Host range as an axis of niche partitioning in the plant-feeding nematode community of banana agroecosystems

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ABSTRACT

The stability and positive functions (such as pest regulation) of intensively managed agroecosystems can be enhanced by increasing biodiversity (in particular, by introducing cover plants or associated crops). Therefore, understanding modes of interspecific interactions among the phytophagous species, such as coexistence via host-plant partitioning, may allow manipulation of the balance between pest and non-pest species.

In the present study, we tested the hypothesis that a community of six plant-feeding nematode species in banana agroecosystems is structured by host plants. This was done using extensive data on the abundance of the different nematodes species on banana and associated weeds in Martinique. Because the purpose of this study was to focus on host-plant range, we eliminated the effects of temperature, rainfall, and soil type using a partial canonical correspondence analysis.

Host plants in banana agroecosystems have a marked influence on the plant-feeding nematode community structure. Host plants allow niche partitioning between some but not all pairs of species. The most evident pattern is the niche partitioning among the three nematodes considered long established in Martinique.

For pairs of species showing no host-plant niche partitioning, additional information regarding the colonisation and population dynamics over time both at the root and agroecosystem scale would allow better understanding of the equilibrium among species of the plant-feeding nematode community.

For management purposes, the modification of abundance of some host plants, which could be used as cover plants in the field, could change the balance among nematode species.

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1. Introduction

The factors structuring phytophagous pest communities must be considered for agroecosystem management. In particular, understanding modes of interspecific interactions among the phytophagous species may allow managers to manipulate the balance between pest and non-pest species. Therefore, it is important to understand how phytophagous pest species coexist in agroecosystems. Species coexistence may be maintained by disturbance and predation and the interaction between these two

factors (Gallet et al., 2007), spatial heterogeneity (Tilman, 1994), and niche partitioning (Giller, 1996; Chesson, 2000).

One way to enhance the stability and positive functions (such as pest regulation) of intensively managed agroecosystems is to increase biodiversity, in particular by introducing cover plants or associated crops (Tilman et al., 2002; Tylianakis et al., 2008). The idea is that the complexity of communities and food webs buffers against perturbations and therefore stabilizes the system (de Ruiter et al., 2005).

While monoculture of dessert bananas (*Musa* spp., AAA group, cv. Cavendish Grande Naine) grown for export involves intensive management, projects for re-introducing biodiversity by the way of plant cover, associated crops, and cultivated fallows have been initiated as parts of integrated pest management. Banana fields represent very simplified agroecosystems that are interesting to

study in part because of the limited number of species in the associated plant community. Moreover, for applied purposes in agro-ecology, knowledge about the relationships among phytophagous species and between phytophagous and their host plants could allow manipulation of the structure of the phytophagous community by the choice of host plant. For example, the planting of cover crops during noncrop periods could modify the phytophagous community. Until now, the diversity of plants associated with the monoculture of dessert banana is limited to weeds. Because plant-feeding nematodes are the most damaging pests in these agroecosystems (Jones, 2000; Gowen et al., 2005), understanding the link between host-plant diversity and the structure of the community of plant-feeding nematodes is important.

Niche partitioning, i.e., the process driving competing species into different patterns of resource use or different niches, may occur through several different modes and on multiple temporal and spatial scales. First, nematode community composition is affected by different environmental factors (Bongers and Ferris, 1999; Ferris and Matute, 2003). At a regional scale, the ecological niches of plant-feeding nematodes may be partitioned by abiotic parameters in the agroecosystems such as climate or soil (Norton, 1989; Cadet et al., 2003; De Waele and Elsen, 2007). At the root scale, feeding on roots at different times of plant development or in different locations may also represent niche partitioning (Yeates, 1987). In this study, we focussed on the host-plant range component of the ecological niche (Yeates, 1999; Brinkman et al., 2008) by determining how six species of plant-feeding nematodes are affected by crop and associated weeds in banana agroecosystems.

Worldwide, bananas are attacked by many species of plant-feeding nematodes but only a few cause economically important damage. In Martinique, the nematode community parasitizing bananas is composed of the migratory endoparasites, *Radopholus similis* (Cobb, 1893) Thorne, 1949, and *Pratylenchus coffeae* Goodey, 1951; the endoparasites *Helicotylenchus multicinctus* (Cobb, 1893) Sher, 1961, and *Hoplolaimus seinhorsti* Luc, 1958; and the sedentary endoparasites *Meloidogyne* spp. and *Rotylenchulus reniformis* Linford & Oliviera, 1940. While all these species exploit the same resource (plant roots) and are able to parasitize a wide variety of host plants (Luc et al., 2005), they differ in life-history (sedentary versus migratory species) and reproductive strategy (parthogenetic versus amphimictic species).

Differences in when and how these species were introduced to Martinique Island and their associations with other crops are also important for understanding differences in nematode/host plant relationships. The burrowing nematode *R. similis* and the spiral nematode *H. multicinctus* are very closely associated with the development of banana crops and have thus arguably been introduced very recently, probably with the first introduced banana plant materials in the Caribbean early in the 16th century (Marin et al., 1998). *R. similis* is native to the Southeast Pacific rim and is the only species within the genus *Radopholus* to be detected outside its centre of origin. Marin et al. (1998) and more recently Price (2006) show how the dispersal of *R. similis* was definitely linked to the dissemination of bananas. The reniform nematode *R. reniformis* is a pan-tropical species associated with many different hosts. Because of its ability to enter into anhydrobiosis (Womersley and Ching, 1989), it can easily be spread by winds and is therefore considered indigenous in the West Indies. The other nematode species (*H. seinhorsti*, *Meloidogyne* spp., and *P. coffeae*) are also widespread as pan-tropical species and are associated with many horticultural crops (Luc et al., 2005). These three species were probably present in the West Indies long before the introduction of bananas.

Beyond banana, these six nematode species are able to exploit a number of weeds present in banana agroecosystems (weed species and families in Martinique are listed in Table 1). While *R. similis* and *H. multicinctus* are closely associated with these banana agroecosystems, the four other nematode species are mostly found in other ecosystems including natural habitats (Luc et al., 2005).

The purpose of this study is to analyse whether and how plant-feeding nematodes partition host plants in banana agroecosystems. While abiotic factors including climate and soil may profoundly affect nematode community structure (Norton, 1989; Cadet et al., 2003), they are not the objects of the present study. The detailed study of the influence of these abiotic factors in Martinique would require the collection of many samples one unique host plant (banana) in different parts of the island. However, climate and soil type were included in our analyses to control for their effects.

In this study, we tested the hypothesis that the plant-feeding nematode community is structured by host plants. We did this by collecting weeds in banana fields and by determining the abundance of each nematodes species on the different host-plant species to answer the following questions: (i) Do the nematodes species have different host ranges? (ii) Is the nematode community structure affected by host-plant weeds associated with bananas? (iii) Is there a host-plant niche partitioning that could promote coexistence among the different species? (iv) Is host-plant niche partitioning related to the introduced versus indigenous status of the plant-feeding nematode species?

2. Materials and methods

2.1. Field data

All samples were collected in Martinique (French West Indies, 14°N, 61°W). Field surveys were regularly conducted between 2002 and 2008. The whole island was prospected year round for associated weeds in banana crops. We used published data on the presence of the nematode species on the different host plants (Quénéhervé et al., 2006) and supplemented them with new data collected with the same method.

We collected 556 weed samples from fields in the different parts of the island. Each sample included the shoots and roots of each plant. After identification of the plant to species (Fournet, 1978; Fournet and Hammerton, 1991), all root samples were carefully washed under tap water to remove soil particles and fine entangled roots. The nematodes were extracted from a 20-g fresh root subsample per plant (carefully picked out under a magnifier) in a mist chamber (Seinhorst, 1950). For 2 weeks, a fine mist of water was sprayed continuously over the roots. Active nematodes emerged and were recovered from the water that collects below. Extracted nematodes were counted twice: after 1 week and again after 2 weeks in the mist chamber using a counting dish and a stereomicroscope. Dry weights of roots were obtained by placing roots at 60 °C in a drying oven. The entire database comprises 247,332 nematodes.

Mean annual temperature and cumulative annual rainfall in the different locations on Martinique were provided for a 30-year period by Météo-France Martinique, Service Climatique. Soil type (Andosol, Ultisol, Vertisol) was determined using Colmet-Daage and Lagache (1965) soil type map.

2.2. Statistical analyses

We used canonical correspondence analysis (CCA) with four factors: temperature, rainfall, soil type, and plant species. This method was introduced by ter Braak (1986). It has been developed to study the relationship between species composition and environment within sites. Here the basic sampling unit is a weed sample separated in space or time from other samples. CCA is an

Table 1
Recorded host plants and relative abundance of six species of plant-feeding nematodes in banana agroecosystems from Martinique. Stars indicate introduced plant species in Martinique (according to Fournet (1978)).

Family	Species	Number of samples	Number of nematodes	Number/g dw[a]	Species relative abundance					
					Meloidogyne spp.	Helicotylenchus multicinctus	Radopholus similis	Pratylenchus coffeae	Rotylenchulus reniformis	Hoplolaimus seinhorsti
Amaranthaceae	1 Amaranthus dubius	19	9206	973	0.40	0.43	0.04	0.01	0.12	
	2 Amaranthus spinosus	5	1652	2361		1.00				
Araceae	3 * Caladium bicolor	5	6224	5460			1.00			
	4 * Colocasia esculenta	15	13661	3614	0.92			0.06	0.02	
	5 Dieffenbachia seguine	5	410	109	0.66				0.32	0.02
	6 Xanthosoma violaceum	10	24621	11191	0.79	0.01			0.20	
Asteraceae	7 * Emilia fosbergii	5	42	28					1.00	
	8 Mikamia micrantha	16	3779	496	0.01				0.99	
	9 Vernonia cinerea	5	12	12	1.00					
Capparidaceae	10 Cleome aculeate	11	120	42	0.36			0.01	0.39	0.24
	11 * Cleome rutidosperma	11	611	25	0.38	0.10	0.11		0.33	0.08
Commelinaceae	12 Commelina diffusa	15	25618	14723			0.13		0.84	0.03
Convolvulaceae	13 * Ipomoea eriocarpa	1	16	6					1.00	
	14 Ipomoea tiliacea	3	0	0						
Cucurbitaceae	15 * Momordica charantia	1	8561	4920	0.99	0.01				
Cyperaceae	16 * Cyperus esculentus	19	1105	111	0.96	0.04				
Euphorbiaceae	17 Euphorbia cyathophora	8	93	42			0.50		0.49	0.01
	18 * Euphorbia heterophylla	21	395	120	0.05	0.72	0.11		0.12	
	19 Phyllanthus amarus	20	1003	141	0.03	0.93	0.02		0.02	
Fabaceae	20 Centrosoma pubescens	1	0	0						
Malvaceae	21 Sida acuta	5	0	0						
	22 Urena lobata	8	131	21	0.83	0.05		0.12		
Melastomataceae	23 Clidemia hirta	11	687	22	0.49		0.51			
Mimosaceae	24 Mimosa pudica	12	2366	219	0.60			0.01	0.04	0.35
Moraceae	25 Cecropia schreberiana	8	1412	200	0.01	0.19	0.01		0.79	
Musaceae	26 * Musa AAA Cavendish	36	68007	1022	0.29	0.40	0.27		0.03	0.01
Myrtaceae	27 * Psidium guajava	1	20	8	0.75	0.25				
Onagraceae	28 * Ludwigia abyssinica	1	3	1			1.00			
Oxalidaceae	29 Oxalis barrelieri	1	6	75		0.67			0.33	
Passifloraceae	30 Passiflora edulis	3	169	220	0.03				0.94	0.03
Piperaceae	31 Peperomia pellucida	11	3080	1721	0.99		0.01			
Poaceae	32 Digitaria horizontalis	15	122	16		1.00				
	33 Echinochloa colona	26	4482	648	0.12	0.16	0.45			0.27
	34 Eleusine indica	38	16854	612	0.69	0.25	0.06			
	35 Eragrostis pilosa	1	181	133			0.03			0.97
	36 Leptochloa filiformis	14	282	47	0.83		0.04	0.06	0.07	
	37 * Panicum maximum	1	7	5			1.00			
	38 Paspalum fasciculatum	15	1052	100	0.23	0.03	0.48	0.20	0.06	
	39 * Rottboellia cochinchinensis	10	138	37		0.28	0.25	0.29	0.18	
	40 * Setaria barbata	15	176	125	0.24	0.39	0.25	0.04	0.08	
	41 * Sorghum halepense	7	129	5	0.34	0.20				0.46
Rubiaceae	42 Spermacoce verticillata	6	0	0						
Solanaceae	43 Physalis angulata	7	191	185		0.85	0.12	0.03		
Solanaceae	44 Solanum americanum	30	12522	510	0.70	0.06	0.06		0.18	
	45 Solanum torvum	20	3068	180	0.02	0.17	0.23		0.58	
Urticaceae	46 Laportea aestuans	10	467	218	0.80	0.11			0.09	
	47 * Phenax sonneratii	40	34508	1610	0.10	0.10	0.15		0.65	
	48 Pilea microphylla	1	144	360	0.97					0.03

[a] Number of nematodes/g dw of root.

extension of correspondence analysis (CA) in which samples are given linear weights so as to maximise the variance among species. CCA looks for coefficients of environmental variables to obtain a site score that maximises the variance of the average positions of species. We completed this analysis by a partial CCA (ter Braak, 1988) to eliminate the effects of temperature, rainfall, and soil type. All computations and graphical displays were carried out using R software, with routines available in the vegan package and the ADE4 package (Chessel et al., 2004).

We then analysed the effects of host-plant species, plant class (monocotyledons or dicotyledons), and plant introduction status (indigenous or introduced) on the abundance of each nematode species using a generalised linear model (GLM) with Poisson error. Plant introduction status is given in Table 1. For each nematode species, a reference model, including all significant terms of environment (temperature, rainfall, and/or soil type) and interactions,

was used for comparing the effect of plant species, plant class, and plant introduction status. Overdispersion was accounted for using Quasi-Poisson in place of Poisson models in R (Crawley, 2007).

3. Results

From field surveys, 48 different plant species hosting the six plant-feeding nematodes species were collected (Table 1). Among these, at least 16 plant species are considered as recently introduced in Martinique (Fournet, 1978; Fournet and Hammerton, 1991).

CCA with all factors shows the influences of temperature, rainfall, and soil type on the relative abundance of nematodes species (Fig. 1a, proportion of variance of axis 1: 0.34, axis 2: 0.24, axis 3: 0.16, axis 4: 0.15, axis 5: 0.11). In the same analysis, some host-plant species were placed along a climate and soil type axis, indicating
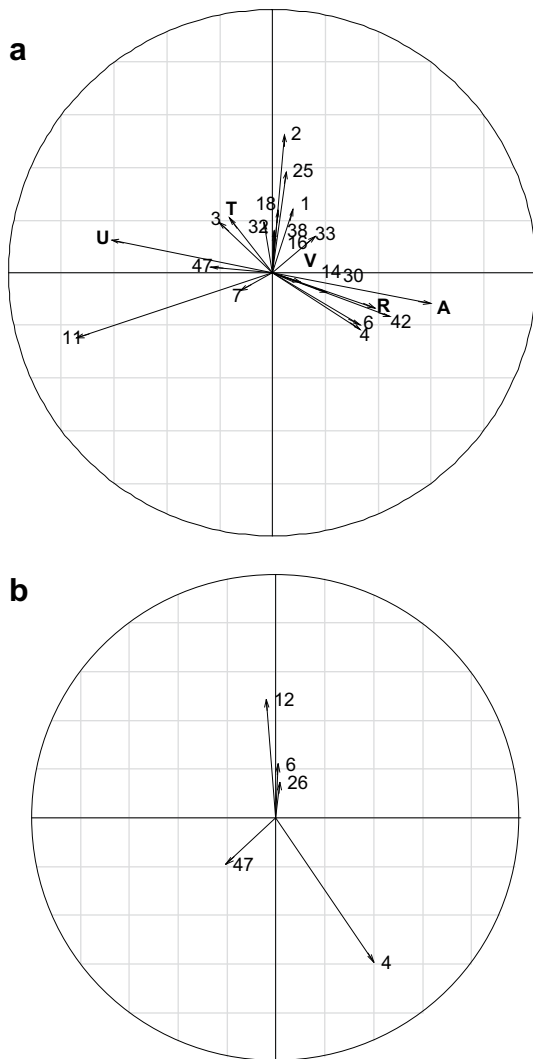
Fig. 1. Canonical correspondence analysis of the relationship between plant-feeding nematodes species and host-plant species. The two plots display correlations >0.1 between variables and the first two axes of the CCA for the first plot (a) and the partial CCA removing the effects of temperature, rainfall, and soil type for the second plot (b). Numbers correspond to the host-plant species presented in Table 1. T: Temperature, R: Rainfall, A: Andosol, U: Ultisol, V: Vertisol.

that these host plants were not randomly distributed regarding climatic and soil conditions. The partial CCA (Fig. 1b, proportion of variance of axis 1: 0.99, axis 2: 0.01) allows controlling for the effect of temperature, rainfall, and soil type. Independent to these environmental variables, five host plants were strongly correlated to changes in abundance of the different nematodes species; these host plants were *Musa* spp. (banana) and four weeds, *Commelina diffusa*, *Colocasia esculenta*, *Phenax sonnerati*, and *Xanthosoma nigrium* (Fig. 1b). The nematodes *Meloidogyne* spp., *H. multicinctus*, and *R. similis* had a large distribution (as indicated by the large ellipse in Fig. 2). The centroids for *Meloidogyne* spp. and *H. multicinctus* were particularly close together. In contrast, the three other species, *P. coffeae*, *R. reniformis*, and *H. seinhorsti* had smaller distributions (as indicated by smaller ellipses in Fig. 2). The centroids of ellipses of these three last species are clearly separated, and the ellipses containing 90% of individuals according to the binormal distribution of points indicate a very weak overlap (Fig. 2).

The frequency distribution of the relative abundance of the six nematode species shows that *H. seinhorsti* and *P. coffeae* have a high

relative abundance on a few plant species: about 80% of the relative abundance of each of these two nematode species derives from only four host plants (*Eragrostis pilosa*, *Sorghum halepense*, *Mimosa pudica*, and *Echinochloa colona* for *H. seinhorsti* and *Rottboellia cochinchinensis*, *Paspalum fasciculatum*, *Urena lobata*, and *C. esculenta* for *P. coffeae*) (Fig. 3). Distribution of the relative abundance is smoother for the four other species, with a maximum relative abundance between 7 and 10% for one host plant. The frequency distributions of relative abundance show that host ranges of *H. seinhorsti*, *R. reniformis*, and *P. coffeae* are mostly separated while the ones of *Meloidogyne* spp, *H. multicinctus*, and *R. similis* overlap.

Results of the GLM analysis are presented in Table 2. Once the significant terms of environment (temperature, rainfall, soil type, and interactions) are accounted for in a reference model, the addition of the 'plant species effect' is significant for all these nematode species. Effect of plant class (monocotyledon or dicotyledon) is significant for *P. coffeae* and *R. reniformis*, these species being more abundant on dicotyledons than on monocotyledons. Effect of plant introduction status is significant for *R. similis*, *P. coffeae*, and *H. seinhorsti*. *R. similis* and *P. coffeae* are more abundant on introduced plant species while *H. seinhorsti* is more abundant on indigenous plant species.

4. Discussion

4.1. Host-plant range and nematode community structure

Host plants in banana agroecosystems have a marked influence on the community structure of plant-feeding nematodes. Results of the CCA and GLM show that host plant greatly affects the abundance of each of the six plant-feeding nematode species. All six nematode species have a wide range of hosts, including from 9 to 30 plant species belonging to numerous families. The six nematode species can thus be considered as polyphagous. Although the host ranges of these species overlap, the relative abundance of each nematode species differs among different host plants, indicating different preferences in host exploitation.

Meloidogyne spp., *H. multicinctus*, and *R. similis* are present on most plants collected. These species are generally considered very polyphagous (Luc et al., 2005). The genus *Meloidogyne* on *Musa* mainly comprises two species, *Meloidogyne arenaria* and *Meloidogyne incognita* (Cofcewicz et al., 2005), which were not differentiated in our study. Species belonging to the *Meloidogyne* genus are generally determined by electrophoresis, and this method could not be used in a wide field survey like the one in our study.

While the six nematode species are polyphagous, i.e., they are able to parasitize many host plants, frequency distribution of relative abundance shows that *P. coffeae*, *R. reniformis* and *H. seinhorsti* specialise on different host plants. In particular, *R. reniformis* and *P. coffeae* are more abundant on dicotyledons than monocotyledons. This preference of *R. reniformis* for dicotyledons was mentioned by Gaur and Perry (1991).

Although ectoparasitic nematodes also occur in the soil of banana agroecosystems, these species are usually in low densities and are less likely to be involved in competitive interactions (Luc et al., 2005). Collection of soil samples, in addition to root samples, would increase our understanding of interactions between endoparasitic and ectoparasitic nematodes.

4.2. Niche partitioning and coexistence via host plants

Host plants allow niche partitioning among some nematode species. The most evident example of this is the niche partitioning among *P. coffeae*, *R. reniformis*, and *H. seinhorsti*. Both the ellipses of the partial CCA and the frequency distributions of relative
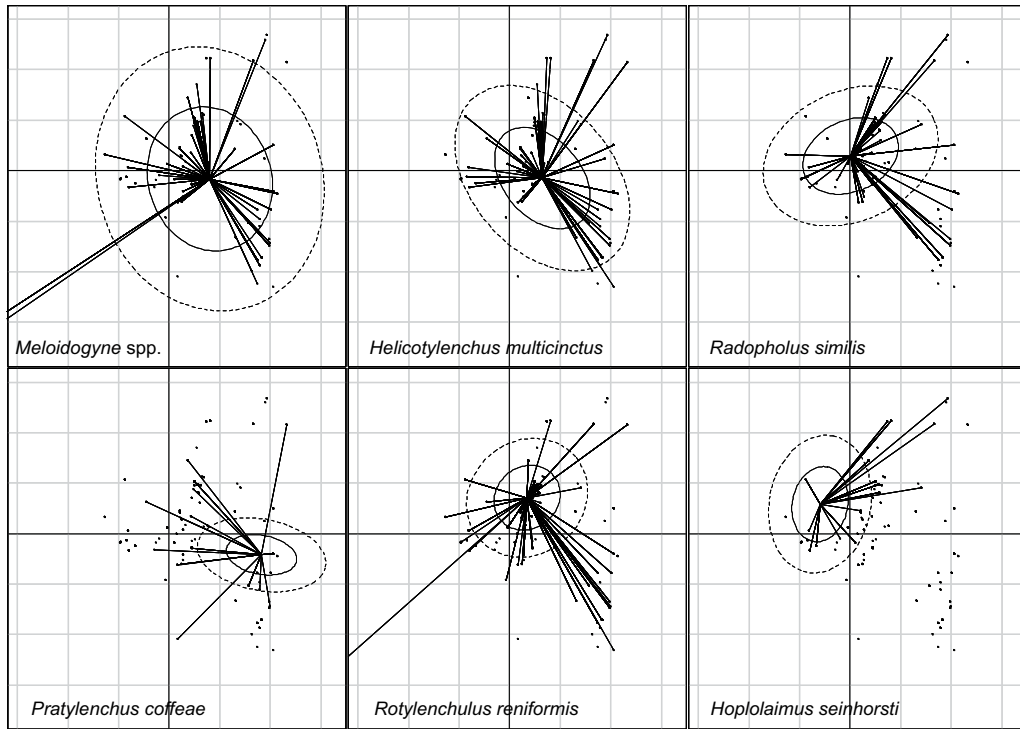
Fig. 2. Biplots of the normalized coordinates of the sites, constrained by the host-plant species, and the coordinates of the nematode species. In each plot, a grid indicates the scale; the length of the square side is 1. In each plot, the dots indicate the samples, the straight lines indicate the presence of nematode species in samples, and the ellipses surround the position of the nematode species providing an index of the dispersion around the species centroid (50% and 90% of individuals collected are expected to be in the ellipse formed by the continuous line and the broken line, respectively). These ellipses are representations of the diversity of the host-plant species used by the nematodes.

abundance show very weak overlap among these species in their exploitation of host plants. This pattern is even stronger between *H. seinhorsti* and *P. coffeae*. Also, ellipses of the partial CCA indicate relatively low overlap between *R. similis* and *P. coffeae*. Overlap is strong between all other pairs and especially with *Meloidogyne* spp.

and *H. multicinctus*, whose dispersion ellipses overlap those of all other species.

Interspecific competition in the field has been strongly suggested between *Meloidogyne* spp. and *R. similis*, *Meloidogyne* spp. and *P. coffeae*, and *H. multicinctus* and *R. similis* (Quénéhervé, 1990; Moens
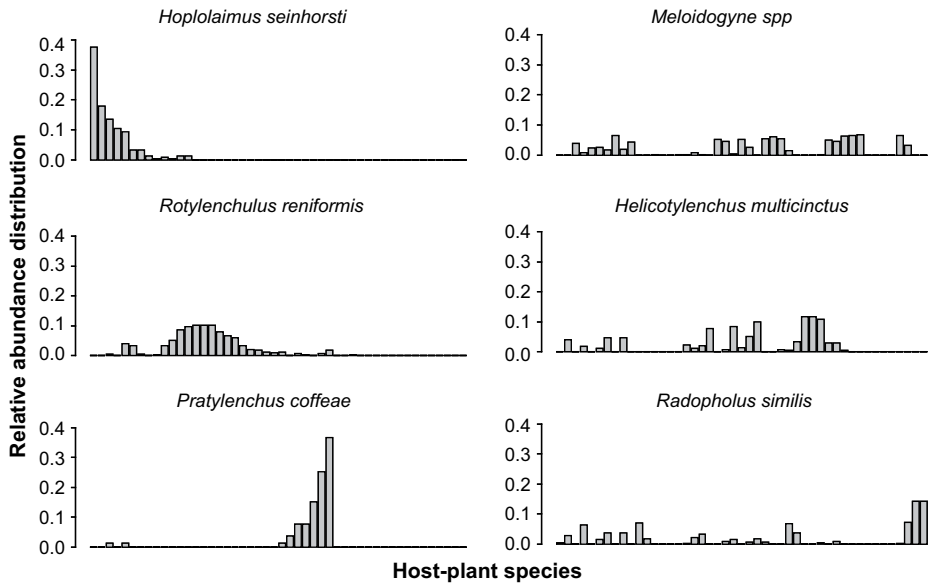

Fig. 3. Frequency distribution of the relative abundance on the 48 host plants for each plant-feeding nematode species. Because *Hoplolaimus seinhorsti*, *Rotylenchulus reniformis*, and *Pratylenchus coffeae* show a strong host-plant partitioning, host-plant species are ordered to illustrate the niche separation between these species. Frequency distributions of *Meloidogyne* spp., *Helicotylenchus multicinctus*, and *Radopholus similis* are given for the same order of host-plant species. It is not possible to order host plants showing niche separation with these three last nematode species. Number of plant species from left to right: 35, 41, 24, 33, 10, 11, 40, 48, 26, 5, 18, 12, 30, 7, 13, 8, 25, 47, 45, 29, 6, 44, 18, 46, 1, 43, 36, 4, 22, 38, 39, 2, 32, 19, 27, 34, 16, 15, 9, 14, 20, 21, 42, 31, 23, 3, 28, 37. Correspondence between number and host-plant names is given in Table 1.

Table 2
Results of the analysis of deviance for abundance of each nematode species. Effects of host-plant species, host-plant class (monocotyledon or dicotyledon), and host-plant introduction status are compared with a reference model for each nematode species; also included are all the significant terms of environment (mean annual temperature = t; mean annual rainfall = r; soil type = s; and interactions). Δ*Dev* corresponds to change in deviance due to the addition of the effect term to reference model. Significant effects are indicated in bold. Introduction status is given in Table 1.

Nematode species	Reference model			Plant species			Plant class			Plant introduction status		
	Terms	residual *d.f*	residual *Dev*	Δ*Dev*	Δ*d.f*	*P*	Δ*Dev*	Δ*d.f*	*P*	Δ*Dev*	Δ*d.f*	*P*
Meloidogyne spp.	1	554	1,648,420	769,865	47	**<0.0001**	48,098	1	0.216	410	1	1
Helicotylenchus multicinctus	1 + t + s + t:s	550	330441	138,003	47	**<0.0001**	1648	1	1	702	1	1
Radopholus similis	1 + t + r + s + t:p + r:s	548	312,411	138,358	47	**<0.0001**	3853	1	0.198	37127	1	**0.0002**
Pratylenchus coffeae	1 + t + r + s + t:s + t:r	548	152,58.7	9011.2	47	**<0.0001**	2233.8	1	**<0.0001**	1938.3	1	**<0.0001**
Rotylenchulus reniformis	1 + r	552	1,865,854	1,150,504	47	**<0.0001**	196,465	1	**0.001**	27544	1	0.284
Hoplolaimus seinhorsti	1 + t + r + s	550	43,100	25,460	47	**<0.0001**	58	1	1	8648	1	**<0.0001**

et al., 2006; Tixier et al., 2006; Quénéhervé, 2008; Tixier et al., 2008). Because exploitation competition for the same resource is likely to occur (and perhaps interference competition via degradation of this resource), coexistence by host-plant niche partitioning is therefore possible among *P. coffeae*, *R. reniformis*, and *H. seinhorsti*, and between *R. similis* and *P. coffeae*. Coexistence among other pairs of species is probably dependent on other mechanisms.

At the root system scale, another axis of the ecological niche is the distance from the rhizome (Quénéhervé, 1990). On banana roots, *R. similis* is more restricted to the closest part of the rhizome compared to other species (Quénéhervé and Cadet, 1985). This is especially evident when *R. similis* competes with *H. multicinctus* (Quénéhervé, 1990). *R. similis* is a migratory endoparasite, able to penetrate any type of root (primary, secondary, and tertiary) and at any position along the root (as is also true for *H. multicinctus* and *H. seinhorsti*) while *R. reniformis* and *Meloidogyne* spp. are sedentary endoparasites that penetrate only at the tip of secondary or tertiary roots just behind the growing meristem.

Coexistence may be insured by mechanisms other than niche partitioning. First, source-sink with migration from outside banana crops is possible; while *R. similis* and *H. multicinctus* seem very associated to banana crops (Gowen et al., 2005), the four other species are found in many other habitats and in particular in vegetables and tuber crops (Luc et al., 2005). Second, coexistence may be enhanced by predation; however, the sampling and extraction methods used in this study do not allow an assessment of predation or of apparent competition mediated through predation. Further studies that included collection of the free-living nematodes, including predacious and omnivorous nematodes, would increase our understanding of these putative species interactions. Third, the life histories of some of these species are still partially unknown, and they may have different colonisation strategies. While plant-feeding nematodes are difficult to rank in the classical *c-p* scale, they can be ranked as *r-K* strategists based on their growth rates (Bongers, 1990). Different colonization abilities and different responses to disturbance (fallow period) and/or spatial heterogeneity (asynchrony of banana trees) may allow coexistence by competition–colonisation trade-off (Tilman, 1994).

4.3. Coexistence and status of introduction of nematodes

Invasions by non-native species often have profound effects on ecosystem function and recipient community structure (Williamson, 1996; Juliano and Lounibos, 2005). However, there are many examples where biological invasions did not lead to the extinction of resident species, i.e., indigenous and invasive species may coexist (Sax et al., 2002; Bruno et al., 2005; Duyck et al., 2006).

Meloidogyne spp., *P. coffeae*, *R. reniformis*, and *H. seinhorsti* were probably already present (being indigenous or previously established) in Martinique when banana was introduced and *R. similis* and

H. multicinctus colonised the island (see Introduction). Niche partitioning via host plant exists among three of the already established species (*P. coffeae*, *R. reniformis*, and *H. seinhorsti*), which is in accordance with the fact that these species have probably been in contact for a long time and have possibly co-evolved. *P. coffeae* occurs more frequently on introduced plant species, however the three nematode species are also found on many indigenous plants. *R. similis* and *H. multicinctus* cover the niche of all pre-existing species, and there is no host-plant niche partitioning except a moderate degree of partitioning between *R. similis* and *P. coffeae*. Thus, in contrast to the strong niche partitioning among already established species (except *Meloidogyne* spp., which have probably more different life-history traits, see above), there is low potential for niche partitioning between recent invaders (*R. similis* and *H. multicinctus*) and established species because most of the host-plant niches of the established species are included in those of the recent invaders.

4.4. Implications for banana agroecosystem management

Our results highlight that modifying the abundance of some host plants may change the balance among nematode species in banana agroecosystems. The burrowing nematode *R. similis* is the most damaging nematode in banana crops (Gowen et al., 2005). No niche partitioning between this species and other nematode species regarding host plant has been observed except with the lesion nematode *P. coffeae*, which is the second most damaging nematode (Quénéhervé, 2008). For example, *C. esculenta* will favour populations of *P. coffeae* and *Meloidogyne* spp. and disfavour populations of *R. similis*. In contrast, some weeds (e.g., *C. diffusa*) support high numbers of *R. similis* and may increase numbers of this species. From a practical point of view, these plant species should be removed during fallow.

H. seinhorsti and *R. reniformis* are considered less damaging nematodes on bananas (Gowen et al., 2005). Because there is host-plant niche partitioning with *P. coffeae*, plants favouring *H. seinhorsti* may prevent population growth of *P. coffeae*. *Eragrostis ilosa* could be a good candidate if additional data confirm that it does not support large numbers of *P. coffeae* or *R. similis*. However, *H. seinhorsti*, *R. reniformis*, and *Meloidogyne* spp. can also damage crops if present in large numbers. For example, high numbers of *Meloidogyne* spp. in the absence of *R. similis* induced severe damage on banana (Jones, 2000: pp. 307–314). An effective strategy for regulation of nematode pests could be to choose a set of associated host-plant species that favour a nematode species that is a weak pest of banana but a good competitor against serious nematode pests of banana on the associated host plant.

In conclusion, host-plant partitioning in banana agroecosystems is considerable among some plant-feeding nematode species, especially those considered long established in Martinique. However, other factors that could promote coexistence and

equilibrium among species should be explored. Additional information about colonisation and population dynamics over time both at the root and agroecosystem scale would increase our understanding of equilibrium among species of the plant-feeding nematode community.

Acknowledgments

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