations, calcium (Ca<sup>2+</sup>; cmol kg<sup>-1</sup> soil), magnesium (Mg<sup>2+</sup>; cmol kg<sup>-1</sup> soil), and potassium (K<sup>+</sup>; cmol kg<sup>-1</sup> soil), were estimated with a flame spectrometer after exchange with ammonium acetate (Page, 1982). The N mineral (NH<sub>4</sub><sup>+</sup>, NO<sub>3</sub><sup>-</sup>, mg kg<sup>-1</sup> soil) content of the soil was determined colorimetrically in 1 M KCl extracts by flow-injection analysis (Bremner, 1965).

The crop that preceded plantain, the frequency of nematicide use, and the age of the plantain planting were determined by interviewing the farmers. Four classes of preceding crop were recognized: (1) long-lasting ( $\geq 1$  year) wild fallow, (2) continuous plantain and/or dessert banana plantation, (3) vegetable market gardening, and (4) tuber plants (yam, dasheen, or sweet potato). Three classes of nematicide use were identified: "no nematicide" (nem0), "occasional treatment" (<2 treatment per year) (nem1), and "frequent treatment" ( $\geq 2$  treatment per year) (nem2). Three classes of plantain planting age were recognized (1-year-old plantings (cycle1), 2-year-old plantings (cycle 2), and >2-year-old plantings (cycle3)).

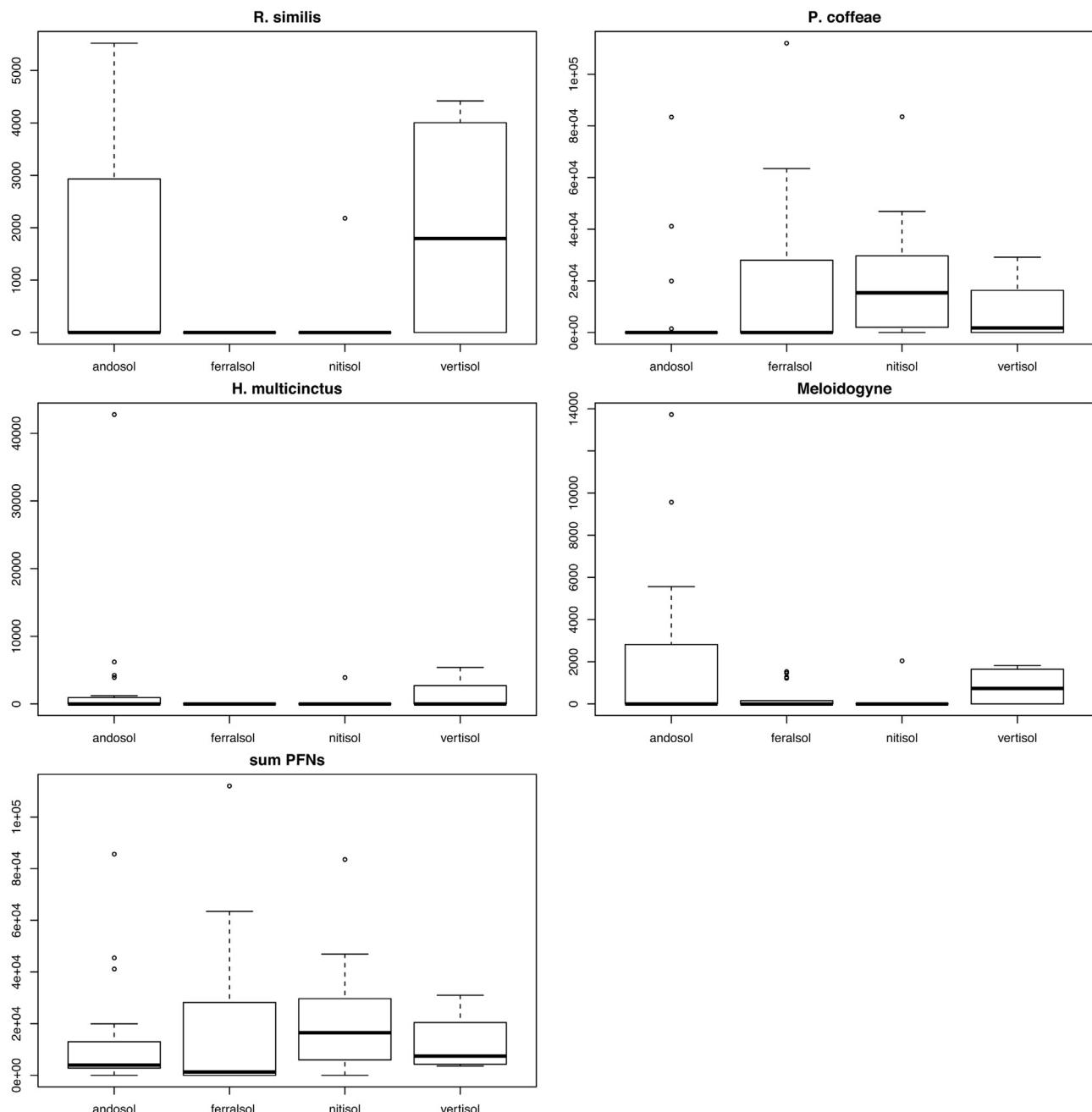
Mean annual temperature and rainfall for the previous 30-year period for each field were obtained from Météo-France Martinique. We assigned a soil type to every field (andosol, ferralsol, vertisol, or nitisol) according to a soil type map (Colmet-Daage and Lagache, 1969). Andosols contain mainly allophanes and have a high meso- and macroporosity with substantial hydrological conductivity. Nitisols contain mainly halloysite and have a substantial macroporosity, while vertisols have poor meso- and macroporosity. Ferralsols are clayey soils but may have many macropores because of sand-like aggregates resulting from the combining of clays with organic matter.

### 2.2. Statistical analysis

Frequencies of occurrence (expressed as a percentage) and average densities were calculated for each PFN species found in

**Table 1**  
Prominence value index of plant-feeding nematode taxa in 301 root samples collected in 53 plantain fields (*Musa* AAB, cv. Crème Blanche) from Martinique, French West Indies.

Nematode species	Frequency of occurrence (%)	Average density (geometric mean)	Prominence value
<i>Radopholus similis</i>	50.6	2249	1601
<i>Pratylenchus coffeae</i>	63	15098	11985
<i>Helicotylenchus multicinctus</i>	53.8	1534	1124
<i>Meloidogyne</i> spp.	70.5	1608	1351



**Fig. 1.** Abundances of four taxa of plant-feeding nematodes in plantain roots as related to soil type.

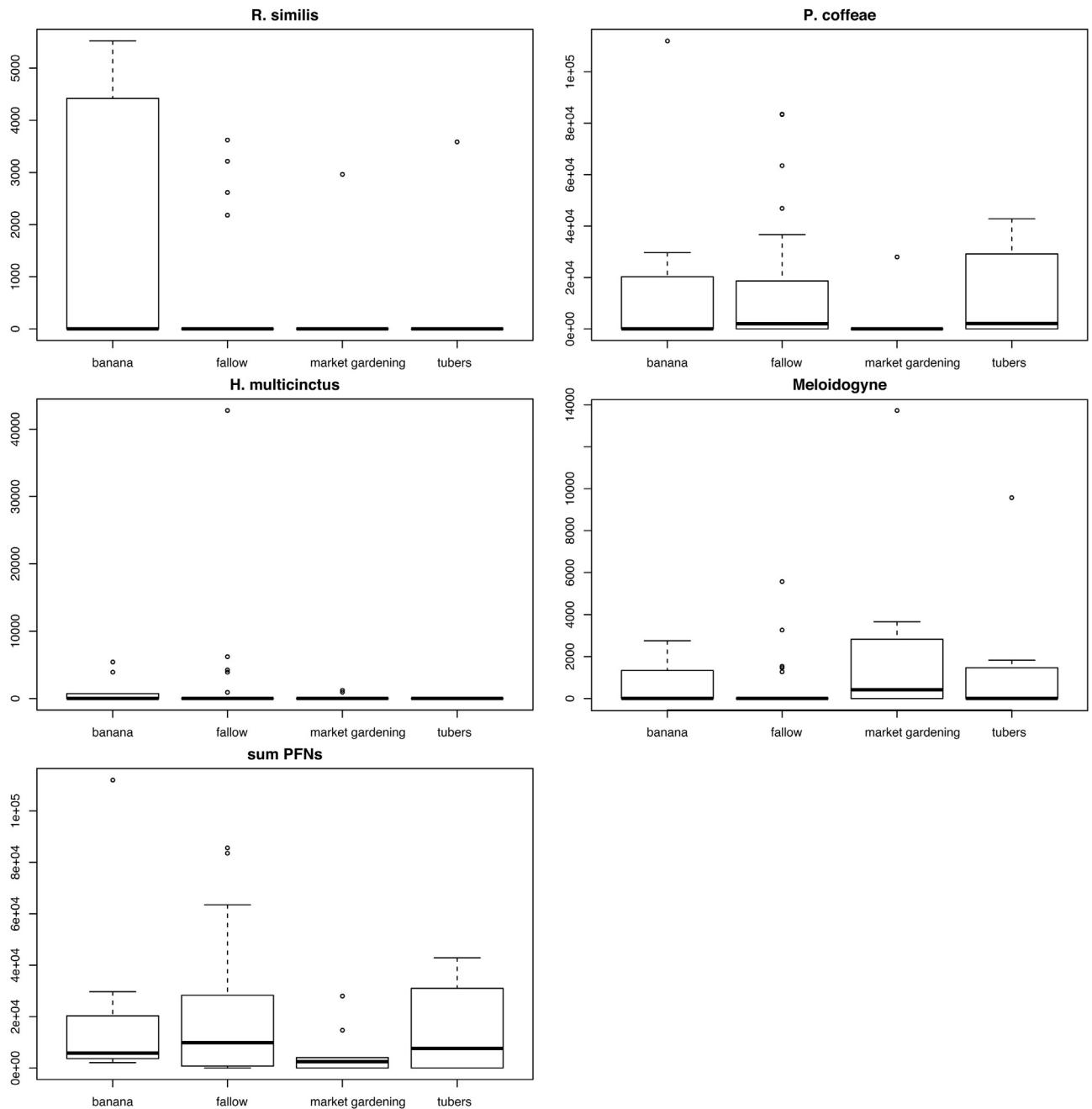
root samples. Prominence values (PVs) of PFN species were calculated according to Quénéhervé and Ferris (1989):

PV = geometric mean of PFN densities \*  $\sqrt{\text{frequency of occurrence of PFN}}$

The variation in climate and soil physico-chemical properties among fields was evaluated with a principal component analysis (PCA). We also ran a PCA on log-transformed geometric mean of abundances of PFNs and a multiple correspondence analysis (MCA) on four qualitative variables (i.e., frequency of nematicide use, age of field, nature of the previous crop, and soil type). Using PCA and MCA outputs, we ran a Coinertia Analysis (CI) to determine the relationships between PFN abundances and field characteristics

(Dolédec and Chessel, 1994; Dray et al., 2003). CI enables the simultaneous analysis of two data tables and has been previously used in nematology (Cadet and Thioulouse, 1998; Godefroid et al., 2013). The significance of the RV coefficient of CI, which measures the correlation between the two tables (Escoufier, 1973), was tested using a Monte-Carlo permutation test with 999 replicates. These multivariate analyses were performed using the ade4 package (Dray and Dufour, 2007) in R (R core team, 2014).

The influence of soil type on the log-transformed average abundance of PFN species in roots was investigated independently for each species using Generalized Linear Mixed-Effects models (GLMMs) with a Poisson distribution of errors (Bolker et al., 2009). In these models, the nature of the previous crop, the frequency of



**Fig. 2.** Abundances of four taxa of plant-feeding nematodes in plantain roots as related to the nature of the previous crop.

nematicide use, and the age of the field were treated as random effects. Similarly, the influence of the previous crop on the log-transformed abundance of PFN species in root samples was investigated independently for each species using GLMMs. In these models, the soil type, the frequency of nematicide use, and the age of plantation were treated as random effects. The significance of each term was assessed by comparing models with and without that term. Difference in Akaike Information Criterion ( $\Delta AIC$ ) was used to assess the difference between models. Models were fitted by the Laplace approximation using the lme4 package (Bates et al., 2014) in R (R core team, 2014).

### 3. Results

Four taxa of PFNs were found in the root samples: *R. similis*, *P. coffeae*, *H. multicinctus*, and *Meloidogyne* spp. The frequencies of occurrence of these PFNs in roots ranged from 50.6% for *R. similis* to 70.5% for *Meloidogyne* spp. (Table 1). The PV was about 10 times higher for *P. coffeae* than for the three other taxa (Table 1). Box plots were used to describe the relationships between PFN abundance and soil type (Fig. 1) and between PFN abundance and the nature of the previous crop (Fig. 2). *P. coffeae* was more abundant in ferralsols and nitisols than in vertisols or andosols (Fig. 1). *R. similis*, *H.*

*M. multicinctus*, and *Meloidogyne* spp. were more abundant in andosols and vertisols (Fig. 1). *R. similis* was more abundant in fields where banana and/or plantain were cultivated before plantain, while *P. coffeae* was more abundant in fields where plantain was preceded by fallow, banana, or a tuber crop (Fig. 2). *Meloidogyne* spp. were more abundant in fields where a market garden was the previous crop (Fig. 2).

The 53 fields included 22 andosols, 17 ferralsols, 10 nitisols, and 4 vertisols. Banana, fallow, a market garden, and tuber were the previous crop for 10, 23, 10, and 10 fields, respectively. Physico-chemical properties greatly differed among the soil types (Fig. 3). The andosols, which were located in cooler and wetter regions, had a higher content in organic matter (C, N) and a lower content of some cations (CEC,  $\text{Ca}^{2+}$ ,  $\text{Mg}^{2+}$ ,  $\text{NH}_4^+$ ) than the other soil types (Fig. 3). Relative to the andosols, the nitisols and ferralsols had lower organic matter contents and higher contents of  $\text{Ca}^{2+}$ ,  $\text{Mg}^{2+}$ , and  $\text{NH}_4^+$  (Fig. 3). The soil types, however, did not greatly differ on the second PCA axis (Fig. 3).

The correlation circle of the PCA computed on PFN abundance data is illustrated in Fig. 4a. The variability on the first PCA axis was mainly explained by the *P. coffeae*, which is opposed to the other taxa (*R. similis*, *Meloidogyne* spp., and *H. multicinctus*) (Fig. 4a). Both *R. similis* and *H. multicinctus* were opposed to *Meloidogyne* spp. on the second PCA axis (Fig. 4a). The correlation circle of the Mca computed on field properties is visualized in Fig. 4b. The outputs of CI are visualized in Fig. 4c and d. The RV coefficient (0.18) was significant ( $p < 0.05$ ) according to a Monte Carlo permutation test. According to the CI axis F1, higher and lower abundances of *P. coffeae* were associated with nitisols and andosols, respectively (Fig. 4c and d). According to the CI axis F1, *Meloidogyne* spp. were relatively more abundant in andosols in fields where a market garden was the previous crop (Fig. 4c and d). According to CI, higher abundances of *R. similis* and *H. multicinctus* were associated with andosols and vertisols where nematicides had been applied and where bananas and/or plantains were continuously cultivated before plantain (Fig. 4c and d).

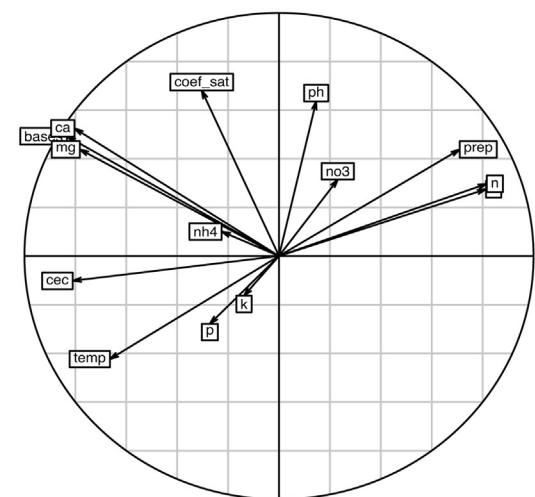
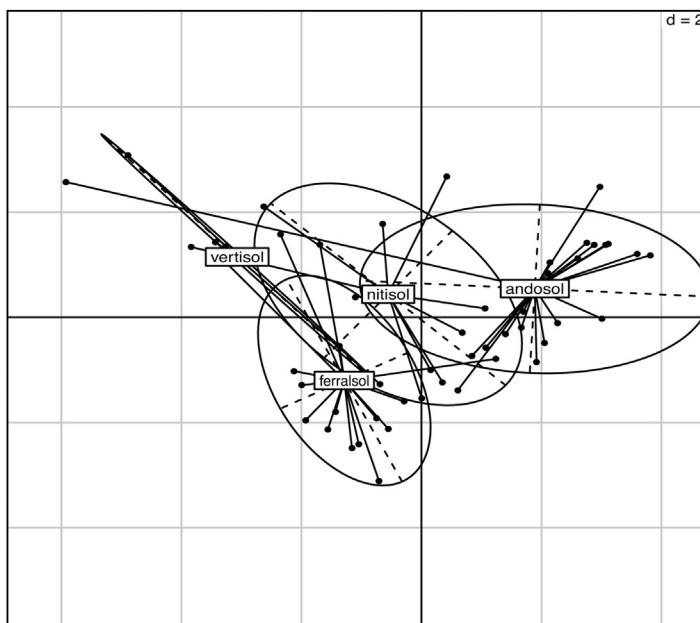
According to GLMMs, the abundance of each PFN was significantly related to soil type ( $P < 0.001$ ). The effect of the previous crop on PFN abundance was significant only for *R. similis*, *H. multicinctus*, and *P. coffeae* ( $P < 0.001$ ).

## 4. Discussion

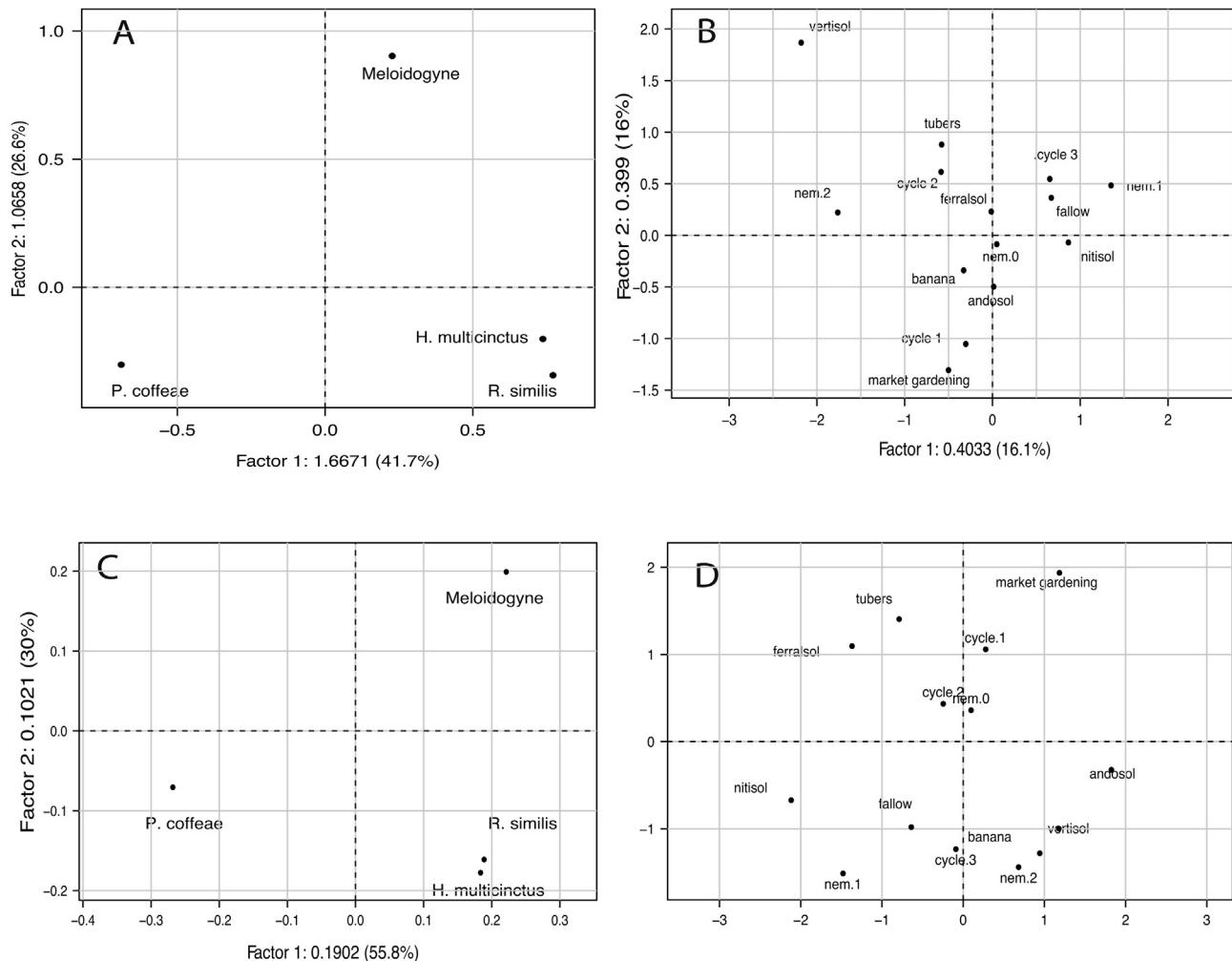
### 4.1. Structure of PFN communities in plantain agrosystems

Because nematological research on *Musa* spp. has focused on dessert banana for export, little information is available concerning the structure of PFN communities in plantain agrosystems in the Caribbean (Quénéhervé, 2009). We provide here the results of the first large-scale nematological survey of plantain agrosystems in the Caribbean region. In this study, large numbers of economically important PFNs were commonly found in plantain roots, and these large numbers may probably partly explain the very short longevity (<2–3 years) of plantain plantings in this region. The PFNs detected in plantain roots were *R. similis*, *P. coffeae*, *H. multicinctus*, and *Meloidogyne* spp. *P. coffeae* was frequently found at very high densities and was by far the predominant PFN in plantain roots. High densities of *P. coffeae* in plantain roots were also reported in previous studies (Osei, 2013; Speijer et al., 2001). These results support the widely accepted view that *P. coffeae* develops very well on plantain (Gowen et al., 2005). This endoparasite may cause severe damage to plantain (Brentu et al., 2004), and should therefore be one of the species targeted for control (Coyne, 2007; Quénéhervé, 2009).

*Radopholus similis*, *H. multicinctus*, and *Meloidogyne* spp. were also frequently found in plantain roots but usually at lower densities than *P. coffeae*. This is not surprising because *R. similis* was less abundant than *Pratylenchus* spp. in plantain agrosystems in other countries (Adiko and N'Guessan, 2002; Osei, 2013; Speijer and De Waele, 2001; Speijer et al., 2001). However, *H. multicinctus* was generally less prominent here (i.e., in the Caribbean) than in plantain-producing regions of Africa (Adiko, 1988; Bridge et al.,



**Fig. 3.** Principal component analysis performed on physico-chemical soil properties in 53 plantain fields throughout Martinique. (A) Factorial scores of the fields. (B) Correlation circle. Symbol meanings: C: carbon ( $\text{mg g}^{-1}$  soil), N: nitrogen ( $\text{mg g}^{-1}$  soil), C/N: ratio carbon/nitrogen, pH: pH, CEC: cation-exchange capacity, bases: sum of exchangeable cations ( $\text{cmol kg}^{-1}$  soil), %: saturation percentage, K<sup>+</sup>: potassium ( $\text{cmol kg}^{-1}$  soil), Ca<sup>2+</sup>: calcium ( $\text{cmol kg}^{-1}$  soil), Mg<sup>2+</sup>: magnesium ( $\text{cmol kg}^{-1}$  soil), P: phosphorus ( $\mu\text{g g}^{-1}$  soil), NH<sub>4</sub><sup>+</sup>: ammonium ( $\text{mg kg}^{-1}$  soil), and NO<sub>3</sub><sup>-</sup>: free ammonia ( $\text{mg kg}^{-1}$  soil).



**Fig. 4.** (A) Correlation circle of the principal component analysis performed on the abundances of four taxa of plant-feeding nematodes in plantain fields. (B) Correlation circle of the multiple correspondence analysis performed on four characteristics of plantain fields. (C) Coinertia factorial plan of nematode data. (D) Coinertia factorial plan of field characteristics. Symbol meanings: “no nematicide” (nem0), “occasional treatment” ( $\leq 2$  treatment per year) (nem1), “frequent treatment” ( $> 1$  treatment per year) (nem2), 1-year-old plantings (cycle1), 2-year-old plantings (cycle2), >2-year-old plantings (cycle3). Banana, market garden, fallow, and tubers are the four classes of crops that preceded plantain in the surveyed fields.

1995; Kamira et al., 2013; Speijer et al., 2001). This finding is also not surprising because we collected samples from relatively young fields (age ranged from 1 to 5 years). The density of *H. multicinctus* in banana roots increases over time because this species is a secondary pest that develops following root necrosis induced by other PFN species such as *R. similis* (Quénéhervé, 1990). For instance, Speijer et al. (2001) sampled fields in Nigeria whose ages ranged from 2 to 25 years. This highlights the difficulty in comparing the structures of PFN communities among different regions because many factors shape the abundances of the different PFN species in agrosystems (e.g., climate, plantation age, soil properties, cultural practices, specific composition of the PFN community, competitive interactions, etc.). In addition, our sampling method and extraction technique are particularly suited for detection of migratory endoparasitic nematodes, and we therefore may have underestimated the prevalence of semi-endoparasitic species such as *Rotylenchulus reniformis* or sedentary endoparasitic species such as *Meloidogyne* spp. in plantain agrosystems.

#### 4.2. Effects of soil properties and cultural practices on PFN communities

Soil physico-chemical properties and climate may greatly affect the structure of PFN communities in agrosystems (Avendano et al., 2004; Bakonyi et al., 2007; Duyck et al., 2012; Ettema and Wardle, 2002; Godefroid et al., 2013; Goodell and Ferris, 1980; Ortiz et al., 2010; Papatheodorou et al., 2004; Quénéhervé, 1988; Ruess et al., 1999). Here, we found that PFN abundance strongly differed among plantain fields that differed in climatic and edaphic conditions.

*P. coffeae* was more abundant in ferralsols and nitisols than in andosols. Relative to nitisols and ferralsols, andosols generally have a low cation content and a high organic matter content (Fig. 3). A previous survey of banana agrosystems in Martinique showed that *P. coffeae* is much more abundant in ferralsols than in andosols (Duyck et al., 2012). However, the abundance of *P. coffeae* in banana roots is generally lower in nitisols than in other soils throughout Martinique (Duyck et al., 2012). One plausible explanation for these observations is that the high contents of

some cations in ferralsols and nitisols may favor the multiplication of *P. coffeae*. Consistent with this possibility is a report that *P. coffeae* in Martinique was more abundant in yams cropped in soils with high concentrations of calcium and magnesium (Cadet and Thioulouse, 1998). A second possibility is that regional climate variation, which is strongly correlated with differences in soil properties (Fig. 3), is the main factor that drives *P. coffeae* abundance (Duyck et al., 2012). Because climate is strongly correlated with soil type in Martinique (Fig. 3), our survey is unable to disentangle the relative importance of these factors for PFN communities. We also observed that *Meloidogyne* spp. were particularly abundant in andosols, which is consistent with a previous study performed in yam agrosystems in Martinique (Cadet and Thioulouse, 1998). Further research is needed to identify the forces driving these patterns.

The previous crop also may shape the structure of the PFN community in agrosystems (Chabrier and Quénéhervé, 2003; Florini et al., 1987). In the current study, the crop planted before plantain was significantly related to the abundances of *P. coffeae*, *H. multicinctus*, and *R. similis*. *P. coffeae* was slightly more abundant in fields in which plantain was preceded by tubers, banana/plantain, or a fallow (Fig. 2). This result is not surprising because *P. coffeae* is well known to develop on tuber crops (Bridge et al., 2005), banana (Gowen et al., 2005), and various weeds that grow during fallow periods (Quénéhervé et al., 2006). Similarly, *R. similis* was more abundant in fields where plantain was preceded by bananas/plantains. This also was expected because *R. similis* is known to develop well on both banana and plantain, and the repeated planting of these crops provides a steady food supply (Chabrier and Quénéhervé, 2003). *Meloidogyne* spp. tended to be more abundant in fields where plantain was preceded by a market garden, although this trend was not statistically significant according to GLMMs (Figs. 2 and 4). Such gardens usually include Solanaceae and Cucurbitaceae that are very good hosts of several *Meloidogyne* species (Quénéhervé et al., 2011; Sikora and Fernandez, 2005). These vegetables and many associated weeds can thus support increases in numbers of *Meloidogyne* spp.

We recognize that correlations between soil factors, cultural practices, and PFN densities may not reflect causal relationships and should be carefully interpreted. Given that many biotic and abiotic factors can affect PFN communities and that correlation does not demonstrate cause-and-effect, determining how these factors help shape PFN communities is difficult in plantain and other agrosystems.

#### 4.3. Future strategies for PFN control

Plantain fields are short-lived in the Caribbean (<2–3 years), and one probable reason is the damage caused by PFNs to the root systems. The control of PFNs on plantain should rely on integrated pest management (IPM) approaches similar to those developed for the cultivation of dessert bananas for export (Quénéhervé, 2009). Starting a plantain planting with PFN-free “healthy” plant material in a “healthy” soil (i.e., a soil with low densities of damaging PFNs) is essential. The use of tissue-cultured plantain plantlets and the adoption of efficient fallow or planting of intercrops might greatly decrease the abundances of harmful PFNs and consequently increase plantain yields, as has been demonstrated for dessert bananas (Chabrier and Quénéhervé, 2003). Our results show that farmers actually use crop rotations that increase the densities of damaging PFNs in soil and that natural fallow does not sufficiently reduce PFN densities probably because of inefficient weed management (Araya and De Waele, 2005; Quénéhervé et al., 2006) and/or the failure to completely eliminate remnant *Musa* plants (Chabrier and Quénéhervé, 2003). Given this situation, the use of antagonistic intercrops that reduce numbers of PFNs should

be seriously considered in the design of future IPM for plantain (Bringel and Silva, 2000). When *in vitro* plants of plantain are not available, planting material that is likely to be pathogen-free can be obtained by macropropagation of plants performed away from the field with false decapitation (Kwa, 2003; Lepoint et al., 2013; Njukwe et al., 2013; Tenkouano et al., 2006), paring (Quénéhervé and Cadet, 1985) or boiling water treatments (Tenkouano et al., 2006). In addition, improved control of *P. coffeae* in plantain will require additional research on the ecology of this PFN (Coyne, 2007). Recent research has focused on *R. similis* in export dessert banana plantations, and the results have led to an important decrease of pesticide use without yield reduction in French West Indies (Achard et al., 2007). A similar effort is needed in plantain with emphasis on *P. coffeae* control. Finally, natural plantain cultivars or recently developed hybrids should be evaluated for PFN resistance (Quénéhervé, 2009; Quénéhervé et al., 2012).

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