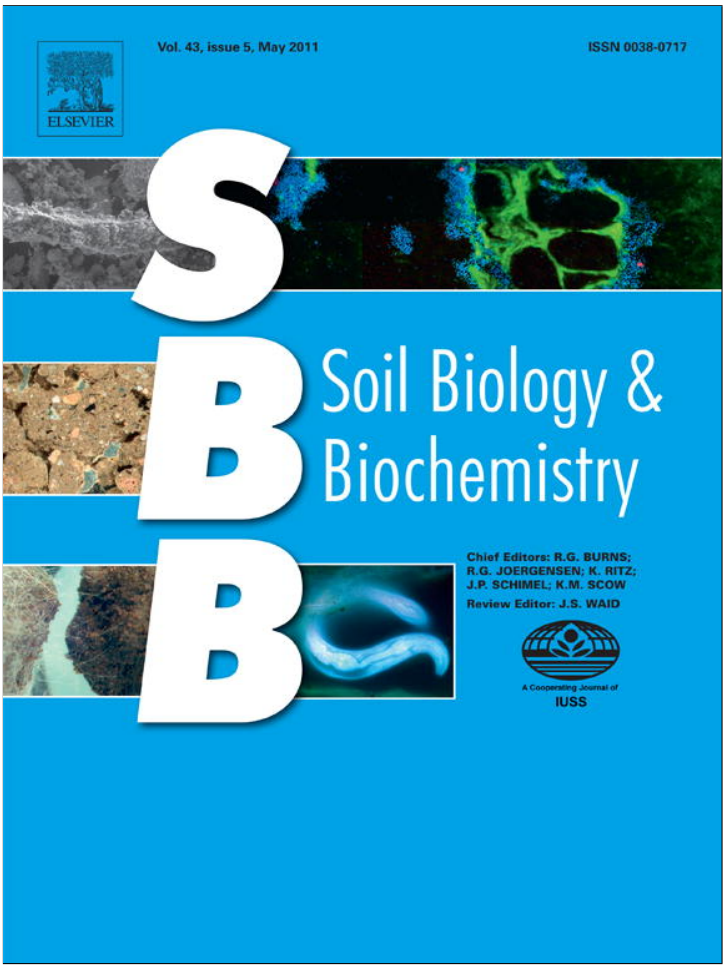

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The distribution of nematodes and soil microbial communities across soil aggregate fractions and farm management systems

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ABSTRACT

We hypothesized that nematode and microbial communities vary between soil aggregate fractions due to variations in physical and/or resource constraints associated with each fraction and that this, in turn, contributes to management impacts on whole soil food webs. Nematode and microbial communities were examined within three soil fractions: large macroaggregates (LM; >1000 μm), small macroaggregates (SM; 250–1000 μm) and inter-aggregate soil and space (IS; <250 μm) isolated from soils of four agricultural management systems: conventional tomato (CON), organic tomato (ORG), a minimum till grain–legume intercrop with continuous cover (CC) and an unmanaged riparian corridor (RC). Aggregate fractions appeared to influence nematode assemblages more than did management system. In general the IS and LM fractions contained higher densities of all nematode trophic groups than did SM. Management × fraction interactions for bacterivores and fungivores, however; suggested a non uniform trend across management systems. The IS fraction exhibited stronger trophic links, per the nematode structure index (SI), while the LM and SM fractions had more active fungal decomposition channels as indicated by the channel index (CI). Higher adult to juvenile ratios in the LM and IS than the SM fraction, and a positive correlation between nematode density in the IS fraction and the proportion of macroaggregates in the soil, indicated an association between soil structure and nematode distribution. Microbial communities varied across both aggregate fractions and management systems. Phospholipid fatty acid (PLFA) analysis suggested that the LM fraction contained greater microbial biomass, gram positive bacteria, and eukaryotes than the IS fraction, while SM contained intermediate PLFA associated with these groups. Total PLFA was greater under RC and ORG than under CC or CON. Total PLFA was positively correlated with % C in soil fractions while nematode abundance exhibited no such relationship. Our findings suggest that microbial communities are more limited by resource availability than by habitable pore space or predation, while nematode communities, although clearly resource-dependent, are better associated with habitable pore space for the soil fractions studied here.

1. Introduction

Soils consist of particles of sand, silt and clay bound into aggregates of various sizes by organic and inorganic agents. The distribution and stability of aggregates, and of the pores within and between them, affect the composition and activity of soil biotic communities (Tisdall, 1994; Mikha and Rice, 2004). Besides access to food sources, a fundamental requirement for all soil organisms is adequate space to accommodate their growth and movement (Jones and Thomasson, 1976) and allow for adequate water and gas exchange (Wallace, 1958). Soil organisms live inside soil aggregates or between the aggregates according to their feeding habits, size and access to resources. For example, bacteria can occupy pores less than 3 μm dia, whereas larger organisms, such as nematodes and protozoa, are limited to larger pores (Hassink et al., 1993; Jones, 1982). In addition to occupying diverse ecological niches in the

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soil, nematodes (and other soil fauna) possess the ability to move toward their food source (Griffiths and Caul, 1993). Given that soil pore spaces depend to a great extent on the size and arrangement of soil aggregates (Wu et al., 1990; Lebron et al., 2002), the distribution of soil fauna, with variable body sizes, likely depends on the degree of soil aggregation and the resources associated with different soil structures (Wallace, 1968; Quénéhervé and Chotte, 1996).

Management practices strongly influence the abundance and diversity of soil faunal communities (Yardim and Edwards, 1998; Neher and Olson, 1999; Briar et al., 2007). Crop rotation, tillage and organic matter inputs alter the soil structure and the size-class distribution of aggregates (Angers, 1992; Kushwaha et al., 2001; Six et al., 2000). However, the extent to which management-driven changes in soil structure affect the composition of faunal communities is not well understood. As the primary regulators of decomposition, bacteria and fungi form key linkages between detritus and soil fauna, and comprise the principal resource base for soil food webs (Ingham et al., 1986; Moore et al., 2004; Ruess and Ferris, 2004). Both agricultural management and location within the soil matrix (i.e., inside or outside of soil aggregates) have been shown to influence the size and diversity of microbial communities (Petersen et al., 1997; Bossio et al., 1998; Mummey et al., 2006). Thus management-induced changes in microbial communities and the associated alterations to aggregate size distribution can have important implications for the functioning and stability of soil food webs.

Nematodes are an abundant and diverse group of soil invertebrates (Yeates, 1979) and are important members of the soil biotic community. Assessment of nematode community composition can provide unique insights into soil biological processes (Ritz and Trudgill, 1999); because different feeding groups of nematodes are specialized with respect to their food sources and play essential roles in functioning of ecosystems (Yeates et al., 1993; Ferris and Bongers, 2006; Ferris and Matute, 2003; Ferris et al., 1996; Ingham et al., 1985). Nematode faunal analysis, based on the relative weighted abundance of colonizer–persister (c–p) guilds, provides a metric of soil food web functioning and associated environmental stresses (Ferris et al., 2001). The analysis includes calculation of indices of food-web enrichment (EI), structure (SI), and decomposition channel (CI) conditions which provide critical information about belowground processes (Ferris et al., 2001; Bulluck et al., 2002; Bongers, 1990). The EI indicates the response of primary decomposers to the available resources, while SI suggests prevalence of trophic linkages (Ferris et al., 2001). The CI measures dominance of fungal or bacterial decomposition channels (Ferris et al., 2001).

We studied the role of soil aggregation in determining nematode and microbial community composition under contrasting management systems. More specifically, we examined nematode and microbial populations, as well as key food-web indices, within soil aggregate fractions across a range of management intensities. We hypothesized that both nematode and microbial communities vary among different aggregate size fractions due to physical and resource constraints associated with each soil fraction. Additionally, we postulated that differences in soil aggregation between management systems and variations in community structure between aggregate fractions explain, in part, observed trends in whole soil food webs across different types of agroecosystem management.

2. Materials and methods

2.1. Selection of habitats

Three agricultural systems and one native habitat were selected at the Russell Ranch long-term agricultural research site near the University of California Davis. The four management systems consisted of: 1) conventional tomato (CON) relying primarily on synthetic fertilizer inputs for fertility, 2) organic tomato (ORG) with annual inputs of leguminous cover crop and compost, 3) a minimum tillage field with continuous cover of grains and legumes (CC), and 4) an unmanaged riparian corridor (RC), with multi-strata vegetation (large trees, shrubs, herbaceous perennials, and annual plants) located adjacent to the production fields. Both ORG and CON management are part of a larger field experiment, detailed by Denison et al. (2004), and were represented by three replicate plots in a completely randomized design. The CC and RC management system were each represented by a single plot of land. Replicates for CC and RC were obtained from three equally spaced 10 m long transects for each treatment.

2.2. Soil sampling

Soil samples were collected in July of 2008, one week after irrigation of all plots to ensure active nematode and microbial communities and to facilitate the removal of intact soil cores. Three soil cores (5 cm dia. × 10 cm deep) were removed from each replicate plot or transect and combined to form one composite sample per replicate plot/transect. Soils were immediately placed on ice following sampling and kept cool prior to laboratory analyses.

2.3. Soil fractionation

Field moist soils were gently broken by hand along natural planes of weakness and passed through an 8-mm sieve. Subsamples (100 g) of moist soil were then wet-sieved using methods modified from Elliott (1986). Soil was placed on a 1000 μm sieve and slaked by submersion in deionized water for 5 min. The sieve was then gently moved up and down by hand for a total of 50 cycles over a 2 min period. Material remaining on the sieve was rinsed into containers, while material passing through the 1000 μm sieve mesh was transferred to a 250 μm sieve for further fractionation, ultimately generating three aggregate fractions: large macroaggregates (>1000 mm; LM), small macroaggregates (250–1000 μm; SM), and fine material (<250 μm). Small aggregates passing through a 250 μm sieve are considered too small for nematodes to enter and this fraction will thus be referred to as inter-aggregate soil and space (IS). The sieving process was repeated for each soil sample multiple times, in order to generate sufficient material from each soil fraction for nematode extraction (~50 g) and phospholipids fatty acid (PLFA) analysis (8 g). Additionally, on the final sieving cycle, sub-samples of the three aggregate fractions were transferred to separate pre-weighed aluminum pans and dried in an oven at 60 °C to determine the proportion of whole soil weight in each fraction. Mean weight diameter (MWD), a weighted average of the three aggregate size classes, was calculated as an index of aggregate stability for each soil using the following equation:

$$\mathrm{MWD} = \sum_i {}^{*}\mathrm{P_i S_i}$$

where S_i is the average diameter (μm) for particles in the ith fraction and P_i is the proportion of the whole soil in this fraction (van Bavel, 1950).

2.4. Elemental analyses

Oven-dried soil fractions were ground and then sub-sampled (30 mg) for analysis of total C and N concentrations using a PDZ Europa Integra C–N isotope ratio mass spectrometer (Integra,

Germany) at the University of California Stable Isotope Facility (for further details see http://stableisotopefacility.ucdavis.edu).

2.5. Nematode analyses

Nematodes were extracted from soil aggregate fractions using a modified sieving and Baermann funnel technique (Barker, 1985). Soil fractions were agitated gently for several minutes by hand to disperse the aggregated particles and enhance the efficiency of extraction of nematodes within the aggregates. The total numbers of nematodes were counted in each sample under a microscope at 50× magnification and the first 200 individuals were identified at 100–400× to genus/family level. If the sample contained fewer than 200 nematodes, all were identified. Nematode counts were expressed as the number of nematodes in each soil fraction (100 g of dry soil fraction).

Each nematode identified in a given sample was recorded as an adult or juvenile to allow determination of the population stage structure. Nematode taxa were assigned to trophic groups (Yeates et al., 1993) and functional guilds (Bongers and Bongers, 1998). Given the uncertain trophic habit of the nematodes in the family Tylenchidae, half of nematodes of such taxa were considered fungal feeders and half as plant feeders (Forge and Simard, 2001; Yeates et al., 1999; Okada et al., 2002). Soil food-web indices: 1) Enrichment Index (EI, indicator of the prevalence of organic matter decomposition pathways mediated by bacteria), 2) Channel Index (CI, indicator of the prevalence of organic matter decomposition pathways mediated by fungi), 3) Structure Index (SI, indicator of soil food-web length and connectance), and 4) Basal Index (BI, indicator of depleted and stressed soil food webs) were calculated following Ferris et al. (2001) to provide diagnostics of soil food-web functioning.

2.6. PLFA analyses of soil

The microbial community composition of each fraction was assessed using PLFA analysis following methods reported previously (Frostegård and Bååth 1996; Bossio et al., 1998; Zelles, 1999; Cordova-Kreylos et al., 2006). Briefly, soil–water solutions for each fraction were centrifuged and excess water poured off. The remaining soil from each fraction was frozen (80 °C) and freeze-dried, while 8 g of dry material was used for lipid extraction. Total lipids were extracted with a one-phase chloroform/methanol/phosphate buffer. Phospholipids were separated from neutral and glycolipid fatty acids with a solid phase extraction column (0.58 Si; Supelco Inc., Bellafonte, PA). Fatty acids were then converted to fatty acid methyl esters for analysis of individual phospholipid fatty acids using a Hewlett-Packard 6890 Gas Chromatograph fitted with a 25 m Ultra 2 (5% phenyl)-methylpolysiloxane column (J & W Scientific, Folsom, CA). Fatty acids were identified using the Sherlock software from Microbial Identification Systems (Microbial ID, Inc, Newark, DE). PLFA biomass was expressed in nanomoles of PLFA per gram (dry weight) soil.

Microbial indices were calculated using key biomarkers in order to compare soil fractions and management treatments (Bossio et al., 1998; Zelles, 1999; Fierer et al., 2003; Kaur et al., 2005; Cordova-Kreylos et al., 2006). The following biomarkers and ratios were used: Total PLFA (sum of all PLFAs detected, nmol/g dry soil), diversity (number of PLFAs detected), fungi:bacteria ratio ((18:2 ω6c)/(i15:0 + a 15:0 + 15:0 + i16:0 + 16:1 ω5c + i17:0 + a17:0 + 17:0cy + 17:0 + 19:0 cy)), gram positive (sum of all branched PLFAs), gram negative (sum of all monounsaturated PLFAs), actinomycetes (10Me PLFAs), fungi (18:2 ω6c), eukaryotes (sum of 20: 20:4 ω6,9,12,15c, 20:2 ω6,9c). The cy:precursor (17:0cy/16:1 ω7c) ratio was also used as an indicator of nutritional stress in bacterial communities. The suffixes 'c' and 't' indicate *cis* and *trans*, the prefixes 'i', 'ai', and 'Me' indicate to iso, anteiso, and mid-chain methyl branching, and the prefix 'cy' refers to cyclopropyl rings (Navarrete et al., 2000).

2.7. Statistical analyses

Management system differences for whole soil properties (e.g., total soil C, N and MWD) were tested by one factor ANOVA. Comparisons were also made among three aggregate size fractions and four management systems for the nematode functional guilds and food-web indices, soil C and N content as well as microbial communities and indices with a variation of a split-plot design, where correlation is allowed between fractions within each sample, using PROC MIXED in SAS Ver. 9.1.3 (SAS Institute, Cary, NC). In the model, management was considered the main effect and aggregate fraction a sub-plot factor. Management and fraction, as well as the management × fraction interaction were considered fixed effects, while replicate plot/transect was treated as a random effect. Comparisons of the means for fractions and management systems were made using Tukey's honestly significant difference. The inability to draw causal inferences for management system effects involving RC and CC is noted and thoroughly recognized in the reporting and interpretation of statistical test results. Simple linear regression was used to examine key relationships between soil C, aggregation characteristics, as well as nematode and microbial indices. Natural log transformations were applied as needed to meet the assumptions of ANOVA. In addition to ANOVA based analyses, principal components analyses (PCA) were performed using Minitab Version 15.1.3 (Minitab, Inc., State College, PA) to gain insights of the multivariate relationship between key nematode and microbial indices as well as aggregate properties using the following variables: total nematode abundance, EI, CI, SI, total PLFA, fungi:bacteria ratio, cy:precursor ratio, and C concentration of each fraction.

3. Results

3.1. Soil aggregation and distribution of C and N among aggregate fractions

Soil structure differed significantly between management systems, as was demonstrated by higher MWD ($P = 0.008$) under ORG and RC (1945 μm and 1887 μm; respectively) relative to CON management (1064 μm; Table 1). Effects on aggregation was also apparent in the percentage of whole soil in the LM fraction, with the highest amounts under RC and ORG management (38.7% and 38.5%; respectively), followed by CC (33.1%), and CON with only 18.1% of the whole soil found in the LM fraction. Correspondingly, the proportion of the whole soil represented by the IS fraction was highest in CON (52%) and lowest under ORG (34.7%). Management systems differences for total C and N in the whole soil were very pronounced, with C concentrations for the bulk soil under RC (1.84%) nearly double that of soil C under CON (0.98%) management ($P < 0.001$; Table 1). When comparing the different fractions, large (LM) and small macroaggregates (SM) consistently displayed higher C and N concentrations than soil in the IS fraction ($P < 0.001$; data not shown). A significant interaction between management and fraction ($P < 0.01$) revealed that differences between the macroaggregate fractions (LM + SM) and IS for both C and N were much greater for RC than other management systems. The relationship between aggregation and soil C was also apparent from a significant correlation between MWD and % C in the bulk soil ($P = 0.007$, $R^2 = 0.52$; data not shown).

Table 1
Aggregate stability, distribution of soil aggregate fractions and total soil C and N under four management systems: conventional tomato (CON), minimum tillage with continuous cover crops (CC), organic tomato (ORG) and unmanaged riparian corridor (RC).

Management System	MWD[a] (μm)	Aggregate Fractions[b]			Soil C (%)	Soil N (%)
		LM (% of Whole Soil)	SM (% of Whole Soil)	IS (% of Whole Soil)		
CON	1064A	18.1A	29.2A	52.7A	0.94A	0.11A
CC	1658AB	33.1B	16.6B	50.3A	1.17B	0.13B
ORG	1945B	38.5B	26.7A	34.8B	1.42C	0.17C
RC	1887B	38.7B	14.1B	47.2AB	1.84C	0.18C

Capital letters to the right of each value indicate significantly different means between management systems according to Tukey's HSD.
[a] MWD = mean weight diameter.
[b] LM = large macroaggregates (>1000 μm); SM = small macroaggregates (250–1000 μm); IS = inter-aggregate soil and space (<250 μm).

3.2. Distribution of nematodes across soil aggregate fractions and management systems

Nematodes in this study were dominated by several key taxonomic groups: *Acrobeloides*, *Aphelenchus* and *Tylenchidae*, cumulatively representing over 70% of all nematodes identified (Table 2).

In general, aggregate fraction appeared to exert greater influence on nematode communities than management system. On average, the IS and LM fractions contained higher nematode densities (2444 and 1829 nematodes per 100 g of soil fraction; respectively) than the SM fraction (1030 nematodes per 100 g of soil fraction). This general trend of IS $\geq$ LM > SM was apparent for both bacterial and fungal feeding nematodes, as well as the sum of omnivorous and predacious nematodes (Table 3). However, significant management × fraction interactions for both bactiverous and fungivorous groups ($P < 0.05$), suggest that this trend was inconsistent across management systems. Plant-parasitic nematodes, on the other hand, were present at significantly higher

Table 2
Mean abundance of nematodes detected within three soil aggregate fractions under four management systems: Conventional tomato (CON), minimum tillage with continuous cover crops (CC), organic tomato (ORG) and unmanaged riparian corridor (RC).

Nematode Genera/Family (*C–p* value)	Management System											
	CON			CC			ORG			RC		
	Soil Aggregate Fraction[a]											
	LM	SM	IS	LM	SM	IS	LM	SM	IS	LM	SM	IS
Dauer larvae (Ba1)	0	0	10.1	4.2	10.1	4.9	2.1	1.8	13.9	13.9	0	11.2
Mesorhabditis (Ba1)	4.3	0	2.6	2.4	6.7	40.5	5.5	0	45.7	2.3	0	32.2
Other Rhabditidae (Ba1)	3.1	0	29.1	52.5	21.1	92	33.1	11.9	78.1	7.1	6.3	26.2
Panagrolaimus (Ba1)	18.2	6.9	20.3	0	2.2	0	31.3	4.2	12.4	0	0	2.1
Monhystera (Ba1)	0	0	11.4	2.4	5.6	7.3	0	2.1	13.2	0	0	2.1
Acrobeloides (Ba2)	145	79	572	131	129	208	177	82	994	112	205	192
Acrobeles (Ba2)	4.5	1.5	0	0	2.2	4.5	0	0	0	4.8	0	16.1
Cephalobus (Ba2)	0	0	25	7	10	18.5	8.2	4.9	64.6	14	7	18.7
Eucephalobus (Ba2)	0	4.3	25	18.6	0	8.9	7.6	4.2	20.9	2.4	29.6	13.2
Chiloplacus (Ba2)	4.5	3.1	2.6	8.2	7.8	0	0	0	0	4.7	10.4	26.2
other Cephalobidae (Ba2)	0	0	0	22.8	11.2	16.5	0	0	6.2	9.1	0	20.2
Plectus (Ba2)	0	2.8	7.5	7	0	8.9	7.6	3.1	20.9	7.2	7	24.3
Wilsonema (Ba2)	0	0	0	0	0	0	0	0	0	0	0	4
Prismatolaimus(Ba3)	0	0	0	0	2.2	0	0	0	0	0	6.8	0
Alaimus (Ba4)	3.1	0	4.9	0	0	0	0	0	9.7	3.3	0	0
Aphelenchoides (Fu2)	212	166	202	39	198	87	352	110	234	46	54	44
Aphelenchus (Fu2)	709	539	589	284	148	870	1247	801	1754	88	51	72
Ditylenchus (Fu2)	0	0	10.3	30.5	6.9	31.8	7.3	0	10.4	0	0	8.2
Psilenchus (Fu2)	0	0	0	0	2.2	0	2.1	0	0	0	0	0
Tylencholaimus(Fu4)	4.5	0	0	1.8	0	0	7.3	9.1	31.3	204	27	115
Mylonchulus (Pr4)	0	0	0	1.8	0	0	0	0	0	0	3.5	0
Discolaimus (Pr5)	0	0	0	1.5	3.3	8.1	0	0	0	0	3.1	0
Mesodorylaimus (O4)	9	0	0	8.2	6.9	21.6	2.1	3.1	0	0	0	8.1
other Dorylaimida (O4)	7.6	2.6	7.6	0	2.2	11.7	7.6	7	6.2	8.1	0	23.4
Qudsianematidae (O5)	11.7	0	11.4	4.8	0	8.1	2.1	0	24.7	12	0	10.7
Eudorylaimus (O5)	24.2	0	2.6	0	0	6.9	3.1	0	25.5	3.3	0	3.1
Aporcelaimidae (O4)	46.4	9.7	26.1	0	0	11.7	6.1	0	20.9	3.3	0	26.1
Paratylenchus (Pp2)	0	0	0	0	0	0	0	0	0	18.7	20.9	40.3
Tylenchidae (Pp2/Fu2)	1001	243	420	484	263	853	294	110	169	911	259	615
Pratylenchus (Pp3)	7.6	2.6	7.3	42.1	18.1	30.3	3.1	8.1	3.5	123.6	298	198
Helicotylenchus (Pp3)	0	0	0	0	0	2.4	11	0	0	0	0	0
Tylenchorhynchus (Pp3)	0	0	0	47	9.1	168	8.4	8.4	25.5	67.8	16.4	80.3
Xiphinema (Pp5)	0	0	0	0	0	3.6	0	0	0	0	0	2.1
Heteroderidae (Pp3)	0	0	0	0	0	0	0	0	0	0	0	13.6

[a] Fraction LM: large macroaggregates (>1000 μm); SM: small macroaggregates (250–1000 μm); IS: inter-aggregate soil and space (<250 μm): Ba: Bacterivore; Fu: Fungivore; O: Omnivore; Pr: Predator; Pp: Plant-parasitic and associated *c-p* value(colonizer-persister).

Table 3
Nematode trophic groups per 100 g^{-1} of three soil aggregate fractions under four management systems: Conventional tomato (CON), minimum tillage with continuous cover crops (CC), organic tomato (ORG) and unmanaged riparian corridor (RC). Presented errors are standard errors of the mean.

Nematode Trophic Group	Soil Fraction[a]	Management System			
		CON	CC	ORG	RC
Bacterivores	LM	183 ± 21	258 ± 51	272 ± 23	181 ± 51
	SM	97 ± 13	215 ± 34	114 ± 5	272 ± 134
	IS	710 ± 154	410 ± 45	1279 ± 406	388 ± 190
Fungivores	LM	1427 ± 126	598 ± 95	1762 ± 589	795 ± 277
	SM	827 ± 322	486 ± 49	975 ± 269	274 ± 12
	IS	1011 ± 120	1415 ± 368	2114 ± 420	548 ± 211
Plant-parasitic	LM	508 ± 123	331 ± 34	169 ± 84	665 ± 86.9a
	SM	124 ± 44	159 ± 51	71 ± 28	465 ± 196b
	IS	218 ± 102	631 ± 182	113 ± 10	662 ± 376ab
		AB	A	B	A
Omnivores + Predators	LM	99.0 ± 35.1	18.7 ± 8.6	21.0 ± 3.4	27 ± 10.6a
	SM	12.3 ± 3.9	12.4 ± 4.2	10.1 ± 4.4	6.6 ± 3.3b
	IS	47.6 ± 5.9	75.1 ± 41.8	77.4 ± 43.0	71.3 ± 5.8a
		A	A	A	A
Total Nematodes	LM	2217 ± 56	1205 ± 170	2225 ± 675	1669 ± 297a
	SM	1061 ± 380	872 ± 63	1170 ± 304	1018 ± 202b
	IS	1987 ± 288	2531 ± 522	3584 ± 672	1674 ± 763a
		A	A	A	A

Capital letters under each column indicate significant differences between agroecosystems managements while lower case letters to the right of each row indicate significant differences between soil aggregate fractions determined using Tukey's HSD. Significant management system × fraction interactions preclude cross treatment comparison of means for bacterivore and fungivore trophic groups.
[a] Fraction LM: large macroaggregates (>1000 μm); SM: small macroaggregates (250–1000 μm); IS: soil and space (<250 μm).

densities in the LM than in the SM fraction, with IS containing intermediate densities ($P = 0.005$; Table 3). The influence of soil fraction on nematode functional guilds translated into effects on food-web indices, such that the IS fraction had a significantly higher SI than the SM fraction ($P = 0.006$; Fig. 1). High *c–p* value nematodes, generally with larger body size, including fungivore *Tylencholaimus* and, omnivores *Eudorylaimus* and *Qudsianematidae* were not observed in the SM fraction, resulting in lower SI

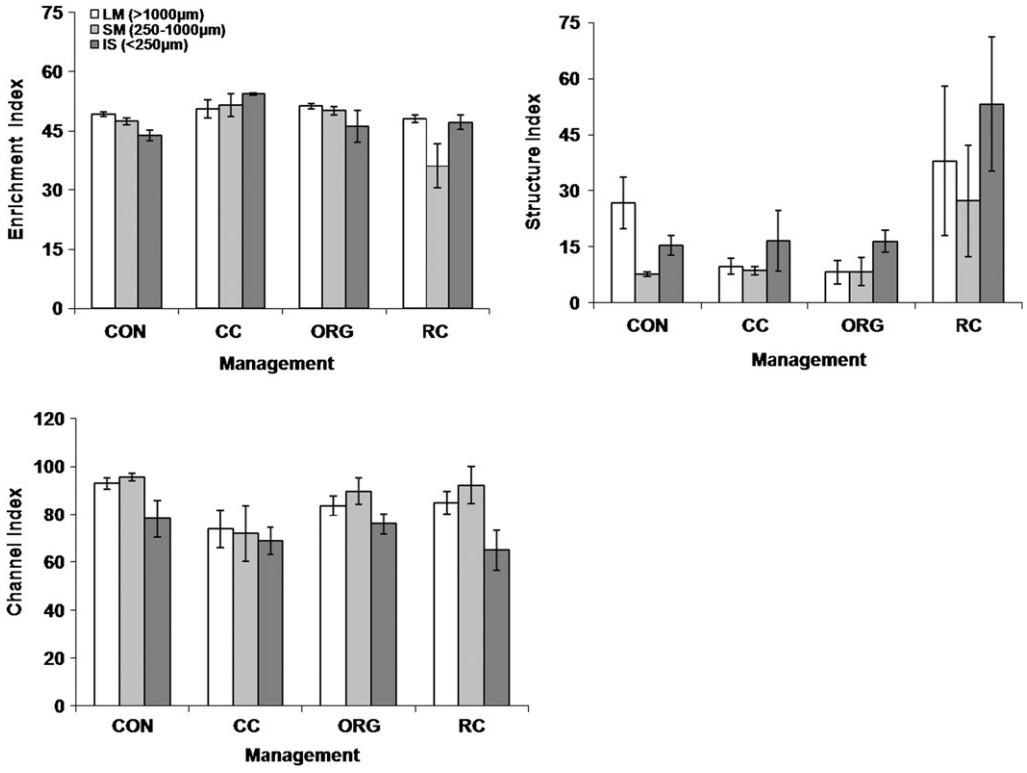

Fig. 1. Mean (±SE) nematode indices in different soil aggregate fractions under four management systems (conventional tomato, CON; organic tomato, ORG; a minimum till grain–legume intercrop with continuous cover, CC; and a riparian corridor dominated by native vegetation, RC) per 100 g dry soil fraction. Error bars denote the standard error of each treatment mean.

compared to other fractions (Table 2). The large plant-parasitic *Xiphinema* (*c*–*p* 5) was only found in the IS fraction. Both LM and SM fractions were found to have a significantly higher CI than the IS fraction ($P = 0.036$; Fig. 1). There were no significant differences in EI between management system and fractions. Stage structure of the nematode assemblage was also affected by soil fraction; there was, a significantly higher juvenile to adult ratio in the SM than in the LM or IS fraction ($P = 0.004$; Fig. 2). Finally, a relationship between overall soil structure and nematode distribution is clear from the positive correlation between the density of all nematodes in the IS fraction and the proportion of the whole soil in macroaggregate (LM + SM) fractions ($P = 0.033$, $R^2 = 0.38$; Fig. 3).

Differences in nematode functional groups between management systems were apparent from significantly higher densities of plant-parasitic nematodes under RC and CC than under ORG management ($P = 0.009$; Table 3). Additionally, management appeared to influence the abundance of fungal feeding nematodes, with higher densities under ORG than RC, but a significant management × fraction interaction ($P = 0.044$) indicates that management system effects on fungivore densities depend on the aggregate fraction in question. There were no significant differences between management systems for any of the other nematode functional groups. Further, although SI was generally highest under RC (Fig. 1), none of the food-web indices demonstrated significant differences between management systems.

3.3. Microbial communities within aggregates and management systems

Both aggregate fraction and management system yielded large differences in microbial functional groups and indices. Total PLFA was significantly higher in the LM fraction (65.2 nmol g^{-1} soil) than in the IS fraction (55.8 nmol g^{-1} soil; $P = 0.042$), with the SM fraction intermediate in value (59.6 nmol g^{-1} soil). Gram positive bacteria and eukaryotes followed this same trend ($P < 0.05$; Table 4), while gram negative bacteria and actinomycetes showed no significant differences between soil fractions. Although the fungi:bacteria ratio in the LM and SM fractions were higher than for IS, the management × fraction interaction indicates that this difference was not significant under ORG. The cy:precursor ratio showed a similar trend, while the total number of biomarkers (microbial diversity) did not significantly differ among fractions (Fig. 4).

In contrast to the findings for nematodes, differences in microbial communities between management systems were generally greater than differences between aggregate fractions. For example, total PLFA was significantly greater ($P = 0.002$) under RC and ORG

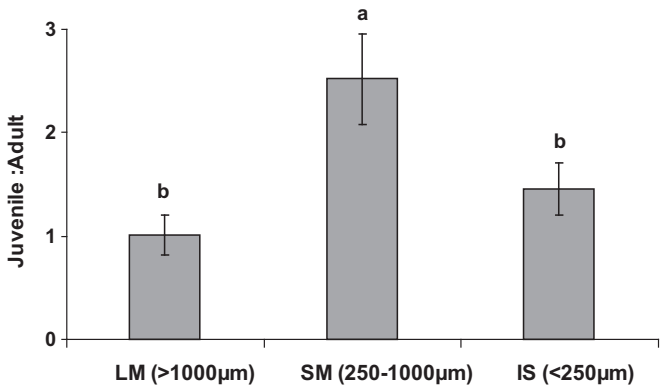

Fig. 2. Mean (±SE) adult to juvenile ratio of nematodes in different soil aggregate fractions. Different letters indicate significant differences between the aggregate fractions.

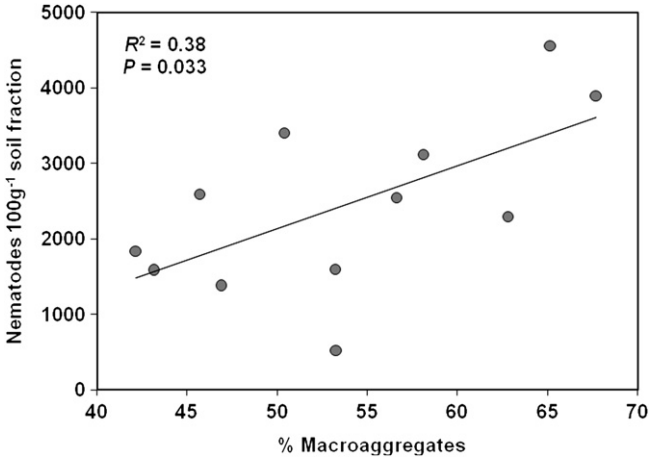

Fig. 3. Relationship between the proportion of the whole soil in the sum of the large and small macroaggregate fractions (>250 µm) and the density of nematodes in the inter-aggregate soil and space (<250 µm).

management (85.1 and 72.2 nmol g^{-1} soil; respectively) than under CC or CON (46.3 and 37.1 nmol g^{-1} soil; respectively). Similar differences between management treatments were found for all microbial groups including gram negative and, gram positive bacteria, actinomycetes, and eukaryotes (Table 4). The total number of distinct PLFA biomarkers, a proxy for microbial diversity, was significantly higher under RC than under CON management (49 versus 40 biomarkers respectively; $P = 0.043$), with intermediate values for ORG and CC (Fig. 4). Both, the fungi:bacteria ratio and the cy:precursor ratio (an indicator of ecosystem stress/disturbance) were generally higher under CON than RC, but significant management × fraction interactions ($P < 0.001$) suggest that this relationship is not uniform across the different aggregate size classes (Fig. 4). For example, fungi:bacteria within the LM fraction was higher than SM or IS under CON and CC, but similar to SM under ORG and RC.

3.4. Relationship between microbial and nematode indices, and soil C

An exploratory PCA highlighted the relationship between nematodes and microbial indices, and the ordination of soil aggregate fractions (Fig. 5a and b). For example, vectors on the loading plot suggest that CI and the fungi:bacteria ratio are positively correlated, while SI and the cy:precursor ratio have a negative association. Total PLFA appears to be highly related to C content of the soil aggregate fraction, and total nematode abundance seems to be negatively associated with total PLFA and C content. In addition, linear regression supports all of these relationships ($P < 0.05$) except for the negative association between total nematodes and soil C concentration (data not presented).

4. Discussion

4.1. Soil aggregation across management systems

Differences in soil structure between management systems were most evident from differences in MWD between treatments. The observed trend of high aggregate stability for the RC and ORG treatments and lower stability under CON management generally follows the inverse gradient of management intensity to which the soils are subjected (RC < CC ≤ ORG < CON; Table 1). However, a significant correlation between MWD and %C for the bulk soil

Table 4
Microbial community groups as determined by PLFA analysis of soil aggregate fractions across and four management systems: Conventional tomato (CON), minimum tillage with continuous cover crops (CC), organic tomato (ORG) and unmanaged riparian corridor (RC). Presented errors are standard errors of the mean.

Microbial Group	Soil Fraction[a]	Management System			
		CON (nmol g^{-1})	CC (nmol g^{-1})	ORG (nmol g^{-1})	RC (nmol g^{-1})
Gram Negative Bacteria	LM	9.10 ± 1.31	13.83 ± 0.93	16.22 ± 1.27	24.45 ± 1.58a
	SM	8.63 ± 0.96	9.36 ± 2.27	16.21 ± 2.08	24.04 ± 1.94a
	IS	7.80 ± 0.87	10.32 ± 0.80	18.84 ± 1.16	19.61 ± 4.66a
		A	AB	BC	C
Gram Positive Bacteria	LM	12.87 ± 1.62	18.02 ± 1.86	23.39 ± 1.92	25.24 ± 1.02a
	SM	11.71 ± 1.28	12.25 ± 3.09	21.32 ± 2.47	27.20 ± 1.42ab
	IS	10.15 ± 1.02	12.86 ± 1.33	23.18 ± 0.84	22.10 ± 4.80b
		A	A	B	B
Actinomycetes	LM	2.76 ± 0.41	3.68 ± 0.50	5.01 ± 0.44	5.77 ± 0.71a
	SM	2.67 ± 0.33	2.56 ± 0.56	4.41 ± 0.44	6.29 ± 0.76ab
	IS	2.22 ± 0.22	2.84 ± 0.26	4.70 ± 0.20	5.03 ± 1.19b
		A	AB	BC	C
Fungi	LM	1.51 ± 0.29	2.09 ± 0.64	1.73 ± 0.11	1.69 ± 0.08
	SM	0.88 ± 0.11	0.71 ± 0.21	1.71 ± 0.24	1.80 ± 0.13
	IS	0.54 ± 0.09	0.51 ± 0.06	1.56 ± 0.11	0.65 ± 0.15
Eukaryotes	LM	0.20 ± 0.02	0.25 ± 0.02	0.36 ± 0.03	0.53 ± 0.09a
	SM	0.17 ± 0.03	0.13 ± 0.06	0.29 ± 0.04	0.50 ± 0.08ab
	IS	0.13 ± 0.02	0.19 ± 0.03	0.33 ± 0.01	0.35 ± 0.08b
		A	AB	BC	C

Capital letters under of each column indicate significant differences between agroecosystems managements, while lower case letters to the right of each row indicate significant differences between soil aggregate fractions determined using Tukey's HSD. A significant management system × fraction interaction precludes cross treatment comparison of means for fungi.

[a] Fraction LM: large macroaggregates (>1000 μm); SM: small macroaggregates (250–1000 μm); IS: inter-aggregate soil and space (<250 μm).

confirms that organic matter inputs also play an important role in governing the structure of soils (Kong et al., 2005). Although the ORG system generally experiences higher disturbance than the CC treatment, it also receives large external inputs of C in the form of manure (2.9 Mg C ha^{-1} yr^{-1}). Furthermore, improved structure under ORG (relative to CC) likely relates to the management history and duration for each treatment, 15 yrs for cropping under ORG versus only 2 yrs since the implementation of the CC plot. Our results thus appear to corroborate the work of other researchers which indicates that C input and tillage are important drivers of soil structure (Kong et al., 2005; Bronick and Lal, 2005).

4.2. The distribution of nematodes

Despite large differences in soil structure and soil C, management system did not demonstrate consistent effects for nematode communities. The most obvious difference was a higher abundance of plant-parasitic nematodes under RC compared to CON (Table 3), which is likely related to the continual presence of live roots of perennial plant species (i.e., trees and shrubs) that provide a habitat and stable food source throughout much of the year. Although a number of studies have reported large impacts of management system on nematode communities (Sohlenius and Wasilewska, 1984; Sohlenius, 1990; Neher and Olson, 1999), the lack of significant differences between cropping systems reported here is not entirely new. It may be that increased disturbance (e.g., tillage) under organic management partially counteracts the benefits to nematodes of higher organic matter input (Briar et al., 2007). Also, the study design employed here allows for better detection of differences between soil aggregate fractions than for differences between management systems, thus rendering tests of management effects on nematode communities less rigorous.

In contrast to management, nematode abundance and community composition appeared to be highly influenced by aggregate fractions. Nematode density was consistently lower in the SM than in the LM or IS fractions (Table 3). Given that nematode distribution in the soil is thought to depend largely on their feeding habits and body size (Jones, 1982; Elliott et al., 1984; Quénéhervé and Chotte, 1996), lower densities in the SM fraction suggests that intra-aggregate pores space may be limiting in these smaller aggregates or that the SM fraction is depleted in nutritional resources relative to the other fractions. While clear differences in the resource quality and availability between SM and LM are not apparent, the higher juvenile:adult ratio observed in small macroaggregates (Fig. 2) suggests that juveniles can more easily access smaller pores and corroborates the idea that habitable pore space is important for determining the distribution of nematodes. This observation also suggests that the SM fraction may offer juveniles a refuge from predators or represents a place of preferential nematode reproduction or development. There were greater densities of higher c–p value nematodes such as omnivores and predators in the IS and LM fractions, contributing to higher SI values. These nematodes are generally larger, and are likely restricted by the smaller pore space of the SM fraction. The distribution of nematodes according to habitable pore space is supported by the findings of Hassink et al. (1993) who found nematode populations across a range of soils to be correlated with the proportion of the soil volume comprised of pores 30–90 μm in diameter. Similar to our findings, Quénéhervé and Chotte (1996) also found low nematode densities in small macroaggregates (200–1000 μm) and attributed this to the inability of nematodes, which are generally >30 μm in diameter, to enter the small pores within this aggregate size class. Despite the strong apparent role of habitable pore space, resource availability within the different size fractions also appears to play some role in determining nematode communities. This is most evident from the higher CI values for macroaggregates (LM + SM) than for the inter-aggregate fraction (Fig. 1). Both large and small macroaggregates are comprised of smaller aggregates that are thought to be held together by fungal hyphae and plant roots (Tisdall and Oades, 1982; Tisdall et al., 1997).

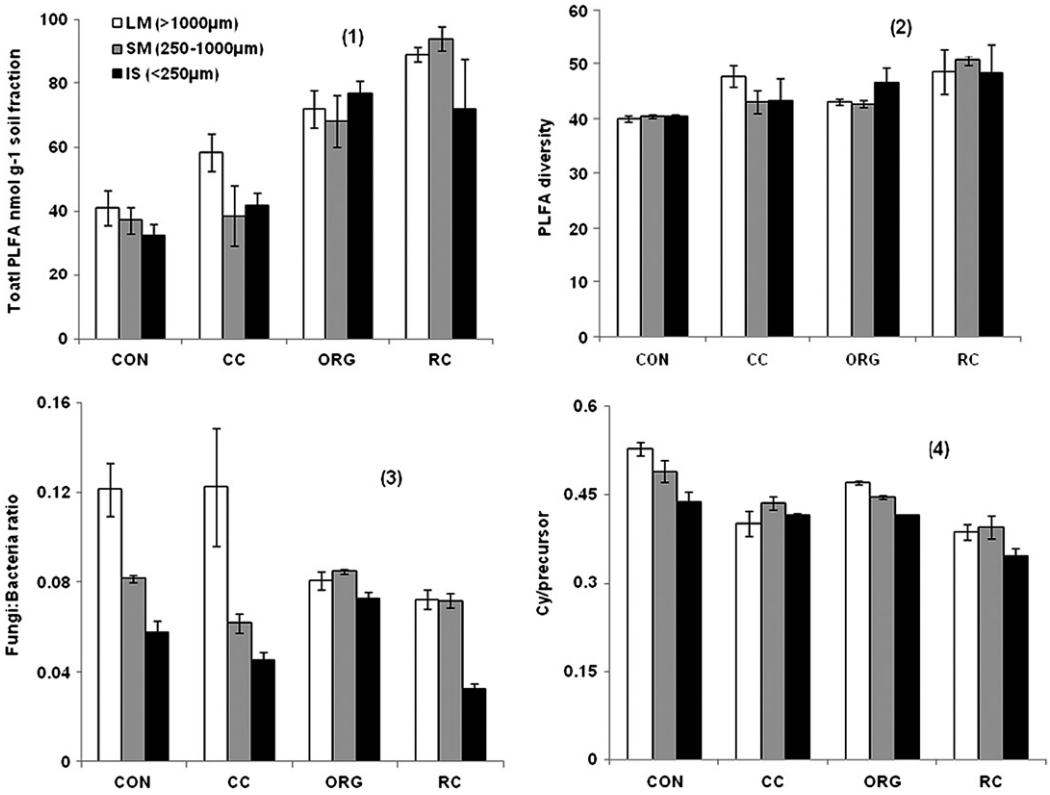

Fig. 4. Mean (±SE) microbial indices in different soil aggregate fractions under four managements systems (conventional tomato, CON; organic tomato, ORG; a minimum till grain–legume intercrop with continuous cover, CC; and a riparian corridor dominated by native vegetation, RC) per 100 g dry soil fraction. Error bars denote the standard error of each treatment mean.

Thus, a higher relative abundance of fungal feeders in macroaggregates, as indicated by the higher CI value (Ferris et al., 2001), suggests nematodes are responding to the greater availability of fungal resources in these fractions. Of all nematode groups, only phytophagous genera were in greater abundance in the LM than the IS fraction (Table 3), suggesting a greater presence of actively growing feeder roots in this fraction to support this nematode group.

The distribution of nematodes in different aggregate fractions varied with management system (Table 3), even if the interaction term was not always significant. Although aggregate fractions are discussed here as isolated entities, they are in fact highly interconnected so that nematodes can move between different fractions. Consequently, the nematodes in one fraction may be influenced by those in other fractions. For example, a greater proportion of large aggregates in a soil would likely correspond to having larger pore sizes and greater pore volume within and between the aggregates (Wu et al., 1990). The positive correlation observed here between macroaggregation (LM + SM) and total nematode density in the IS fraction (Fig. 3) suggests that habitable pore space (and associated nematode communities) in the IS fraction depends on the overall aggregation of a soil. These findings indicate that the relationship between soil structure and soil fauna communities depends on additional factors and is perhaps more complex than we originally postulated.

4.3. Microbial communities

In contrast to the observations for the distribution of nematodes, microbial communities showed strong differences between management systems, with aggregate fraction having a lesser effect. Total PLFA, an indicator of microbial biomass, as well as PLFA associated with specific functional groups, were higher under RC and ORG than CON (Fig. 4 and Table 4) and this trend appeared to correspond to differences in soil C content between the systems. This relationship is supported by a strong association between C concentration of each sample and total PLFA, apparent from the PCA (Fig. 5) as well as from a linear correlation between these variables ($P < 0.001$; $R^2 = 0.54$; data not shown). Higher microbial diversity under RC than CON may be related to higher resource availability (total soil C) and reduced nutritional stress, as indicated by a lower cy:precursor ratio under RC than for CON (Fig. 4). However, other factors, such as increased plant diversity and lower soil disturbance under RC, likely contribute as well (Bossio et al., 1998; Chaer et al., 2009; Eisenhauer et al., 2010).

Along with significant effects of management system, the association between C content and PLFA may explain differences in microbial groups across aggregate fractions, as C rich large macroaggregates demonstrated consistently higher PLFA from all functional groups than was observed in the relatively C-poor IS fraction (Table 4). As mentioned earlier, higher C content in macroaggregates fits with the theory of aggregate hierarchy which suggests that larger aggregates are composed of smaller aggregates held together by organic materials (i.e., plant roots and fungal hyphae). Increased C content of the macroaggregate fractions translated directly into increased food availability for microbial communities.

4.4. Associations between nematodes and microbes

In general, nematode populations were not strongly correlated with microbial communities across soil fractions and management

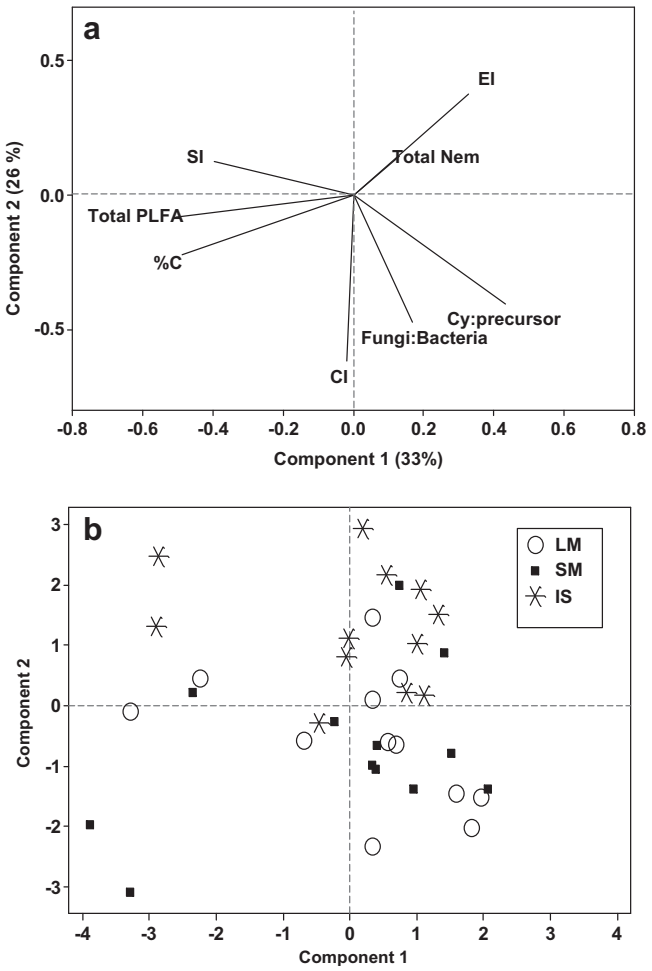

Fig. 5. Principal components analysis: (a) Loading plot (association between the original loading variable and each principal component) for the first two component showing relationship among key nematode and microbial indices, and % C. (b) Score plot showing the distribution of the soil aggregate fractions including LM: large macroaggregates (>1000 μm) as open circles; SM: small macroaggregates (250–1000 μm) as stars; IS: inter-aggregate soil and space (<250 μm) as small squares.

systems. Nematodes were most abundant in the IS fraction and under ORG management (Table 3), while microbial communities had the greatest biomass under RC and in the LM fraction (Table 4 and Fig. 4). This disassociation may reflect differences in the factors limiting these two groups. The high correlation between soil C and microbial communities suggests that bacteria and fungi are highly limited by resource availability, while habitable pore space likely plays a lesser role (Postma and van Veen, 1990). As indicated earlier, findings from our study and others (Hassink et al., 1993; Quénéhervé and Chotte, 1996) suggest that nematodes are strongly limited by habitable pore space, mainly by availability of water filled pores of 30–90 μm in diameter. This limitation, along with highly restricted access of bacterial-feeding nematodes to their food sources (microbes residing in pores <30 μm diameter), likely explains the lack of correlation between nematodes and microbial communities.

Despite the apparent disconnect between nematodes and microbial communities, nematode components of food webs do reflect microbial community composition in some ways. For example, the suggestion of greater prevalence of fungal-dominated pathways (higher CI values) in macroaggregates than in the IS fraction is corroborated by a greater concentrations of fungi and generally higher fungi:bacteria ratios in the SM and LM fractions (Table 4 and Fig. 4). This, along with significant correlation between CI and the fungi:bacteria ratio (Fig. 5), provides a clear link between fungivorous nematodes and their food sources. Additionally, SI (an indicator of nematode food-web stability) was negatively associated (Fig. 5) with the cy:precursor ratio (an indicator of nutritional stress in microbial communities), suggesting that both nematodes and microbial communities respond similarly to adverse conditions.

5. Conclusions

This study suggests important influences of soil structure and management on soil food webs and decomposer communities. Our hypothesis, that communities of soil biota are determined in part by physical and/or resource constraints associated with different aggregate size fractions was supported by significant differences between fractions for both nematode and microbial community composition and abundance. However, the differences between soil fractions did not indicate that management associated variations in soil structure had predictable effects on nematode and microbial communities in whole soil. Despite the new insights offered by this study, further research is needed to fully elucidate how management both directly and indirectly (via changes to soil aggregation) impacts the structure and functioning of soil communities.

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