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Original article

Long-term effect of a legume cover crop (*Mucuna pruriens* var. *utilis*) on the communities of soil macrofauna and nematofauna, under maize cultivation, in southern Benin

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Abstract

In southern Benin like in other tropical areas, natural fallows, which were traditionally used in order to improve soil fertility, are no longer possible in a context of high population pressure. Many studies have underlined the advantages of legume cover crops to ensure the sustainability of plant productivity: increase in soil organic matter content, increase in crop yields, improvement of the water regime of soils, and decrease in runoff and erosion. Nevertheless the mechanisms responsible for these modifications are not completely understood. The characterisation of biological activity and diversity in a soil can help in understanding the dynamics of soil structure and the flux of nutrients. For this purpose, the density, diversity and functional composition of soil nematodes and soil macroinvertebrates were measured in different treatments under maize cultivation. The three treatments were: (1) a pure traditional maize crop without any fertilisation (T); (2) a maize crop with a mineral fertiliser (NPK); and (3) a maize crop inter-cropped with *Mucuna pruriens* var. *utilis* (M). Soil in plot M presented different biological properties when compared with T and NPK: higher macrofauna density (especially termites, earthworms, millipedes, centipedes) and biomass (especially earthworms and termites), higher density of facultative phytophagous, bacterial-feeding and predatory nematodes, and lower density of obligatory phytophagous (*Criconemella*, *Scutellonema* and *Meloidogyne*) nematodes. The modification of the composition and activity of soil biota under *Mucuna* might partly explain the potential of *Mucuna* for soil restoration.

Keywords: Cover crop; Soil biodiversity; Nematodes; Soil macrofauna; Soil biofunctioning

1. Introduction

In southern Benin where the density of the human population is as high as 400 inhabitants per km^2, agricultural pressure on soil is very high and soil fertility is seriously depleted. Moreover, this population pressure induces a reduction in the duration of natural fallows traditionally used to restore soil fertility [3,24]. In order to replace natural fallows, different techniques have been tested to ensure the sustainability of plant productivity of rainfed crops (maize, beans, cassava, and peanuts). Legume cover crops seem a good way to restore and/or to conserve soil fertility by controlling weeds and erosion and by enhancing carbon and nitrogen stocks in soil [4,6,12,13,26].

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In 1988, an experiment was set out in southern Benin to study the effect of the association of the legume cover crop *Mucuna pruriens* var. *utilis* with maize on plant productivity, soil fertility, erosion and soil organic carbon dynamics (Table 1) [3,5,6]. Previous results have revealed that the association of *Mucuna* with maize induced a decrease in runoff and erosion, an increase in soil organic matter content and in the production of maize grains, and an improvement of the water regime of soils [4,6]. However, the mechanisms responsible for these modifications are not fully understood. Positive (direct or indirect) effects of *Mucuna* on microbes and soil fauna activity could partly explain the observed modifications in soil physical and chemical properties. Indeed, most of the studies evaluating the potential of *Mucuna* for soil restoration have mostly considered changes in soil physical properties and plant yield [2]; but no studies have been done on the biologically mediated processes occurring with this legume cover crop.

This present paper aims at investigating the effect of the presence of a legume cover crop in a maize crop on soil macrofauna and soil nematofauna using the same experiment that was studied by Azontonde [2] and Barthès et al. [6]. Macrofauna and nematodes are often seen as indicators of soil quality and plant productivity as they integrate most of physical, chemical and biological soil properties, which determine soil functions, and offer information at different scales [9, 17,19,30]. Soil macrofauna comminute and redistribute organic debris, thereby increasing microbial activity, and improve soil structure [15,18,19,23,33]. Through their feeding activity nematodes control bacterial and fungal communities, thereby enhancing organic matter decomposition and nutrient availability; they also affect plant pathogens and plant diseases [11,22,27,36]. We address the question of the difference between taxonomic and functional groups of soil macrofauna and nematofauna in maize crops with or without legume cover crop. We hypothesize that the presence of a legume cover crop would support higher density, biomass and diversity of macrofauna and nematofauna than conventional maize crops.

2. Materials and methods

2.1. Site and soil characteristics

The experiment was located in the southern part of Benin at Agonkanmey near the town of Cotonou (6°24′N, 2°20′E, elevation 20 m above sea level). This area is characterised by a sudano-guinean climate with two dry seasons (November–March and July–August) and two wet seasons (March–July and September–November). The mean annual rainfall is about 1200 mm, and the mean daily temperature is ca. 27 °C throughout the year. The soils are classified as slightly desaturated impoverished ferrallitic soils developed on a clayey-sandy sedimentary material [37]. They are also classified as Typic Tropudults (USDA) or Dystric Nitosols (FAO) and are locally called "Terres de Barre". The pH (1:2.5 soil/water suspension) ranges from 5.0 to 5.5 across the area. The soil has a sandy loam surface layer overlying a sandy clay loam layer at a depth of about 50 cm.

2.2. Experimental design

The experiment has been described in detail by Azontonde [2] and Barthès et al. [5,6]. It was set up in 1988 in order to test soil conservation and rehabilitation techniques in maize cropping systems including the

Table 1
Effect of the utilisation of mineral fertiliser or introduction of *Mucuna* in maize crops on grain yield and some litter and soil parameters in our experiment in south Benin

	Treatment T	Treatment NPK	Treatment M	Reference
Maize grain yield				
(kg ha^{-1}) (1988)	500	500	500	[3]
(kg ha^{-1}) (1996)	200	2500	3500	
Residue biomass (dry matter)				
(Mg ha^{-1} per year)	7.99 ± 1.85	13.0 ± 0.98	19.94 ± 0.33	[6]
(Mg C ha^{-1} per year)	3.48 ± 0.74	6.37 ± 0.41	10.02 ± 0.28	
N input (including fertiliser, dust, rain, N-fixation) (kg ha^{-1} per year)	11	90	389	[3]
Total soil C content (0–10 cm) (g kg^{-1} soil)	5.3 + 0.1	6.7 ± 1.8	11.5 ± 2.0	[6]
Soil C stock (0–40 cm) (1999) (Mg C ha^{-1})	24.2 ± 0.5	28.8 ± 5.7	41.4 ± 4.9	[6]
Macroaggregates (%) (1999) (coarse sand corrected)	42.3 a	59.2 b	68.7 c	[5]
Annual soil losses (1998) (Mg ha^{-1} per year)	34.0	9.3	2.9	[5]

T: traditional maize crop; NPK: maize crop with mineral fertiliser; M: maize crop intercropped with *Mucuna*. * Numbers of the same row followed by different letters are significantly different ($P < 0.05$).

introduction of *Mucuna* [2] and consisted of three plots (30 × 8 m, slope 4%). It lasted up to 1999 when our study was conducted. Plot replication and randomisation was not achieved in this trial, as it is usually not done for long-duration trials [5,29], especially when they include runoff plots, as it was the case in our experiment. Three treatments were compared:

- Treatment T (control): this traditional pure maize (*Zea mays* var. DMR) crop was characterised by the absence of fertilisers and cover plants;
- Treatment NPK: a pure maize system with a mineral fertiliser (NPK, 15–15–15) used every year at a rate of 200 kg ha^{-1} with 100 kg ha^{-1} urea, which represents an annual input of 75 kg N ha^{-1}, 30 kg P_2O_5 ha^{-1} and 30 kg K_2O ha^{-1};
- and Treatment M: maize and *M. pruriens* var. *utilis* were inter-cropped every year, without fertiliser.

Maize was always cropped during the first rainy season, with manual superficial hoe cultivation. In treatment M, *Mucuna* was sown 1 month after maize and constituted a relay-crop after maize harvesting. During the second rainy season, a natural fallow covered treatments T and NPK.

In 1988, at the beginning of the experiment, there was no or only slight differences between plots for topsoil clay content, pH, soil organic carbon SOC content, C to N ratio [6]. In 1999, strong differences were measured between plots and linked to the management of maize crops [6].

2.3. Sampling of soil macrofauna and nematodes

Soil fauna was sampled in November 1999, at the end of the rainy season.

For soil macrofauna, six soil monoliths (2 5 × 2 5 × 30 cm) were excavated from each plot (two in the upper part of plots, two in the middle, and two in the lower part of plots) after sampling litter layer and digging a trench around each monolith (modified TSBF method [1]). Monoliths were cut into three horizontal layers (0–10, 10–20 and 20–30 cm), and visible soil invertebrates were hand-sorted before being placed in a mixture of alcohol/formalin. In the laboratory, invertebrates were identified at order/family level and then counted and weighed. Density (ind m^{-2}) and biomass (g m^{-2}) were calculated.

For the nematofauna, three samples (each made of five subsamples) (upper, middle and lower part of each plot) were collected with a shovel from the upper 10 cm of soil; likewise three samples (each made of three subsamples) were taken from the 10–20 to 20–30 cm depth strata. Twenty-seven bulked samples, carefully hand-mixed, were obtained in total. Nematodes were extracted from 250 cm^3 of soil using the Seinhorst elutriation method [28], counted, fixed with formalin, transferred to glycerin and subsequently mounted in bulk on glass slides. From each sample, a mean of 190 nematodes was identified under a microscope at 400×, to family or genus level. Nematode taxa were assigned to trophic groups following Yeates et al. [38] and then allocated to cp-classes following Bongers [9]. Nematodes that could not be assigned to a trophic group with certainty were classified in the group of the taxon having the most similar morphological feeding structure. Different indices relative to the nematofauna were calculated. The ratio fungal feeding nematodes/bacterial feeding nematode (F/B) was calculated as well as the Maturity Index (MI), according to Bongers [9].

2.4. Statistical analyses

For nematofauna, differences between treatments were assessed by *U*-test of Mann–Whitney ($P < 0.05$) using the Statview software. The whole dataset (nematodes and macrofauna) was also subjected to a Principal Component Analysis (PCA) with the ADE-4 software [31]. In order to make possible the joint analysis of macrofauna and nematodes densities, densities obtained from the upper, middle and lower parts of each plot (M1, M2, M3, respectively, for M plot; N1, N2, N3, respectively, for NPK plot; T1, T2, T3, respectively, for T plot) were used. As a consequence, the mean for two macrofauna samples was calculated. A permutation test ($N = 1000$) was used to discriminate between treatments.

3. Results

3.1. Soil macrofauna

A total number of 5648 individuals were hand-sorted from the monoliths of the three plots: 1281, 1413 and 2954, respectively, in T, NPK and M. Thus, mean densities were equal to 3423, 3765 and 7887 ind m^{-2}, respectively, in T, NPK and M (Table 2). In all plots, termites were the most abundant invertebrates in soil (from 70% of the mean density in NPK to 86% in M). Ants were the second group in abundance (2.5% of density in M, 16% in NPK and 17% in T). Earthworms were relatively abundant with a mean density of 121 (3%), 360 (10%) and 579 (7%) ind m^{-2}, respec-

tively, in T, NPK and M. Each other taxonomic group represented less than 1% of mean density.

In T and M, there was a decrease in the mean density from the upper layer (0–10 cm) down to the deeper layer (20–30 cm) whereas in NPK, the invertebrates were more abundant in the 10–20 cm layer (Fig. 1). Only a few animals were collected from the upper layer in plot NPK. This result was mainly due to the fact that most termites and ants were found in the 10–20 cm layer in NPK whereas they were found mainly in the 0–10 cm in the other two plots.

Mean biomass was measured as 10.1, 22.1 and 40.6 g m^{-2}, respectively, in T, NPK and M (Table 2). Termites and earthworms were the main groups. Termite contribution to biomass ranged from 31% (in NPK) to 39% (in T). Earthworm biomasses were relatively high: 3.8 g m^{-2} (38%) in T, 10.5 g m^{-2} (48%) in NPK, and 20.7 g m^{-2} (51%) in M. Ant contribution to biomass was relatively high in T and NPK (12% and 11%, respectively) and very low in M (less than 1%). The last group with contribution to biomass higher than 3% was that of the Coleoptera larvae (4%, 7% and 5%, respectively, in T, NPK and M). Each other taxonomic group represented less than 3% of mean biomass. As for density, most of biomass was observed in the 0–10 cm layer, except for termites and ants in NPK (Fig. 1).

3.2. Soil nematofauna

About 20,000 nematodes were extracted from soil samples, more than 5000 were identified under microscope. The mean nematode density was not significantly different between T, NPK and M; however in the 20–30 cm depth strata the nematode density in M was significantly higher than in T. Most nematodes occurred in the 0–10 cm layer (Fig. 2).

Whereas the dominant trophic group was plant feeder in T and NPK, the dominant and significantly more abundant group in M was bacterial feeding nematodes (Table 3). Facultative plant-feeding nematodes (Tylenchidae) were significantly more abundant in M than in T and NPK. Omnivorous and fungal-feeding nematodes were less abundant in NPK than in T and M. Absolute abundance of predators was significantly greater in M than in T. The fungal-feeders/bacterial-feeders ratio (F/B) was significantly lower in M (0.47) than in T (1.33) and was intermediate for NPK (0.56). No significant difference between the three treatments was measured for the MI (2.41, 2.46 and 2.61, respectively, in M, NPK and T).

The structure of the phytoparasitic nematode community was very different in the three treatments: in T, dominant plant feeders were *Scutellonema* and *Meloidogyne*; the dominant nematodes of NPK were *Pratylenchus*, *Helicotylenchus* and *Meloidogyne* whereas *Pratylenchus* was the most abundant plant-feeder in M (Table 3). *Scutellonema* which was very abundant in T was quite absent in NPK and M. The only plant-feeder nematode that was more abundant in M than in the two other treatments was the *Trichodorus* which was mainly represented in the 20–30 cm depth strata. The main differences for the fungal-feeding nematodes between treatments were the lower density of *Ditylenchus* in NPK than T and M, and the detection of Belondiridae only in T. Bacterial feeders were dominated in the three treatments by Cephalobidae. The density of this taxon was significantly higher in M (300.9 × 10^3 ind m^{-2} soil in the 0–30 cm depth strata) than in

Table 2
Mean density (ind m^{-2}) and biomass (g m^{-2}) of taxonomic groups of the soil macrofauna (0–30 cm) in different treatments

	Treatment T		Treatment NPK Plot NPK		Treatment M Plot M	
	Density	Biomass	Density	Biomass	Density	Biomass
Earthworms	121 ± 109	3.80 ± 3.63	360 ± 136	10.53 ± 6.12	579 ± 365	20.68 ± 15.16
Termites	2632 ± 5744	3.92 ± 7.82	2637 ± 3007	6.81 ± 8.81	6747 ± 9561	15.04 ± 21.45
Ants	597 ± 857	1.22 ± 1.49	605 ± 1220	2.37 ± 5.47	197 ± 285	0.36 ± 0.41
Millipedes	21 ± 31	0.34 ± 0.61	35 ± 31	0.45 ± 0.42	135 ± 75	1.15 ± 0.64
Centipedes	2.7 ± 6.5	0.02 ± 0.06	29 ± 31	0.10 ± 0.09	72 ± 34	0.44 ± 0.35
Coleoptera adults	8 ± 13	0.19 ± 0.44	8 ± 13	0.03 ± 0.06	19 ± 23	0.63 ± 0.85
Coleoptera larvae	5.3 ± 8.2	0.37 ± 0.68	29 ± 41	1.64 ± 3.02	29 ± 32	2.03 ± 4.56
Dermaptera	8 ± 19	0.08 ± 0.19	0	0	0	0
Hemiptera	8 ± 8.7	0.08 ± 0.11	5.3 ± 8.3	0.01 ± 0.01	8 ± 13	0.03 ± 0.05
Diptera	0	0	2.7 ± 6.5	0.01 ± 0.03	5.3 ± 13	0.01 ± 0.02
Isopoda	2.7 ± 6.5	0.01 ± 0.01	0	0	21 ± 45	0.02 ± 0.03
Diplura	16 ± 27	0.07 ± 0.14	43 ± 46	0.10 ± 0.13	69 ± 34	0.17 ± 0.12
Arachnida	0	0	8 ± 13	0.02 ± 0.04	5.3 ± 13	0.03 ± 0.07
Total	3423 ± 5656	10.08 ± 8.87	3765 ± 3401	22.05 ± 11.73	7887 ± 9410	40.59 ± 23.08

T: traditional maize crop; NPK: maize crop with mineral fertiliser; M: maize crop intercropped with *Mucuna* (mean ± standard deviation, $N = 6$).

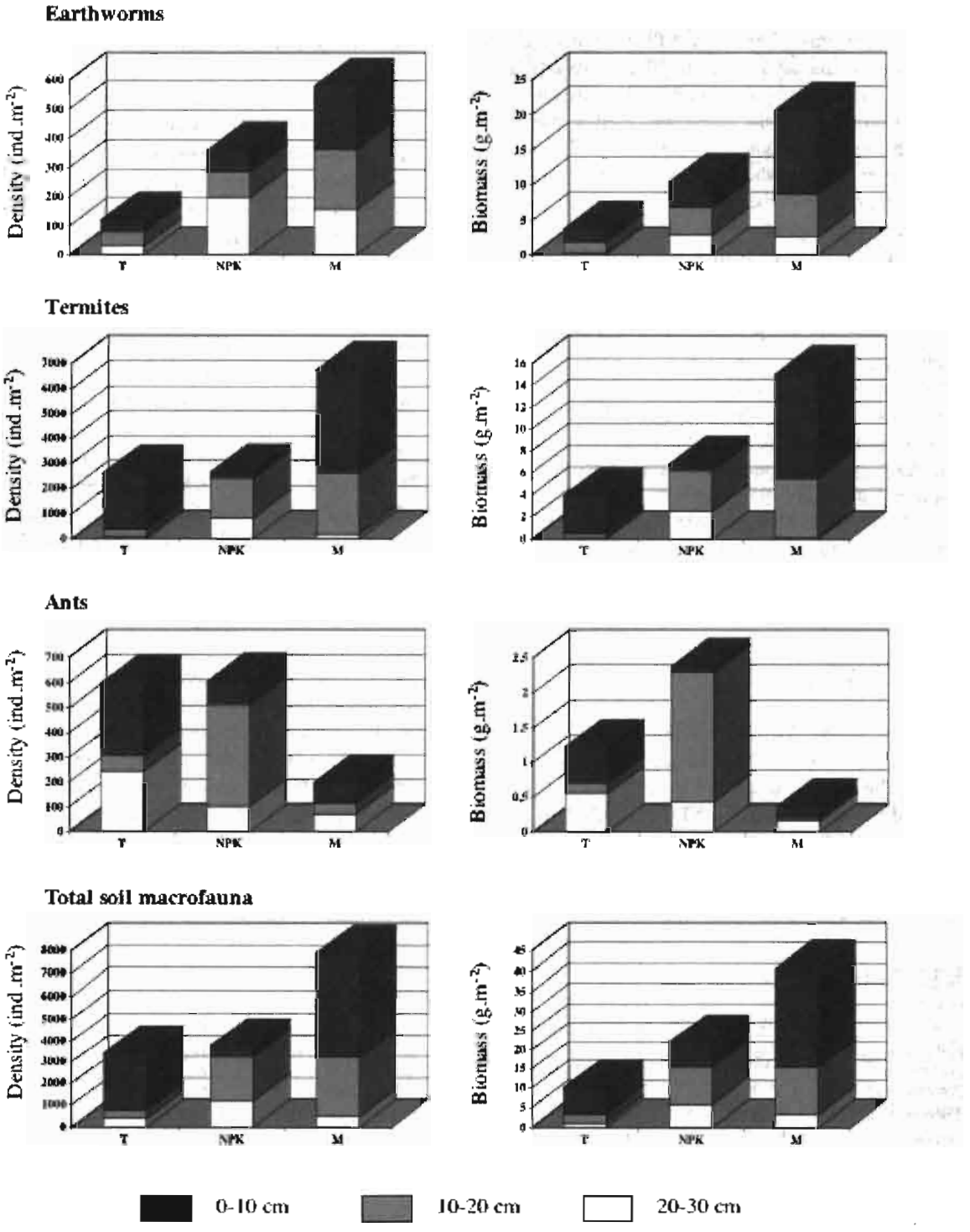

Fig. 1. Depth distribution of soil macrofauna (earthworms, termites, ants and total soil macrofauna) density and biomass in different maize cropping systems. T: pure maize cropping system; NPK: pure maize cropping system with mineral fertiliser; M: maize cropping system intercropped with *M. pruriens*.

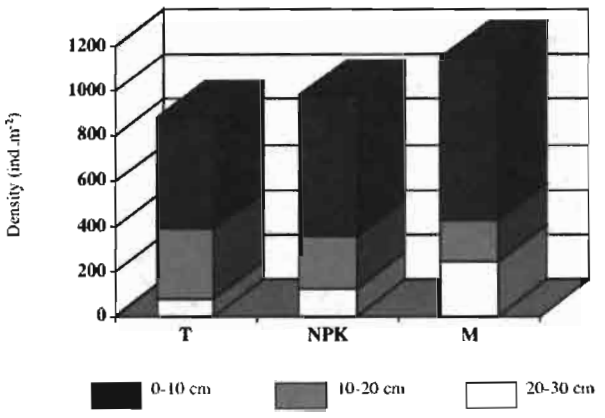

Fig. 2. Depth distribution of soil nematofauna density (10^3 ind m^{-2} soil) in different maize cropping systems. T: pure maize cropping system; NPK: pure maize cropping system with mineral fertiliser; M: maize cropping system intercropped with *M. pruriens*.

NPK (166.6 × 10^3 ind m^{-2} soil) and T (136.1 × 10^3 ind m^{-2} soil). Rhabditidae were also more abundant in M than NPK and T, in which these nematodes were undetected.

3.3. Multivariate analysis of macrofauna and nematofauna densities

PCA performed on the whole fauna dataset separated on the first axis (28% of total variance):

- plot M characterised by high densities of earthworms, isopods, Coleoptera, centipedes, millipedes, and facultative plant feeders;
- and plot T characterised by high densities of Dermaptera, ants and fungal feeder nematodes (Fig. 3). The permutation test was significant at $P < 0.07$ which means that composition of soil fauna discriminates treatments.

4. Discussion

Plot M presented a higher maize productivity and different soil properties if compared with T and NPK: higher C content, higher litter amount, higher nutrient availability, higher aggregate stability and less erosion (Table 1). Our study shows that soil fauna was also deeply affected by the introduction of *Mucuna* in maize crops.

Macrofauna density and biomass were two to four-fold higher in the plot with *Mucuna* than in plots without *Mucuna* (T and NPK). This underlines how sensitive the macrofauna community response is to the presence of a legume cover crop [20,23]. The introduction of *Mucuna* favoured the development of earthworms, millipedes, centipedes, Coleoptera adults, Diptera larvae and Isopoda and decreased the density of ants and Dermaptera. Our results confirm other studies showing that soil macrofauna is deeply affected by management and land-use changes [19]; this has been widely demonstrated for earthworms [15]. However only rare data are available for legume cover crop in the tropics. The modifications observed in our study may result from qualitative and quantitative changes in organic inputs, N availability, and a different soil microclimate [32]. The accumulation of organic matter in the *Mucuna* treatment (Table 1) may provide a resource base for soil macrofauna community and especially for "litter transformers" and "ecosystem engineers" (*sensu* Lavelle) [18,21]. There is well-documented literature showing macro-invertebrates are positively affected by organic matter content in cropping systems, and especially by leguminous residues [19,21]. The increase (five times more) in earthworm density and biomass may possibly favour the production of stable casts which play an important role in the improvement of soil water regimes, resistance to erosion and physical protection of organic matter [8,35]. This hypothesis is confirmed by a better aggregate stability and lower soil losses by erosion measured under *Mucuna* (Table 1).

Nematodes were also affected, with considerable modifications in the structure of communities. Under *Mucuna*, facultative plant feeders (Tylenchidae), bacterial feeders (mainly Rhabditidae and Cephalobidae) and predatory nematodes were favoured while obligatory plant feeders (mainly *Criconemella*, *Scutellonema* and *Meloidogyne*) were slightly reduced. The increased presence of bacterial-feeding nematodes and the decrease in F/B ratio under *Mucuna* (if compared to treatment T) may indicate that *Mucuna* promotes bacterial activity. This increase in bacterial activity may be explained by modifications of microclimate, organic inputs (both qualitatively and quantitatively) and by the size, composition and activity of the soil macrofauna community. This stimulation of soil microorganisms, principally bacteria, and grazing by nematodes may possibly result in a higher release of microbial N and, conceivably, efficiency of nutrient acquisition by plants [7,10,14, 16]. Moreover, the presence of *Mucuna* restricts the development of some phytophagous nematodes like *Meloidogyne*, which have deleterious effects on crops; this effect of *Mucuna* has already been observed [22,25, 27,34].

Table 3
Mean density (10^3 ind m^{-2} soil) and relative abundance (%) of nematode taxa and trophic groups (0–30 cm) in different treatments

	Treatment T	Treatment NPK	Treatment M
Plant feeders			
Pratylenchus	56.1 ± 41.4	127.0 ± 78.7	97.2 ± 55.6
Criconemella	12.5 ± 8.2	45.6 ± 31.4	12.1 ± 16.4
Xiphinema	9.7 ± 14.0	48.0 ± 9.5	35.6 ± 25.0
Scutellonema	116.6 ± 185.3	5.0 ± 2.9	1.6 ± 2.7
Helicotylenchus	1.5 ± 1.5	81.3 ± 86.7	32.2 ± 28.4
Meloidogyne	78.7 ± 121.6	76.5 ± 117.6	25.8 ± 15.3
Rotylenchulus	1.4 ± 2.4	0	1.4 ± 2.4
Trichodorus	7.3 ± 5.8	5.6 ± 6.6	51.6 ± 47.3
Total	284 ab	389 b	258 a
Percentage	32.2 ab	39.8 b	22.4 a
Facultative plant feeders			
Tylenchidae	44.6 ± 13.6 a	102.6 ± 28.3 a	160.9 ± 116.5 b
Percentage	5.1 a	10.5 ab	14.0 b
Fungal feeders			
Aphelenchina	84.3 ± 13.1	64.0 ± 44.9	53.7 ± 12.0
Anguinidae (*Ditylenchus*)	112.4 ± 53.1	56.7 ± 16.9	109.9 ± 31.7
Tylencholaimoidea	37.9 ± 21.9	18.5 ± 6.0	26.0 ± 6.6
Belondiridae	6.5 ± 1.1	0	0
Total	241 b	139 a	190 b
Percentage	27.3 a	14.3 a	16.5 a
Bacterial feeders			
Rhabditidae	0	1.8 ± 2.1	39.5 ± 26.5
Diplogasteridae	0.9 ± 1.6	0	1.4 ± 1.6
Panagrolaimidae	6.8 ± 8.3	37.4 ± 30.8	8.6 ± 8.1
Prismatolaimidae	16.8 ± 3.0	7.8 ± 2.7	10.7 ± 11.6
Rhabdolaimidae	2.3 ± 0.4	5.8 ± 3.7	7.1 ± 1.5
Alaimidae	4.8 ± 0.6	21.3 ± 15.9	17.0 ± 4.1
Plectidae	6.2 ± 5.5	1.8 ± 1.8	9.3 ± 8.9
Monhysteridae	4.1 ± 3.5	3.6 ± 1.0	4.0 ± 7.0
Leptolaimidae	3.1 ± 2.9	0.8 ± 0.7	1.6 ± 0.5
Cephalobidae	136.1 ± 91.3	166.6 ± 71.2	300.9 ± 96.4
Total	181 a	247 a	400 b
Percentage	20.5 a	25.3 b	34.8 b
Omnivorous			
Dorylaimoidea	97.9 ± 12.5 ab	59.4 ± 28.9 a	104.3 ± 99.2 b
Percentage	11.1 a	6.1 a	9.1 a
Predators			
Ironidae	1.0 ± 1.7	0	0
Discolaiminae	5.7 ± 7.7	5.8 ± 6.4	4.9 ± 5.0
Mononchidae and Anatonchidae	26.8 ± 19.4	33.3 ± 10.4	32.6 ± 25.1
Total	33 a	39 ab	37 b
Percentage	3.8 a	4.0 a	3.3 a
Total	*882.0 ± 240.6*	*976.0 ± 77.3*	*1150 ± 223.1*

T: traditional maize crop; NPK: maize crop with mineral fertiliser; M: maize crop intercropped with *Mucuna* (mean ± standard deviation, $N = 3$). Numbers of the same row followed by different letters are significantly different ($P < 0.05$).

5. Conclusion

Our study showed that the presence of *Mucuna* in a maize cropping system modified the structure, composition and diversity of soil biota and stimulated the development of organisms that can promote soil structure and nutrient availability. More research is needed to understand: (i) the reasons of these modifications even if different parameters can be proposed: quality and quantity of organic matter, N availability, and microclimate, and (ii) the effect of a specific fauna community under *Mucuna* on maize productivity. These results also confirm the idea that soil animals should be considered for inclusion in indices of soil quality through their positive contribution to soil processes [39]. Secondly a better use of resource biota (sensu Swift and Anderson [30]), i.e. cover plant and decomposer organisms, may increase the functional properties of ecosystems and allow a better agricultural ecosystem productivity and sustainability [7].

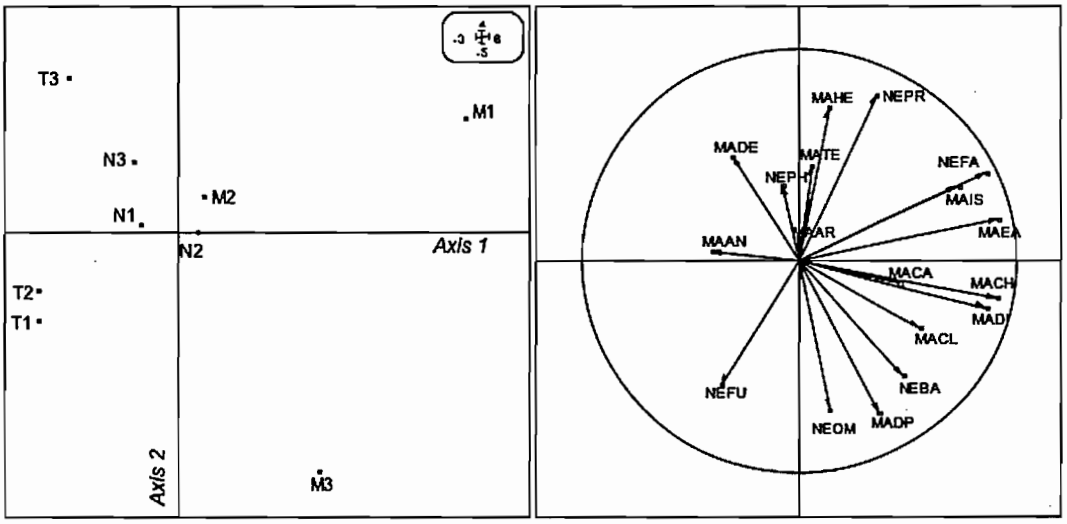

Fig. 3. PCA performed on the whole dataset (0–30 cm).
Left: projection of plots on axes 1 and 2. M1: upper part of M plot, M2: middle part of M plot, M3: lower part of M plot, N: upper part of NPK plot, N2: middle part of NPK plot, M3: lower part of M plot, M1: upper part of M plot, M2: middle part of M plot, M3: lower part of M plot.
Right: correlation circle of variables, on axes 1 and 2. NEFU: Fungus-feeding nematodes; NEPH: phytophagous nematodes; NEOM: omnivorous nematodes; NEPR: Predatory nematodes, NEFA: facultative phytophagous nematodes, NEBA: bacterial-feeding nematodes; MAAN: Ants; MADE: Dermaptera; MATE: Termites; MAHE: Hemiptera; MAAR: Arachnida; MAIS: Isopods; MAEA: earthworms; MACA: Coleoptera adults; MACL: Coleoptera larvae; MACH: Chilopoda; MADI: Diplopoda; MADP: Diptera larvae.

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