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Nematode assemblages in banana (*Musa acuminata*) monocultures and banana plantations with Juçara palms (*Euterpe edulis*) in the southern Mata Atlântica, Brazil

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Summary – The composition of the nematode fauna at two different agrosystems (banana monocultures and mixed banana-palmito plantations) was investigated at six study sites on the coastal plain of southern Brazil. Nematode abundance was higher and the number of families was lower (25 compared to 33) in the soil of banana monocultures. The assemblages in the soil of the banana monocultures were dominated by bacterial feeders and plant parasites, whereas in the soil of the mixed plantations the proportion of the other trophic groups was higher. In the monocultures, the percentage of families categorised as colonisers (*c-p* 1 families) was higher and the persisters lower. The difference in the assemblage of *c-p* groups was significant between sites of the two different systems. Principal component analysis (PCA) ordination of the samples by nematode family composition showed site-specific assemblages, similarity between two sites of each system and significant dissimilarities between the two systems. The MI 1-5 and the MI 2-5 were lower in the banana monocultures. Additionally, the MI 2-5 of banana site B2 was significantly higher than that of the two other banana sites. The ratio F/B was higher and the ratio (F + B)/plant feeders was lower in the banana-palmito plantations. The differences between the systems in nearly all measured parameters indicate a higher degree of disturbance and nutrient enrichment of the soil under monocultures. However, a low number of plant parasites and dominance of *c-p* 3 taxa at both agroecosystems show that the soil of both agroecosystems seems to be of an advanced successional stage. This may be a result of a less intensive 'organic' cultivation without the use of plant protection products and fertilisers and with additional non-host plants. Despite many non-controlled variables in the smallholder systems, according to the results the nematodes can be regarded as suitable indicators of soil disturbance in banana and banana-palmito agro-ecosystems.

Keywords – agriculture, community composition, diversity, eutrophic conditions, maturity index, nematode assemblage, trophic structure.

Nematodes are amongst the most numerous soil animals, and show a high diversity (Bongers, 1994; Andrássy, 2009). However, due to their small size and the difficulty in extracting them from soil samples, they are still relatively rarely studied (s'Jacob & Van Bezooijen, 1984; Nicholas, 1984). In forest soils of tropical regions in general, and of South America in particular, almost nothing is known about free-living nematodes. Most taxonomic efforts have been addressed towards important plant-parasitic nematodes (Huang & Cares, 2006), which cause major yield losses in some important tropical crops. Examples are the root-lesion nematode *Pratylenchus coffeae* and the burrowing nematode *Radopholus similis* in banana cultures (Sarah, 1989; Kashaija *et al.*, 1994), one of the main crops in the tropics.

In 2008, the abundance and structure of nematode assemblages were studied in six agroecosystem sites (three banana monocultures and three banana-palmito plantations), located in the southern coastal region in Paraná originally covered by forest. The Brazilian Atlantic Forest (Mata Atlântica) is among the most diverse and most threatened ecosystems of the world (Fun-

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dação SOS Mata-Atlântica, 1993). The region has been largely impacted by colonisation, which resulted in extensive deforestation, conversion into farmland and urbanisation (Ribeiro *et al.*, 2009). Our study was part of the German-Brazilian co-operative project SOLOBIOMA (see www.InBioVeritas.net), which aimed to assess the ecosystem quality of different sites in this region and their potential to conserve biodiversity and related ecosystem services. The main objective of the present study was to investigate whether and how the nematode assemblages differ in two different agroecosystems. Differences in diversity (richness) and trophic structure (function) could help identify drivers of biodiversity reduction.

Materials and methods

The study sites were located on the coastal plain of the state of Paraná, in the municipality of Antonina. Soils are classified as gley soils (Römbke *et al.*, 2009). Further details on site and soil characteristics are presented in Table 1. The climate of the region can be described as mesothermic subtropical humid, corresponding to the Cfa-type of Köppen's classification (Schröder, 2000; Strahler & Strahler, 2005). Mean annual temperature is between 20.0-22.1°C, and mean annual rainfall in the region is 2545 mm (Ferretti & Britez, 2006) and shows seasonality. Lower rainfall occurs from the end of autumn to winter (April-August), and higher rainfall during the warmer Brazilian summer (September-March) (IPARDES, 2001).

Nematodes were sampled at six different sites of two agroecosystems (banana (B) and banana-palmito (BP)), considered as replicates. All sites are situated around the village Rio Pequeno, about 20 km north of Antonina, within the marginal zone of the Environmental Protection Area (EPA) Guaraqueçaba, and are cultivated by smallholders. Within the EPA, the use of chemical fertilisers and pesticides is officially prohibited. To our knowledge no chemicals were applied at the studied sites. In the banana (*Musa acuminata*) monocultures understorey was sparse, whilst in the mixture of banana and palmito (*Euterpe edulis*) herbs and secondary trees were found (see Table 1).

At each site, five plots (of about 5 m^2) were established. In each plot, ten samples were taken with a soil core sampler (2.5 cm diam. × 10 cm depth), subsequently mixed and reduced to five composite samples. Nematodes were extracted from these samples through the modified sieving and decanting method of Cobb (Cobb, 1918; s'Jacob & Van Bezooijen, 1984; Southey, 1986). All samples were treated in the same way: each composite sample was thoroughly mixed and a sub-sample of 50 g soil fresh weight was taken in small portions randomly. This 50 g soil was steeped in 400 ml tap water for approximately 15 min. Soil and water were then stirred for 60 s, and after 15 s of sedimentation the supernatant was carefully decanted in a collecting plastic bowl (nematode suspension). This procedure was repeated twice, each time with 400 ml tap water. The remaining sediment was discarded, and the combined nematode suspension poured through a cascade of several sieves with decreasing mesh sizes (1000, 350, 175, 100, 45 μm). To improve cleaning, the nematode suspension was poured five times through the 45 μm sieve. The nematodes on the 45 μm sieve were rinsed with tap water and transferred into a separate plastic bowl. The collected supernatant of the nematode suspension was then carefully decanted and the remaining nematodes were poured into an extraction sieve containing a cotton-wool filter. The extraction sieve was placed in a shallow tray filled with tap water. Within the following 24 h the nematodes actively moved through the cotton wool into the tray. This nematode suspension was poured through a small 20 μm sieve to separate the nematodes from the water. Subsequently, extracted nematodes were carefully rinsed from the 20 μm sieve into a counting dish and counted alive under an inverse microscope (magnification ×160). Counted samples were transferred into 5 ml polypropylene tubes. For identification of nematodes, samples were heated up to 60°C and preserved in formaldehyde (4%). Until identification, the samples were stored in a refrigerator at 4-6°C.

The identification of nematodes (100 nematodes per sample) was conducted either to the family or genus level. The identification and taxonomical classification was performed by using the keys of Bongers (1994) and Andrássy (2005, 2007, 2009). Classification of the nematodes into trophic groups was done according to Yeates *et al.* (1993). The following trophic groups were distinguished:

- Algivores (ALG)
- Bacterivores (BAC)
- Fungivores (FUN)
- Omnivores (OMN)
- Predators (PRE)
- Herbivores, separated into obligatory plant parasites (PP) and facultative epidermal cell and root hair feeders (WEP)

The following characteristics of the nematode populations of each site were also evaluated: abundance (ind.

Table 1. *Location, age of the plantation, size, soil and crop characteristics and further observations on the use of the six study sites.*

	B1	B2	B3	BP1	BP2	BP3
UTM coordinates (East/North)	727013/7206145	728835/7202908	727662/7203747	731179/7202942	730852/7202331	727032/7206176
Age (years)	approx. 5-10	approx. 10-15	approx. 2	10	10	approx. 5-10
Size (ha)	approx. 2.0	2.3	approx. 1.0	4.6	3	approx. 2.0
Soil type	Gley soil	Gley soil	Gley soil	Gley soil	Gley soil	Gley soil
pH*	4.8-5.2	4.5-4.7	5.4-5.6	4.3-4.7	4.0-4.4	4.8-5.5
C (%)	3.3	4.1	2.5	4.4	4.3	5.3
N (%)	0.3	0.4	0.2	0.5	0.5	0.5
C/N (%)	10.2	9.9	10.7	9.2	9.5	10.6
P (mg (dm soil)$^{-3}$)	96.8	20.5	40.8	12.4	18.4	56.7
Observations on soil	very sandy, clearly more dry, poor WHC	very loamy, many earthworms	fertilisation with goat dung, regularly soil cultivation, removal of litter	very loamy, many roots	very loamy, many roots, many earthworms, polluted with household waste	very sandy, clearly more dry, poor WHC
Microbial biomass (μg C_{mic} (g soil)$^{-1}$)*	453-738	661-982	459-493	991-1037	685-1205	301-489
Flood events	none	none	none	2 months/year	2 months/year	none
Invading domestic animals	not observed	cows	not observed	chickens, soil scratched up	chickens, soil scratched up	not observed
Banana plants (no./site)	440	946	283	243	171	196
Palmito plants (no./site)	–	–	–	166	402	264
Secondary trees (no.)	8	–	–	27	40	71
Understorey/general condition	Sparse, once a year totally removed	partly very high/fallow aspect with many dead banana trunks	no under-storey/very open system	up to 1 m high/strong shading, fallow aspect but some places without litter layer and with compacted soil	up to 0.4 m high, strong shading	up to 0.4 m high, dense
Additonal cultivation	none	fallow for a long time, old banana material inserted	manioc, cabbage, courgette	none	none	none

B = banana, BP = banana-palmito.

* Data from Heine (2007).

(100 g dry soil)$^{-1}$), number of families (total), number of families in the different trophic groups, trophic structure (% part of the different trophic groups over total abundance), % part of families with *c-p* 1, *c-p* 2, or *c-p* 3-5 value, Maturity Indices (MI 1-5 (excluding plant parasites), MI 2-5 (excluding plant parasites and all *c-p* 1 organisms)), Plant Parasite Index (PPI), the ratio fungal to bacterial feeders (F/B) and the ratio of F + B to plant feeders.

The maturity index (Bongers, 1990) uses the structure of nematode assemblages as an instrument to assess the condition of soils or sediments. Based on their ability to colonise new habitats, nematode families are classified on a coloniser-persister (*c-p*) scale ranging from 1 (colonisers) to 5 (persisters). Nematode families comprising species that rapidly increase in number in early stages of succession are considered to be colonisers and receive a low *c-p* value. They have similar characteristics to r-strategists. The persisters among the nematodes are comparable with K-strategists and generally live in habitats with a long durational stability. Phytophagous nematodes differ in their reaction to a chemical stressor and eutrophication from non parasitic nematodes (Bongers, 1990; Yeates, 1994; Bongers *et al.*, 1997). Therefore, they were excluded from the calculation of the maturity index (MI) and were combined to calculate a plant parasite index (PPI). The MI and the PPI were calculated as the weighted mean of the single *c-p* values:

$$\text{MI or PPI} = \sum_{i=1}^{n} v(i) * f(i),$$

where $v(i)$ is the *c-p* value assigned to taxon i and $f(i)$ is the abundance of the taxon i.

The ratios F/B (Twinn, 1974) and (F+B)/plant feeders (McSorley & Frederick, 1996) were both calculated as indicators for decomposition of organic matter. The higher the F/B ratio, the lower the degradation/transition rate, and the higher the ratio (F + B)/plant feeders the younger the soil and the stronger the plant growth.

A univariate analysis of variance (ANOVA) followed by a Bonferroni test was performed using Statistica 8 software to determine whether the sites differed in the abovementioned variables (at significance level of $P < 0.05$). Abundance data were log-transformed to reach variance homogeneity. The assemblage of *c-p* groups of the different sites was tested for significant differences by the χ^2-test ($P < 0.05$). Differences in family composition of the nematode communities of the sample sites were analysed by multivariate PCA using CANOCO 4.5 software. In order to check if PCA was suitable, the length of gradient was calculated by discriminant component analysis (DCA) (2.095) beforehand. Within CANOCO the options log-transformation ($\ln(2x + 1)$) of abundance data and centring by family were chosen. Dissimilarities between the two agro-ecosystems were tested for statistical significance by the multivariate analysis of similarity (ANOSIM) using the Bray-Curtis matrix using PRIMER ($P < 0.05$).

Results

The mean nematode abundance in the soil of the banana monocultures was significantly higher (1293.9 ± 750.7 to 2214.7 ± 1275.6 ind. (100 g soil)$^{-1}$ (dw)) compared with the soil of the banana-palmito sites (355.0 ± 208.7 to 1284.4 ± 762.5 ind. (100 g soil)$^{-1}$ (dw)) (ANOVA, $F_{5,24} = 7.3$, $P < 0.001$) (Fig. 1). The differences between all banana sites and the banana-palmito site BP1 ($P = 0.0003$-0.02), between B1 and BP3 ($P = 0.02$) and between BP1 and BP2 ($P = 0.02$) were significant.

In total, 35 families of nematodes were identified from the six sites of two different agroecosystems, 25 in the banana plantations and 33 in the banana-palmito plantations (Table 2). Two families comprised more than 50% of the total abundance at the banana monocultures; the greatest mean abundance was determined for Hoplolaimidae followed by Rhabditidae. At the mixed plantations four families covered more than 50% of the total abundance, with Hoplolaimidae showing the greatest mean abundance; next in density were Aporcelamidae followed by Rhabditidae and Leptonchidae.

The mean number of families per site was significantly lower in monocultures (10.2 ± 3.4, 11.2 ± 1.9 and 11.8 ± 0.8) than in mixed cultures (12.6 ± 1.7, 13.4 ± 2.9 and 17.0 ± 1.9) (ANOVA, $F_{5,24} = 5.62$, $P < 0.01$) (Fig. 2). The differences between all banana sites and the banana-palmito site BP3 were significant ($P = 0.006$-0.02).

The trophic structure of the nematode assemblages in the soil of the banana plantations showed a strong dominance of the plant parasites and the bacterial feeders (Table 2; Fig. 3). The family Hoplolaimidae (*c-p* 3) contributed the major part of the plant parasites and the family Rhabditidae (*c-p* 1) of the bacterial feeders. At two sites the Aporcelaimidae (*c-p* 4) and at one site the Thornenematidae (*c-p* 5) contributed most to the omnivores. The Aphelenchoididae (*c-p* 2) and Leptonchidae (*c-p* 4) contributed most to the group of the fungal feeders at two sites and one site, respectively. The agro-ecosystems did not

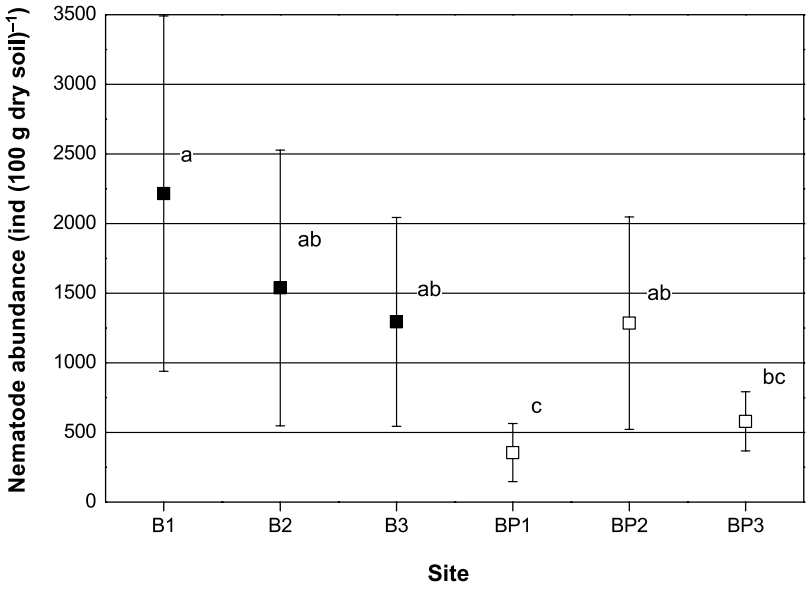

Fig. 1. *Mean (± s.d.,* n = *5) nematode abundance in the soil of three banana (B) and three banana-palmito (BP) plantations. Data with different letters are significantly different according to Bonferroni test at* P = *0.0003 to 0.02.*

differ in the proportion of plant parasites, whereas the percentage of bacterivorous nematodes was more than 10% lower in the soil from the banana-palmito sites. The percentage of the trophic groups of omnivores, fungal feeders, predators, as well as the root hair and epidermal feeders was higher in the banana-palmito sites than in the banana plantation. By contrast to the banana sites, in the banana-palmito sites algal feeders occurred. In both systems the family Hoplolaimidae dominated the plant parasites, but at two banana-palmito sites also the Dolichodoridae (*c-p* 3), and at one site the Criconematidae (*c-p* 3) were found abundantly. The bacterial feeders were not dominated by the family Rhabditidae, as in the banana sites. Instead, several families with *c-p* values of 1-3 were found. Finally, the Aporcelaimidae contributed most to the omnivores and the Leptonchidae most to the fungal feeders.

The proportion of *c-p* 1 families was higher, whereas the proportion of the *c-p* 3-5 families was lower in the banana plantations compared with the banana-palmito site (Fig. 4). The assemblage of the different *c-p* groups differed significantly (χ^2-test, $P < 0.05$) between banana site B1 and all banana-palmito sites and between B3 and BP1.

The eigenvalues of the first two PCA ordination axes were 0.24 and 0.16, cumulatively explaining together 39.3% of the total variance in family composition between the sites. In general, the five individual samples per site (*e.g.*, site points B1-1 to B1-5) were ordinated closely together, indicating that differences in the composition of the nematode communities of the different samples within one site were small, which means that there is a site-specific assemblage. Furthermore, the site points B1 and B3 (banana) and BP1 and BP3 (banana-palmito), respectively, were ordinated close to each other (Fig. 5). The composition of family at these sites of the respective system is similar. On the other hand, the site points of B2 (banana) and BP2 (banana-palmito) are clearly situated apart from their corresponding sites, indicating that the composition of their nematode assemblages is different from their respective sites. However, B2 and BP2 are also on the left side of the diagram as are BP1 and BP3, meaning that the nematode communities of the banana sites B1 and B3, which are the only site points on the right side of the diagram, are clearly distinct from all others. According to ANOSIM, using the Bray-Curtis similarity matrix, the dissimilarities between the two agroecosystems with regard to the nematode communities are statistically significant ($P = 0.001$).

The families presented in the diagram have a fit of >30%, thus lying far away from the centre of the diagram and are important for indicating sample differences. The bacterivore family Rhabditidae and the fungivore family Aphelenchoidiae, with low *c-p* values of 1 and 2, re-

Table 2. *Mean relative abundance (%) of nematode families in two different agroecosystems.*

Family	*c-p*	Banana								Banana-palmito							
		B1		B2		B3		Overall		BP1		BP2		BP3		Overall	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Algal feeders																	
Achromadoridae	3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6	1.4	0.2	0.4	2.2	1.7	1.0	1.0
Bacterial feeders																	
Alaimidae	4	0.2	0.4	1.0	0.7	0.2	0.4	0.5	0.5	3.5	2.3	1.0	1.4	1.4	1.5	2.0	1.4
Aulolaimidae	3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.5	1.0	1.7	0.5	0.5
Cephalobidae	2	2.4	2.5	2.8	1.9	1.2	0.8	2.1	0.8	4.0	3.6	1.2	1.3	3.2	2.5	2.8	1.5
Diplogastridae	1	0.0	0.0	0.6	1.3	0.0	0.0	0.2	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Halaphanolaimidae	3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.8	1.1	0.3	0.5
Onchulidae	3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.4	0.2	0.4	1.2	0.5	0.5	0.6
Panagrolaimidae	1	0.4	0.5	2.8	0.8	0.4	0.9	1.2	1.4	0.5	0.7	3.2	2.9	1.2	0.8	1.6	1.4
Plectidae	2	0.0	0.0	0.6	0.5	0.2	0.4	0.3	0.3	2.0	3.2	0.2	0.4	0.6	0.9	0.9	1.0
Prismatolaimidae	3	2.2	2.8	0.0	0.0	0.4	0.5	0.9	1.2	0.6	0.9	0.0	0.0	1.0	1.2	0.5	0.5
Rhabditidae	1	35.1	34.4	22.8	18.0	24.8	20.6	27.6	6.6	7.3	8.0	11.0	14.4	16.9	18.0	11.7	4.9
Teratocephalidae	3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.7	0.2	0.4	0.0	0.0	0.2	0.3
Hyphal feeders																	
Anguinidae	2	0.0	0.0	0.0	0.0	0.2	0.4	0.1	0.1	0.0	0.0	3.1	6.9	0.0	0.0	1.0	1.8
Aphelenchidae	2	0.0	0.0	0.0	0.0	0.6	0.9	0.2	0.3	0.0	0.0	0.0	0.0	0.2	0.4	0.1	0.1
Aphelenchoididae	2	15.6	13.8	0.2	0.4	6.4	5.0	7.4	7.7	1.1	1.2	0.4	0.5	0.2	0.4	0.6	0.5
Diphtherophoridae	3	0.4	0.5	0.0	0.0	0.2	0.4	0.2	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Leptonchidae	4	0.0	0.0	8.0	5.1	0.2	0.4	2.7	4.6	24.8	15.8	4.7	2.9	4.8	2.7	11.4	11.6

Table 2. *(Continued.)*

Family	*c-p*	Banana								Banana-palmito							
		B1		B2		B3		Overall		BP1		BP2		BP3		Overall	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Omnivores																	
Aporcelaimidae	4	13.0	6.0	3.6	2.5	7.0	3.5	7.9	4.7	11.7	7.0	8.6	5.1	19.9	9.6	13.4	5.8
Belondiridae	5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6	1.3	0.0	0.0	0.0	0.0	0.2	0.3
Nordiidae	4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.2	2.2	0.4	0.7
Qudsianematidae	4	1.0	1.2	0.6	0.9	1.4	0.9	1.0	0.4	4.7	7.8	0.4	0.5	3.4	3.1	2.8	2.2
Thornenematidae	5	1.4	1.3	15.2	7.3	3.0	2.2	6.5	7.6	3.9	2.2	0.8	1.3	3.6	2.6	2.8	1.7
Plant feeders																	
Criconematidae	3	0.8	1.8	3.6	8.0	1.6	1.8	2.0	1.4	0.3	0.6	12.4	17.4	0.2	0.4	4.3	7.0
Hoplolaimidae	3	19.0	13.5	24.1	16.5	41.9	17.0	28.3	12.0	10.6	10.0	36.0	24.4	16.3	11.5	21.0	13.3
Longidoridae	5	5.8	8.4	0.0	0.0	1.4	2.1	2.4	3.0	8.7	7.6	0.2	0.4	7.6	4.3	5.5	4.6
Paratylenchidae	2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.4	0.0	0.0	0.0	0.0	0.1	0.1
Pratylenchidae	3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.5	0.0	0.0	0.1	0.2
Predators																	
Actinolaimidae	5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.4	0.1	0.1
Anatonchidae	4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.6	2.2	0.0	0.0	0.5	0.9
Discolaimidae	5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.5	0.1	0.2
Mononchidae	4	0.6	0.5	3.2	2.8	2.6	2.4	2.1	1.4	7.6	7.1	5.0	5.2	4.6	3.7	5.7	1.6
Nygolaimidae	5	0.0	0.0	0.0	0.0	0.4	0.5	0.1	0.2	0.0	0.0	0.0	0.0	0.2	0.4	0.1	0.1
Tobrilidae	3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.4	0.1	0.1
Tripylidae	3	1.2	2.2	0.6	1.3	0.0	0.0	0.6	0.6	0.0	0.0	0.2	0.4	0.4	0.9	0.2	0.2
Epidermal and root hair feeders																	
Tylenchidae	2	1.0	1.7	10.2	3.1	6.0	3.7	5.7	4.6	6.6	6.1	8.7	6.9	7.3	5.8	7.6	1.1

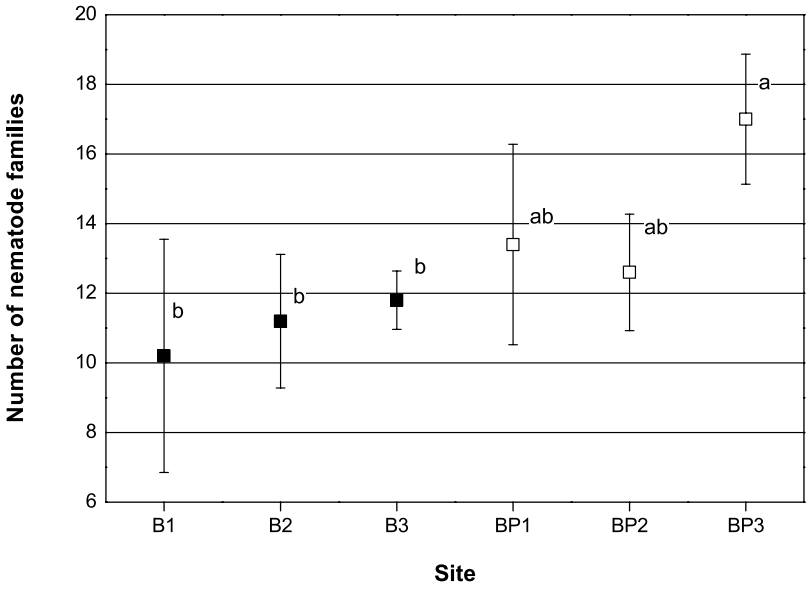

Fig. 2. *Mean (± s.d.,* n = *5) number of nematode families in the soil of three banana (B) and three banana-palmito (BP) plantations. Data with different letters are significantly different according to Bonferroni test at* P = *0.006 to 0.02.*

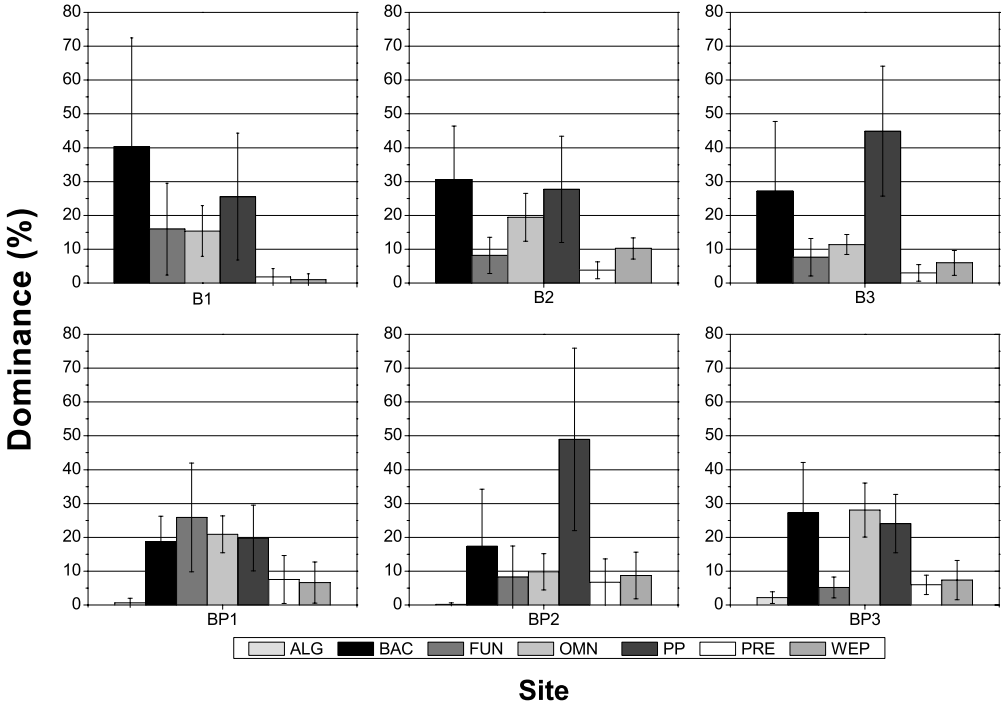

Fig. 3. *Mean (± s.d.,* n = *5) trophic structure of the nematode communities in the soil of banana and banana-palmito plantations. ALG = algivores, BAC = bacterivores, FUN = fungivores, OMN = omnivores, PP = plant parasites, WEP = epidermal and root hair feeders, PRE = predators.*

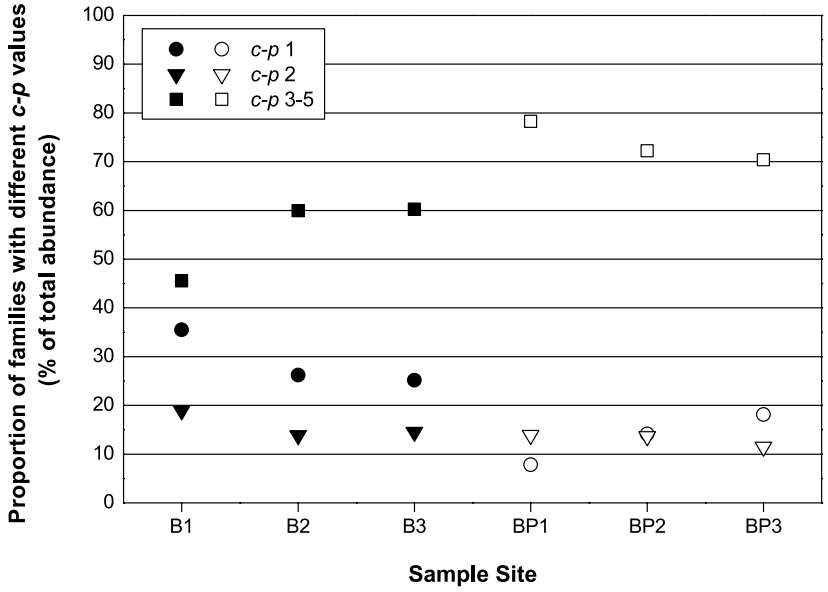

Fig. 4. *Percentage part of total nematode abundance of families with* c-p *1,* c-p *2 and* c-p *3-5 values (mean of five samples) in the soil of three banana (B) and three banana-palmito (BP) plantations, and the resulting respective means ± s.d.*

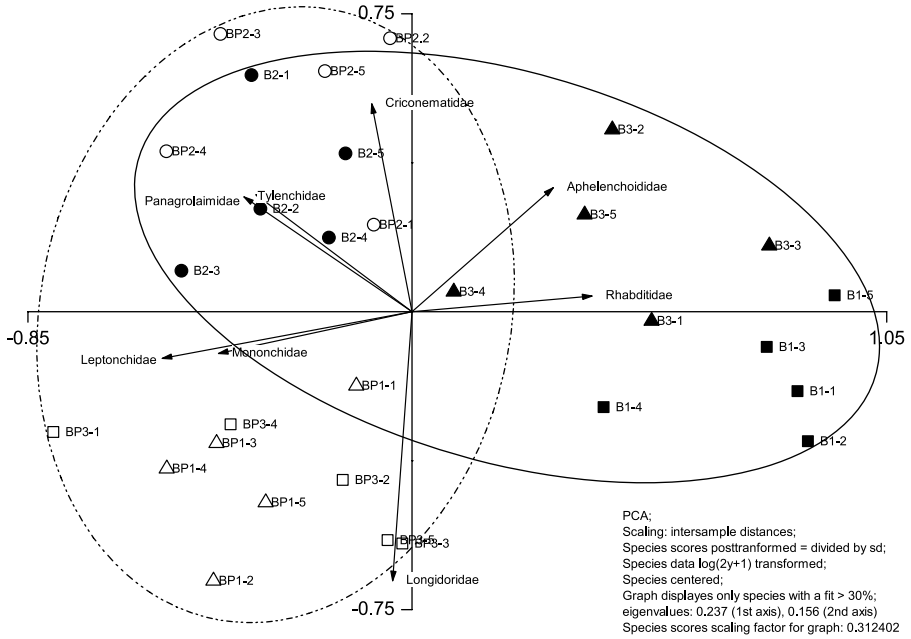

Fig. 5. *PCA (principal component analysis) ordination diagram of nematode families and samples (biplot) in the three sites of each system (B1-1 = banana site 1-plot 1; B1-2 = banana site 1-plot 2,* etc.*).*

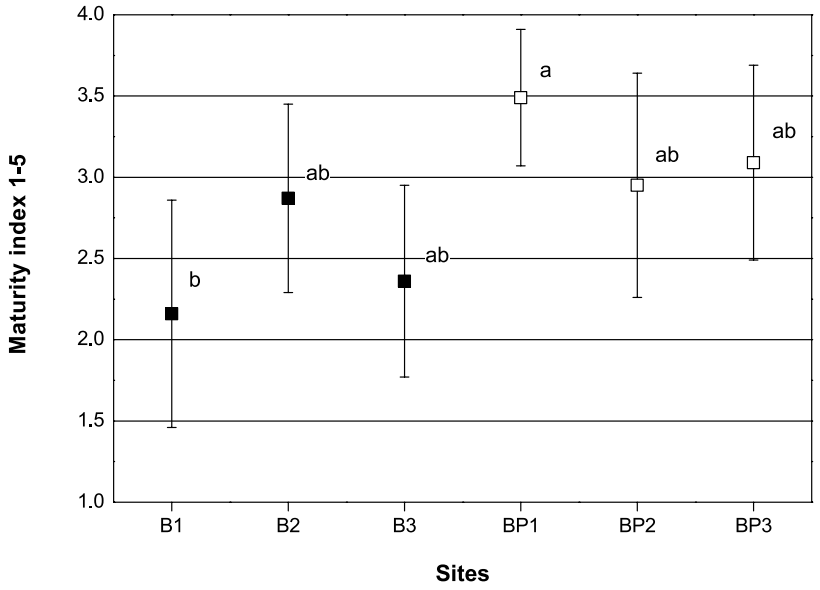

Fig. 6. *Mean (± s.d.,* n = *5) Maturity Index 1-5 for the nematode community of the soil of three banana (B) and three banana-palmito (BP) plantations. Data with different letters are significantly different according to Bonferroni test at* P = *0.03.*

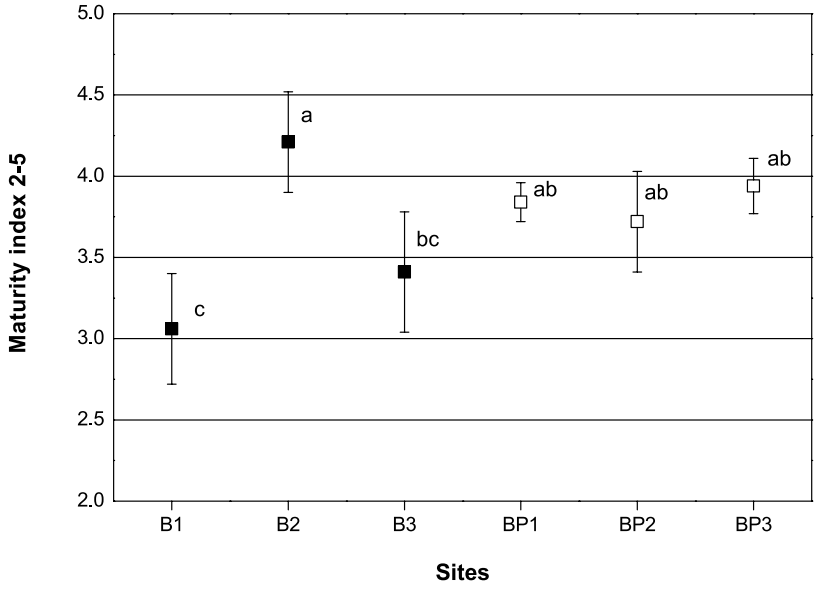

Fig. 7. *Mean (± s.d.,* n = *5) Maturity Index 2-5 for the nematode community of the soil of three banana (B) and three banana-palmito (BP) plantations. Data with different letters are significantly different according to Bonferroni test at* P = *0.00002 to 0.02.*

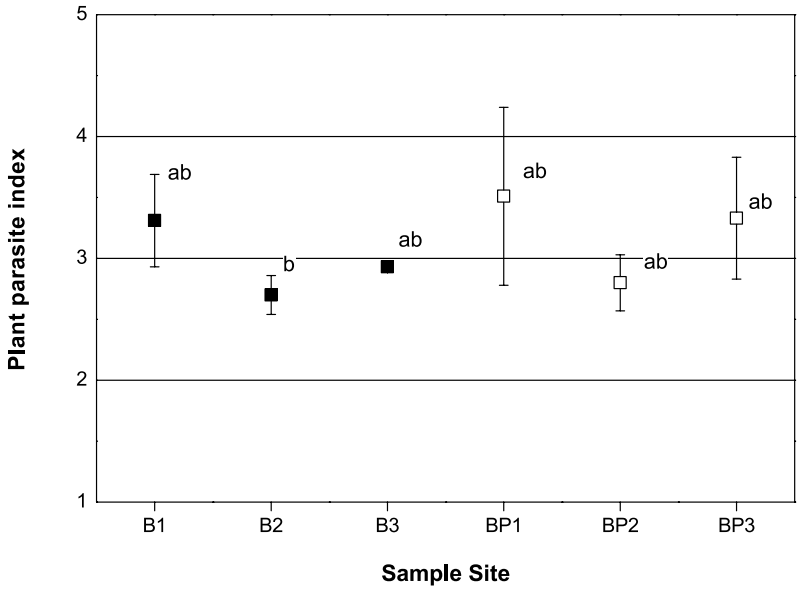

Fig. 8. *Mean (± s.d.,* n = *5) Plant Parasite Index for the nematode community of the soil of three banana (B) and three banana-palmito (BP) plantations. Data with different letters are significantly different according to Bonferroni test at* P = *0.03.*

spectively, are most important for B1 and B3, whereas the fungivore family Leptonchidae, the predatory family Mononchidae and the plant parasite family Longidoridae, all with high *c-p* values of 4 and 5, respectively, are most important for BP1 and BP3. For B2 and BP2 the bacterivore family Panagrolaimidae (*c-p* 1) together with the plant parasite families Criconematidae (*c-p* 3) and Tylenchidae (*c-p* 2) are most important.

The mean nematode maturity index 1-5 in the banana stands (2.16 ± 0.70 to 2.87 ± 0.6) was significantly below that of the banana-palmito plantations (2.95 ± 0.69 to 3.49 ± 0.42) (ANOVA, $F_{5,24} = 3.23$, $P < 0.05$) (Fig. 6). The Bonferroni test revealed a significant difference between the banana site B1 and the banana-palmito site BP1 ($P = 0.03$).

The mean MI 2-5 was 3.06 ± 0.34 to 4.21 ± 0.31 in the banana and 3.72 ± 0.31 to 3.94 ± 0.17 in the banana-palmito plantations (ANOVA, $F_{5,24} = 10.22$, $P < 0.0001$) (Fig. 7). The Bonferroni test revealed a significant difference between the banana site B1 (3.06) and all banana-palmito sites ($P = 0.0008$-0.02). Additionally, banana site B2 (4.21) differed significantly from the two other banana sites ($P = 0.00002$ and $P = 0.003$), indicating a high intra site variation in the banana sites. The mean PPI was 2.89 ± 0.31 and 3.21 ± 0.37 in the banana and the banana-palmito plantations, respectively (ANOVA, $F_{5,24} = 3.27$, $P < 0.05$) (Fig. 8). The Bonferroni test revealed a significant difference between the banana sites B1 and B2 ($P = 0.03$). The mean ratio of fungal feeders/bacterial feeders was higher at the banana-palmito plantation and the mean ratio of sum fungal feeders + bacterial feeders/plant feeders was higher at the banana plantation. However, there were no significant differences between the sites.

Discussion

According to Bongers (1990), a decrease in nematode maturity is correlated with an increase in nematode density under eutrophic conditions. Furthermore, Pattison *et al.* (2004) and Huang and Cares (2006) stated that nutrient-enriched soils show a reduced biodiversity and a higher degree of soil disturbance. The observed nematode abundance was more than two times higher at the banana-monocultures than at the banana-palmito plantations, with significant differences between all banana sites and BP1 and between B1 and BP3. At the same time the number of families (significantly between all banana sites and BP3) and the MI (significantly between B1 and BP1) were clearly lower. The differences in nematode assemblages observed between the two systems studied may indicate a higher degree of disturbance and more eutrophic conditions in the monocultures. Under such conditions the population of short-lived r-strategists (bacterial-

feeding Rhabditidae, Panagrolaimidae and Diplogastridae) increase relative to other nematode groups (Ferris & Matute, 2003). The higher portion of colonisers (Rhabditidae) at the banana plantations indicates resource enhancement as these enrichment opportunists reproduce explosively when microbial activity is high (Bongers & Bongers, 1998; Bongers, 1999).

As a result of the high number of Rhabditidae the mean percentage of the *c-p* 1 taxa was more than twice as high at the banana plantations compared to the banana-palmito cultures, causing a significant difference in the assemblage of *c-p* groups between B1 and all BP sites and between B3 and BP1. On the other hand, *c-p* 1 taxa, which indicate nutrient enrichment when dominant, are only the second most dominant at the banana plantations as well as at the banana-palmito agroecosystems. At both sites the *c-p* 3-5 taxa were dominant with 55% (banana) and 73% (banana-palmito), respectively. Bongers and Bongers (1998) stated that the presence of *c-p* 3, 4 and 5 taxa indicate low disturbance and a more advanced successional stage.

At all banana-palmito plantations secondary trees and a high understorey were present (Heine, 2007), while only a few additional trees were observed at all banana monocultures. High understorey and a thick litter layer (dead banana leaves were added) with a lot deadfall trees was present at B2. At B3 additional vegetables were planted, but litter was removed and soil was raked and regularly fertilised by goat dung. The high rate of shading by trees, a high understorey and ground coverage by additional plants may be the reason for the high percentage of *c-p* 3-5 taxa, especially at the banana-palmito plantations. In other words, these sites were in an anthropogenically-enhanced more advanced successional stage than the banana-monocultures. In this context it has to be mentioned that B1 (assemblage of *c-p* groups significantly different from all BP sites), the only site without any additional plantings and compared to all other sites with the highest phosphorus value in soil (see Table 1), showed the lowest portion of *c-p* 3-5 taxa and the highest portion of *c-p* 1 taxa. This result is supported by the MI 1-5 value, a measure for stability, functioning and eutrophication of a soil ecosystem. The MI 1-5 values determined for the banana (2.46) and the banana-palmito plantations (3.17), and the respective differences (significantly lower at B1 compared to BP1) between the sites, also reflected a higher degree of succession at the banana-palmito sites. According to Bongers and Bongers (1998) values around 4 are reached under undisturbed conditions and values < 2 in disturbed situations (Bongers & Ferris, 1999). The MI 1-5 value determined for the site B2, the banana site with the highest degree of additional vegetation and the lowest degree of disturbance, was clearly higher (2.87) than at the other two banana-monocultures B1 and B3. The MI 2-5, an indicator for environmental pollution (Korthals *et al.*, 1996a; Bongers & Bongers, 1998) differed significantly between B1, the only site without additional plantings, and all banana-palmito sites. Furthermore, a significantly higher MI 2-5 was determined at B2 compared with B1 and B3, reflecting also a lower degree of disturbance at B2 and indicating the presence of an environmental stressor at B1 and B3. The significantly lower PPI at B2 compared with B1 is also an indication of a greater extent of eutrophication at B1 (highest phosphorus value determined), since an increase of primary production of higher plants as a result of fertilisation caused an increase of the PPI. However, in general, the number of plant-parasitic nematodes was relatively low at both systems compared to more intensively used agroecosystems (Huang & Cares, 2006). The differences between the sites in the trophic structure of the nematode communities, with lower portions of fungivores, omnivores and predators at the banana monocultures, also indicate organic enrichment that caused increased microbial activity. Furthermore, the lower number of omnivores at the banana monocultures could be caused by the high sensitivity of this group, since they are known to be most sensitive to environmental stressors (Korthals *et al.*, 1996b; Parmelee *et al.*, 1997), thus being considered as indicators of ecosystem disturbances (Thomas, 1978). In addition, Pattison *et al.* (2004) found that the abundance of omnivores is negatively correlated with total N in the soil, which cannot be confirmed by the present results. The lower F/B ratio at the banana monocultures also indicates a higher microbial activity with a higher degradation rate at these sites compared with the mixed plantations (Twinn, 1974) and the higher $(F + B)$/plant feeders ratio at the banana sites indicates younger soils and stronger plant growth (McSorley & Frederick, 1996). In addition, litter quality and host plant biomass may play a role in this context, but no data of these factors have been measured at the study sites.

Similarities and dissimilarities between the family structures of the assemblage of the investigated sites as determined by PCA can also be attributed to their respective characteristics. The banana monocultures B1 and B3, with clearly distinct nematode communities from all other sites, are the sites with the lowest ground cover and the

lowest amount of litter. B1, the site where points were separated most from the other sites, was the only monoculture without any additional vegetable crops and trees or shrubs due to yearly removal, as well as the highest value of phosphorus in soil. B3 was an open banana system with additional annual crops but litter was removed regularly and no shady trees are present. At these two sites the enrichment opportunistic Rhabditidae (*c-p* 1) and the general opportunistic Aphelenchoididae (*c-p* 2) contributed most to the calculation of the site points. By contrast with B1 and B3, B2 was left fallow for several years with understorey and incorporated banana litter material At this site, and also at BP2, not only the enrichment opportunists Panagrolaimidae (*c-p* 1) and the general opportunists Tylenchidae (*c-p* 2), but also the persisters Criconematidae (*c-p* 3) were most important. All three banana-palmito stands contained additional trees, part understorey and a litter layer. The heterogeneity of site BP2 and the homogeneity of the two other banana-palmito sites (BP1 and BP3) might explain the dissimilarities and similarities, respectively, between these sites. At the two latter sites the persister families Leptonchidae (*c-p* 4), Longidoridae (*c-p* 5) and Mononchidae (*c-p* 4) were most important for the calculation of the site points. It has to be mentioned that the percentage of omnivores was similar (and highest) at the two banana-palmito sites with the highest similarity (BP1 (28.1%) and BP3 (20.9%)). Equal observations were made at the two banana sites with the highest similarity.

Differences in nematode populations between the systems and between the sites can be attributed to a different degree of soil disturbance. The banana monocultures B1 and B3 were found to be most different from the banana-palmito sites and also from the banana site B2. It can be summarised that at these sites, in particular at B1, soil disturbance and eutrophication was highest. However, a low number of plant-parasitic nematodes and dominance of cp-3 taxa at both agro-ecosystems show that the soil of both agroecosystems seems to be of advanced successional stage (Ettema & Bongers, 1993; Korthals *et al.*, 1996; Bongers & Ferris, 1999). This may be a result of a less intensive 'organic' cultivation without the use of plant protection products and fertilisers and with additional non-host plants. This method of cultivation usually improves soil fertility and reduces the susceptibility to plant parasites (Sarah, 1989). Despite many non-controlled variables in the smallholder systems, according to the results the nematodes can be regarded as suitable indicators of soil disturbance in banana and banana-palmito agroecosystems.

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