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Effects of agricultural management on nematode–mite assemblages: Soil food web indices as predictors of mite community composition

Sara Sánchez-Moreno^{a,*}, Nicole L. Nicola^b, Howard Ferris^a, Frank G. Zalom^b

^aDepartment of Nematology, University of California Davis, Davis, CA 95616, USA

^bDepartment of Entomology, University of California Davis, Davis, CA 95616 USA

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ABSTRACT

Biological indicators based on abundances of soil organisms are powerful tools for inferring functional and diversity changes in soils affected by agricultural perturbations. Field plots, combining organic and conventional practices with no tillage, conservation tillage and standard tillage maintained different nematode assemblages and soil food webs. Soil food web indices based on nematode assemblages were reliable predictors of the trophic composition of functional characteristics of soil mite assemblages. Bacterial-feeding and predatory nematodes, together with predatory mites, were abundant in the organic-no till treatments and were associated with high values of the Enrichment and the Structure Index based on nematode assemblages. Conventional-Standard tillage treatments had high abundances of fungal- and plant-feeding nematodes and algivorous mites, associated with high values of the Basal and Channel Index. This study validates the hypothesis that nematode-based soil food web indices are useful indicators of other soil organisms such as mites, with similar functional roles and environmental sensitivities.

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1. Introduction

Soil food webs are complex assemblages of organisms; they have received much attention from terrestrial ecologists (Scheu, 2002; Hedlund et al., 2004; van der Putten et al., 2004). Because of the great biological diversity and the large sampling and identification effort required in working with soil organisms, many soil ecologists focus their studies on a few taxa. Several indicator systems, based on specific taxonomic groups of organisms, have been developed to infer structure and function of the whole soil food web from analysis of some of its components. The analyses are based on phyla (nematodes, Protozoa), classes (Collembola) or species

(annelids) (Wasilewska, 1997; van Straalen, 1998; Foissner, 1999). Thus, a relevant goal for soil ecologists is the verification of the assumptions that indicator taxa are representative of other organisms in the food web.

Nematodes are highly diverse soil-dwelling metazoans that occupy, usually in great abundance, many habitats. Up to several million nematodes may inhabit a square meter of soil, representing numerous trophic groups, soil food web links, and life strategies (Bongers, 1990; Yeates et al., 1993; Yeates and Bongers, 1999; Ferris et al., 2001). Nematodes have been used as indicators of soil perturbations that include chemical, physical and agricultural effects on ecosystem health and functioning. The indicators include trophic group abundances

* Corresponding author. Present address: Departamento de Protección Vegetal, Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria, Crta. Coruña km 7.5, Madrid 28040, Spain. Tel.: +34 913478710; fax: +34 913471479.

E-mail address: sarasm@inia.es (S. Sánchez-Moreno).

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and ratios (Wasilewska, 1998), diversity indices (Urzelai et al., 2000) and soil food web indices (Ferris et al., 2001).

Nematodes exhibit complex and numerous interactions with other soil organisms. They have close relationships with their food sources and with other soil animals that may constitute their prey or their predators (Ingham et al., 1985; Yeates and Wardle, 1996; Fu et al., 2005). The indicator capacity of soil food web indices (Ferris et al., 2001) is based on available knowledge about these relationships and the food web functions of component taxa. The Enrichment Index (EI) and the Channel Index (CI) are indicators of organic matter decomposition pathways; the EI, based on the prevalence of fast-growing enrichment opportunistic nematodes, is an indicator of rapid, bacteria-mediated, organic matter decomposition (high EI), while the CI, based on the prevalence of fungal-feeding in relation to other microbivorous nematodes, is an indicator of slower organic matter decomposition mediated by fungi (high CI). The Basal Index (BI) is derived from the abundance of persistent microbial-feeding nematodes; high BI values indicate short and depleted soil food webs. The Structure Index (SI) weights the prevalence of omnivore and predatory nematodes in the soil food web as an indicator of long and complex soil food webs with high connectance and numerous trophic links. Soil food web indices have been used to infer soil food web responses to soil disturbance (Berkelmans et al., 2003; Ferris and Matute, 2003; Bulluck et al., 2002; Okada et al., 2004).

In a similar way, the high diversity of microarthropod communities, and their intricate relationships within the soil ecosystem, qualify them as bioindicators (van Straalen, 1998; Koehler, 1999; Čoja and Bruckner, 2006). Mites are some of the most abundant soil arthropods, and play important roles in the interactions of soil biota. Among the soil mites, Uropodina and Gamasida are important in agroecosystems as effective predators capable of regulating their prey populations, while some Gamasina are also indicators of soil conditions, ecological disturbance and anthropogenic impact (Koehler, 1999). Some mite species, such as *Alliphis siculus*, are efficient nematode predators especially important in soils managed without the use of pesticides (Koehler, 1999).

On a global basis, agricultural practices cause significant and extensive soil disturbance and soil contamination, with concomitant contributions to the loss of biodiversity (Wood et al., 2000). More sustainable agricultural practices, including organic management and reduced tillage, enhance soil diversity and fertility (Mäder et al., 2002); and soil dwelling animals are, in general, more abundant in organic than in conventional farming systems (Bengtsson et al., 2005).

The objectives of the study reported herein were to: (1) analyze the effects of different agricultural management systems on nematode assemblages and on the soil food web, (2) compare nematode and mite sensitivity to organic and conventional management practices under different tillage intensities, (3) seek robust relationships between nematodes and mites, including causal (e.g., predation) and casual (e.g., trophic redundancy) relationships, and (4) test the efficacy of soil food web indices, based on nematode abundances, as indicators of the characteristics of the soil mite community.

2. Materials and Methods

2.1. Study area and treatments

The Long Term Research in Agricultural Systems project (LTRAS) was established at the University of California, Davis, in 1993 with the aim of studying the long-term effects of tillage, chemicals and cover crops on the biology, productivity and economics of different agricultural systems. The plots used in this study had been rotated with tomato (*Lycopersicon esculentum*) and corn crops (*Zea mays*) in 2-year cycles for 12 years. Samples were collected in 0.4 ha plots which included two management practices: organic (ORG) and conventional (CONV). During the winter, CONV plots were maintained fallow while legume cover crops were planted in the ORG plots. Both systems were irrigated in summer. CONV plots received mineral fertilizer and compost was added, when necessary, to the ORG plots. Each plot was divided into two subplots; standard tillage (ST) and conservation tillage (CT). Tillage was applied whenever needed in the standard tillage sections of each plot (about five times a year) for creating planting beds, incorporating crop residues, and for weed control. Conservation tillage sections were only tilled when weed problems were overwhelming, usually once or twice a year. In the CT subplots, two 3 m² microplots were hand weeded instead of tilled, comprising the no-till treatment (NT) in the ORG plots. Thus, five treatments were sampled: Conventional-Standard Tillage (CST), Conventional-Conservation Tillage (CCT), Organic-Standard Tillage (OST), Organic-Conservation Tillage (OCT), and Organic-No Tillage (ONT). All the treatments were planted with tomato (2005) and corn (2006).

Three replicates of each treatment were established and three samples were taken in each treatment plot. Thus, 45 soil samples were collected at each of eight sampling dates: March, June, August, and November 2005, and April, May/June, August/September, and November 2006. At the sixth and seventh sampling dates, plots in the later-planted ORG system were sampled approximately 1 month later than those in the CONV systems so that the plants were in comparable phenological states at the time of sampling.

2.2. Soil sampling and extraction and identification of nematodes and arthropods

Mites were sampled by taking an undisturbed soil core (5 cm diam. × 10 cm deep) by pushing a metal cylinder into the soil. Immediately after the mite sampling, nematodes were sampled by removing a 20 cm × 20 cm × 20 cm cube of soil around the position of the arthropod core. Samples were transported to the laboratory and arthropods were extracted immediately. Soil samples for nematodes were stored at 4 °C for no more than 1 week before extraction.

Mites were extracted by placing the intact soil cores in Berlese-Tullgren funnels for 7 days and collecting in 70% ethanol. Mites were identified to lowest possible taxonomic level, and classified into four trophic groups: fungivores/saprophytes, predators, omnivores, and endeostigmatid or algivores. Those data were used to compare nematode and mite assemblages and trophic composition. More specific details on arthropod assemblages will be published elsewhere.

Abundances of mite taxa were expressed on an absolute basis (number of mites in taxon *i* per core).

Nematodes were extracted from a subsample of 250 g of fresh soil from the 20 cm × 20 cm × 20 cm soil sample using a modification of sieving and Baermann funnel techniques (Barker, 1985). All nematodes collected in each sample were counted under a dissecting microscope. The nematode suspension was then centrifuged and nematodes spread on a microscope slide. At least 200 nematodes were identified to genus or family level. Nematodes were then assigned to main trophic groups (Yeates et al., 1993) and to colonizer–persister groups (Bongers and Bongers, 1998). Bacterial-feeding nematodes are fast-growing nematodes with short life cycles, r-strategists that behave as general opportunists (e.g., family Cephalobidae) or enrichment opportunists (e.g., Rhabditidae, Panagrolaimidae). Fungal feeders (e.g., Aphelenchidae) are also fast-growing nematodes, while predators and omnivores are large, k-strategists nematodes often sensitive to soil perturbation. Plant-feeders include migratory and sedentary plant-parasites and herbivores. Nematode taxa and trophic group abundances were expressed on an absolute basis (number of nematodes in taxon *i* per 100 g of fresh soil).

Mites were classified into four trophic groups (Krantz, 1979; Norton, 1985; Walter, 1988; Smith et al., 1996). Fungivorous-saprophagous mites are K- (e.g., Oribatida, Oehserchestidae) or r-strategists (e.g., Astigmata), particulate feeders that enhance soil structure and fertility and are favored by moist organic soils. Algivorous mites (Nanorcherstidae) are usually small, K-strategists mites abundant in dry soils, and the only fluid-feeders within the suborder Endeostigmata. Omnivores are r-strategist mites with broad trophic habits (e.g., Eupodidae), while predators are r- (e.g., Rhagidiidae) or K-strategists (Gamasida) that include the most important nematophagous mites.

Soil food web indices, based on nematode functional guild abundances, were calculated after Ferris et al. (2001). The Enrichment Index (EI) is based on the abundance of enrichment opportunistic nematodes, and indicates rapid decomposition of low C:N organic matter mediated by bacteria. The Channel Index (CI), on the contrary, is based on the abundance of fungal-feeding opportunistic nematodes and indicates slower decomposition of high C:N organic matter mediated by fungi. The Structure Index (SI) is based on the abundance of large omnivore and predatory nematodes, an indicator of soil food web length and connectance. Finally, the Basal Index (BI), based on the abundance of generally opportunistic nematodes, is an indicator of depleted-perturbed soil food webs.

2.3. Statistical analysis

Nematode data from the three samples were averaged as the aggregate faunal assemblage for each plot so that three replicates for each treatment were subjected to statistical analysis. Due to the lack of normality in the datasets, non-parametric statistics were used in univariate analyses. Kruskal–Wallis ANOVA was used to detect significant differences between treatments and the Mann–Whitney test was used post hoc. All samples from every sampling date were used in univariate and multivariate analyses. To study the effect of time on the nematode and mite assemblages, non-parametric Friedman repeated measures ANOVA was used to

test dependence of trophic groups and community descriptors at each sampling time on the previous sampling date. Spearman rank-order correlation coefficients were used to infer relationships among continuous variables.

Canonical Correspondence Analysis (CCA) was applied to log-transformed nematode and mite trophic group abundances to infer associations between nematode and arthropod trophic groups with agricultural treatments. CCA is used to assess relationships between groups of variables, and results in a bidimensional plot in which dependent and independent variables score along unrelated canonical roots. Independent variables (agricultural treatments) are marked with arrows, and the distance between dependent variables and the arrows indicates the strength of the association.

Discriminant Analysis (DA) was applied to log-transformed nematode and mite absolute abundances to measure dissimilarity of soil biotic composition between treatments. DA was used to test whether chosen variables (composition of nematode and mite assemblages) significantly discriminate among groups (treatments). Once the analysis was performed, Squared Mahalanobis distances were used as a measure of the distance between centroids of each group, showing the degree of similarity existing in composition of nematode and mite assemblages among treatments.

Simple regression was used to determine significant soil food web predictors of mite trophic group abundance and to infer associations among the soil biota.

All statistical analyses were performed using the STATISTICA software (StatSoft, 1996).

3. Results

3.1. Effects of agricultural treatments on nematode abundance

Across all sampling dates and treatments, 37 nematode taxa (genera and families) were found in soil samples (Table 1). Five taxa (*Aphelenchus*, *Tylenchidae*, *Acrobeloides*, *Panagrolaimus*, and *Aphelenchoides*) comprised the majority of the nematode assemblage, constituting more than 75% of the total number of nematodes found.

Abundances of nematode taxa were compared among the five treatments. In general, nematode abundances were higher in the ORG plots, where bacterial-feeding nematodes were more abundant than in CONV. *Mesorhabditis*, *Plectus*, *Tylenchorhynchus* and *Helicotylenchus* were more abundant in all the ORG treatments, whether tilled or not tilled, than in CONV plots. *Panagrolaimus* and *Prismatolaimus* were more abundant in OCT and ONT, while other bacterial-feeding nematodes, such as *Eumonhystera*, *Cruznema* and *Acrobeloides*, together with the fungal-feeder *Aphelenchoides* and omnivores of the Dorylaimida were associated with some of the ORG treatments.

Of the dominant taxa, only one fungal-feeder (*Aphelenchus*) was primarily associated with CONV plots. Scarcer taxa, such as the bacterial-feeders *Metacrolobus* and *Alaimus*, and the predator *Discolaimus* were more abundant in CCT. The bacterial-feeder *Acrobeloides* and the fungivore *Diphtherophora* were less abundant in CST, and *Xiphinema* was the only plant-feeding nematode associated with CONV treatments.

Table 1 – Average (\pm S.E.) nematode abundance in each treatment (number of nematodes/100 g fresh soil). Trophic group of each taxon and significant effects of management, tillage, and management \times tillage are indicated. Data were averaged across eight sampling dates.

	CST	CCT	OST	OCT	ONT	Manag.	Tillage	Manag. \times tillage
Dauerlarva (Ba-F)	0.09a (\pm 0.06)	0.07a (\pm 0.05)	3.98ab (\pm 2.74)	2.17b (\pm 1.07)	3.51b (\pm 1.05)	P < 0.01		P < 0.01
Rhabditidae (Ba-F)	1.73 (\pm 0.95)	2.77 (\pm 1.27)	13.74 (\pm 9.19)	5.85 (\pm 3.43)	5.39 (\pm 3.10)			
Panagrolaimus (Ba-F)	13.40a (\pm 3.63)	37.58b (\pm 9.91)	77.85bc (\pm 17.61)	199.25c (\pm 39.59)	154.03c (\pm 22.61)	P < 0.01	P < 0.01	P < 0.01
Rhabditis (Ba-F)	0.03 (\pm 0.03)	0.14 (\pm 0.11)	1.07 (\pm 0.67)	0.59 (\pm 0.51)	1.02 (\pm 0.62)			
Mesorhabditis (Ba-F)	7.48a (\pm 1.70)	12.26a (\pm 2.86)	63.14b (\pm 11.59)	47.46b (\pm 8.82)	33.93b (\pm 5.40)	P < 0.01		P < 0.01
Eumonhystera (Ba-F)	0.45a (\pm 0.16)	0.52a (\pm 0.22)	1.82ab (\pm 0.63)	4.40b (\pm 1.60)	1.83ab (\pm 0.53)	P < 0.01		P < 0.01
Cruzanema (Ba-F)	4.21a (\pm 1.08)	1.85a (\pm 0.75)	13.61b (\pm 3.63)	5.79ab (\pm 1.23)	9.83ab (\pm 4.71)	P < 0.01		P < 0.01
Acrobeles (Ba-F)	0.82a (\pm 0.25)	0.78a (\pm 0.34)	1.93a (\pm 1.16)	4.47ab (\pm 1.82)	7.98b (\pm 4.45)	P < 0.05	P < 0.01	P < 0.01
Acrobeloides (Ba-F)	71.03a (\pm 11.83)	109.54b (\pm 12.89)	102.75b (\pm 11.98)	118.17b (\pm 10.99)	115.65b (\pm 16.02)	P < 0.05	P < 0.05	P < 0.05
Cephalobidae (Ba-F)	3.02b (\pm 0.58)	0.90a (\pm 0.22)	5.64b (\pm 1.13)	2.85b (\pm 0.60)	2.49ab (\pm 0.76)		P < 0.01	P < 0.01
Wilsonema (Ba-F)	0.05 (\pm 0.05)	0.09 (\pm 0.07)	0.00 (\pm 0.00)	0.04 (\pm 0.04)	0.00 (\pm 0.00)			
Plectus (Ba-F)	1.29a (\pm 0.33)	1.17a (\pm 0.37)	4.76b (\pm 1.11)	4.66b (\pm 0.93)	4.45b (\pm 1.12)	P < 0.01		P < 0.01
Metacrolobus (Ba-F)	0.29ab (\pm 0.09)	0.69b (\pm 0.15)	0.17a (\pm 0.10)	0.37a (\pm 0.21)	0.34a (\pm 0.16)	P < 0.05		P < 0.01
Achromadora (Ba-F)	0.05 (\pm 0.04)	0.07 (\pm 0.05)	0.23 (\pm 0.12)	0.21 (\pm 0.16)	0.37 (\pm 0.20)			
Prismatolaimus (Ba-F)	1.07a (\pm 0.45)	3.15a (\pm 1.34)	4.24ab (\pm 1.32)	14.38b (\pm 5.67)	16.87b (\pm 5.11)	P < 0.01	P < 0.01	P < 0.01
Alaimus (Ba-F)	3.50ab (\pm 1.75)	1.23b (\pm 0.29)	1.12a (\pm 0.58)	1.84ab (\pm 0.41)	2.55ab (\pm 1.29)		P < 0.05	
Leptolaimus (Ba-F)	0.86 (\pm 0.51)	1.25 (\pm 0.73)	0.19 (\pm 0.18)	1.05 (\pm 0.72)	0.54 (\pm 0.32)			
Aphelenchoides (Fu-F)	52.71a (\pm 9.45)	54.54a (\pm 12.54)	92.27ab (\pm 18.39)	89.99ab (\pm 15.78)	81.69b (\pm 10.68)			P < 0.05
Aphelenchus (Fu-F)	189.25 (\pm 37.63)	179.63 (\pm 26.24)	175.41 (\pm 33.91)	142.51 (\pm 22.05)	139.24 (\pm 21.80)	P < 0.01		
Ditylenchus (Fu-F)	0.06 (\pm 0.03)	0.26 (\pm 0.11)	0.32 (\pm 0.22)	1.58 (\pm 0.77)	1.10 (\pm 0.66)		P < 0.05	
Diphtherophora (Fu-F)	4.98a (\pm 2.00)	7.54b (\pm 1.55)	15.42b (\pm 6.17)	21.72b (\pm 5.85)	21.09b (\pm 6.07)		P < 0.05	P < 0.01
Tylencholaimus (Fu-F)	0.26 (\pm 0.13)	0.13 (\pm 0.09)	0.49 (\pm 0.26)	1.06 (\pm 0.74)	0.35 (\pm 0.21)			
Tylenchidae (Fu-F, Pp-F)	145.73 (\pm 16.16)	138.14 (\pm 18.45)	134.25 (\pm 22.45)	126.39 (\pm 18.65)	130.73 (\pm 17.64)	P < 0.01		
Psilenchus (Pp-F)	0.00 (\pm 0.00)	0.00 (\pm 0.00)	0.08 (\pm 0.08)	0.00 (\pm 0.00)	0.00 (\pm 0.00)			
Ecphyadophora (Pp-F)	0.30 (\pm 0.14)	0.87 (\pm 0.33)	0.90 (\pm 0.49)	0.99 (\pm 0.32)	1.68 (\pm 0.93)			
Paratylenchus (Pp-F)	0.53 (\pm 0.51)	0.00 (\pm 0.00)	0.11 (\pm 0.08)	0.06 (\pm 0.06)	0.00 (\pm 0.00)			
Pratylenchus (Pp-F)	10.94 (\pm 3.03)	17.96 (\pm 3.96)	11.61 (\pm 4.08)	19.15 (\pm 5.76)	22.47 (\pm 8.53)			
Tylenchorhynchus (Pp-F)	0.87a (\pm 0.29)	6.81a (\pm 4.58)	48.33b (\pm 9.93)	48.86b (\pm 10.61)	36.35b (\pm 5.06)	P < 0.01	P < 0.01	P < 0.01
Helicotylenchus (Pp-F)	0.44a (\pm 0.30)	0.24a (\pm 0.15)	2.07ab (\pm 1.39)	3.41ab (\pm 1.88)	4.95b (\pm 1.15)	P < 0.01	P < 0.01	P < 0.01
Meloidogyne (Pp-F)	2.24 (\pm 2.02)	0.10 (\pm 0.08)	0.06 (\pm 0.04)	0.00 (\pm 0.00)	0.08 (\pm 0.08)			
Xiphinema (Pp-F)	0.29ab (\pm 0.12)	1.39b (\pm 0.37)	0.17a (\pm 0.11)	0.29a (\pm 0.19)	0.51ab (\pm 0.27)	P < 0.05		
Tripyla (P)	0.00 (\pm 0.00)	0.02 (\pm 0.02)	0.07 (\pm 0.07)	0.04 (\pm 0.04)	0.00 (\pm 0.00)			P < 0.05
Qudsianematidae (O)	7.58 (\pm 1.24)	7.47 (\pm 1.44)	9.61 (\pm 1.93)	9.57 (\pm 1.96)	11.52 (\pm 2.03)			
Mylonchulus (P)	0.29 (\pm 0.15)	0.03 (\pm 0.03)	0.31 (\pm 0.16)	0.46 (\pm 0.24)	0.13 (\pm 0.06)			
Dorylaimidae (O)	1.19a (\pm 0.32)	6.07ab (\pm 2.35)	8.77b (\pm 2.23)	6.51b (\pm 1.48)	7.73b (\pm 1.44)	P < 0.01	P < 0.05	P < 0.01
Aporcelaimidae (P)	0.01 (\pm 0.01)	0.00 (\pm 0.00)	0.13 (\pm 0.09)	0.13 (\pm 0.13)	0.00 (\pm 0.00)			
Prionchulus (P)	0.03 (\pm 0.02)	0.00 (\pm 0.00)	0.00 (\pm 0.00)	0.00 (\pm 0.00)	0.05 (\pm 0.05)			
Discolaimus (P)	0.35a (\pm 0.17)	1.10b (\pm 0.29)	0.23a (\pm 0.11)	1.43ab (\pm 0.49)	1.17ab (\pm 0.47)		P < 0.01	P < 0.05

Letters following a mean indicate significant differences in abundance, based on post hoc tests, of a taxon among system \times tillage combinations (CST, CCT, OST, OCT, ONT, where C = Conventional Management, O = Organic Management, ST = Standard Tillage, CT = Conservation Tillage, NT = No Tillage). Nematode trophic groups are indicated as Ba-F = bacterial feeders; Fu-F = fungal feeders, Pp-F = plant-feeders, O = omnivores, P = predators.

The most important factor affecting abundance of nematode taxa was the combination of management system (ORG or CONV) with tillage (ST, CT, or NT). Management system alone affected a greater number of nematode taxa (15) than tillage (12 taxa significantly affected).

3.2. Effects of agricultural treatments on nematode trophic groups and soil food web indices

Across all treatments and sampling dates, the nematode assemblage was primarily composed of bacterial- and fungal-feeding nematodes, which comprised more than 75% of the individuals present.

Bacterial-feeder abundance was higher in ORG than in CONV plots ($P < 0.01$, Table 2). Abundances of predatory nematodes and of all nematode taxa combined were higher in the ORG plots than in CST. Plant feeders were more abundant in the ORG treatment, and fungal-feeding nematodes were not affected by treatments. The relative contribution of plant- and fungal-feeding nematodes to the whole assemblage was greater in CONV plots ($P < 0.01$, data not shown). Across all sampling dates, numbers of fungal-feeding, plant-feeding and omnivore nematodes did not differ among the five treatments, although plant feeders were affected by management system.

Taxa richness and EI values were higher in ORG than in CONV plots ($P < 0.01$, Table 2). In contrast, both the CI and BI values were significantly higher in CONV than in ORG plots ($P < 0.01$, Table 2). The SI was higher in the ONT treatment than in CONV plots ($P < 0.05$).

The soil food web faunal profile (Ferris et al., 2001) shows mean EI and SI values in different treatments in a bidimensional space with SI values on the x-coordinate and EI values on the y-coordinate. The progression from low SI and EI values, associated with CST and CCT, to highest values in OST, OCT, and ONT, represents a gradient from depleted and simple to enriched and complex soil food webs (Fig. 1).

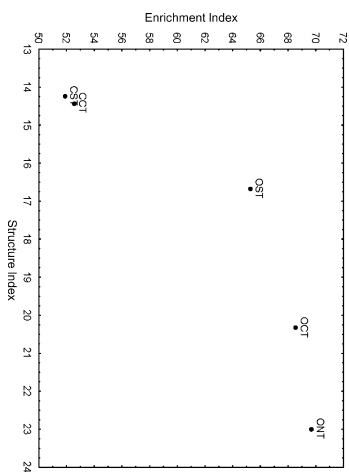


Fig. 1 – Faunal profile based on nematode abundance for the five treatments (note that scales of axes are adjusted to facilitate comparisons); CST = Conventional-Standard Tillage; CCT = Conventional-Conservation Tillage; OST = Organic-Standard Tillage; OCT = Organic-Conservation Tillage; ONT = Organic-No Tillage).

	CST	CCT	OST	OCT	ONT	Manag.	Tillage	Manag. × tillage
Total density	527.40a (±57.38)	596.34ab (±54.98)	796.85b (±78.83)	887.70b (±77.01)	821.60b (±55.02)	$P < 0.01$	$P < 0.01$	$P < 0.01$
Ba-F	109.36a (±16.35)	174.05b (±20.76)	296.24c (±30.99)	413.55c (±49.67)	360.77c (±26.93)	$P < 0.01$	$P < 0.01$	$P < 0.01$
Fu-F	320.42 (±41.92)	312.03 (±32.75)	351.94 (±42.82)	321.05 (±28.72)	310.51 (±29.59)			
Pp-F	88.18 (±10.77)	95.56 (±13.64)	129.47 (±19.26)	134.96 (±20.52)	129.73 (±18.16)	$P < 0.05$		
P	1.85a (±0.44)	7.22ab (±2.39)	9.38b (±2.26)	8.44b (±1.62)	9.08b (±1.76)	$P < 0.01$	$P < 0.05$	$P < 0.01$
O	7.59 (±1.24)	7.47 (±1.44)	9.74 (±1.93)	9.70 (±1.96)	11.52 (±2.03)			
S	11.27a (±0.46)	11.69a (±0.31)	13.17b (±0.50)	14.03b (±0.46)	13.81b (±0.44)	$P < 0.01$	$P < 0.05$	$P < 0.01$
EI	51.91a (±0.94)	52.57a (±1.15)	65.31b (±2.20)	68.58b (±2.41)	69.74b (±2.10)	$P < 0.01$	$P < 0.01$	$P < 0.01$
CI	75.61b (±2.86)	67.17b (±3.15)	42.25a (±4.07)	35.29a (±3.69)	33.19a (±3.08)	$P < 0.01$	$P < 0.01$	$P < 0.01$
SI	14.23a (±2.37)	14.42a (±2.35)	16.66ab (±2.48)	20.32ab (±2.74)	22.98b (±2.72)	$P < 0.05$		
BI	44.27a (±1.10)	43.37a (±1.05)	32.43b (±2.16)	28.29b (±2.07)	26.77b (±1.67)	$P < 0.01$	$P < 0.01$	$P < 0.01$
PredM	4.79a (±1.77)	8.44ab (±2.03)	6.98ab (±1.29)	11.60b (±1.75)	13.67b (±2.05)	$P < 0.01$	$P < 0.01$	$P < 0.05$
OmnM	7.26a (±1.90)	9.52ab (±1.19)	7.12a (±1.10)	16.63b (±2.21)	16.86b (±2.60)	$P < 0.01$	$P < 0.01$	$P < 0.01$
FS	36.86 (±6.63)	65.31 (±14.09)	64.50 (±12.28)	81.90 (±13.77)	101.52 (±17.48)	$P < 0.01$	$P < 0.05$	
Alg	16.68 (±4.34)	19.97 (±6.14)	8.26 (±2.10)	7.42 (±1.66)	7.00 (±1.43)	$P < 0.05$		

Mean (±S.E.) of total number of nematodes (total density) and nematode trophic groups (see Table 1 for nematode trophic group abbreviations) and mite trophic groups (PredM = predators; OmnM = omnivores; FS = fungivore-saprophyte, Alg = algivore; number of mites/core (5 cm diam. × 10 cm deep), nematode taxa richness (S) and soil food web indices (EI = Enrichment Index; CI = Channel Index, SI = Structure Index, BI = Basal Index). Letters following a mean indicate significant differences in abundance, based on post hoc tests, of a taxon among system × tillage combinations (CST, CCT, OST, OCT, ONT, where C = Conventional Management, O = Organic Management, ST = Standard Tillage, CT = Conservation Tillage, NT = No Tillage).

3.3. Effect of treatments on mite trophic groups

Seventy-five mite genera and species were identified in samples from the field. Mite taxa were then grouped into 25 higher categories (families or suborders) and classified into trophic groups. Over all treatments and time, most mites (70%) were classified as fungivores/saprophytes, followed by algivores (11.8%), omnivores (11.5%) and predators (6.7%) (Table 2). Predators, omnivores and fungivores were more abundant in the least disturbed ORG plots. Predators and omnivores were affected by management, tillage and the management × tillage interaction. Fungivores were not affected by the management × tillage interaction. Algivores were only affected by management system; they were in greatest abundance in CONV plots.

3.4. Time trends for nematodes

Abundances of predator, omnivore and plant-feeding nematodes at each sampling date were highly dependent on their abundances on previous dates (coefficient of concordance *k* between 0.48 and 0.53) (Table 3). Bacterial-feeding nematodes were more abundant in summer, and predators were very scarce in winter. Plant feeders showed the clearest pattern, with greatest abundances in August 2005 and 2006, when plants were mature and before crop harvest.

Of all soil food web and diversity descriptors, taxa richness and the SI at each sampling date had greatest dependence on their values at preceding samplings. The SI was a good indicator of the temporal trend of mite predator abundance, and follows a very similar temporal pattern to nematode predator abundance as well (Fig. 2).

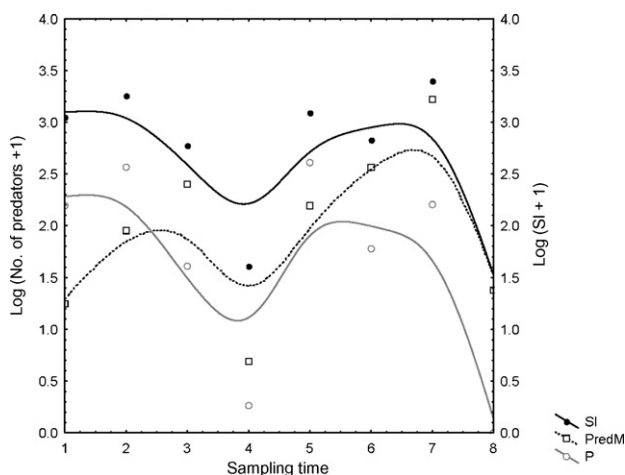


Fig. 2 – Log-transformed values of the Structure Index (SI) and abundance of predatory mites (PredM) (Log + 1 number per core) and nematodes (P) (Log + 1 number/100 g fresh soil) across eight sampling dates (1–8 correspond to March, June, August, and November 2005, and April, May/June, August/September, and November 2006). Curves were fitted by distance-weighted least squares.

Table 3 – Effect of sampling date (month/year) on total number of nematodes, trophic group abundance, taxa richness and soil food web indices.

	3/05	6/05	8/05	11/05	4/06	5-6/06	8-9/06	11/06	k	P
Total	796.11 (±88.53)	654.95 (±48.81)	838.17 (±91.68)	511.74 (±57.26)	590.77 (±73.61)	805.53 (±127.11)	632.71 (±73.95)	977.83 (±82.27)	0.24	0.001
Ba-F	206.53 (±25.43)	253.53 (±26.93)	273.31 (±40.14)	199.03 (±42.13)	255.13 (±39.77)	405.97 (±88.37)	205.27 (±37.27)	367.58 (±40.12)	0.20	0.004
Fu-F	390.38 (±48.83)	258.21 (±22.54)	351.55 (±40.28)	260.55 (±21.04)	241.26 (±35.04)	289.50 (±34.64)	260.83 (±29.50)	533.24 (±60.41)	0.25	0.001
Pp-F	175.51 (±23.96)	112.28 (±7.69)	197.39 (±22.56)	47.73 (±5.99)	75.02 (±18.12)	94.84 (±15.90)	147.93 (±24.98)	73.97 (±12.98)	0.48	0.000
P	8.94 (±1.65)	12.91 (±2.93)	4.77 (±1.44)	1.34 (±0.35)	13.62 (±3.89)	5.87 (±1.66)	9.09 (±2.29)	1.02 (±0.51)	0.53	0.000
O	14.63 (±2.97)	18.03 (±1.69)	11.16 (±2.55)	3.09 (±0.84)	5.75 (±1.11)	9.34 (±2.07)	9.59 (±1.26)	2.03 (±0.53)	0.51	0.000
S	13.09 (±0.41)	13.92 (±0.52)	13.62 (±0.56)	9.62 (±0.29)	13.96 (±0.41)	12.67 (±0.48)	14.60 (±0.57)	10.87 (±0.49)	0.62	0.000
EI	54.54 (±1.15)	55.17 (±1.85)	57.47 (±1.93)	61.15 (±3.03)	68.56 (±3.37)	66.62 (±4.05)	61.16 (±3.11)	68.32 (±2.97)	0.34	0.000
CI	63.77 (±2.90)	51.98 (±3.63)	50.90 (±4.32)	55.80 (±6.37)	40.13 (±8.81)	44.30 (±8.25)	55.97 (±7.86)	42.76 (±5.97)	0.19	0.006
SI	21.30 (±3.49)	26.03 (±2.32)	15.88 (±2.36)	5.03 (±0.89)	21.57 (±2.36)	18.56 (±3.26)	29.72 (±2.60)	3.70 (±1.14)	0.56	0.000
BI	40.37 (±1.48)	38.52 (±1.66)	39.17 (±1.93)	38.02 (±3.00)	28.56 (±3.01)	31.28 (±4.04)	32.88 (±2.54)	31.44 (±2.98)	0.26	0.000

Repeated measures non-parametric Friedman ANOVA. Mean (±S.E.) of total number of nematodes and nematode trophic group abundances (numbers/100 g of fresh soil), nematode taxa richness (S) and soil food web indices (see Table 2 for definition of abbreviations). Coefficient of concordance (*k*) and level of significance (*P*) are shown.

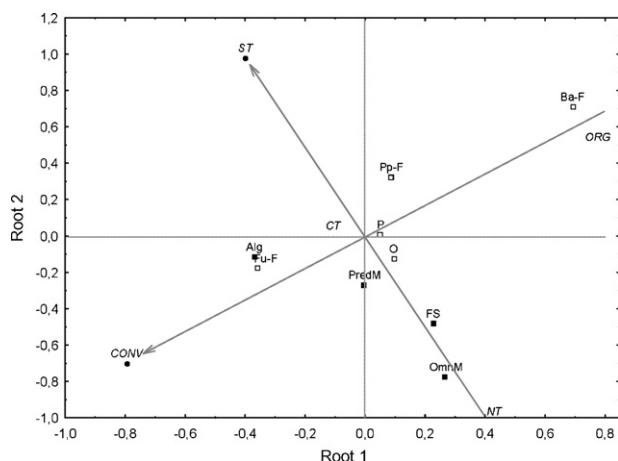


Fig. 3 – Canonical Correspondence Analysis biplot of associations between nematode and mite trophic groups with treatments (CONV = Conventional Management, ORG = Organic Management, ST = Standard Tillage, CT = Conservation Tillage, NT = No Tillage. See Table 1 for other definitions).

3.5. Relationships between nematodes, mites and treatments

The relationships between nematode and mite trophic groups can be summarized in a canonical correspondence analysis (CCA) bi-plot (Fig. 3). The first extracted root ($P < 0.01$) accounted for 65% and 19% of the management and nematode variables respectively, while the second root ($P = 0.14$) accounted for 19% and 11% of the variance. Bacterial-feeding nematodes were strongly associated with ORG, while fungal-feeding nematodes and algivororous mites were associated with CONV. Abundances of all the other trophic groups were more strongly associated with tillage than with the management system; predator and omnivore nematodes, and predator, omnivore, and fungivore/saprophyte mites were associated with CT or NT (Fig. 3).

Nematode and mite abundances were subjected to discriminant analysis to determine differences among biological assemblages in each treatment. As determined by the squared Mahalanobis distances between group centroids, the five treatments differed significantly from each other. Treatments OCT and ONT differed by the smallest distance (1.72) while the greatest distances were between the OCT and ONT treatments and CST (9.16 and 10.07 respectively). The difference between OST and OCT was greater than that between CST and CCT (6.07 and 2.43 respectively) (Table 4).

Simple regression analyses showed that the EI was a significant positive predictor of bacterial-feeding and predatory nematodes and of predatory and omnivorous mites, and a significant negative predictor of fungal- and plant-feeding nematodes and algivororous mites (Table 5). The CI provided the exact opposite indication and was also a significant negative predictor of fungivore/saprophyte mites. The SI was related to the abundance of bacterial-feeding and omnivore nematodes, fungivore/saprophyte mites and predatory nematodes and mites; it was a negative predictor of

Table 4 – Squared Mahalanobis distances between group centroids in the discrimination between treatments by nematode and mite taxa abundances.

	CST	CCT	OST	OCT	ONT
CST	0.00				
CCT	2.43**	0.00			
OST	2.61**	4.29**	0.00		
OCT	9.16**	6.16**	6.07**	0.00	
ONT	10.07**	5.81**	7.89**	1.72*	0.00

Discriminant analysis performed on nematode and mite taxa abundances in different treatments (CST, CCT, OST, OCT, ONT, where C = Conventional Management, O = Organic Management, ST = Standard Tillage, CT = Conservation Tillage, NT = No Tillage).

* $P < 0.05$.

** $P < 0.001$.

fungal-feeding nematodes. Finally, there was a negative relationship between the BI and bacterial-feeding nematodes, omnivore mites, and predatory mites and nematodes, and a positive relationship with fungal- and plant-feeding nematodes, and with algivororous mites (Table 5). Such relationships can be summarized in a model that characterizes the two different soil assemblages. The model was constructed based on the associations detected by simple regression among trophic group abundances and experimental treatments and among soil food web indices and trophic groups of nematodes and mites (Fig. 4). Each association was composed of nematode and mite trophic groups that were most abundant in the same treatments, and soil food web indices were considered predictive when they had a significant positive or negative relationship with trophic group abundances. Thus, Association I was composed of bacterial-feeding and predatory nematodes and mites, and was typically present in the OCT/ONT plots. High values of the SI and EI were positive predictors of this association, which comprised, together with omnivore nematodes and mites, and fungivore/saprophyte mites, the biological assemblage in the ORG management system, irrespective of tillage treatment. Association II was composed by fungal- and plant-feeding nematodes and algivororous mites, and it was indicated by high values of the BI and CI.

Table 5 – Significant regression coefficients between soil food web indices and nematode and mite trophic groups. Only significant coefficients ($P < 0.05$) are indicated.

	EI	CI	SI	BI
Ba-F	0.79	-0.88	0.29	-0.80
Fu-F	-0.69	0.81	-0.50	0.78
Pp-F	-0.32	0.31		0.26
P	0.21	-0.28	0.54	-0.34
O			0.51	
PredM	0.23	-0.20	0.38	-0.30
OmnM	0.41	-0.36		-0.42
FS		-0.24	0.34	
Alg	-0.30	0.26		0.30

See Table 2 for definition of abbreviations.

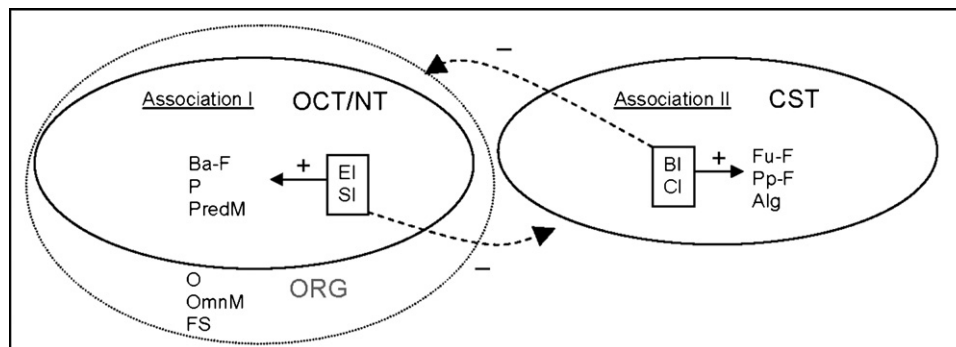


Fig. 4 – Association of nematode and mite trophic groups with soil food web indices. Relationships were inferred by ANOVA and simple regression. EI and SI were higher in organic systems (ORG) than in conventional ($P < 0.01$, see Table 2), while BI and CI were associated with conventional standard tillage (CST) ($P < 0.01$, see Table 2). Each pair of indices was a significant predictor (positive, solid line) of the abundances of the trophic groups within the same association and of the abundances of the trophic groups in the other association (negative, dotted line) ($P < 0.05$, see Table 5) (OCT/NT = Organic Conservation and No Tillage). See Table 2 for abbreviations.

4. Discussion

The aim of this study was to test the hypothesis that soil food web indices based on nematode assemblages are reliable indicators of other soil-dwelling organisms. At the same time, we expected to develop inferences in regard to mite-nematode interactions under different agricultural practices.

Tillage, application of mineral fertilizers and chemical pest control are basic components of conventional agricultural systems. They influence soil nematode biodiversity by altering nematode abundance (Sánchez-Moreno et al., 2006), and generally suppressing predatory and omnivorous taxa (Tenuta and Ferris, 2004; Sánchez-Moreno and Ferris, 2007).

Of the 37 nematode taxa identified, 14 taxa had the following ranking according to a gradient of management and tillage practices from lowest to highest abundance: ONT < OCT < OST < CCT < CST. The type of management – organic or conventional – was the most important factor determining the taxal composition of the nematode community. Organic systems generally sustain higher N mineralization rates (Forge and Simard, 2001), enhanced soil fertility, higher biodiversity and greater bacterial biomass than conventional farms (Mäder et al., 2002; Mulder et al., 2003; van Diepeningen et al., 2006).

Increase in bacterial- and fungal-feeding nematodes is associated with higher N availability (Ferris et al., 2004). Both the EI and Rhabditidae abundance were significantly higher in ORG plots in this study, indicating more abundant microbial populations and eventually more effective organic matter decomposition and higher soil fertility (Ferris et al., 2004). Enrichment-opportunistic bacterial-feeding nematodes with short life cycles (such as Rhabditidae and *Panagrolaimus*) respond rapidly to organic matter or fertilizer incorporation, and were more abundant in the ONT treatment than were basal bacterial feeders (such as *Acroboloides* and *Cephalobidae*), which do not disappear when the soil is perturbed or chemically fertilized (Ferris et al., 2001; Forge and Simard, 2001). Basal bacterivorous nematodes were more abundant in the CONV system plots and contributed to the low values of the EI and the high values of the BI. Higher BI values in CONV

plots indicate the presence of a basal soil food web, typically representative of highly perturbed natural and agricultural soils with low organic input (Ferris et al., 2001). The CI, indicator of fungal-mediated decomposition channels and slower organic matter decomposition (Ferris et al., 2001), was significantly higher in the CONV plots. Input of readily decomposed organic materials from compost in ORG plots may have favored bacterial decomposition channels and opportunistic bacterial-feeding fauna (Bardgett and Cook, 1998). In CONV plots organic matter derived from leaf litter and crop residues with high C/N ratios, more recalcitrant to decomposition, increased the ratio of fungal- to bacterial-feeding nematodes (Ferris and Matute, 2003). Although it has been reported that residue decomposition by fungi increases under no-till due to the lack of disruption of hyphal networks (Minoshima et al., 2007), we found a tendency towards higher fungal participation under standard tillage practices. The incorporation of organic matter into the soil through tillage may have had an effect on the EI and CI values, but the tillage effects were obscured by the stronger effect of the management system.

SI values are usually low in agricultural systems (Berkelmans et al., 2003; van Diepeningen et al., 2006), and the SI values in our study were extremely low (14–23). However, SI values were highest in the ONT treatment, indicating the presence of a more complex and longer soil food web, while CONV treatments had the lowest indication of soil food web complexity. As indicated from laboratory studies (Tenuta and Ferris, 2004), the reduction of the higher links of the soil food web is correlated with the application of fertilizers and pesticides. In a field trial near our study site, Minoshima et al. (2007) did not find higher values of the SI under no-till compared to standard tillage, probably due to the large influence of many years of conventional management on the higher levels of the soil food web. In general, our results agree with the observations of Bouwman and Zwart (1994), who reported that biomasses of bacterial-feeding and predatory nematodes were higher while those of plant- and fungal-feeding nematodes were lower in “integrated” than in CONV fields 4 years after the establishment of the treatments.

Similarly to bacterial-feeding and predatory nematodes, predatory and omnivorous mites were in greater abundance in the ORG plots. Cultivation intensity reduces mite populations (Bedano et al., 2006) including Oribatida (fungivore/saprophyte) and the predatory Gamasina, some of the mite taxa most sensitive to soil perturbation; their abundances may be reduced to 50% after tillage (House and Parmelee, 1985; Hülsmann and Wolters, 1998). Absolute abundances of both groups were significantly higher in ONT and OCT than in CST, and mites in the Gamasina were always more abundant in the ORG plots. Oribatids are associated with high soil organic matter content in most terrestrial ecosystems (Behan-Pelletier, 1999) and are negatively affected by herbicides (Moore et al., 1984), which could explain their association with the ORG plots.

Soil microarthropods may reduce nematode populations; in a microcosm study, Hyvönen and Persson (1996) found greater nematode abundances in soils free of arthropods, and consecutively smaller abundances when fungivorous arthropods (collembola and oribatid mites) and predators were introduced into the soil. Fungivorous arthropods seemed to reduce fungal-feeding nematode populations by increasing the competition for food, although there was no decrease in fungal hyphal biomass. On the contrary, other studies have suggested that fungivory by arthropods may induce compensatory fungal growth (Krivtsov et al., 2003), which could enhance fungal-feeding nematode populations. Our results do not allow the inference of a competitive relationship; algivorous mites and fungal-feeding nematodes were both abundant in CONV plots.

In a microcosm study, Ruf et al. (2006) found ^{13}C derived from plant litter in bacterial-feeding nematodes (*Rhabditis*) and the predatory mite *Hypoaspis* (*Geolaeaps*) *aculeifer*. The predatory mite obtained the ^{13}C from the bacterivorous nematode and from fungivorous Collembola (the only two food sources in the experiment), suggesting that mites were more closely connected to the bacterial than to the fungal decomposition channel. In contrast, our study suggests that, at least in soils under organic management, predatory mites are more closely connected to the bacterial-channel, probably due to higher mite predation rates on bacterial-feeding nematodes. High mite predation rates on bacterivorous nematodes such as *Wilsonema*, *Acrobeloides* and *Metateratocephalus*, have been previously reported (Hyvönen and Persson, 1996).

Absence of physical perturbation and chemical inputs in ONT plots led to a nematode–mite assemblage characteristic of high soil food web structure, with abundant predators and a large bacterial-feeding community, probably supported by large microbial populations which provide a consistent food source for the higher trophic levels of the soil food web. Some authors have reported increased abundances of nematodes and mites under reduced tillage correlated with soil total N (Nakamoto et al., 2006). In other studies, living mulch increased the abundances of nematodes and mites associated to the fungal decomposition channel, and large populations of higher trophic groups (Nakamoto and Tsukamoto, 2006). We did not observe a shift from bacterial to fungal dominance linked to abundant populations of predators; the ORG plots maintained active bacterial decomposition channels 2 years after the treatment began. However, ORG plots had cover

crops and crop residues incorporated into the soil periodically throughout the experiment, that provided resources to support large populations of bacterial-feeding nematodes which, together with reduced perturbation, maintained higher trophic levels. Bacterial-feeding nematodes, predatory nematodes, and predatory mites may exhibit prey preference (Bilgrami, 1994; Khan et al., 1995; Venette and Ferris, 1998; Newsham et al., 2004). By inducing compensatory growth and feeding preference in certain nematode taxa, the higher diversity and abundance of predatory nematodes and mites in organic plots may have enhanced prey availability and diversity for bacterial-feeding nematodes (thus the EI values).

The conventional and organic systems in this study supported two different assemblages characterized by different abundances of nematode and mite trophic groups and assessed by high values of different soil food web indices. One of the most abundant mite taxa found in this study, the fungivore/saprophyte Oribatida, is associated with organic matter in most terrestrial ecosystems (Behan-Pelletier, 1999). Both fungivore/saprophyte mites and bacterial-feeding nematodes were more abundant in ONT; however, fungivore/saprophyte mites were excluded from Association I, which characterizes the assemblage present in the ORG system, because its abundance was not predicted by the BI and EI indices.

The strong bacterial decomposition channel and the presence of large populations of predators were the main attributes of the organic assemblage. Predatory nematodes and mites exhibited a very similar temporal pattern and the SI, as expected, was especially reliable in reflecting the abundance of predatory mites.

Algivorous endeostigmatid mites and fungal-feeding nematodes shared common soil food web predictors. Algae are abundant components of the soil microflora and occupy similar niches to soil bacteria and fungi. Although algal-feeding has been described as a nematode trophic habit, no nematode taxa have been exclusively assigned to this trophic group (Yeates et al., 1993). The CI reflected both higher numbers of fungal-feeding nematodes and algivorous mites, but until more knowledge is available regarding food sources for mites and nematodes, no further functional relationships can be inferred between both groups. High abundances of fungal- and algal-feeding organisms, and the absence of predators, characterized the conventional assemblage.

Functional groups are “abstractions that help us to view more clearly the resulting emergent properties and processes that have become part of the environment” (Brussaard, 1998) and, in this case, functional groups of different taxa are associated in solid relationships. These associations or assemblages of nematode and mite trophic groups can be considered as “guilds” in the sense of Blondel (2003), sharing resources and exploiting them similarly.

5. Conclusions

Nematode and mite populations in agricultural fields respond similarly to agricultural management. There were functional parallels between predatory nematodes and mites, fungal- and plant-feeding nematodes and algivorous mites, and

bacterial-feeding nematodes and fungivore/saprophyte mites. Soil biota provided high-resolution discrimination of agricultural practices, with greatest differences in the soil biota composition between CST/ONT and smallest differences between OCT/ONT.

Bacterial-feeding nematodes, fungivore/saprophyte mites and predatory nematodes and mites were more abundant in organic-no till plots, supporting a soil food web with abundant organisms at higher trophic levels. Cover crops, crop residues and composts as surface mulches, together with lack of physical disturbance, were sufficient to support and maintain this structure. Conventional farming systems, with high C/N crop residues and much lower organic matter input supported fungal-mediated food webs mainly composed of fungal-feeding nematodes and algivorous mites.

Soil food web indices, based on the abundances of nematode functional guilds, reflected the characteristics of the mite community. Our results validate hypotheses regarding the bioindicator potential of the nematode fauna, at least with regard to soil mite assemblages.

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