

Structure, functions and interguild relationships of the soil nematode assemblage in organic vegetable production

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ABSTRACT

The abundance and metabolic footprints of soil nematodes were quantified during four of eight years of an intensive organic vegetable production system. Treatment variables included cover crop mixtures and compost application rates. The abundances of bacterivore and fungivore nematodes were enhanced by the annual use of winter cover crops but showed no relationship to the level of residual soil organic matter. Metabolic footprints, based on biomass and respiratory activity, were calculated for functional guilds and ecosystem services of the nematode assemblage. The enrichment footprint, representing the ecosystem service of nutrient mineralization, was related to the level of soil organic carbon. It was strongly related to the metabolic footprint of bacterivore nematodes and both were enhanced in treatments that were cover cropped annually. Cover-cropped treatments also had a slightly higher herbivore footprint, suggesting support of some taxa of plant-feeding nematodes. The structure footprint, reflecting the metabolic activity of higher trophic level nematodes, including the predators of opportunistic species, did not differ among cover crop and compost amendment treatments. However, enrichment footprints were correlated with bacterivore footprints, which represented the predominantly bacterivore resources available to predators. Abundance of predators increased as a function of the abundance of those nematode prey that can be amplified by organic inputs. The functional connectance, represented by spatial co-location, between predators and amplifiable prey was greater in treatments with a greater abundance of predators. The functional connectance between predators and herbivore prey, representing a management target, was strongly related to the functional connectance between predators and amplifiable prey. We conclude that cover crops not only affect organisms at the entry level of the web but that resources are also transferred to higher trophic links which increases top-down pressure on plant-parasitic nematodes.

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1. Introduction

A fundamental goal of organic agriculture is stewardship of the functions of the soil food web to optimize essential ecosystem services. Important among such services are the mineralization of molecules from organic to inorganic forms available to plants, and the regulation or suppression of pest species (Ferris et al., 1998; Ingham et al., 1985; Sánchez-Moreno and Ferris, 2007). During mineralization, organic molecules are metabolized by rhizosphere organisms to release energy and to obtain elements essential for their growth. In the regulatory process, feeding by generalist and specialist predators affects the abundance and biomass of organisms that are assimilating resources at the entry level of the soil food web, including herbivores (Sánchez-Moreno et al., 2009). To

achieve adequate levels of such ecosystem services, it is necessary to have sufficient biomass and activity of appropriate functional guilds in the soil food web. That requires a frequent or consistent supply of new organic material to fuel the system (Ferris, 2010a).

Through use of cover crops that are incorporated into the soil or mulched on the surface, and the application of composts and manures, soil carbon and soil microbial biomass are usually higher in organic than in conventional agricultural systems (DuPont et al., 2010). Over time, organic systems, with their greater overall C input, retain soil C in progressively more recalcitrant forms and in the elevated biomass of soil organisms. Increased soil C is usually associated with higher soil moisture content, greater retention of essential minerals and improved soil quality (Clark et al., 1999; Glover et al., 2010; Pimentel et al., 2008).

Whereas the nutrient status of soils in conventionally-managed systems can be precisely adjusted with mineral fertilizers, that of organic systems is more difficult to accurately calibrate due to seasonal differences in rates of cover crop growth, differences in their C:N ratios and decomposition rates, and differences in

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compost quality. In conventional systems, chemical fertilizers are often at extremely high concentrations in the water films around soil particles. Such concentrations are toxic to sensitive organisms inhabiting those small volumes of water (Tenuta and Ferris, 2004). Among the nematodes, sensitive taxa include the slow-reproducing, large-bodied predator species that contribute to the regulation of population levels of pest species (Bongers and Ferris, 1999; Ferris, 2010a). The cover crop residues, composts and supplemental fertilizers of organic systems decompose through the metabolic activities of bacteria and fungi. Minerals released slowly from organic amendments are unlikely to achieve levels toxic to soil organisms. Unless organisms that feed on bacteria and fungi are present in abundance, nutrients may become bound in the organic molecules that comprise the biomass of decomposers and, consequently, be unavailable for plant uptake (Ferris et al., 2004).

A stronger conceptual base for soil ecology will emerge from application of broader ecological concepts in interpretation of soil processes (Barot et al., 2007). Applications of synoptic assessments that are explanatory or predictive of ecosystem functions and environmental impacts range from community respiration, the net carbon flux of a system, to the ecological footprint, the area necessary to provide the resources for, and to assimilate the wastes of, a population (Costanza, 2000; Ngao et al., 2012; Regaudie-de-Gioux and Duarte, 2012). Environmental effects of the metabolic activity of microbes, expressed through their production of extracellular metabolites, are described as their metabolic footprint (Mapelli et al., 2008). In soil systems, Mulder et al. (2008) propose faunal biomass flux and distribution as descriptors of ecosystem function. The structure of the nematode assemblage is a useful bioindicator of decomposition pathways, soil nutrient status, environmental quality, and the effects of contaminants (Bongers, 1990; Ferris et al., 2001; Höss et al., 2004; Heininger et al., 2007; Yeates et al., 2009). Besides utilization of C in body and egg production, nematodes have size-dependent metabolic costs (Ferris et al., 1995; Klekowski et al., 1972, 1974). Since both nematode biomass and respiration can be calculated from published morphometric parameters (Andrássy, 1956; Atkinson, 1980), Ferris (2010b) derived the nematode metabolic footprint (NMF). The NMF is a metric of metabolic activity and ecosystem function based on carbon utilization in production and respiration. When integrated with other faunal analysis tools, the NMF infers the activity level of functional guilds.

Food web structure and function are determined by resource supply and by predation and competition among trophic levels of organisms. The diverse organisms in a functional guild may occupy different niches and differ in attributes so that each contributes in a complementary manner to the system function. Consequently, there is a positive relationship between magnitude of the function and diversity within a functional guild (Loreau, 2004; Loreau and Hector, 2001) and loss of biodiversity has negative effects on ecosystem functioning (Heemsbergen et al., 2004). Further, a functional guild is not comprised of a single group of organisms; organisms of different taxonomic groups perform similar functions and services. Diversity thus underpins functional resilience whereby an ecosystem service continues even if conditions become unfavorable for some components of the guild (Ferris, 2010a; Loreau, 2004).

High values of land in the Salinas Valley of California (rental costs currently US \$3000–7000 ha⁻¹ yr⁻¹) typically necessitate the production of two or more crops per year to maintain economic viability. Winter cover cropping to improve nutrient cycling and add organic matter to soil is considered a “best management practice” in high-input, intensive vegetable systems in California (Hartz, 2006; Wyland et al., 1996). However, winter cover cropping in addition to production of two cash crops can be challenging because of the time needed to incorporate the cover crop into the soil and allow adequate decomposition before planting subsequent cash crops. The

overall objective of this research is to establish a sound basis for stewardship of the structure and function of the soil food web in an intensive organic agricultural system producing two vegetable crops per year and supported by winter cover crops, composts and supplemental organic fertilizers. We explore the application of some novel analyses to interpret and illustrate soil food web structure and function.

2. Materials and methods

2.1. Field characteristics

The field site of this experiment is in the Salinas Valley of California at 36° 37' 20.82", 121° 32' 55.32". The Salinas Valley is an area of intensive irrigated vegetable production with climate moderated by proximity to the ocean. Between 2003 and 2011, the average air temperature during the winter cover cropping period (October–March) was 11 °C and during the vegetable cropping period (May–September) was 15 °C. (<http://wwwcmis.water.ca.gov>, Station #89, Salinas South). The average annual rainfall during the eight years of the experiment was 302 mm, concentrated between October and March. The soil type at the experimental site is a uniform Chualar loamy sand (fine-loamy, mixed, thermic Typic Argixerol). The field was used for conventional oat hay production and mixed vegetable and sugar beet trials from 1990 to 1996. Organic production with mixed vegetable and cover crops began at the site in 1997 and the field has been certified organic by California Certified Organic Farmers since 1999. Since organic certification, the field has been in cover crops and in the current experiment.

2.2. Cropping sequence

A legume–rye mixture cover crop was grown on the experimental site in the winter of 2002–2003 and a buckwheat (*Fagopyrum esculentum*) cover crop during the following summer. The Salinas Organic Cropping Systems experiment was initiated by planting cover crops and applying compost treatments (per treatment list, Table 1) in October, 2003; these treatments were repeated each fall. Two cash crops were grown each summer, starting in 2004. Cover crops were incorporated in February or March and followed by a transplanted spring lettuce crop (May–June or June–July) and a summer crop of either spinach (July–August, 2004) or transplanted broccoli (July–September/October 2005 to 2010). Each lettuce crop received preplant supplemental organic fertilizers at a total N application rate of 73 kg ha⁻¹ from a combination of pelleted poultry manure and drip-irrigation-applied liquid fish emulsion. Each broccoli crop received 134–168 kg N ha⁻¹ from the same pelleted and liquid sources. Green-waste compost (7.6 Mg ha⁻¹ d.w., C:N ratio ≈22) was applied to all treatments before each spring and summer crop, except for Treatment 1, which never received compost. Treatments 1 and 2 were fallow during all winter periods except 2006–2007 and 2010–2011, when they were cover cropped with the legume–rye mixture at the high seeding rate. Treatments 3–8 were cover cropped each winter (Table 1). Cover crops in Treatments 4, 6 and 8 were seeded at three times the rate of Treatments 3, 5 and 7 (Brennan and Boyd, 2012a,b).

2.3. Experimental design

The experimental design was a randomized complete block with the eight treatments arranged in each of four blocks in an area 49 m wide and 156 m long. Each plot was 19.5 m long and 12.2 m wide. During the vegetable crops, each treatment area consisted of 12 beds, 102 cm wide. The center 10 beds were used for data collection and the outer beds functioned as inter-plot buffers. Drip irrigation

Table 1
Compost and winter cover crop treatment descriptions. Nematode samples were taken in spring and summer of 2005, 2006, 2008, and spring 2011.

Treatment code ^a	Annual compost rate (Mg ha ⁻¹) ^b	Cover crop		
		Type ^c	Seeding rate (kg ha ⁻¹) ^d	Frequency ^e
1	0	Legume/rye	336	Every 4th winter
2	15.2	Legume/rye	336	Every 4th winter
3–4	15.2	Legume/rye	112, 336	Every winter
5–6	15.2	Mustard	10, 30	Every winter
7–8	15.2	Rye	90, 270	Every winter

^a The experiment included eight treatments, however, because nematodes were unaffected by cover crop seeding rate, treatments that differed only in seed rate were combined as 3–4, 5–6, and 7–8.

^b Green waste compost applied on a dry weight basis and split application prior to each vegetable crop.

^c Legume/rye cover crop mixture included 90% legume and 10% 'Merced' rye (*Secale cereale* L.) by seed weight. Legumes were 35% *Vicia faba* L., 25% *Pisum sativum* L., 15% *Vicia benghalensis* L., and 15% *Vicia sativa* L. Mustard was a mixture of 69% 'Ida Gold' (*Brassica juncea* L.) and 31% 'Pacific Gold' (*Sinapsis alba* L.), by seed weight.

^d For the combined treatments (3–4, 5–6, 7–8), the low and high seeding rates are listed, respectively for each pair.

^e Treatments 1 and 2 were maintained as weed-free fallows for all winter periods (October–March) except those of 2006–2007 and 2010–2011 when they were cover cropped.

tape, with emitters 20–30 cm apart, was installed on or slightly below the soil surface at the center of each bed during the vegetable crops. The irrigation tape was removed before the winter cover crop was planted and installed again prior to planting of the spring lettuce crop. Depending on field conditions following the commercial harvest of the lettuce, the beds were either reshaped with a reduced-tillage disc or flattened with a tandem disc or spader before being reformed for the summer crop. Deep tillage with ripper shanks to approximately 1 m was performed as needed after the vegetable crops to break up compaction caused by the commercial harvest operations. Lettuce, and broccoli crops were harvested and marketed by commercial crews, resulting in export of nutrients from the field; the spinach crop of 2004 and the broccoli crop of 2005 did not meet market standards due disease or insect damage and were not harvested for commercial sale (Brennan and Boyd, 2012a).

2.4. Soil organic carbon and crop yield measurements

Soil samples, 20 cores to a depth of 30 cm in an 'x' pattern across each plot, were taken during October each year for analysis at the UC Davis Analytical Laboratory. The soil was pulverized to pass through a 2 mm screen and then ground to pass through a 0.25 mm screen. Total soil C was determined on a subsample by the combustion method (<http://anlab.ucdavis.edu/analyses/soil/320>) and inorganic C by titration with 0.025 N H₂SO₄ of carbonate and bicarbonate in a saturated paste extract (<http://anlab.ucdavis.edu/analyses/soil/220>). Soil organic C was estimated by subtracting inorganic C from total soil C (Nelson and Sommers, 1982).

Aboveground dry matter of the vegetable crops was determined by harvesting 32 randomly chosen lettuce plants and 20 randomly chosen broccoli plants from each plot at or immediately prior to the commercial harvest. Total fresh weight of the harvested plants was determined and a subsample oven dried at 60 °C. Those data are presented on a per plant basis averaged across lettuce and broccoli

crops in summary form herein (Table 2) and will be reported in detail elsewhere (Brennan and Boyd, unpublished).

2.5. Nematode analyses and interpretation

Soil samples for nematode analysis were taken, starting in the second year of the crop sequence, at the ends of the spring lettuce crop (June/July) and the summer broccoli crop (September/October) in 2005, 2006 and 2008, and again at the end of the spring lettuce crop in June, 2011. Soil samples from each plot were a composite of 15 cores, 2.5 cm diam., 30 cm deep, dispersed across the inner eight beds of the plot. Samples were transported to the laboratory in insulated boxes and stored at 4 °C for no more than one week before nematode extraction.

Soil samples were gently homogenized by hand and 350 cc subsamples were weighed for nematode extraction. Nematodes were extracted using a combination of decanting and sieving and Baermann funnel methods (Barker, 1985). Samples were washed through a 0.25 mm aperture sieve to remove larger particles and onto a 36 μm sieve to separate nematodes from excess water. Nematodes and residue from the 36 μm sieve were washed into beakers and placed on Baermann funnels for 48 h to allow active nematodes to separate from the residual debris. Nematodes were counted using a dissecting microscope and then the sample concentrated by centrifugation and placed on a microscope slide. The first 200 nematodes encountered in the sample were identified at 200× or 400× to genus or family within one week of extraction.

Nematodes were assigned to trophic groups according to Yeates et al. (1993) and colonizer-persister (cp) groups based on Bongers (1990) and Bongers and Bongers (1998). For the purpose of these analyses, we treated nematodes feeding on soil organisms other than plants, bacteria or fungi as predators (pr), so that specialist (e.g., Mononchidae) and generalist predators (e.g., Aporcelaimidae) were considered to have the same feeding habit. Additionally, there were some algal feeders (al) in the assemblages, presumably inhabitants of the topmost layer of soil. The cp scale classifies

Table 2
Dry weight and C:N ratios of cover crop incorporated, soil organic carbon (SOC), and average per plant crop yield, across years in which nematode populations were sampled (2005, 2006, 2008, 2011).

Treatment	Dry wt. cover crop incorporated (kg ha ⁻¹)	C:N ratio cover crop incorporated	Crop yield dry wt. (plant ⁻¹)	SOC (kg ha ⁻¹)
P (86 df)	<0.05	<0.05	<0.05	<0.05
No cover/No compost ^a			42.6a	6.2a
No cover ^a			46.4ab	7.9b
Legume/rye	6360b	19a	55.0c	8.6b
Mustard	5090a	21a	53.6c	8.6b
Rye	6337b	28b	53.1bc	8.5b

^a A cover crop was grown in these plots in 2010–2011 resulting in average dry matter incorporated of 6901 and 7057 kg ha⁻¹.

nematodes into five groups from microbial feeders with short life cycles and high fecundity (cp1 and 2) to omnivores and predators with long life cycles and greater sensitivity to perturbation (cp4 and 5) (Bongers, 1990). Herein, we refer to the cp groups as “structural guilds” since they indicate the relative abundance of nematodes of different life history strategies and sensitivities to enrichment and disturbance. Soil food web indices were calculated after Ferris et al. (2001) and Berkelmans et al. (2003). The indices are based on “functional guilds” of nematodes as categorized by the matrix of feeding habits and life history strategy. We use the concatenation of feeding habit and structural guild category to represent functional guild designation so that the ba1 functional guild is comprised of bacterivores with cp1 life history characteristics while pr5 represents predators of the cp5 group.

Various indices developed and implemented for the assessment of environmental quality and food web structure indicate the potential for ecosystem functions and services based on the relative abundance of structural and functional guilds (e.g., Bongers, 1990; Bongers and Ferris, 1999; Ferris and Bongers, 2009). However, they do not indicate the probable magnitude of the services. A measure of magnitude is provided by assessment of metabolic footprints based on biomass and metabolic activity of components of the nematode assemblage calculated from published dimensions of each species and averaged across species for genera and families (Ferris, 2010b). The ecophysiological attributes of nematodes, assembled at species, genus and family levels are available at <http://plpnemweb.ucdavis.edu/nemalex>. The Nematode Metabolic Footprint has a production component, the lifetime amount of C partitioned into growth and egg production, and a respiration component, the C utilized in metabolic activity. The Enrichment Footprint (EF) is NMF enrichment opportunist nematodes (Bongers and Ferris, 1999). The Structure Footprint (SF) is the NMF of nematodes which may have a regulatory function in the food web and which are indicative of the abundance of organisms of similar functions in non-nematode taxa (Ferris et al., 2001). The Herbivore, Bacterivore and Fungivore Metabolic Footprints are based on NMF assessments for nematode indicators of C and energy entering the soil food web through their respective channels.

Connectance is defined as the proportion of possible linkages among taxa that are realized in the food web (Cohen, 1989; Martinez, 1992). In this case, we apply the concept to the *functional connectance* represented by the co-occurrence of predator and prey nematodes in individual soil samples (Sánchez-Moreno et al., 2011). For four samples representing each treatment on each date, potential connectance (F) between predators and prey is the product of the number of occurrences of predator and prey taxa, $F = ab$. Then we determined the number of times that any predator and any prey taxa co-occurred in a sample, averaged across the four samples of each treatment ($S = (\sum a_i b_j) / m$ where $i = 1$ to n for the n prey taxa and $j = 1$ to k for the k predator taxa in each sample and m is the number of samples representing each treatment). Functional connectance (C) is expressed as a percentage of the potential functional connectance for samples from each treatment ($C = 100S/F$). By categorizing nematode guilds into the “management cohorts” of Amplifiable Prey, Target Prey, and Predators, we determine C among any pair of the cohorts for each treatment. Amplifiable Prey are those species that are either neutral or beneficial to management objectives and whose abundance can be enhanced by provision of specific resources, for example, bacterial- and fungal-feeding nematodes. Target Prey is the cadre of undesirable species in relation to management objectives for the system; in the current case they are plant-feeding nematodes. Predators may be generalists (often termed omnivores), which feed on nematodes and other soil organisms) or specialists (which utilize nematode prey as their primary resource). The predators are shared as common natural enemies by Amplifiable and Target Prey.

We analyze the structure and function of the soil food web in the organic vegetable production system of the Salinas Valley in relation to taxonomic diversity of the nematode assemblage, structural guild configuration and, based on NMF assessments, magnitude of services of the soil food web that contribute to soil fertility and the regulation of opportunistic pest species. Statistical analyses were performed with the Advanced Linear/Nonlinear Models of Statistica Release 8 (StatSoft, Tulsa, Oklahoma, USA); those within time periods were conducted with Main Effects ANOVA and those across years with Repeated Measures ANOVA.

3. Results and discussion

3.1. Crop and cover crop biomass, and soil organic carbon

In the treatments with a cover crop each year, the biomass of legume/rye and rye incorporated was greater than that of mustard while the C:N ratio of the rye cover crop was greater than that of the other two (Table 2). However, differential effects on soil organic carbon (SOC) levels were minimal. Annual SOC levels were higher and similar wherever cover crops were grown annually (Treatments 3–8) and/or compost was applied (Treatment 1). Aboveground biomass production per plant, of the lettuce and broccoli crops averaged across the years of the nematode study, was significantly greater in Treatments 3–8, which received cover crops and compost annually, than in treatments with cover crop every fourth winter without compost (Treatment 1) or with compost (Treatment 2) (Table 2). The introduction of cover crops into Treatments 1 and 2 during the winter of 2006–2007 and 2010–2011 did not reduce the difference between the organic matter level of Treatment 1 and that of other treatments.

3.2. Nematode diversity and abundance

The nematode assemblage at the experimental site included at least 44 taxa representing 30 nominal families with frequencies of detection ranging from <1% to >99% of the samples (Table 3). Their feeding habits included plant feeding (pl), fungal feeding (fu), bacterial feeding (ba), specialist predators and omnivores (pr) (Yeates et al., 1993). Nematode taxa at the experimental site represented all the cp (structural guild) categories of Bongers and Bongers (1998). The taxa ranged in fresh body mass, calculated per Andrassy (1956), from 0.01 to 44.3 μg with the majority <1 μg and with higher structural-guild predators generally of greatest body mass.

Where cover crops were grown annually (Treatments 3–8), there were no effects of seeding rates on yields of either vegetable crop, therefore, we simplify illustration by combining faunal and metabolic analyses on the nematode assemblages across seeding rates in those treatments. The resultant analyses did not differ substantially from those conducted on an individual treatment basis.

In previous studies in organic production systems in California, the economic crop following a winter cover crop exhibited nutrient deficiency due to immobilization of N and other minerals in the flush of microbial biomass that followed cover crop incorporation. Irrigation and additional organic matter during the dry post-harvest period of the previous year increased the abundance of fungal- and bacterial-feeding nematodes and, by inference, the abundance of protozoa, at the time of cover crop incorporation. Available mineral N was at higher levels in plots with abundant bacterial-feeding organisms, thus alleviating the N-deficiency (Ferris et al., 2004). Soil mineral N levels were increased by 20% or more by the metabolic activity of bacterial- and fungal-feeding nematodes in microcosm experiments (Chen and Ferris, 1999; Ferris et al., 1998). However, continuous cropping reduced the abundance of predators and the magnitude of their regulatory

Table 3
Feeding habit (adapted from Yeates et al., 1993), structural guild (cp group) (Bongers and Bongers, 1998), body weight (calculated per Andr ssy, 1956), and frequency of occurrence of nematode taxa in 192 samples taken on six occasions from 32 plots representing eight treatments and four replications. Nematodes were identified to either genus (italicized) or family (not italicized) level.

Genus/family	Feeding habit ^a	cp group	Body wt. (�g)	Freq.%	Genus/family	Feeding habit ^a	cp group	Body wt. (�g)	Freq.%
<i>Acroboloides</i>	ba	2	0.15	99.5	<i>Aporcelaimidae</i>	pr	5	44.27	19.3
<i>Aphelenchus</i>	fu	2	0.24	97.9	<i>Cruznama</i>	ba	1	10.34	18.8
<i>Tylenchidae</i>	pl	2	0.15	96.9	<i>Rhabditis</i>	ba	1	7.73	17.7
<i>Tylenchorhynchus</i>	pl	3	0.18	95.8	<i>Mesorhabditis</i>	ba	1	0.57	17.2
<i>Panagrolaimus</i>	ba	1	0.68	95.3	<i>Heterodera</i>	pl	3	0.13	16.1
Dauerlarvae ^b	0(ba)	1	(0.0)	94.3	<i>Chiloplacus</i>	ba	2	0.54	15.6
<i>Aphelenchoides</i>	fu	2	0.17	90.1	<i>Metacrolobus</i>	ba	2	0.14	15.6
<i>Acrobelles</i>	ba	2	0.63	81.8	<i>Tylencholaimus</i>	fu	4	0.54	12.5
<i>Rhabditidae</i>	ba	1	6.80	80.2	<i>Longidorella</i>	pl	4	0.52	12.5
<i>Prismatolaimus</i>	ba	3	0.63	65.6	<i>Achromadoridae</i>	al	3	0.32	9.4
<i>Pristionchus</i>	ba,pr	1	3.75	62.0	<i>Mesodorylaimus</i>	pr	5	1.68	8.9
<i>Trichodorus</i>	pl	4	0.74	56.8	<i>Ditylenchus</i>	fu	2	0.59	8.3
<i>Monhysteridae</i>	ba	2	0.43	47.9	<i>Tripyla</i>	pr	3	4.19	8.3
<i>Plectus</i>	ba	2	0.99	44.8	<i>Pratylenchus</i>	pl	3	0.13	4.2
<i>Eudorylaimus</i>	pr	4	3.60	34.9	<i>Leptolaimidae</i>	ba	2	0.35	3.6
<i>Ecphyadophora</i>	pl	2	0.01	28.6	<i>Ecumenicus</i>	pr	5	0.72	2.6
<i>Seinura</i>	pr	2	6.35	28.1	<i>Helicotylenchus</i>	pl	3	0.37	2.1
<i>Mylonchulus</i>	pr	4	1.90	25.0	<i>Dorylaimidae</i>	pr	5	7.46	1.6
<i>Paratylenchus</i>	pl	2	0.06	25.0	<i>Cephalobidae</i>	ba	2	0.37	1.0
<i>Diploscapter</i>	ba	1	0.30	24.0	<i>Discolaimus</i>	pr	5	2.82	0.5
<i>Qudsianematidae</i>	pr	4	2.00	21.4	<i>Tylencholaimellus</i>	fu	4	0.88	0.5
<i>Alaimus</i>	ba	4	0.53	19.3	<i>Prodorylaimus</i>	pr	5	6.35	0.5

^a 0, not feeding, pl, plant feeding, fu, fungal feeding, ba, bacterial feeding, pr, specialized predation and omnivory, al, algal feeding. Functional guilds are designated by concatenation of feeding habit and structural guild categories.

^b Dauerlarvae are non-feeding stages with reduced metabolic activity.

service, probably because of the frequency of soil disturbance (S nchez-Moreno et al., 2006).

In the current study, we grouped the nematode taxa into structural guild categories to illustrate the effects of cover crop and compost treatments on the structure of the nematode assemblage averaged over the seven samplings and four years of the study (Table 4). Treatments (3–8), receiving compost and cover crops annually, had greater population levels of the cp1 enrichment opportunist structural guild, when measured at the end of the subsequent economic crop, than treatments (1–2) without cover crops annually (Table 4). There were no differences in abundance of cp1 nematodes among cover crop types where cover crops were grown annually (Treatments 3–8). Of the nematode indicators of enrichment, the EF but not the enrichment index (EI), measured in the spring was related to SOC (Fig. 1). However, by the end of the summer broccoli crop, the EF was no longer related to SOC levels and, by inference, SOC no longer reflected the magnitude of activity in the soil food web.

Although the EF differed significantly among cover crop treatments (Table 5A), it was not related to the dry weight of material incorporated, presumably reflecting differences in decomposition rates and quality of the materials. Population levels of the general opportunists that survive under a wide range of conditions (cp2), also were more abundant in annually cover-cropped treatments than in Treatments 1 and 2 (Table 4). Neither cp1 nor cp2

Table 4
Abundance (nematodes kg⁻¹ soil) of the 44 taxa detected at the experimental site, categorized by structural guilds and averaged across two samplings per year for 2005, 2006 and 2008.

Treatment	Structural guild			
	cp1	cp2	cp3	cp4–5
<i>P</i> (181 df)	<0.05	<0.05	<0.05	ns
1. No cover/No compost	613a	1379a	160a	79a
2. No cover	914a	1286a	195a	82a
3–4. Legume/rye	1165b	1587ab	363b	135a
5–6. Mustard	1082b	1985b	392b	112a
7–8. Rye	1250b	2091b	351b	92a

nematodes exhibited a significant response to compost alone (Treatment 2 vs. 1). Similarly, cp3 nematodes were enhanced by annual cover crops but not compost while abundances of those in the cp4–5 groups, mainly larger, longer-lived generalist and specialist predators, showed no relationship with the manipulative treatments (Table 4). However, the abundance and prevalence of the opportunistic (cp1) generalist predator nematode, *Pristionchus* sp., which feeds on bacteria, protozoa and small nematodes, were always greater in the plots receiving cover crops (data not shown).

In summary, while residual SOC at the end of each cropping year appeared to be a function of compost application (Table 2), nematode abundance in the lower functional guilds was related to cover crop frequency. That suggests that the organic input from the cover crops was labile and readily accessible to the micro-organisms that are resources for these nematodes. Conversely, the most recalcitrant components of the compost persisted in the soil, as reflected by effects on SOC. Such persistent C fractions are not available to most decomposer organisms (Allison, 2006). Therefore we conclude that cover crops had a greater effect on the soil food web than compost additions.

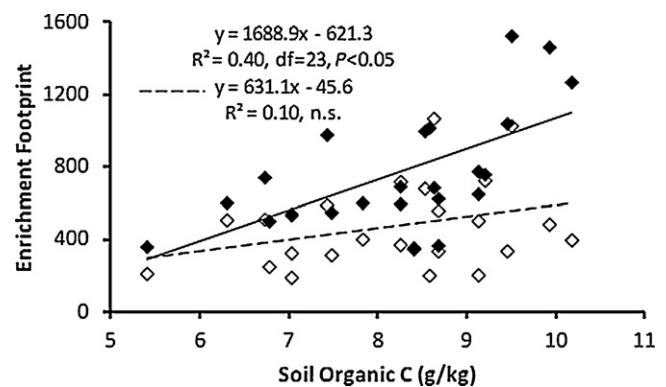


Fig. 1. Relationship between the Enrichment Footprint based on spring (solid line, solid symbols) and summer (dashed line, open symbols) nematode faunal analysis and soil organic carbon level measured at the end of summer. Data for each treatment averaged across replications in 2005, 2006 and 2008.

Table 5

Mean nematode metabolic footprints of functional components of the nematode assemblage after the spring lettuce crop (A) Across years, (B) Within years, across treatments.

Treatment	Enrichment ^a	Structure	Herbivore	Bacterivore	Fungivore
(A) Nematode metabolic footprints across years					
<i>P</i> (<i>df</i> = 48)	<0.05	ns	<0.05	<0.05	ns
1. No cover/no compost	544a	96a	42a	679a	38a
2. No cover	461a	112a	30a	574a	28a
3–4. Legume/rye	648ab	95a	68ab	804ab	34a
5–6. Mustard	864b	145a	86b	1023b	42a
7–8. Rye	713sb	134a	82b	862ab	36a
(B) Nematode metabolic footprints across treatments					
<i>P</i> (<i>df</i> = 48)	<0.05	<0.05	<0.05	<0.05	<0.05
2005	912c	28a	101b	1058c	30a
2006	745bc	110b	109b	937bc	72b
2008	627ab	120b	47a	781ab	18a
2011	445a	220c	16a	540a	25a

^a Enrichment and structure designations refer to assessments based on nematodes that represent these characteristics of the soil food web. Herbivore, bacterivore and fungivore designations refer to nematodes with specific feeding habits.

3.3. Nematode metabolic footprint analysis

All treatments were cover cropped during the winter after the 2006 and 2010 growing seasons, therefore we conducted metabolic footprint assessments (MFA, Ferris, 2010b) separately on nematode assemblages for 2005–2006, 2008, and spring 2011. We use MFA as an indicator not only of responsiveness to resources of the nematode assemblage, but also their likely effect on the magnitude of the functions and services provided by the different functional guilds (Tables 5 and 6).

To determine the duration of impact of the resources provided by the cover crops and compost amendments, we assessed NMF values of the functional components of the nematode assemblage at the end of the spring lettuce crop across the four years in which nematode samples were taken (Table 5A and B). Across years, the EF, based on the abundance and metabolic activity of the ba1 and fu2 functional guilds, was clearly in parallel with the metabolic footprint of bacterivores (BF). The EF and BF levels were enhanced in treatments receiving cover crops annually (Table 5A). Both EF and BF levels were smaller after the summer broccoli crops than after the spring lettuce crops in treatments averaged across years (Tables Table 55A, B and Table 66A, B), reflecting the annual diminution of organic resources from cover crops. The EF and BF averages decreased almost linearly across years following both the spring lettuce crop and summer broccoli crop (Tables Table 55B and Table 66B), perhaps suggesting gradual exhaustion of the systems.

The SF differed little among treatments averaged across years (Tables Table 55A and Table 66A), reflective of the amount of disturbance from tillage in this and other intensive cropping systems (Berkelmans et al., 2003; Sánchez-Moreno et al., 2006). However, the SF did increase over time (Tables Table 55B and

Table 66B) in response to the continued application of labile carbon through cover crops and crop residues. In fact, the SF, and the higher trophic level nematodes on which it is based, is impacted by two opposing forces, the stimulus of continued resource application to the system and the detrimental effects of frequent soil tillage. In small, rapidly-developing soil mesofauna, such as bacterial-feeding nematodes, 50% of the C in the body tissue may be attributed directly to recently-incorporated plant material while larger and slower-developing species, such as predatory nematodes have proportionally less of this material (Albers et al., 2006).

We consider enrichment, bacterivore, herbivore and fungivore footprints to be indicators of resource entry into the soil food web while the structure footprint is an indicator of higher trophic level predation. Using that framework, resource entry indicators declined both within years and across years. Predation indicators were not affected within years but increased across years perhaps suggesting advances in system maturity. The decline in resource entry indicators across years may reflect net resource export of this intensive production system perhaps in combination with increased top-down predation pressure. It is interesting to speculate that the observed differences among footprint types might represent snapshots of long-term predator-prey cycling. In that case, the decline in available prey would be followed by decline in predators and allow, resources permitting, resurgence in prey footprints. Longer-term study would be necessary to detect such cycles and they would be dampened by alternative resources available to predators.

One concern in the use of cover crops for providing carbon and energy to fuel the services of the soil food web is the potential for direct or indirect increase in plant-feeding nematodes which

Table 6

Mean metabolic footprints of functional components of the nematode assemblage after the summer broccoli (A) across years, (B) within years, across treatments.

Treatment	Enrichment ^a	Structure	Herbivore	Bacterivore	Fungivore
(A) Nematode metabolic footprints across years					
<i>P</i> (<i>df</i> = 36)	ns	ns	ns	ns	ns
1. No cover/no compost	325a	24a	46ab	423a	16a
2. No cover	400a	73a	42a	492a	32a
3–4. Legume/rye	563a	108b	72ab	686a	27a
5–6. Mustard	415a	62a	87b	496a	33a
7–8. Rye	544a	73a	77ab	674a	27a
(B) Nematode metabolic footprints across treatments					
<i>P</i> (<i>df</i> = 36)	ns	<0.05	<0.05	ns	<0.05
2005	537a	43a	112c	686a	40c
2006	466a	77ab	72b	584a	28b
2008	409a	98b	24a	465a	16a

^a Enrichment and structure designations refer to assessments based on nematodes that represent these characteristics of the soil food web. Herbivore, bacterivore and fungivore designations refer to nematodes with specific feeding habits.

Table 7
Correlation coefficients between measures of soil health based on nematode faunal analysis and plant dry weights calculated cumulatively across the sampling period.

	Enrichment index ^a	Enrichment footprint	Structure index	Structure footprint
Cum. yield lettuce	0.51*	0.41*	0.52*	0.35
Cum. yield broccoli	0.44*	0.42*	0.35	0.32
Cum. yield total	0.49*	0.46*	0.46*	0.37*

* $P < 0.05$, $df = 31$.

^a Enrichment and structure designations refer to assessments based on nematodes that represent these characteristics of the soil food web.

could damage the economic crops. Damaging effects might occur if the cover crop supported a nematode species whose host range included the economic crops. For cover crops grown in the fall and winter months, those direct effects often are avoided because soil temperatures are too low for increase of the nematode populations. Indirect effects are more subtle; if the cover crop enhances growth of the economic crop through nutrient availability or soil structure effects, that enhancement provides more resources for herbivore increase. The effects of herbivore species in that case may not be seen during the current crop but may present problems for a second annual crop or for those of subsequent years. Thus, the beneficial effects of amendments on crop growth are more likely to be due to their positive effects on beneficial nematodes rather than on negative effects on herbivore nematodes (Thoden et al., 2011).

The NMF values of herbivore nematodes in most cover-cropped treatments were small but significantly greater than those in the no cover-crop controls after both the spring lettuce and summer broccoli crops of 2005 and 2006 (Tables Table 55A and Table 66A). However, the differences among treatments were not detectable in 2008 and 2011 (data not shown). Averaged over all treatments, the herbivore footprint decreased across years after both vegetable crops (Tables Table 55B and Table 66B), somewhat coincident with increase in the SF and perhaps suggesting an increase in top-down predation pressure on the plant-feeding nematodes. The fungivore footprint was not affected by treatment although it did decline over time at the end of the summer broccoli crop (Table 6B). Based on the much smaller sizes of the herbivore and fungivore than the bacterivore metabolic footprints, we conclude that direct herbivory and fungivore activity were not consistent or important channels of resources into the soil food web; most resource assimilation was via the bacterial channel.

Relative dry matter yields of the spring lettuce crops of 2005 and 2006 were related to the EF measured at the end of those

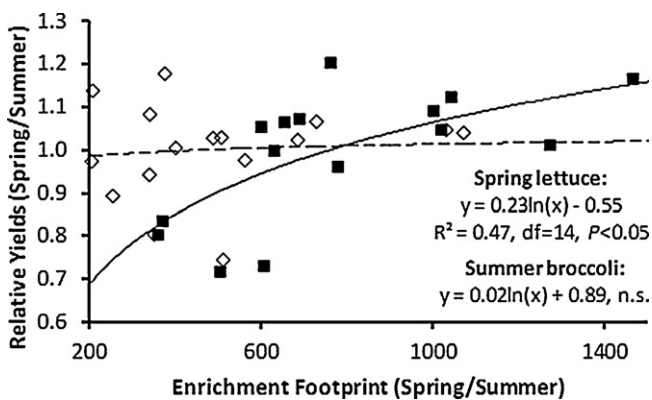


Fig. 2. Relationship between relative per plant aboveground biomass (based on crop type and seasonal averages) and the Enrichment Footprint of the nematode assemblage measured after spring lettuce (solid line, solid symbols) and summer broccoli (dashed line, open symbols) (A) and prior to summer broccoli (B). Data from 2005 and 2006.

crops (Fig. 2). By the end of the summer broccoli crops, the enrichment effect of the winter cover crop and compost amendments was depleted (Table 6) and broccoli yield was not related to the EF measured either before (data not shown) or after at the end of the crop. In fact, the fungivore footprint, either before or after the broccoli crop, had a stronger, although not significant, relationship with broccoli yield (data not shown) than did the EF. That suggests that the probable increase in C:N ratio of the residual organic resources, as opportunistic organisms utilized the more labile components, resulted in succession to a fungal dominated food web (Ferris and Matute, 2003).

Our monitoring of nematode assemblages seven times during seven-year duration provided discontinuous snapshots of food web biology during temporal shifts in baseline and functional activities within the various treatments. To better integrate effects over time, we examined the relationships between crop yields and various indicators of soil health on a cumulative basis. By the end of the experiment, cumulative crop yields were related to all measures of soil health based on nematode faunal analysis (Fig. 3, Table 7).

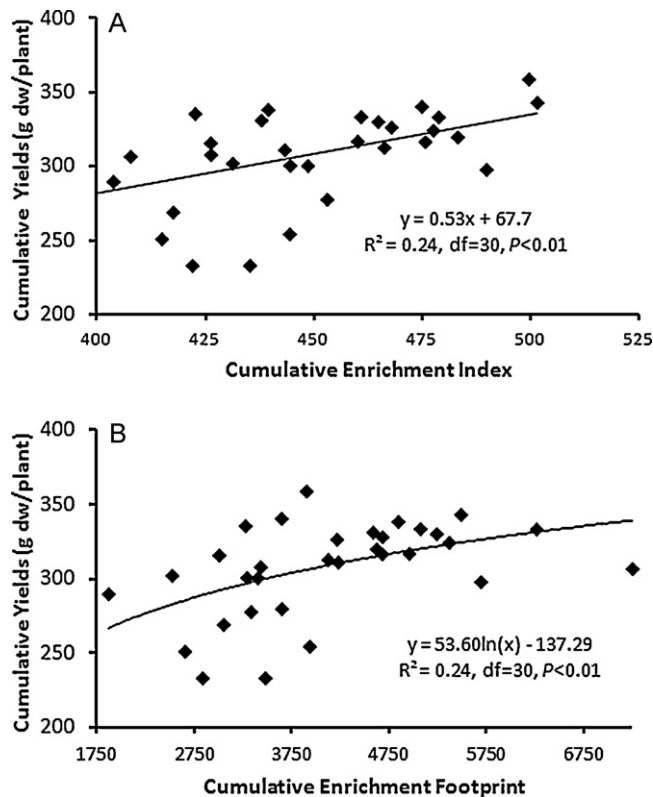


Fig. 3. Cumulative total of annual crop dry weight (g/plant) across years of nematode sampling in relation to A. Enrichment Index and B. Enrichment Footprint of the nematode faunal assemblage.

3.4. Functional connectance

Predator nematodes represent top down pressure on the prey species; they are also indicative of the abundance of other organisms in the same management cohort (Ferris, 2010a; Ferris et al., 2001; Sánchez-Moreno et al., 2009). Here we test whether increased functional connectance between predators and amplifiable prey results in increased functional connectance between predators and target prey and, consequently, increased regulatory pressure on target prey.

As an important intermediate step, we demonstrate a relationship between amplifiable prey abundance and that of predators ($P < 0.01$, Fig. 4A). The relationship between predator abundance and amplifiable prey biomass is similar (data not shown) and we have already determined that nematode metabolic footprints of the bacterivore component of amplifiable prey are increased by cover crops, particularly during a subsequent spring crop (Table 5). Positive relationships between abundance of predator and prey nematodes are uncommon in agricultural systems due to the differences in environmental characteristics that favor the two functional guilds (Sánchez-Moreno and Ferris, 2007). In this case, cover crops and compost incorporation may have favored organisms at the entry level of the soil food web while the absence of mineral fertilizers and pesticides may have been conducive to increase in predators as the experiment progressed. Thus, bottom-up effects of compost and cover crops may have increased predator populations mediated through their prey, which was particularly evident by the 8th year of the experiment (Fig. 5). The bottom-up effect of residue incorporation has also been shown to increase the NMF levels of the nematode assemblage in other studies (Zhang et al., 2012).

There was greater functional connectance between predators and amplifiable prey ($P < 0.01$, Fig. 4B) in treatments with a greater abundance of predators. The functional connectance between predators and target prey was strongly related to the functional connectance between predators and amplifiable prey ($P < 0.01$, Fig. 4C). We conclude that cover crops not only affect organisms at the entry level of the web but that resources are also transferred to higher trophic links which in turn increases top-down pressure on plant-parasitic nematodes. However, there are inefficiencies in the system. Interpolation across the three relationships portrayed in Fig. 4 reveals that a doubling of amplifiable prey abundance increases the functional connectance between predators and target prey by less than 5%. This dilution of effect must represent, among other things, differences in spatial patterns of amplifiable prey associated with cover crop and compost incorporation and target prey associated with plant roots.

A high degree of functional connectance suggests many interactions among organisms with resultant functional redundancy in the regulatory process and hence functional resilience to perturbation in that ecosystem service. However, food web functional connectance is susceptible to frequent disturbance, even in organic systems (Sánchez-Moreno and Ferris, 2007). This experimental farming system, and the organic production systems that it represents, involves several tillage operations each year which imposes disproportionate disturbance pressures on predator taxa (Berkelmans et al., 2003). Also, since the plant-fixed C is diminished through respiration at each trophic level, maintenance of higher trophic levels requires continued resource flow through the system (Ferris, 2010a). Management of predator–prey relationships through organic inputs to fuel the soil food web might be explored more definitively in less disturbed and no-till systems.

For an organic system to function efficiently, it is necessary for stewardship to support and foster a diversity of organisms,

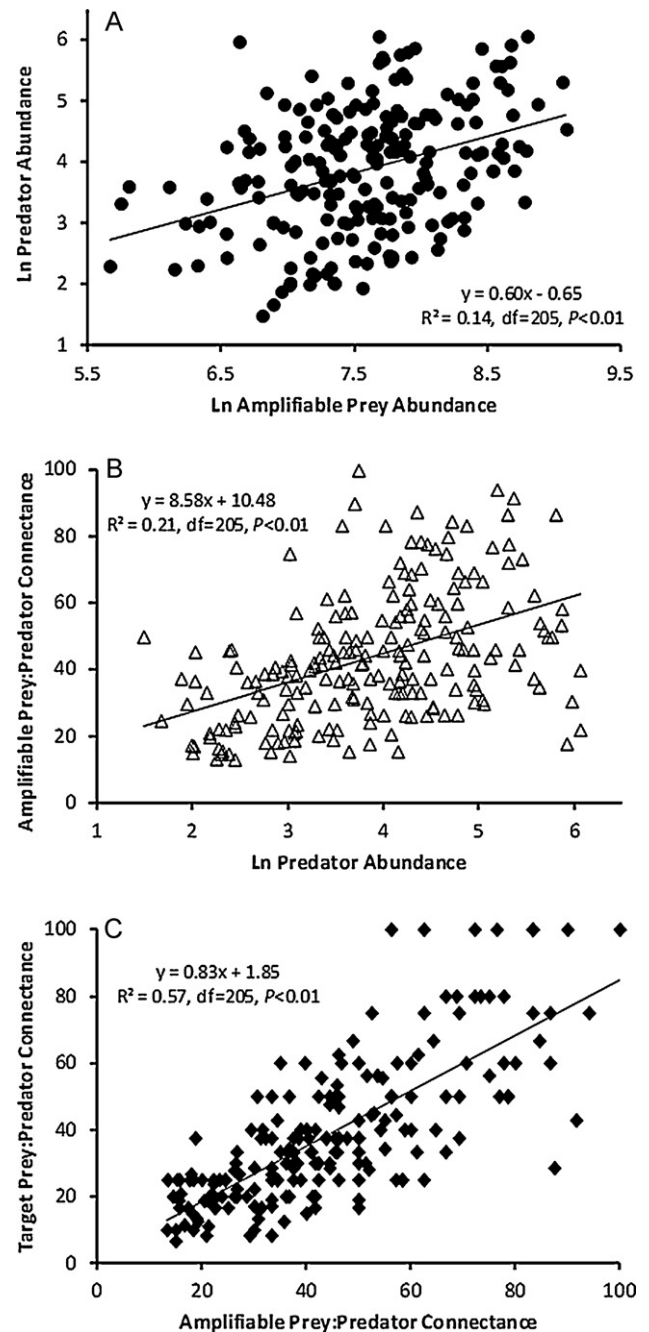


Fig. 4. (A) The relationship between the abundance of predators and the abundance of amplifiable prey. (B) The relationship between predator:amplifiable prey functional connectance and predator abundance. (C) The relationship between predator:target prey functional connectance and predator:amplifiable prey functional connectance. Relationships are across all years of the study.

representing a variety of functional guilds, in sufficient abundance for nutrients to become available to plants and for populations of pest species to be regulated. Because their quality changes over time, residual organic resources are exploited by a succession of diverse organisms, which may select for specific groups of predators. Through the duration of the growing season, cohorts of organisms are favored that are adapted to the changing ambient conditions and available resources (Ferris and Bongers, 2009; Ferris and Matute, 2003; Sánchez-Moreno et al., 2009; Semenov et al., 2002).

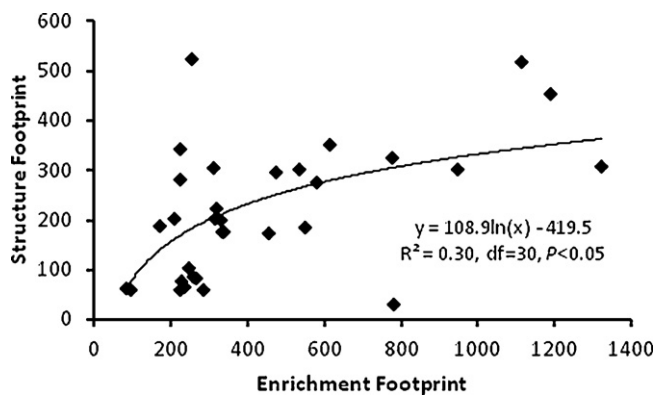


Fig. 5. Relationship between the Structure Footprint and Enrichment Footprint of the nematode faunal assemblage at 8th year of the experiment in spring 2011.

4. Conclusions

- Abundances of bacterivore and fungivore nematodes were enhanced by the use of winter cover crops.
- Cover crops had a greater effect than compost additions on the structure and functions of soil food web.
- The metabolic footprint of enrichment indicator nematodes, representing the ecosystem service of nutrient mineralization, was comprised mainly of the contribution of bacterivore nematodes and less of fungivores.
- The metabolic footprint of herbivore nematodes increased slightly with use of cover crops, suggesting need to consider the host status of economic crops to the plant-parasitic nematode taxa.
- In this experiment, most resource assimilation into the soil food web was via the bacterial channel; herbivore and fungivore channels were less active.
- The structure footprint, reflecting the metabolic activity of higher trophic level nematodes, did not differ among cover crop and compost amendment treatments but it did increase over years, suggesting increases in system maturity.
- Abundance of predators increased with abundance of the amplifiable nematode prey, predominantly bacterivores, that are readily amplified by organic inputs.
- The functional connectance between predators and amplifiable prey was greater in plots with a greater abundance of predators.
- Functional connectance between predators and herbivore prey, which represent a management target, was strongly related to the functional connectance between predators and amplifiable prey.
- Crop plant biomass was correlated with measures of soil health based on nematode faunal analysis.
- Cover crops not only affect organisms at the entry level of the web but resources are transferred to higher trophic links which in turn increases top-down pressure on plant-parasitic nematodes.

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Corrigendum

Corrigendum to “Structure, functions and interguild relationships of the soil nematode assemblage in organic vegetable production” [Appl. Soil Ecol. 6 (2012)16–25]

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The authors regret that Tables 1 and 2 contained erroneous data. The corrected tables appear below. The authors apologize for any inconvenience caused.

Table 1

Compost and winter cover crop treatment descriptions. Nematode samples were taken in spring and summer of 2005, 2006, 2008, and spring 2011.

Treatment code ^a	Compost rate (Mg ha ⁻¹ crop ⁻¹) ^b	Cover crop		
		Type ^c	Seeding rate (kg ha ⁻¹) ^d	Frequency ^e
1	0	Legume/rye	420	Every 4th winter
2	7.6	Legume/rye	420	Every 4th winter
3–4	7.6	Legume/rye	140, 420	Every winter
5–6	7.6	Mustard	11, 33	Every winter
7–8	7.6	Rye	90, 270	Every winter

^a The experiment included eight treatments, however, because nematodes were unaffected by cover crop seeding rate, treatments that differed only in seed rate were combined as 3–4, 5–6, and 7–8.

^b Green waste compost applied on a dry weight basis prior to each vegetable crop. For the treatments receiving compost, the annual application rate was 15.2 Mg ha⁻¹ for years 1 to 7 when two vegetables were grown annually and 7.6 Mg ha⁻¹ during year 8 when only one vegetable was grown.

^c Legume/rye cover crop mixture included 90% legume and 10% ‘Merced’ rye (*Secale cereale* L.) by seed weight. Legumes were 35% *Vicia faba* L., 25% *Pisum sativum* L., 15% *Vicia benghalensis* L., and 15% *Vicia sativa* L. Mustard was a mixture of 61% ‘Ida Gold’ (*Sinapis alba* L.) and 39% ‘Pacific Gold’ (*Brassica*

juncea (L.) Czern.), by seed weight.

^d For the combined treatments (3–4, 5–6, 7–8), the low and high seeding rates are listed, respectively for each pair.

^e Treatments 1 and 2 were maintained as weed-free fallows for all winter periods (October–March) except those of 2006–2007 and 2010–2011 when they were cover cropped.

Table 2

Dry weight and C:N ratios of cover crop shoots incorporated during the winter prior to nematode sampling, soil organic carbon (SOC) and average per plant crop shoot yield averaged across years in which nematode populations were sampled (2005, 2006, 2008, 2011).

Treatment	Dry wt. cover crop incorporated ^a (kg ha ⁻¹)	C:N ratio cover crop incorporated ^b	Crop yield dry wt. (g plant ⁻¹)	SOC (g C kg ⁻¹ soil)
P (86 df)	< 0.05	< 0.05	< 0.05	< 0.05
1. No cover/ no compost			42.6a	5.0a
2. No cover			46.4ab	6.7b
3–4. Legume/rye	6360b	19a	55.0c	7.4b
5–6. Mustard	5090a	21a	53.6c	7.4b
7–8. Rye	6337b	28b	53.1bc	7.4b

^a Cover crop was only grown in treatments 1 and 2 during the 2010–2011 winter resulting in average shoot dry matter incorporated of 6901 and 7057 kg ha⁻¹, respectively. Cover crop dry weights and the respective C:N ratios for treatments 3–4, 5–6, and 7–8 are averaged across the years.

^b C:N ratios of the cover crop shoots for treatments 1 and 2, grown during the 2010–2011 winter, were 23 and 22, respectively.

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