Niche partitioning based on soil type and climate at the landscape scale in a community of plant-feeding nematodes

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ARTICLE INFO

ABSTRACT

Understanding how environmental factors structure communities is important in conservation biology and ecosystem management. The aim of this study was to test the hypothesis that a plant-feeding nematode community composed of six species is structured by soil type and climate at the landscape scale, and that niche partitioning via these factors is consistent with the coexistence of the species. Martinique has an impressive diversity of abiotic factors (climate and soil type) over a relatively small land area, which facilitates the study of how soil type and climate affect the nematode community.

We conducted this study by building an extensive data set containing the abundance of each nematode species on banana (3708 samples and 5,673,705 nematodes) in a wide range of sites in Martinique. The data set also contained environmental data (soil, climate) and plantation age. We analyzed the response of each nematode species to climate and soil type with a generalized linear model in order to understand whether niche partitioning of factors could contribute to the coexistence of the nematode species.

Temperature, rainfall, soil type, and plantation age significantly affected the abundance of the six nematode species. While some pairs of species shared the same environmental niches, other showed clear niche partitioning along climatic axes. The two dominant species, *Radopholus similis* and *Helicotylenchus multicinctus*, have similar convergent ecological niches regarding climate, soil type, plantation age, and host range. These two species, which often co-occur, probably have different resources at the root scale. Soil type and climate structure plant-feeding nematode species community at the island scale. Further studies need to evaluate coexistence at the root scale among dominant species.

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1. Introduction

Understanding how communities of competing species are structured at the landscape scale is important in conservation biology, e.g., for predicting coexistence following biological invasions (Dangles et al., 2008), and in ecosystem management, e.g., for predicting the development of pest populations (Teodoro et al., 2008). The geographic distribution of species is influenced by niche requirements (i.e., by the effect of environmental factors on life-history traits) and by interspecific interactions such as competition (Costa et al., 2008). Stable coexistence in communities is predicted at larger scales when competing species have niche partitioning

mechanisms that reduce interspecific competition (Gilbert et al., 2008). At landscape scale, communities of competing species are usually structured by niche partitioning among abiotic factors. This is the case for soil nematodes communities, which are structured mostly by soil type and climatic factors (Bongers and Ferris, 1999; Cadet et al., 2003; Ferris and Matute, 2003).

Because the soil nematode community structure is widely used as a bioindicator of ecosystem changes (Bongers, 1990) and because soil nematodes affect plant growth and vigour (Freckman and Caswell, 1985; Coleman, 2008), understanding how niche partitioning contributes to the coexistence of soil nematodes is important (Ettema et al., 1998; Bongers and Ferris, 1999). The study of the effect of abiotic factors such as climate and soil type on the community structure of plant-feeding nematode in the field is difficult for at least two reasons. First, it is difficult to separate the effect of plants and the effects of the abiotic environment because

plant-feeding nematodes are greatly affected by their host plants (Yeates, 1999; Brinkman et al., 2008; Duyck et al., 2009) whose distribution is greatly affected by abiotic factors (Yeates and Boag, 2004). Second, the distribution of nematodes at landscape scale may result from dispersal by humans and may therefore reflect invasion history.

The study of the plant-feeding nematode community in the banana agroecoystem on the island of Martinique may reduce these two difficulties. First, although plant-feeding nematodes in banana agroecosystems are linked to host plants, the significance of host plant as a variable is reduced because the same host plant (banana) is grown widely on the island; it is therefore easy to restrict sampling to one host. Second, like many volcanic tropical islands, Martinique has an impressive diversity of abiotic factors (climate and soil type) in a relatively small area, which facilitates the study of these factors. In a radius of less than 10 km, soil type and climate may vary substantially. Because rainfall is linked to topographic relief and because elevation of banana plantations on Martinique range from 0 to more than 500 m a.s.l., annual rainfall can range from 1000 mm at sea level to >6000 mm at higher elevations. Given this great range of climate and also a great range in the nature and age of the source rocks, soil on Martinique is quite variable.

To understand the effects of abiotic factors on the community structure of plant-feeding nematodes, we studied six species of plant-feeding nematodes in competition on the same host plant (*Musa* spp., AAA group, cv. Cavendish Grande Naine). Worldwide, bananas are attacked by many species of plant-feeding nematodes but only a few causes economically important damage (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. 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; Duyck et al., 2009), they differ in life history (sedentary versus migratory species) and reproductive strategy (parthenogenetic vs. amphimictic and syngonic species).

In this study, we tested the hypothesis that this plant-feeding nematode community composed of six species is structured by soil type and climate at landscape scale. We conducted this study by building an extensive data set that contained the abundance of each nematode species on banana and associated environmental information in many different locations on Martinique. Our analysis also included the time elapsed since planting (=plantation age) because host-plant quantity and quality change as the plant ages and because plant-feeding nematodes are greatly affected by root quantity and quality (Van der Stoel et al., 2006). We analyzed the response of each nematode species to climate and soil type using a generalized linear model in order to understand whether niche partitioning of these factors could contribute to the coexistence of the nematode species.

2. Materials and methods

2.1. Field data collection

A systematic survey of nematode infestation on bananas was undertaken between 2003 and 2009. All banana root samples were collected in commercial banana plantations of Martinique (French West Indies, 14°N, 61°W). 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 (Fig. 1).

Soil types (young soils on pumice, andosols, nitisols, ferralsols, vertisols, and fluvisols) were determined using a soil type map (Colmet-Daage et al., 1969). Young soils (containing sandy primary minerals and allophane in the clay fraction) are composed of many tubular mesopores (from 3 to 30 μm diameter) and macropores (from 30 to 300 μm diameter) that allow high hydraulic conductivity at saturation ($Ksat$) (Cabidoche et al., 2009). Andosols (containing mainly allophane) have a high hydrological conductivity ($Ksat = 50-200$ mm h^{-1}) and have substantial meso- and macroporosity but that porosity can be irreversibly damaged by heavy ploughing. Nitisols contain mainly halloysite and have many macropores ($Ksat = 10-70$ mm h^{-1}). In ferralsols, the primary materials have been degraded and Fe-oxihydroxides have accumulated, resulting in cementation of the clay fraction. Ferralsols are clayey (>90% clay) but the clayey materials combine with organic matter to produce sand-like aggregates, such that macropores are abundant ($Ksat = 20-150$ mm h^{-1}). Vertisols usually have poor meso- and macroporosity. When wet, vertisols have only few pores as wide as 3–300 μm and a very low water conductivity ($Ksat = 1-10$ mm h^{-1}); pores >3 μm occur in vertisols only when these soils are dry, which is also when megapores (>300 μm) appear. Fluvisols, which occur on fluvial terraces, result from erosion of upper lands ($Ksat = 10-50$ mm h^{-1}).

2.2. Laboratory identification

Each root sample was collected from 10 adjacent banana plants. Root samples were carefully washed, cut into 0.5-cm lengths, and thoroughly mixed in the laboratory. The nematodes were then extracted from a 20-g fresh root subsample using the maceration and centrifugal-flotation method (Coolen and D'Herde, 1972). Nematode abundance was expressed as number per 100 g of fresh roots. Nematodes were identified to species by examining living or fixed specimens with a stereomicroscope. The entire database comprised 3708 samples and 5,673,705 specimens of plant-feeding nematodes identified to species. Number of sampling points for fluvisol, andosol, young soil on pumice, ferralsol, nitisol and vertisol were 378, 618, 834, 210, 1470 and 198, respectively.

2.3. Statistical analyses

Nematode abundance data were analyzed using a Poisson log-linear model (analysis of deviance with Poisson error) as a function of species, temperature, rainfall, soil type, plantation age, and interactions. We used standard simplification procedures to eliminate non-significant terms from the model. The significance of each term was assessed through the change in deviance between models with and without that term. Overdispersion was accounted for using quasi-Poisson instead of Poisson models in R (O'Hara and Kotze, 2010). We started from the most complex model (including all interactions) and kept eliminating higher-order terms as long as they remained insignificant (Crawley, 1993). All models were fitted using R (R Development Core Team, 2010).

3. Results

Temperature, rainfall, soil type, and plantation age significantly affected the abundance of the six nematode species (Table 1). The significant interactions between these factors and the species factor indicate that the six species react differently to these factors. The interaction between temperature, rainfall, and soil type, however,
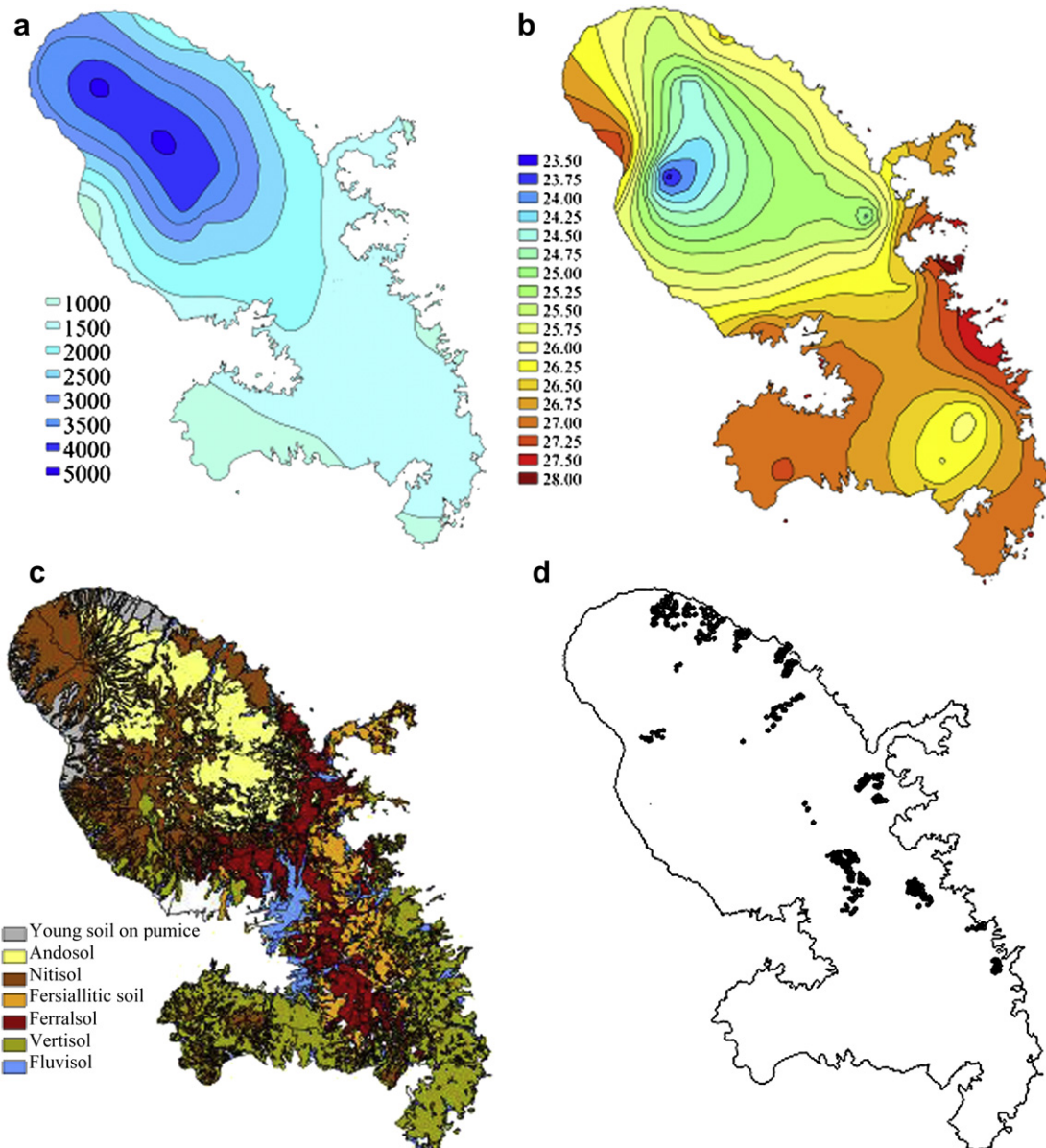
Fig. 1. Rainfall, temperature, soil types, and sampling locations on Martinique. a. Mean annual rainfall (mm) from 1971 to 2000; b. Mean annual temperature (°C) from 2007 to 2008; c. Distribution of soil types (Colmet-Daage and Lagache, 1965); d. Distribution of sampling points.

Table 1
Results of the analysis of deviance for the abundance of six plant-feeding nematode species in Martinique. Only those effects retained in the final model (see Methods) are presented. Δdev corresponds to changes in deviance. The residual deviance and df relate to the reference model. P values indicate the significance of the effect. sp = species, d = duration after plantation, t = mean annual temperature, r = mean annual rainfall, soil = soil type.

Effect	Δdf	Δdev	Residual df	Residual dev	P value
sp	5	6,802,457	3702	13,543,400	<0.0001
d	1	245,195	3701	13,298,205	<0.0001
t	1	265,243	3700	13,032,962	<0.0001
r	1	131,679	3699	12,901,283	<0.0001
soil	5	584,755	3694	12,316,528	<0.0001
sp × d	5	154,001	3689	12,162,527	<0.0001
sp × t	5	233,657	3684	11,928,870	<0.0001
sp × r	5	92,745	3679	11,836,125	0.0023
sp × soil	25	717,637	3654	11,118,488	<0.0001
d × soil	5	316,967	3649	10,801,521	<0.0001

was not significant, indicating that the effect of climate was independent from that of soil type. The significant interaction between plantation age and soil type indicated that change in nematode abundance with time since planting differed among soil types.

R. similis and *H. multicinctus* were most abundant in the dry and cool areas of the island (Fig. 2). *P. coffeae* and *Meloidogyne* spp. were most abundant in wet and cool areas, while *R. reniformis* and *Hoplolaimus seinhorstii* were most abundant in dry and warm areas. Overall, *Meloidogyne* spp, *H. multicinctus,* and *R. similis* were most abundant compared to the three other species. The abundance of *P. coffeae* was intermediate while the abundances of *R. reniformis* and *H. seinhorstii* were the lowest of the six species.

The relative composition of the nematode community depended on soil type (Table 1; Fig. 3). *H. multicinctus* was abundant in all soil types, especially in young soils on pumice and in nitisols, where it represented about 50% of all plant-feeding nematodes. The presence of some species greatly depended on soil type; for
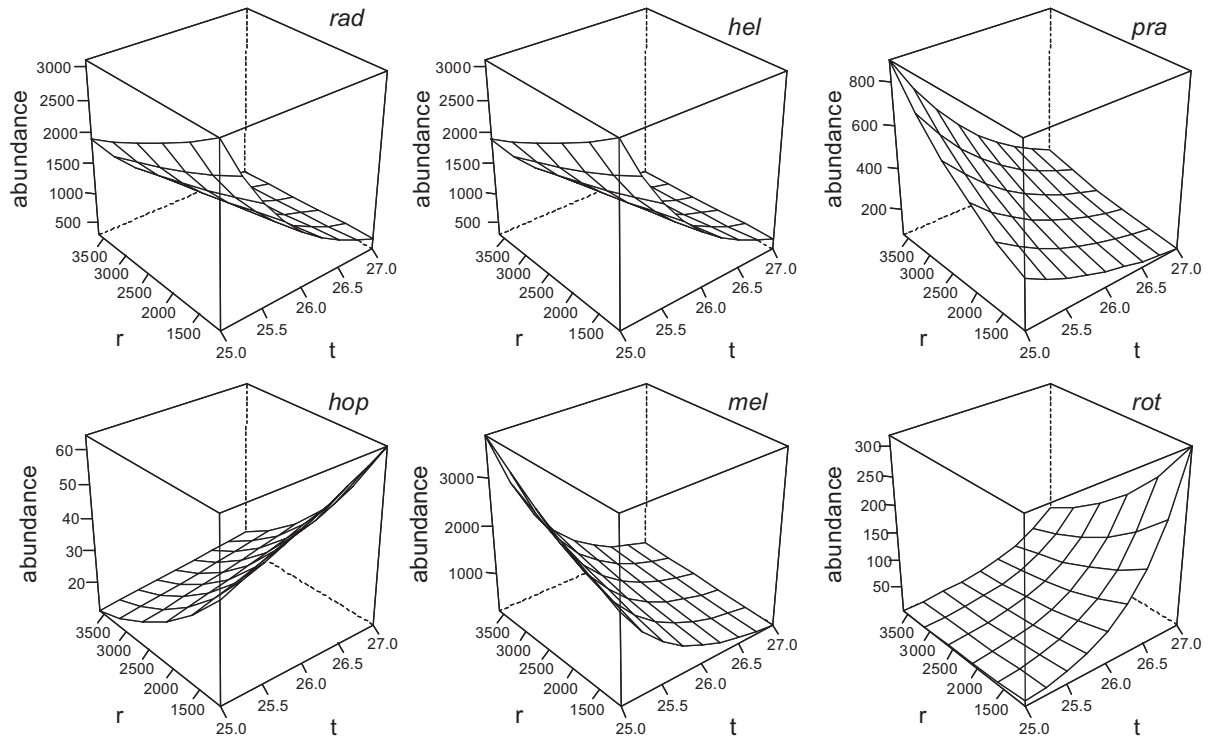
Fig. 2. Influence of temperature (t, °C) and rainfall (r, mm) on the abundance (number/100 g of fresh root) of six nematode species. rad: *Radopholus similis*, hel: *Helicotylenchus multicinctus*, pra: *Pratylenchus coffeae*, hop: *Hoplolaimus seinhorsti*, mel: *Meloidogyne* spp., rot: *Rotylenchulus reniformis*. Because there was no interaction between climate (rainfall and temperature) and soil type and plantation age, the effect of climate is presented using data from andosols and 3-year-old banana plants. For other soil types and plant ages, the absolute values may differ but the effect of temperature and rainfall will be the same.

example, *P. coffeae* was abundant in ferralsols but absent from nitisols and vertisols. Contrary to nematode communities in other soil types, communities in vertisols were dominated by large numbers of *H. multicinctus* and *Meloidogyne* spp. and contained only small number of the other nematode species.

Plantation age strongly influenced nematode abundance, and depended on species and soil type (Table 1). On nitisols, the abundances of *R. similis*, *H. multicinctus*, and *Meloidogyne* spp. were high at planting and continued to increase over time (Fig. 4A). In contrast, the abundances of *H. seinhorsti*, *P. coffeae*, and *R. reniformis* were low at planting and decreased over time (Fig. 4B). The pattern was different in the andosols, which had low abundances of *R. similis*, *H. multicinctus*, and *Meloidogyne* spp. (Fig. 5A) at planting and increasing abundances of *P. coffeae* and *R. reniformis* over time (Fig. 5B).
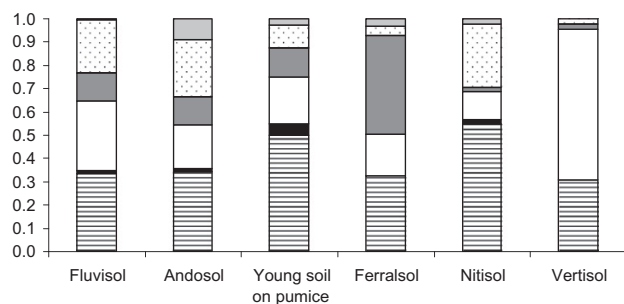

Fig. 3. Relative abundance of plant-feeding nematodes in relation to soil type (after 3 years at 27 °C with average rainfall of 3100 mm). rad: *Radopholus similis*, hel: *Helicotylenchus multicinctus*, pra: *Pratylenchus coffeae*, hop: *Hoplolaimus seinhorsti*, mel: *Meloidogyne* spp., rot: *Rotylenchulus reniformis*.

4. Discussion

4.1. Influence of environmental factors on species abundance

Temperature, rainfall, and soil type strongly influenced the abundances of the six species of plant-feeding nematodes common in Martinique banana plantations. In our study, the abundance of *R. similis* decreased as rainfall increased. This observation agrees with previous studies that reported a decline in numbers of *R. similis* during wet seasons (Jimenez, 1972; McSorley and Parrado, 1981; Hugon et al., 1984; Quénéhervé, 1989). Recent experimental results also confirm that *R. similis* survivorship is shorter in water-saturated soils than in drier soils in both andosols and nitisols (Chabrier et al., 2010). The abundance of *H. multicinctus*, also decreased with increasing rainfall. This behaviour has already been observed on plantains in the Caribbean (Hutton, 1978). *P. coffeae* is a pantropical species that was first observed in the roots of plantains in Grenada and described as *Tylenchus musicola* by Cobb in 1919. In our study, the abundance of *P. coffeae* greatly decreased as rainfall decreased, and this could explain why *P coffeae* abundance increases with elevation. Although *Pratylenchus* spp. can enter a state of anhydrobiosis (Glazer and Orion, 1983; Townshend, 1984) and thereby survive dry conditions, this species is probably unable to increase its numbers in dry conditions.

Based on experiments in growth chambers, the reproduction of different isolates of *R. similis* and of different species of *Pratylenchus* is highest between of 25 and 30 °C (Radewald et al., 1971; Fallas and Sarah, 1995; Pinochet et al., 1995). In addition, the multiplication rate of *R. similis* was always 3—5 times greater than that of *P. coffeae* (Pinochet et al., 1995).

Whereas *Meloidogyne* spp. was more abundant in wet and cool areas (higher elevation), *R. reniformis* was more abundant in dry
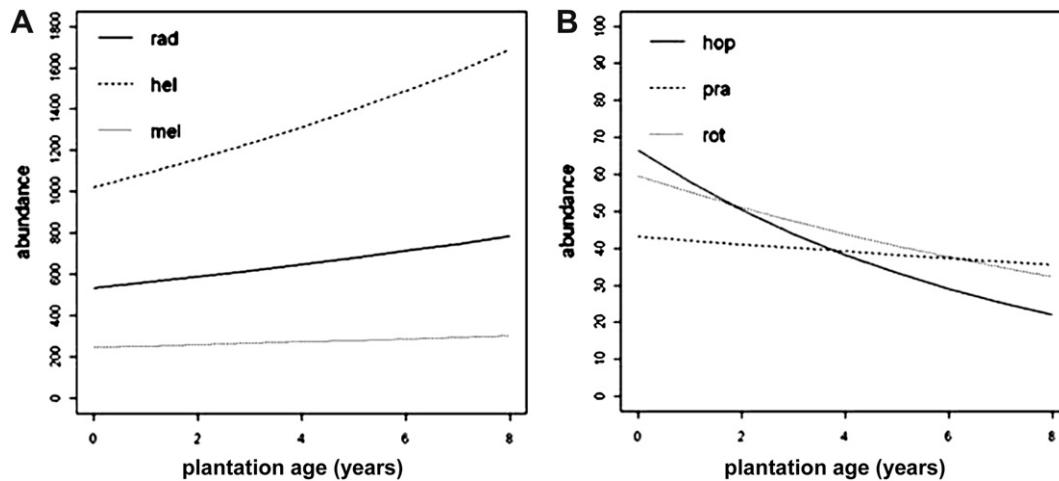
Fig. 4. Change in nematode abundance as a function of plantation age in nitisols (27 °C, 3100 mm). Nematode abundance is expressed as number per 100 g of fresh roots. rad: *Radopholus similis*, hel: *Helicotylenchus multicinctus*, pra: *Pratylenchus coffeae*, hop: *Hoplolaimus seinhorsti*, mel : *Meloidogyne* spp., rot: *Rotylenchulus reniformis*.

and warm areas (sea level). Both species are sedentary endoparasites that share the same ecological niches (secondary and tertiary banana roots) and that can be competitively excluded *R. similis* or *P. coffeae*. The geographic distributions of *Meloidogyne* spp. and *R. reniformis* are strongly influenced by soil type (especially clay content) and soil ionic content (Koenning et al., 1996; Le Saux and Quénéhervé, 2002).

The abundance of the six nematode species responded differently to the different soil types. In particular, abundances in vertisols were very different from those in other soils, in part because vertisols supported very small numbers of both *R. similis* and *P. coffeae*. In contrast, *P. coffeae* was very abundant in ferralsols in Martinique, which confirms observations that *P. coffeae* is much more abundant than *R. similis* in ferralsols in Cameroon and Gabon (Loubana et al., 2007). These different responses may be linked to differences in soil porosity. Because of their diameters, *R. similis* and *P. coffeae* require soil pores that have water films and diameters of 30−300 μm in order to move through the soil (Wallace, 1959, 1968). In vertisols, these two conditions rarely occur together. Thus, nematode movement in vertisols is restricted to a short time when rain occurs just after tillage. A species with a low ability to survive suboptimum conditions, such as *R. similis*, is unlikely to increase in

number in vertisols. In contrast, species with a high ability to survive suboptimum conditions, such as *H. multicinctus* and *Meloidogyne* spp., are able to persist and then increase in number in the short periods when conditions are favourable in vertisols. Other soil types in Martinique contain numerous pores of favourable diameter (30−300 μm) and often have favourable water potential (−1 to −10 kPa); in these soils, even species with a low ability to survive adverse conditions are able to increase in number.

Fertility may vary regarding of soil type (young soils on pumice have 2.5−5.9% of organic matter; andosols 2.2−10.5%; nitisols, ferralsols, vertisols, and fluvisols between 2 and 3%). However the nutrition of banana plants can be considered as optimal in all soil types due to fertilization and irrigation that are optimized (Delvaux et al., 1990). Climatic factors, those vary according to different zones of Martinique (especially altitude), affect plant growth and development. Because temperature is the main driver of banana plant development, temperature variations (between 23.5 and 28 °C of annual mean values) lead to a cropping cycle (time between two consecutive harvests) comprised between 7 and 12 month. Nevertheless, the fact that cropping cycles overlap leads to a relatively constant production of root biomass all over the production period. The main damage of plant-parasitic nematodes on banana
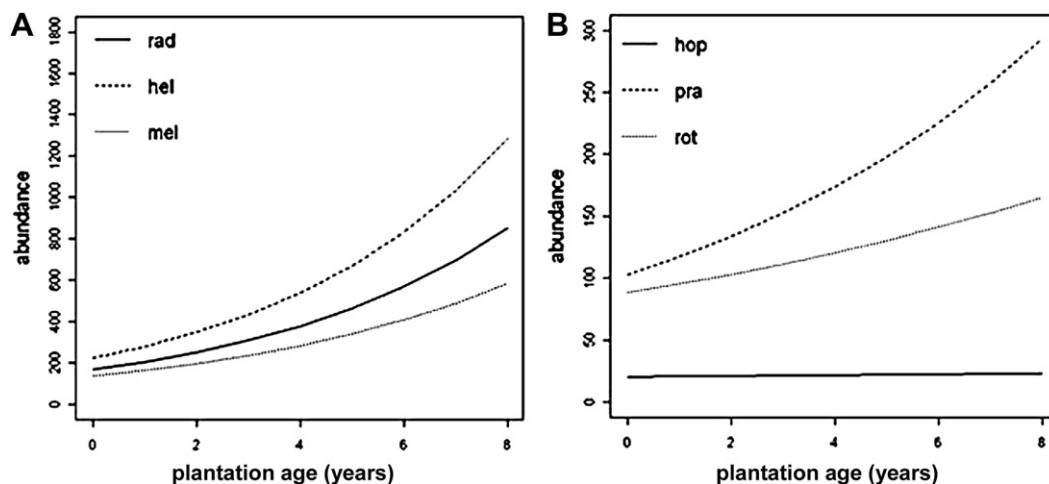

Fig. 5. Change in nematode abundance as a function of plantation age in andosols (27 °C, 3100 mm). Nematode abundance is expressed as number per 100 g of fresh roots. rad: *Radopholus similis*, hel: *Helicotylenchus multicinctus*, pra: *Pratylenchus coffeae*, hop: *Hoplolaimus seinhorsti*, mel : *Meloidogyne* spp., rot: *Rotylenchulus reniformis*.

plant is the topple over due to root necrosis, thus reducing the anchoring capacity of plants. In intensive production, fields are fertilized in excess (between 300 and 500 kg of N every year, while only 100 are exported) leading to a moderate effect of plant-parasitic nematodes on the nutrition of the banana plant.

Because the studied nematodes are able to complete many life-cycles within banana root tissues without passing through soil, direct interaction between these nematodes and other soil organisms such as earthworm is not probable (Lafont et al., 2007). However indirect impact of earthworms on nematodes community via modified soil composition and structure is possible (Lavelle et al., 1992; Lafont et al., 2007). In this paper we studied the influence of environment at the landscape, however, modifications of the local environment at the root scale will also influence the community of plant-feeding nematodes and need to be further studied.

4.2. Niche partitioning and coexistence

Some pairs of species seem to share the same climatic niche. For example, both R. similis and H. multicinctus prefer relatively dry and warm conditions. Coexistence of these two species is probably the result of weak interspecific competition because they partition roots of different ages and conditions. Quénéhervé (1990) observed successive multiplication of R. similis followed by H. multicinctus on the same type of root. R. similis is able to increase quickly on the fresh resource (undamaged roots) while H. multincinctus is able to increase later by utilizing R. similis-damaged roots. When these two species co-occur, there is a niche differentiation at the root scale: R. similis restricts its niche to the cortical part of the rhizome while H. multicinctus restricts its niche at a certain distance from the rhizome where decomposing resource is present (Quénéhervé, 1990). At the field scale, the biomass of old roots increases more quickly than that fresh roots, which explains the greater intrinsic rate of increase for H. multicinctus than for R. similis on banana (Tixier et al., 2008).

Other pairs of species show clear niche partitioning along climatic axes. This is the case of the two most damaging nematode species, P. coffeae and R. similis. At the island scale, these species segregate along a climatic gradient and especially along a rainfall gradient. This results from the different tolerances of these two species to saturated vs. dry soils.

Compared to the abundances of other species, the abundances of R. reniformis and H. seinhorstii were very low in banana plantations on Martinique. While the two species occupy the same climate and soil niches, they have different alternative host plants (weeds) (Duyck et al., 2009).

4.3. Conclusion

The global distribution of nematode species reflects their origin, natural dispersal, and human-mediated dispersion, while their potential distributions are limited by their biological traits. On a regional scale, assessment of the distribution of nematode species should reflect not only the range of land use and vegetation but also climate, topography, and soils. Moisture, temperature, and soil type, as well as the presence of suitable host plants in the case of plant-feeding nematodes greatly affect the distribution of terrestrial nematodes (Yeates and Boag, 2004). Our study shows a clear niche partitioning among some species according to these abiotic factors. In contrast to the other studied species, the two dominant species, R. similis and H. multicinctus, are very closely associated with banana and have probably been introduced very recently, probably with the introduction of banana plant material in the Caribbean early in the 20th century (Marin et al., 1998). These two species have convergent ecological niches regarding climate, soil

type, plantation age, and host range (Duyck et al., 2009). The four other species were probably already present (being indigenous or previously established) in Martinique when banana was introduced and when R. similis and H. multicinctus colonized the island. These previously established species are likely to partition their ecological niches via host range (Duyck et al., 2009) and climate with the two dominant species.

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