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Original article

The influence of a shrub-based intercropping system on the soil nematofauna when growing millet in Senegal

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ABSTRACT

Woody shrubs commonly co-exist with annual food crops in farmers' fields throughout the Sahel. Management strategies that deliberately include the native shrub *Piliostigma reticulatum* in Senegalese cropping systems result in soil functioning enhancement that benefits to the associated cereal. The objective of this work was to evaluate shrub effect on soil nematode communities. Soil samples were collected from an experimental design where pearl millet (*Pennisetum glaucum*) was cultivated alone or with *P. reticulatum* stands and mulch. Soil nematofauna characteristics were determined and compared with results from soil under pure shrub stands and from bare soil. The analysis of soil nematofauna, characterized by the abundance of different trophic groups and related indices (MI, maturity index; EI and SI, enrichment and structure indices), allowed discrimination between treatments with or without shrub presence. The soil nematode community in millet cultivation was dominated by plant feeding nematodes, mainly from the Hoplolaimidae family, but their abundance decreased when *P. reticulatum* was associated to the cereal. The shrub also impacted other nematode trophic groups. The abundance of opportunistic bacterial feeders (mainly Cephalobidae) was increased in shrub treatments. Further research should explore consequences on cereal nutrition and nematicidal properties of *P. reticulatum*.

1. Introduction

In Sub-Saharan Africa, food security remains a major concern [1,2]. West African soils exhibit a poor inherent fertility [3] while agriculture is based on small-scale farming with very low external inputs. Moreover agricultural systems in this semi-arid region are mainly rain fed and thus highly vulnerable to climate variability and drought. Such constraints encouraged the development of alternative cropping systems tailored to social and environmental local conditions.

Native perennial woody shrubs are dominant in the West Africa landscape. *Piliostigma reticulatum*, one of the most common Sahelian shrubs, provides rural people with fuel, materials for construction, fodder for livestock and traditional medicine [4]. Native shrubs co-exist with staple food crops in farmers' fields. The accumulation of fertile soil particles beneath the shrub canopies resulting from a landscape-scale redistribution of resources generates nutrient-rich soil plots known as "fertility islands" [5,6]. Shrubs also confer improved microclimatic regimes within the vicinity of their canopy due to their deep rooting systems and associated hydraulic lift [7–9]. In semi-arid Senegal, traditional management of native perennial woody shrubs involves coppicing and burning aboveground residues in the spring, prior to the planting of row crops, to clear fields. Alternative systems in which annual crops and shrubs are intercropped while shrub residues return to soil as mulch are receiving increasing attention all over Sub-Saharan Africa [10]. Such a shrub management resulted in both nutrient and moisture-related benefits to pearl millet (*Pennisetum glaucum*) when associated with common shrubs in the Senegalese peanut basin [8,11]. Better carbon storage and nutrient cycling, and higher soil moisture improved cereal yields [8,9,11,12]. Microbial communities beneath shrubs are more diverse, more active, and different from soil outside the influence of the shrub [11,13].

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Abundant and functionally diverse, soil nematodes are important members of the soil biotic community and play an essential role in ecosystem functions [14–16]. Different nematode trophic groups are defined according to their feeding habits. Plant feeding nematodes, i.e. plant parasitic and root-hair feeders, cause damage to roots that alter the plant's ability to take up nutrients and water [17]. Bacterial and fungal feeding nematodes affect soil organic matter decomposition and nutrient cycling [14,18]. Other important trophic groups of free-living nematodes are the predators and omnivores for their role in regulating the populations of other soil organisms [15]. While plant species identity and diversity may affect soil nematode community [19], its analysis provides useful indicators to document soil processes and assess changes in soil conditions of agricultural systems [20].

This study aims at evaluating the response of soil nematode communities, as well as key food web indices, to intercropping pearl millet with *P. reticulatum*. We attempted to highlight possible impacts on plant feeding nematodes when millet is cultivated with shrub. We also postulated that beneficial nematode communities vary as a result of the acknowledged impacts of shrubs on soil water balance, increased biological activity, soil organic matter build-up, and fertility replenishment.

2. Materials and methods

2.1. Experimental field site

The study site was located at Nioro-du Rip in the Southern region of the Senegalese Peanut Basin (13°45 N, 15°47 W, and 18 m above sea level). The climate is semi-arid with mean annual precipitation of 750 mm distributed from July to September and mean air temperatures ranging from 20 °C in December–January to 35.7 °C in April–June (i.e. BSh climate unit according to the Köppen–Geiger's classification). The soil is a fine-sandy, mixed Haplic Ferric Lixisol [21], locally referred to as a Deck-Dior [22]. The dominant native shrub species at the site is *P. reticulatum* (DC.) Hochst (Caesalpinioideae), with stand of about 185 shrubs ha^{-1}.

The study was carried out on an existing experiment established in 2003 at a local agricultural research station. A 2500 m^2 area was fenced to prevent cattle grazing and public access. Pearl millet (*P. glaucum* (L.) R. Br.) was planted with presence or absence of *P. reticulatum* (four plots each). Plots (10 m × 4.5 m in size) were neither tilled nor fertilized. In the four plots randomly assigned to shrub and millet association, *P. reticulatum* stands were periodically pruned according to farmers' practices to minimize competition for light between shrub and crops: it was cut at the starting of the rainy season to install the main crop and the pruned biomass was chopped to approximately 1 cm length and surface-applied as a mulch to the plot from which it was harvested. Then subsequent sprouts were allowed to continue growing and reform into the shrub. The millet grain yields in 2011 were 500 kg ha^{-1} in no shrub plots (M) and 886 kg ha^{-1} when millet was associated with *P. reticulatum* (M + S), along with chopped shrub residues at the soil surface. Two additional treatments were randomly selected in the untouched part of the fenced area: Four shrubs with canopy diameter of approximately 2 m serving individually as a replicate for shrub (S) treatment and four areas of bare soil (5 m^2 each) as a control (C).

2.2. Soil sampling

Soils were collected from each subplot in August 2011 when ears were emerging in treatments with millet. Ten individual soil cores (3 cm in diameter) were randomly sampled at a depth of 0–10 cm in the individual root system for the shrub or millet treatments and between interlacing roots for shrub-millet association. The soil cores were mixed to make one composite sample per subplot. Fresh soils were transferred to the laboratory in a cooler and stored at 4 °C for a maximum of 5 days before analysis. A small portion of each soil sample was air-dried and sieved prior to soil physico-chemical analyses.

2.3. Soil parameters

Soil moisture was determined gravimetrically by drying at 105 °C for 48 h. Total carbon and nitrogen contents were quantified after dry combustion using an elemental analyzer (Flash *EA 1112* series, Thermo Finnigan, France) and total phosphorus was determined by colorimetry [23]. Soil pH values were measured in 1:2.5 (w:v) soil-to-water suspensions. Soil mineral N content was determined colorimetrically in KCl 1 M extracts by flow injection analysis [24]. Microbial biomass carbon was estimated by the fumigation–extraction method, using the gain in ninhydrin-reactive N after fumigation and multiplied by 21 [25].

2.4. Nematode community characterization

For each sample, nematodes were extracted from approximately 250 g of wet soil using a modified Seinhorst method [26]. Collected nematodes were counted at 40× magnification using a dissecting microscope before being fixed in a formaldehyde–glycerol mixture. A representative sub-sample mounted on mass slides was used for identification to genus or family level at a higher magnification (400×). Nematode taxon richness (S) was calculated based on the number of taxa identified. The Shannon–Weaver diversity index (H′) was used to evaluate the taxonomic diversity of the nematode community [27]. Nematode taxa were assigned to one of five trophic groups: bacterial feeders (Ba), fungal feeders (Fu), plant feeders (H), omnivores (Om) and predators (Pr) [28]. The Nematode Channel Ratio (NCR) was calculated to quantify the relative importance of fungal-fed and bacterial-fed trophic channels of the soil decomposer food web [29]. Nematodes were categorized into a 1–5 colonizer–persister (cp) series [28,30], ranging from extreme r- to extreme K-strategists. The cp classification allows the calculation of the free-living nematode Maturity Index (MI) as the weighted mean frequency of the cp classes for non-plant feeding taxa [28]. The Plant Parasitic Index (PPI) is comparable to the MI but computed only for the plant feeding nematodes [28]. The PPI/MI ratio was calculated [31] as a useful indicator of nutrient status in the soil [32]. Other nematode ecological indices [33] were also used to evaluate the soil nematofauna under the different plant treatments. The Enrichment Index (EI) measures the number of opportunistic bacterial and fungal feeders that respond quickly to the input of C and N sources [33]. The Structure Index (SI) indicates soil food web length and connectance.

2.5. Statistics

The treatment effects were analyzed with a one-factor ANOVA. Data normality was checked to ensure that the distribution met the underlying assumptions for further statistical analysis. If the variance was not sufficiently homogeneous even after logarithmic transformation, data were analyzed using the non-parametric Kruskal–Wallis test in combination with an appropriate post hoc analysis. Statistical analyses were performed with XLStat-Pro (v2010 AddinSoft®) to test for significant differences between the different treatments (at $P < 0.05$ unless otherwise stated). In order to assess the similarity of the nematode communities between treatments, cluster analysis (hierarchical agglomerative clustering, group average method) of Bray–Curtis similarity matrices was conducted on square-root transformed abundance data (64 taxa) and an ordination plot was produced by non-metric multidimensional scaling (MDS) using PRIMER software. This analysis relies on a two-dimensional map where the degree of similarity among observations is indicated by the proximity of their representative points (the closer, the more similar). Axes of the map hold no specific value and can be rotated or mirrored without influencing the relative distances between the observations. A permutational multivariate analysis of variance (perMANOVA) was used to statistically evaluate if the four treatments led to different nematode communities. perMANOVA constructs an F-ratio from sums of squared distances within and between groups that is analogous to Fisher's F-ratio [34].

3. Results

3.1. Soil properties under the different treatments

There is no significant difference in the soil total carbon or nutrient status between control (C) and millet (M) (Table 1). Soil contents of total carbon, nitrogen and phosphorus were significantly higher under shrub canopy (S) than in bare soil (C). However these parameters did not significantly differ between millet cultivated alone (M) or millet in the presence of the shrub (M + S; Table 1). Similar trends were observed for soil ammonium (NH_4^+-N) while soil nitrate content was significantly increased in the presence of the shrub (from 1.5 to 4.1 μg NO_3^--N g^{-1} soil in M and M + S treatments respectively). Soils were acidic and no significant difference was observed in pH values between treatments (Table 1). Soil microbial biomass was slightly higher in both millet treatments (with or without the shrub) but not significantly different in bare soil or under shrub stands (Table 1).

3.2. Composition of the soil nematofauna

Sixty-four soil nematode taxa were identified during the study, representing 39 families with contributions above 0.1% of the total soil nematodes in the respective treatments (Table 2). Plant and bacterial feeders dominated the nematode communities representing 45% and 35% of the nematodes, respectively. The plant feeding nematode community was dominated by the cp-3 Hoplolaimidae (Table 2), especially *Helicotylenchus* and *Scutellonema* (data not shown). The other plant feeders, Tylenchidae, Pratylenchidae and Dolichodoridae, have densities greater than 20 individuals 100 g^{-1} in some treatments. The bacterial feeding nematodes were represented by 16 different families with Cephalobidae (cp-2) being the most abundant (mainly represented by *Acrobeles*, *Acrobeloides* and *Zeldia*; data not shown). Bacterial feeders from cp-1, cp-3 and cp-4 classes (noted as Ba1, Ba3 and Ba4, respectively) were also present but less abundant than Ba2. Fungal feeders were primary composed of the families Belondiridae, Leptonchidae and Aphelenchoididae, with cp classes from 2 to 5 (Table 2). Qudsianematidae (Om4) was the most represented family in the omnivores, and Discolaimidae (Pr5) for the predators.

Table 1
Selected soil parameters ($n = 4$) for the different treatments.

Soil parameters	Treatment			
	Control (C)	Shrub (S)	Millet (M)	Millet w/Shrub (M + S)
Total C (mg C g^{-1})	2.5 a[a]	4.0 b	3.0 a	3.2 ab
Total N (mg N g^{-1})	0.22 a	0.36 b	0.26 a	0.29 ab
Total P (μg P g^{-1})	42.3 a	59.5 b	48.8 ab	51.5 ab
NH_4^+-N (μg N g^{-1})	1.5 a	5.6 c	3.2 ab	4.0 bc
NO_3^--N (μg N g^{-1})	1.0 a	5.6 b	1.5 a	4.1 b
pH (H_2O)	5.5 a	5.5 a	5.2 a	5.6 a
Microbial biomass (μg C g^{-1})	49.0 a	51.5 a	67.6 a	69.1 a

[a] Different letters within a row indicate significant difference between treatments at $P < 0.05$.

3.3. Distribution of nematodes across treatments

The total nematode density did not significantly vary between treatments while all of the trophic groups except the omnivore group were significantly affected (ANOVA, $P < 0.1$; Fig. 1). Table 2 showed details on abundance at family and functional guild levels. The number of plant feeders was lower in millet when associated with the shrub than in millet cultivated alone (Fig. 1). Indeed, the families Hoplolaimidae and Dolichodoridae, both in H3 functional guild, were significantly depressed from M to M + S treatments ($P < 0.01$; Table 2). The presence of the shrub increased the abundance of the bacterial feeding nematodes (Fig. 1), especially for Cephalobidae (Ba2) and Rhabditidae (Ba1; Table 2). However, treatment effect was not statistically significant for Rhabditidae due to high variability in the abundance within M + S treatment. The treatment effects on the abundance of fungal feeders (Fig. 1) mainly consisted of a significant increase of Belondiridae (Fu5) in the millet either in shrub presence or absence (M + S and M respectively) compared to both control (C) and shrub (S) treatments (Table 2). However Aphelenchoididae (Fu2) tended to be more abundant and Leptonchidae (Fu4) less abundant when millet was associated with *P. reticulatum* rather than cultivated alone but the differences were not statistically significant (Table 2). Three different families of predatory nematodes were significantly impacted by treatments (Table 2) generating an overall significant effect on the abundance of predators (Fig. 1). For these 3 families, a higher abundance was measured in treatments with plants than in the control ($P < 0.05$), regardless of plant type.

3.4. Nematode community structure and indices

The nematode taxon richness (S) and the diversity index (H′) showed a similar trend with the highest values in the presence of the shrub. The treatment effect was highly significant for richness ($P < 0.001$) while the H′ index was slightly affected ($P = 0.123$; Fig. 2). The Enrichment Index (EI) was very low in control and millet treatments (1.2 and 6.2 in C and M, respectively). The treatment effect was significant ($P = 0.002$; Fig. 2) and the EI values were significantly higher in the shrub presence (31.4 and 46.8 in S and M + S, respectively). The Structure Index (SI) was significantly affected by the treatments ($P = 0.013$) with no difference between M and M + S treatments (Fig. 2). The treatments significantly affected the Maturity Index (MI; $P = 0.001$; Fig. 2). MI values were lower in the presence of the shrub (3.40 vs. 2.52 in C and S treatments, and for treatment with millet 3.33 vs. 2.67 in M and M + S, respectively). No significant differences in the values of Plant Parasitic Index (PPI) were observed among the different treatments while the presence of the shrub affected the ratio between PPI and MI ($P = 0.001$; Fig. 2). The Nematode Channel Ratio values were higher in the presence of the shrub (Fig. 2). The perMANOVA analysis underlined an overall significant effect of treatment ($P = 0.001$; Table 3) on the composition of the nematode community. These results are illustrated in Fig. 3, which represents the MDS analysis. The treatments were well aggregated and clearly separated according to the shrub presence.

4. Discussion

Abundance of nematodes in the control soil (C) was very low (400 individuals 100 g^{-1} soil) while the nematode community was

Table 2
Nematode abundance per family (individuals 100 g^{-1} dry soil; mean and standard error) and associated functional guild for the different treatment ($n = 4$).

Family	Functional guild[a]	Treatment			
		Control (C)	Shrub (S)	Millet (M)	Millet w/Shrub (M + S)
Tylenchidae	*H2*	47.6 (16.7)	24.8 (10.6)	56.4 (10.0)	44.2 (18.6)
Paratylenchidae	*H2*	1.1 (0.7)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Pratylenchidae	*H3*	18.9 (11.4)	25.9 (6.6)	16.9 (6.8)	64.8 (25.2)
Criconematidae	*H3*	0.0 (0.0)	0.0 (0.0)	1.2 (1.2)	2.3 (2.3)
Hoplolaimidae**[b]	*H3*	148.1 (28.7)	97.0 (19.8)	509.6 (80.3)	237.6 (103.3)
Dolichodoridae**	*H3*	7.7 (3.3)	7.3 (3.4)	50.6 (15.6)	39.3 (8.1)
Trichodoridae	*H3*	0.0 (0.0)	2.1 (0.7)	0.9 (0.9)	1.8 (1.2)
Longidoridae	*H5*	1.1 (0.7)	8.1 (4.0)	1.2 (1.2)	10.5 (4.7)
Neodiplogasteridae	*Ba1*	0.0 (0.0)	0.8 (0.8)	0.0 (0.0)	0.0 (0.0)
Panagrolaimidae	*Ba1*	0.0 (0.0)	4.3 (4.3)	0.0 (0.0)	0.0 (0.0)
Rhabditidae	*Ba1*	0.0 (0.0)	24.2 (6.4)	1.2 (1.2)	166.8 (130.0)
Cephalobidae*	*Ba2*	63.9 (6.0)	261.1 (70.5)	179.2 (25.7)	268.0 (53.9)
Leptolaimidae	*Ba2*	0.0 (0.0)	0.8 (0.8)	0.0 (0.0)	0.0 (0.0)
Monhysteridae	*Ba2*	0.0 (0.0)	0.6 (0.6)	0.0 (0.0)	3.1 (2.5)
Ostellidae	*Ba2*	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	2.3 (2.3)
Plectidae	*Ba2*	1.6 (1.1)	14.7 (1.9)	9.2 (8.0)	20.7 (9.0)
Chromadoridae	*Ba3*	0.6 (0.6)	0.0 (0.0)	3.0 (2.0)	0.0 (0.0)
Desmodoridae	*Ba3*	0.0 (0.0)	0.8 (0.8)	0.0 (0.0)	1.3 (1.3)
Diplopeltidae	*Ba3*	0.6 (0.6)	0.8 (0.8)	0.0 (0.0)	2.6 (2.6)
Odontolaimidae	*Ba3*	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	1.3 (1.3)
Prismatolaimidae	*Ba3*	2.7 (1.2)	3.7 (2.0)	7.0 (4.2)	3.2 (2.1)
Rhabdolaimidae	*Ba3*	0.0 (0.0)	0.6 (0.6)	0.0 (0.0)	0.0 (0.0)
Alaimidae	*Ba4*	1.8 (1.1)	2.4 (2.4)	2.5 (2.5)	6.5 (6.5)
Bathyodontidae	*Ba4*	0.0 (0.0)	0.0 (0.0)	2.5 (2.5)	0.0 (0.0)
Anguinidae (Ditylenchus)	*Fu2*	1.5 (0.9)	2.8 (1.0)	0.0 (0.0)	2.3 (2.3)
Aphelenchidae	*Fu2*	0.8 (0.8)	0.7 (0.7)	0.9 (0.9)	2.7 (2.7)
Aphelenchoididae	*Fu2*	0.0 (0.0)	6.1 (1.7)	4.6 (2.7)	21.2 (12.1)
Leptonchidae	*Fu4*	44.6 (18.0)	24.2 (8.3)	53.7 (3.7)	24.7 (6.8)
Belondiridae*	*Fu5*	24.8 (5.4)	8.9 (3.7)	79.6 (15.9)	52.1 (22.1)
Tripylidae	*Pr3*	0.0 (0.0)	2.2 (2.2)	0.0 (0.0)	3.2 (2.1)
Mononchidae	*Pr4*	0.7 (0.7)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Nygolaimidae	*Pr5*	0.0 (0.0)	0.0 (0.0)	1.3 (1.3)	0.5 (0.5)
Carcharolaimidae***	*Pr5*	4.2 (2.3)	3.1 (1.3)	10.9 (1.5)	0.0 (0.0)
Aporcelaimidae*	*Pr5*	0.0 (0.0)	8.3 (3.6)	0.0 (0.0)	0.9 (0.9)
Discolaimidae*	*Pr5*	15.4 (3.7)	25.7 (9.0)	51.7 (18.2)	74.8 (13.5)
Dorylaimidae	*Om4*	3.8 (1.2)	0.8 (0.8)	2.1 (2.1)	0.0 (0.0)
Nordiidae	*Om4*	0.5 (0.5)	0.0 (0.0)	0.0 (0.0)	2.3 (2.3)
Qudsianematidae	*Om4*	8.3 (3.7)	14.1 (2.8)	17.4 (9.6)	30.6 (13.1)
Thornenematidae	*Om5*	0.0 (0.0)	0.0 (0.0)	1.2 (1.2)	0.0 (0.0)

[a] Functional guilds : H, plant feeders; Ba, bacterial feeders; Fu, fungal feeders; Pr, predators; Om, omnivores; numbers following the trophic group indicate cp values.
[b] Asterisks indicate P values of ANOVA from abundance data per family with treatment as the main factor; $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

well structured (SI = 88) with a dominance of cp-3 to 5 guild classes. The MDS representation clearly separates treatments according to shrub presence, which affected both taxa composition and relative abundance of nematodes trophic groups. The taxa diversity (Shannon–Weaver index) and richness were higher in the presence of shrubs. The change in composition was related to the presence of new taxa (e.g. Panagrolaimidae, Tripylidae) in treatments with shrub presence.

The nematode community in millet cultivation was dominated by plant feeding nematodes (60% of the total abundance), with *Helicotylenchus* and *Scutellonema* as the most abundant genera. Previous studies reported high populations rates of these endoparasites in cropping systems in Senegal causing damages to millet [35–40]. The ectoparasite nematodes *Tylenchorhynchus* ssp. were also reported to be abundant in Senegalese soils cultivated with millet [38]. No overall treatment effect was acknowledged on plant parasitic index (PPI) while the dominance of the cp-3 guild class in plant feeders was unlikely to stress differences in the index. However the abundance of plant feeding nematodes decreased by 23% when millet was cultivated with *P. reticulatum* (M vs. M + S treatments), mostly due to a decrease in Hoplolaimidae abundance. Many plant constituents and metabolites have been investigated for activity against plant parasitic nematodes [41,42]. *P. reticulatum* is ethnomedicinally used for the antioxidant and antimicrobial activities of its bark, root, pod, young stem or leaves [43–46]. Nemato-toxic compounds may be released through volatilization, exudation, leaching and decomposition [41,47–49]. Alkaloids, polyphenols, flavonoids and anthocyanins have been identified in *P. reticulatum* [45,50–52] while their nematicidal effects have not been demonstrated yet. Plant feeding taxa may be not equally sensitive to the shrub presence as families other than Hoplolaimidae and Dolichodoridae were not significantly affected by the presence of the shrub ($P < 0.05$). The effect of shrub on plant feeding nematodes deserves further research.

Shrub also led to changes in free-living nematode communities. The lower MI in S and M + S treatment compared to control (C) and millet alone (M) indicated an environmental disturbance due to the presence of the shrub. The structure index (SI) observed in millet cultivation was unchanged when *P. reticulatum* was associated, indicating that the length of food chains was not increased to include more predators and omnivores. However, higher abundance of Discolaimidae (Pr5) may indicate a top-down regulation of plant parasitic nematodes [33,53]. Shrub enhanced the abundance of the opportunistic guilds, increased the enrichment index (EI) and decreased the maturity index (MI) but the bacterial feeding nematodes benefited more from the presence of the shrub than the fungal feeders. Bacterial feeding nematodes represented the dominant trophic group in treatment associating millet and *P.*

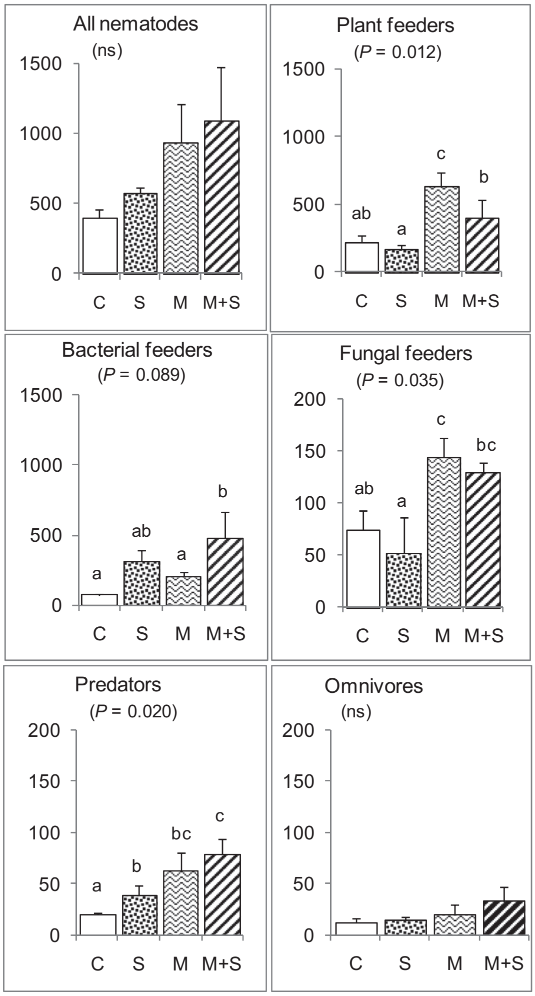

Fig. 1. Abundance (number of individuals 100 g^{-1} dry soil; means with standard errors as bars) of total and nematode trophic groups for different treatments (C: control soil; S: shrub; M: millet; M + S: millet with shrub). Significance values for treatment effect in ANOVA are in parentheses (ns = not significant when $P < 0.1$). Different letters between columns indicate significant difference between treatments at $P < 0.05$.

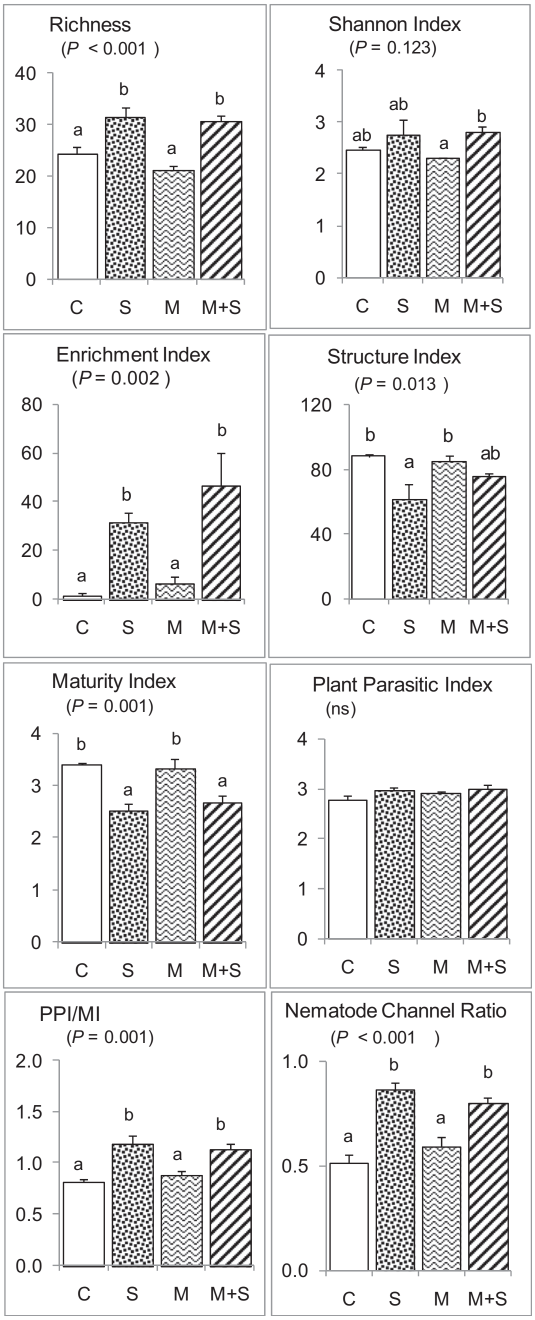

Fig. 2. Nematode ecological indices for different treatments (C: control soil; S: shrub; M: millet; M + S): millet with shrub. Significance values for treatment effect in ANOVA are in parentheses (ns = not significant when $P < 0.1$). Different letters between columns indicate significant difference between treatments at $P < 0.05$.

reticulatum stands and mulch, with Cephalobidae (Ba2) and Rhabditidae (Ba1) the most abundant taxa. The enrichment index (EI) provides an indicator of resources available to the soil food web and the response of primary decomposers to those resources. Low values of EI in control (C) and millet (M) treatments may be related to low resource status at the sampling date in the studied sandy soil (Table 1). The soil mineral N content was higher when millet was cultivated with *P. reticulatum* and shrub residues at the soil surface. Previous studies reported rapid response of bacterial feeders (especially cp-1) to change with resources and microbial biomass [16,54,55] while the enhancement of enrichment opportunists (mainly Rhabditidae) clearly indicated microbial grazing by nematodes [55]. Decomposition of organic matter may proceed through different pathways or channels in the soil food web [56–59]. The accumulation of residues on the soil surface may be readily exploited by fungi, resulting in slow decomposition rates and a dominance of fungivores [60], especially when materials have high lignin, high cellulose and high C-to-N ratio [33,58]. In the present study, abundances of bacterivores and values of the Nematode Channel Ratio (NCR; Figs. 1 and 2) indicated that bacterial decomposition may dominate in the presence of the shrub, and was likely related to a moderate C-to-N ratio in shrub materials (values of 20

Table 3
Results, presented as *P* values, of the PerMANOVA analysis for the comparison of the soil nematode community structure (density of 64 taxa) of the 16 plots among the four treatments.

	Control	Shrub	Millet	Millet w/Shrub
Control	–			
Shrub	0.035	–		
Millet	0.081	0.024	–	
Millet w/Shrub	0.024	0.022	0.028	–

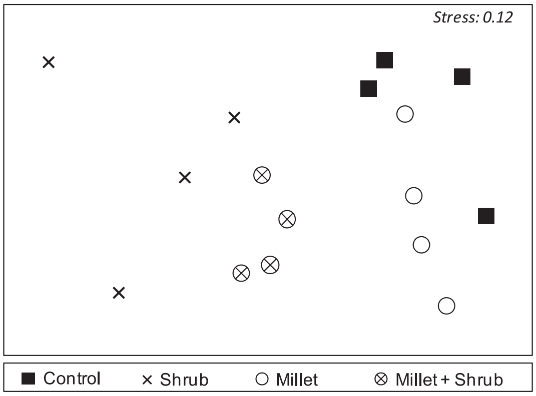

Fig. 3. Non-metric multidimensional scaling (MDS) representation showing similarity in nematode community composition between treatments.

and 27 in the leaves and leaves + stem respectively [11]). Moreover, bacterial-mediated decomposition pathways are reported to be predominant in agricultural soils [58]. Opportunistic nematodes that feed on bacteria and fungi accelerate the decomposition of soil organic matter and the turnover of N in soil, thereby releasing nutrients for plant growth [54,61–63] and that may have contributed to better millet yields observed in association with *P. reticulatum* (Table 1). A previous study in the region showed that shrub residues applied at the soil surface in millet fields may provide short-term plant available N when added to soil [11].

The presence of shrub residues at the soil surface also contributed to changes in soil microclimate [8] while some families like Rhabditidae are vulnerable to thermal stress [64]. The mulch also contributed to moister but probably more heterogeneous soil conditions that may contribute to explain high and variable abundance of Rhabditidae in the M + S treatment. *P. reticulatum* also performs hydraulic lift [65] (passive movement of water through roots from moist subsoil to dry surface layers [66]) and allows greater soil microbial diversity year around than outside its vicinity [13] that may explain larger abundance of bacterial feeders in the shrub presence. On the contrary, Cephalobidae produce an anabiotic form resistant to dessication [67] that may explain their predominance in millet as previously observed in other fields of the region [40]. Abundance of Cephalobidae as well as those of opportunistic fungal feeders (mainly Aphelenchoididae, Fu2) increased when millet was cultivated with *P. reticulatum*. These taxa appear to have wide ecological amplitude through adaptation to stress conditions while the competitive ability of different nematode species may change along with environmental conditions [33]. Further research may document climate-related questions of the soil food web in the shrub vicinity.

5. Conclusion

The analysis of soil nematofauna, characterized by abundance of the different trophic groups and related maturity and enrichment indexes, allowed discriminating for the presence of *P. reticulatum* in the studied Senegalese agricultural soils. When millet is cultivated with *P. reticulatum*, (i) plant parasitic nematodes abundance was decreased, (ii) the nematode community was dominated by enrichment opportunistic and general opportunistic bacterial feeders, and soil food web was characterized by bacterial-mediated decomposition pathways. This increase in microbivorous nematode abundance, both general opportunists and enrichment opportunists, indicates that the presence of *P. reticulatum* led to a better nutrient availability in the soil than where it is not present. Further research is needed to clarify this point, that shrub presence is potentially conducive to a more efficient nutrition for cereals and to evaluate the nematicidal potential of *P. reticulatum*.

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