Suppressive service of the soil food web: Effects of environmental management

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Abstract

Soil food webs perform the important ecosystem services necessary to maintain both agricultural productivity and ecosystem health. Higher trophic levels in soil food webs can play a role suppressing plant parasites and affecting nutrient dynamics by modifying abundance of intermediate consumers. Natural and agricultural landscapes were sampled to compare soil faunal structure. Top-down soil suppressiveness of a parasitic nematode, *Meloidogyne incognita*, was determined in laboratory assay. Five treatments, including two nitrogen fertilizers, two herbicides and simulated tillage were established in experimental microcosms to evaluate the effects of simulated agricultural practices on top-down suppressiveness. Soil food web indices, based on the composition of the nematode fauna, were calculated to infer soil food web condition. Long and complex soil food webs in natural areas, with more trophic links and abundant predatory nematodes, effectively suppressed plant–parasite populations, while disturbed communities in agricultural soils did not. Soil suppressiveness was related to the ratio of predators to prey and to the prevalence of omnivore and predator species. Agricultural management led to a reduction in the suppressive capacity of the soil food web. Abundance of predatory nematodes was related to soil NH_4^+, probably due to excretory products of nematodes and other organisms grazing on microbes. Soil suppressiveness, soil food web dynamics and agricultural management are strongly inter-related.

1. Introduction

Understanding the function of soil food webs is an important priority for soil ecologists (Hedlund et al., 2004). Aboveground trophic webs are quite well understood but belowground communities require further study since they are the basic biological system supporting many ecological functions and services (De Deyn et al., 2003; Schröter et al., 2004). Indeed, recent studies suggest that above and belowground biological communities are strongly related so that changes aboveground have important consequences belowground and vice versa (Wardle et al., 2004, 2005; van der Putten et al., 2004).

Species loss can alter the goods and services provided by ecosystems (Hooper et al., 2005). The destruction of natural systems and agricultural intensification, has produced important changes in soil biological communities, reducing biodiversity, eliminating key species and altering trophic relations. Forest clearcutting, drought, acid rain or soil pollution can decrease diversity and cause species loss (Dmowska, 1996; Korthals et al., 1996a; Bengtsson, 2002). In contrast, increasing plant diversity, or designing agricultural management to enhance soil faunal diversity, leads to more productive and stable ecosystems (Bardgett and Cook, 1998; Spehn et al., 2005).

Nematodes play important roles in soil functioning. As participants in several links of the food web, they interact with many other organisms, consuming and being consumed by other components of the soil fauna. Their diversity is the basis for their multiple functions and roles;

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for example, regulating bacteria and fungal populations, feeding on roots (sometimes at levels damaging to the plant host) and, possibly, acting as top-down regulators of lower trophic levels (Khan and Kim, 2005). Indeed, abundance and diversity of nematodes are indicators of the soil faunal structure (length, complexity, connectivity and abundance of organisms at high trophic levels) and functioning (Bongers and Ferris, 1999; Ekschmitt et al., 2001; Yeates, 2003). Soil food web indices based on the nematode community have been developed and applied to assess ecosystem health (Ferris et al., 2001; Berkelmans et al., 2003; Hohberg, 2003) and nutrient cycling (Bulluck et al., 2002; Ferris et al., 2004). The Basal Index (BI) is an indicator of soil food webs that are diminished due to stress (resource limitation, pollution or adverse environmental conditions) and comprised mainly of opportunistic nematodes with survival capabilities. The Structure Index (SI) indicates lack of, or recovery from, stress and/or resource depletion, abundance of predators and omnivores and food web connectance and length. The Enrichment Index (EI) increases when resources become available; bacterial flush is followed by increase in bacterial feeders. Finally, the Channel Index (CI) indicates the percentage of opportunistic grazers feeding on fungi or bacteria, and the predominant decomposition pathway (Ferris et al., 2001).

Soil functioning is strongly dependent on soil food web diversity. Soil invertebrate fauna enhance plant growth (Wardle, 1999) and plant diversity (De Deyn et al., 2003). Setälä et al. (1998), after analyzing a number of studies on soil fauna and ecosystem functions, concluded that soil faunal diversity clearly affects primary production and carbon mineralization. Several functions important in agricultural soils have relationships with the nematode faunal components of the soil food web. For example, soil suppressiveness against root-knot nematodes was found to be negatively correlated with BI and CI (Berkelmans et al., 2003), and the EI may indicate available mineral N and crop yield (Ferris et al., 1998, 2001) or the amount of N mineralized (Ferris and Matute, 2003).

The interaction of the components of the soil food web drive such functions as organic matter decomposition, plant productivity and nutrient cycling; they also may influence the diversity of the soil system. In the case of nematode communities, other than the direct effects of plant feeding, most research has been focused on the effects of intermediate trophic levels (microbial grazers) on microorganism-mediated soil processes (Chen and Ferris, 1999; Savin et al., 2001; Djigal et al., 2004). The effects of predators and omnivores on the soil food web, and thus on ecosystems functions, have been studied less (Wardle and Yeates, 1993; Mikola and Setälä, 1998; Laakso and Setälä, 1999) and results are often contradictory or difficult to interpret (Wardle, 1999).

Both natural and anthropogenic chemical components of the soil (e.g., nitrate, ammonium, pH, organic matter, pesticides and pollutants) have reciprocal relationships with soil food web structure. The soil fauna regulate soil functioning by grazing on fungi and bacteria, affecting carbon and nitrogen mineralization, altering primary production and directly enriching the soil with nutrients (Bouwman et al., 1994; Mikola and Sulkava, 2001; Hunt and Wall, 2002; De Deyn et al., 2003). At the same time, nutrient and organic matter addition, and soil physical perturbations (mainly in agricultural systems), modify the composition and abundance of soil fauna. But the effect of perturbations on the food web is inconsistent. Among the nematode fauna, large, k-strategist, predator and omnivore nematodes are more likely than other functional guilds to be adversely affected by physical or chemical changes in the soil (Bongers, 1990; Korthals et al., 1996b).

Mechanisms underlying suppressiveness of soil to plant disease organisms are well documented. Suppression of plant–parasitic root-knot nematodes has been ascribed mainly to nematode-trapping fungi and other microorganisms (Westphal and Becker, 2001a; Wang et al., 2004) and is reduced when the soil is fumigated or managed as a monoculture (Westphal and Becker, 1999, 2001b; Pyrowolakis et al., 2002). Biological suppressiveness is transferable to non-suppressive (conducive) soils (Westphal and Becker, 2000). The suppressive capacity of nematodes, such as entomopathogenic Rhabditidae also has been tested (Pérez and Lewis, 2004), but the capacity of higher trophic levels to regulate plant-feeding species by predation is not well understood.

We studied the nematode community of neighboring disturbed and undisturbed habitats. Nematode community composition and abundance, soil suppressiveness and soil food web indices were used to determine if (a) suppressiveness to introduced organisms is greater in undisturbed soil than in soil that has been agriculturally managed, (b) the level of soil suppressiveness can be indicated by the faunal structure of soil nematodes (as indicated by the SI) and (c) the suppressiveness of undisturbed soils is reduced after the soil has been subjected to simulated agricultural management.

2. Material and methods

2.1. Study site

The study site is situated near Oakville (Napa Valley, California). Two different environments, a mature oak woodland and a 20-year-old vineyard, were sampled. The woodland is situated on a hill slope and the vineyard at the base of the hill. The oak woodland is well conserved and the soil is covered by a thick layer of leaf litter. The vineyard begins 20 m from the woodland and is separated from it by a narrow road. The vineyard has been organically managed for the last 7 years; before being converted to organic, the vineyard was managed with conventional practices.

2.2. Determination of physical environment and food web structure

2.2.1. Sampling methods

In June 2005, 15 samples were collected from the woodland (from the upper, intermediate and lower part of the hill, five samples at each location) and 20 from the vineyard (four sampling points separated by about 100 m, five samples from each site), along a transect from the top of the hill at N38°25.945′; W122°25.339′ to the center of the vineyard (N38°26.076′; W122°25.025′). Each sample consisted of 2 kg of soil collected at a single point from 0 to 20 cm depth and with minimal soil disturbance. In October 2005, 24 samples were collected in the woodland, at the intermediate elevation of the hill, for use in a medium-term experiment (see below). At each date, samples were transported to the laboratory in insulated containers and stored at 4 °C until processed.

2.2.2. Physical and chemical analyses

From the June samples, 500 g of air-dried soil was submitted to the University of California's Agriculture and Natural Resources Analytical Laboratory (ANR). Concentrations of NO_3^--N and NH_4^+-N were determined by an automated flow injection analyzer method (Hofer, 2003; Knepel, 2003). Total organic matter was determined by weight loss on ignition (Rible and Quick, 1960) and soil texture was determined by soil suspension and hydrometer (Sheldrick and Wang, 1993).

From the October samples, 8 g of fresh soil was mixed with 40 ml of 2 M KCl and shaken for 1 h. Each sample was centrifuged at 5 G for 5 min at room temperature. The supernatant was filtered and sent to the ANR analytical lab where NO_3^--N and NH_4^+-N were determined. Soil pH was measured by the saturated paste method (Hesse, 1971).

2.2.3. Biological analyses and suppressiveness determination

Soil suppressiveness was tested in samples taken in both June (samples from the vineyard and the woodland) and October (samples from the woodland only). A subsample of 300 g of fresh soil was removed from each sample; 100 g was used as a control to check if the target nematodes, *Meloidogyne incognita* juveniles, were present in the soil, 100 g was defaunated (3 h 65 °C) and 100 g was non-defaunated. The 100 g portions were placed in Petri dishes and *M. incognita* juveniles (500) were inoculated on the surface of the defaunated and non-defaunated replicates. The control soil was inoculated with distilled water. The defaunated replicates provided baseline data on the mortality of the nematodes in the absence of any predator or antagonist.

Defaunated, non-defaunated and control replicates were incubated for 5 days in the dark at room temperature. Nematodes were extracted from the soil in each Petri dish using a modified Baermann method. Nematodes in each

sample were counted at 50× magnification. Each nematode suspension was then concentrated by centrifugation and the concentrate spread on a microscope slide. At least 200 nematodes from each sample were identified at higher magnification to genus or family level.

Soil suppressiveness was tested once in each sample and average values in each area (vineyard and woodland) were used to compare habitats (see Section 2.4). In the experimental approach, suppressiveness was checked in four different replicates in each treatment (see Section 2.3). Two measures of suppressiveness were used. For each sample, absolute suppressiveness was calculated as the percentage of inoculated nematodes that did not survive in the non-defaunated sample, and relative suppressiveness was calculated as absolute suppressiveness in non-defaunated sample minus absolute suppressiveness in the defaunated replicate.

Different ecological indicators were used to infer the effects of agricultural management on the soil food web. Relative and absolute abundances of nematode trophic groups, nematode taxa abundance and taxa richness (number of taxa in each sample) were used as descriptors of the nematode community. Five nematode trophic groups were used (bacterial feeders, fungal feeders, plant feeders and parasites, predators and omnivores (Yeates et al., 1993)). Food web indices (SI, CI, EI and BI) were calculated following Ferris et al. (2001).

2.3. Simulated agricultural disturbance experiment

Soil samples collected in October were used to establish a microcosm experiment. Five treatments were applied to the soil; two nitrogen fertilizers (ammonium nitrate (NH_4NO_3) and calcium nitrate ($Ca(NO_3)_2\cdot4H_2O$)), two herbicides (diuron ($C_9H_{10}Cl_2N_2O$) and simazine ($C_7H_{12}ClN_5$)) and simulated tillage. The experiment consisted of 96 microcosms that represented four replicates of six treatments for each of four time intervals. To minimize experimental heterogeneity, one soil sample was used to establish each temporal series. To simulate tillage, soil for that treatment was mixed in a cement mixer for 20 min. Chemical treatments were applied by adding 50 ml of a solution of fertilizer or herbicide in distilled water. Herbicides were applied at 2.68 kg a.i./ha of simazine and 1.79 kg a.i./ha of diuron (as recommended by the University of California Integrated Pest Management Program—http://www.ipm.uc-davis.edu/PGM/r302700211.html). The nitrogen fertilizer treatments were applied at 11.2 kg/ha. The control and time zero (T0) microcosms received 50 ml of distilled water. Although plants influence biological processes in the rhizosphere (Phillips et al., 2003), they were excluded from our experimental design to avoid any effects on nematode community dynamics that might obscure the effects of the experimental treatments.

Two days after establishment of the experimental treatments, soil moisture content reached 10% and nematodes

were extracted from the T0 microcosms to represent soil conditions prior to treatment application. Soil moisture was maintained by daily watering throughout the experiment, at a predetermined rate, to offset evaporative loss. For each subset of the experiment, nematodes were extracted from four replicates of each treatment (including the control) 10, 20 and 30 days after the T0. For each exposure time, soil suppressiveness was tested as described above.

2.4. Statistical analyses

Due to lack of normality in the data, non-parametric methods were used to test differences between habitats and between treatments. June data from both environments (vineyard and woodland) were compared by the Mann–Whitney U test. Multiple differences between treatments were tested by Mann–Whitney and, post hoc, by the Kruskal–Wallis test.

To examine relationships between variables, all variables were subjected to Spearman rank order correlation.

In the microcosm experiment, GLM was used to test the influence of continuous and discrete variables on the nematode community. Soil pH was considered a continuous variable and sampling time (before and 10, 20 and 30 days after treatments were applied) and treatments (ammonium nitrate, calcium nitrate, diuron, simazine and simulated tillage) were considered discrete variables. The interaction of discrete variables (time × treatment) was also tested. As high numbers of tardigrades were recovered in some samples, tardigrade abundance was included as a continuous independent variable.

In a second analysis, influence of nematodes and treatments on NH_4^+ and NO_3^- was tested by GLM using trophic group abundances, food web indices, sampling time and treatments as categorical or continuous predictors of soil nitrogen concentration.

All statistical analyses were carried out with the STATISTICA program (StatSoft, 1996).

3. Results

3.1. Nematode community composition and relationships between nematode faunal analysis and physical/chemical environmental conditions

Thirty two nematode taxa were identified in the woodland and 26 in the vineyard. *Acrobeloides*, *Aphelenchoides*, Rhabditidae (dauerlarvae), *Eudorylaimus*, *Mesorhabditis*, Tylenchidae and *Tylencholaimus* were the most abundant taxa (Table 1). Eleven taxa were found only in the woodland while five taxa were found only in the vineyard. *Achromadora*, Qudsianematidae, *Prionchulus*, *Panagrolaimus*, *Pratylenchus*, *Tripyla*, *Eudorylaimus*, *Metacrolobus*, *Tylencholaimus*, *Wilsonema* and Criconematidae were more abundant in the woodland than in the vineyard, while *Aphelenchus*, *Mesorhabditis*, Tylenchidae and *Tylenchorhynchus* were more abundant in the vineyard.

There were no differences in soil texture or soil pH between habitats. NH_4^+ and organic matter were higher in the woodland, while NO_3^- was higher in the vineyard (Table 2).

Total number of nematodes was greater in the vineyard, mainly due to the abundances of bacterial-, fungal- and plant feeders, which were almost double those in the woodland

Table 1
Average number of nematodes (±S.E.)/100 g soil

	Woodland	Vineyard			Woodland	Vineyard	
Achromadora	2.9 ± 1.3 a	0.0 ± 0.0 b	W	*Leptolaimus*	0.0 ± 0.0	0.5 ± 0.6	V
Acrobeles	0.2 ± 0.2	0.0 ± 0.0	W	*Mesorhabditis*	8.6 ± 3.2 a	35.0 ± 8.7 b	
Acrobeloides	42.9 ± 10.0	76.1 ± 12.4		*Metacrolobus*	1.7 ± 0.9 a	0.5 ± 0.23 b	
Alaimus	0.4 ± 0.2	0.7 ± 0.54		Monhysteridae	0.8 ± 0.4	1.5 ± 0.6	
Aphelenchoides	10.5 ± 5.6	18.2 ± 5.4		*Odontolaimus*	0.0 ± 0.0	0.2 ± 0.2	V
Aphelenchus	0.6 ± 0.4 a	15.8 ± 3.5 b		*Panagrolaimus*	7.07 ± 1.8 a	3.9 ± 1.8 b	
Aporcelaimidae	0.0 ± 0.0	0.2 ± 0.2	V	*Paratylenchus*	3.8 ± 3.2	0.0 ± 0.0	W
Cephalobidae	0.4 ± 0.3	0.0 ± 0.0	W	*Plectus*	5.8 ± 2.3	6.0 ± 1.7	
Criconematidae	0.8 ± 0.4 a	0.1 ± 0.1 b		*Pratylenchus*	4.5 ± 2.3 a	0.1 ± 0.1 b	
Dauerlarvae	10.0 ± 2.6	17.6 ± 6.0		*Prionchulus*	3.4 ± 1.0 a	0.2 ± 0.2 b	
Diphterophora	0.1 ± 0.1	0.0 ± 0.0	W	*Prismatolaimus*	0.6 ± 0.3	0.4 ± 0.3	
Diplogasteridae	0.1 ± 0.1	0.0 ± 0.0	W	Qudsianematidae	2.4 ± 1.0 a	1.1 ± 0.5 b	
Discolaimus	0.5 ± 0.5	0.0 ± 0.0	W	*Rhabditis*	4 ± 2.6	5.5 ± 3.4	
Ditylenchus	0.0 ± 0.0	0.3 ± 0.3	V	*Tripyla*	2.3 ± 0.6 a	1.6 ± 1.2 b	
Ecphyadophora	1.1 ± 1.0	0.2 ± 0.2		Tylenchidae	65.9 ± 18.1 a	202.1 ± 37.7 b	
Eudorylaimus	19.6 ± 3.7 a	11.6 ± 3.2 b		*Tylencholaimus*	25.1 ± 10.3 a	6.4 ± 2.7 b	
Eumonhystera	0.3 ± 0.3	0.0 ± 0.0	W	*Tylenchorhynchus*	0.6 ± 0.3 a	11.0 ± 4.5 b	
Gracilacus	1.9 ± 1.5	0.0 ± 0.0	W	*Wilsonema*	0.5 ± 0.2 a	0.0 ± 0.0 b	W
Helicotylenchus	0.1 ± 0.1	0 ± 0.0	W	*Xiphinema*	0.0 ± 0.0	0.5 ± 0.4	V

W and V indicate the exclusive presence of a taxon in one habitat (woodland or vineyard, respectively).
Letters (a and b) indicate significant differences between habitats ($P < 0.05$).

Table 2
Soil physical and chemical properties, trophic group abundances and community descriptors[a] in the study area

	June Woodland	June Vineyard[b]	October Woodland[b]
pH	5.8 ± 0.2 a	5.7 ± 0.1 a	5.56 ± 0.09 a
NH_4^+	12.7 ± 1.6 a	1.6 ± 0.1 b	3.85 ± 0.32 b
NO_3^-	6.9 ± 1.6 a	11.3 ± 1.7 b	6.20 ± 1.17 a
OM	9.9 ± 0.6 a	3.7 ± 0.1 b	–
Sand	52.0 ± 2.4 a	49.6 ± 0.6 a	–
Silt	29.0 ± 2.0 a	32.4 ± 0.3 a	–
Clay	19.0 ± 1.0 a	18.1 ± 0.3 a	–
Ba	86.8 ± 49.3 a	147.7 ± 85.1 b	42.98 ± 8.26 b
Fu	68.1 ± 58.7 a	141.7 ± 86.5 b	21.84 ± 3.92 b
Pp	47.5 ± 36.7 a	111.4 ± 69.3 b	23.58 ± 4.73 b
O	18.5 ± 13.2 a	11.8 ± 12.0 b	5.11 ± 1.82 b
P	8.1 ± 4.4 a	2.9 ± 4.7 b	0.89 ± 0.37 b
Sup. Ab.	89.8 ± 1.4 a	85.5 ± 5.3 b	97.28 ± 0.59 b
Sup. Rel.	41.6 ± 9.78 a	48.8 ± 8.9 a	51.28 ± 3.92 b
N	247.6 ± 119.8 a	416.9 ± 227.5 b	94.40 ± 16.17 b
S	14.6 ± 3.5 a	11.9 ± 1.6 b	8.63 ± 0.84 b
EI	59.7 ± 16.1 a	60.5 ± 9.8 a	51.28 ± 3.92 a
SI	60.5 ± 21.5 a	26.3 ± 17.2 b	23.66 ± 4.37 b
CI	30.8 ± 21.1 a	40.7 ± 13.7 b	29.01 ± 4.79 a
BI	24.1 ± 11.8 a	33.1 ± 7.6 b	38.18 ± 3.83 b

[a] OM: organic matter content, Ba: bacterial-feeders, Fu: fungal-feeders, Pp: plant–parasites and herbivores, O: Omnivores, P: predators, N: total number of nematodes, S: taxa richness, Sup.: suppressiveness (absolute (Ab) and relative (Rel.)), EI: Enrichment Index, SI: Structure Index, CI: Channel Index and BI: Basal Index.

[b] Data from June vineyard and October woodland were both compared with June woodland data. Letters (a and b) indicate differences between habitats ($P < 0.05$).

(Table 2). In contrast, abundances of omnivores and predators were higher in the woodland.

Taxa richness, SI and soil suppressiveness were significantly higher in the woodland, while CI and BI were significantly higher in the vineyard (Table 2). The different states of the soil food web can be clearly distinguished in the faunal profiles of the two habitats (Fig. 1); samples from the vineyard represented an enriched soil food web compared to the woodland, with more abundant bacterial- and fungal-feeding nematodes. Woodland samples represented a food web with more abundant organisms at the higher levels of the soil food web, with more trophic links and greater connectance.

The relationships of NH_4^+ and NO_3^- with the nematode community structure were almost opposite. NH_4^+ was positively correlated with abundances of higher trophic levels and the SI, while NO_3^- was negatively correlated with omnivores, predators and the SI. Similarly, NH_4^+ was inversely correlated with the BI and fungal feeders, while NO_3^- was positively correlated with plant parasites and bacterial feeders. Organic matter was also positively correlated with higher trophic levels and NH_4^+ and negatively with the BI (Table 3).

Percent sand was correlated negatively with NO_3^- and positively with fungal feeders. Percent silt was correlated negatively with the SI and predators and positively with plant parasites and NO_3^-. Percent clay was negatively correlated with the total number of nematodes and with abundances of plant parasites (Table 3).

3.2. Relationship between suppressiveness and inferred food web structure

Absolute soil suppressiveness was more strongly related to the soil food web descriptors than was relative suppressiveness. It was positively related to the SI, omnivores, predators and organic matter, and negatively to total number of nematodes and to abundance of bacterial and fungal feeders (Table 3; Fig. 2). Suppressiveness was also negatively correlated with the biomass of nematodes at lower trophic levels in the soil food web (Fig. 3).
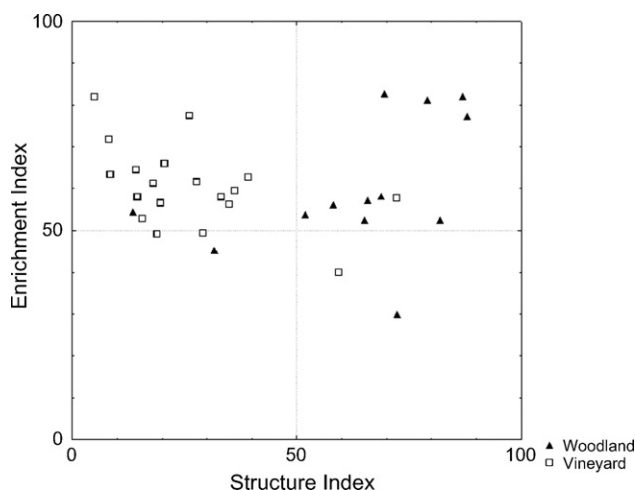

Fig. 1. Faunal profile of woodland and vineyard soil communities.

Table 3
Spearman rank order correlation coefficients between nematode community descriptors and soil chemistry

	NH$_4^+$	NO$_3^-$	OM	Sand	Silt	Clay	Sup. Rel.	Sup. Ab.	O Rel.	P Rel.
N	−0.24	0.33	−0.14	0.15	0.21	**−0.36**	−0.17	**−0.38**	**−0.35**	**−0.41**
S	**0.37**	−0.04	**0.36**	−0.16	0.05	0.09	0.07	−0.12	0.31	**0.36**
EI	−0.10	0.14	−0.06	0.03	−0.11	0.02	−0.32	−0.16	**−0.36**	−0.01
SI	**0.48**	**−0.50**	**0.59**	0.22	**−0.52**	0.14	0.08	**0.41**	**0.83**	**0.65**
CI	−0.32	0.08	−0.31	0.18	0.09	−0.30	0.25	−0.06	0.08	−0.33
BI	**−0.39**	0.28	**−0.48**	−0.01	0.32	−0.21	−0.01	−0.23	**−0.45**	**−0.60**
Ba Rel.	0.11	0.06	0.04	0.04	−0.18	0.15	0.12	−0.02	−0.26	−0.02
Fu Rel.	**−0.40**	0.15	−0.21	**0.42**	−0.16	−0.30	0.09	−0.08	−0.27	**−0.47**
Pp Rel.	−0.20	**0.37**	−0.14	−0.01	**0.39**	**−0.48**	0.05	−0.20	−0.13	−0.32
O Rel.	**0.49**	**−0.40**	**0.51**	0.11	−0.32	0.08	0.26	**0.50**	1.00	**0.55**
P Rel.	**0.62**	**−0.39**	**0.61**	−0.01	**−0.37**	0.28	0.13	**0.38**	**0.55**	1.00
Ba Ab.	−0.21	**0.38**	−0.18	−0.01	0.33	−0.23	−0.29	**−0.40**	**−0.50**	**−0.42**
Fu Ab.	**−0.37**	0.29	−0.27	0.31	0.03	−0.35	−0.14	**−0.38**	**−0.39**	**−0.51**
Pp Ab.	−0.31	0.31	−0.26	0.11	0.33	**−0.45**	−0.10	−0.03	−0.27	**−0.49**
O Ab.	0.31	−0.22	**0.36**	0.17	−0.18	−0.07	0.17	0.21	**0.86**	0.31
P Ab.	**0.58**	−0.35	**0.56**	0.01	−0.30	0.21	0.22	0.27	**0.48**	**0.94**
NH$_4^+$	1.00	−0.22	**0.86**	−0.10	−0.14	0.08	0.18	0.30	**0.49**	**0.62**
NO$_3^-$		1.00	−0.16	**−0.49**	**0.71**	0.01	−0.02	−0.13	**−0.40**	**−0.39**
OM			1.00	−0.02	−0.16	0.02	0.26	**0.45**	**0.51**	**0.61**
Sand				1.00	**−0.81**	**−0.59**	0.15	0.12	0.11	−0.01
Silt					1.00	0.13	−0.11	−0.20	−0.32	**−0.37**
Clay						1.00	−0.14	−0.03	0.08	0.28

Samples from woodland and vineyard.

Relative (Rel.) and absolute (Ab.) abundances of trophic groups are included. Bold numbers indicate significant relationships ($P < 0.05$).

3.3. Effects of disturbance on food web structure

There were 36 nematode taxa in the samples collected in October in the woodland and used in the experiment. Although not detected in June, tardigrades were in high abundance in the woodland soil in October. The three independent variables included in the analysis (soil pH, time of exposure and treatments) had a significant impact on the abundance of the nematode taxa. Time of exposure and treatments were the two variables affecting a larger number of nematode taxa (11 and 9, respectively) (data not shown).

Soil pH did not vary across time in the control samples, and varied slightly with treatments. The only change in pH values was detected in samples treated with ammonium nitrate, 20 days after the application (Table 4). NH$_4^+$ was strongly influenced by the nitrogen fertilizer treatments. Both ammonium nitrate and calcium nitrate increased the amount of ammonium in the soil after the first sampling time. This effect remained in the soil until the last sampling (T3, 30 days after the treatments were applied). NO$_3^-$, however, did not change in the calcium nitrate treatment, and only increased in the microcosms receiving ammonium
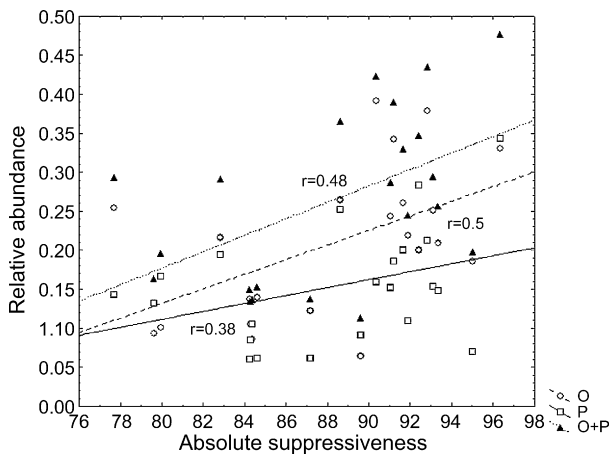

Fig. 2. Relationship between soil suppressiveness and relative abundance of predators (P), omnivores (O) and the sum of both (O + P). Correlation coefficients are $P < 0.05$.
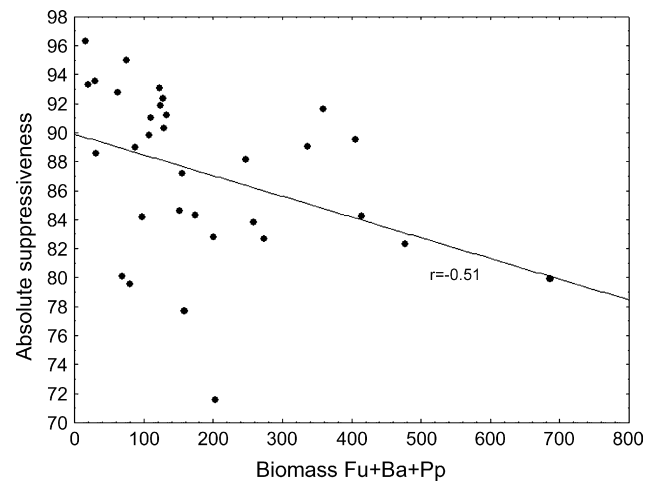

Fig. 3. Relationship between soil suppressiveness and available biomass in the soil food web. Correlation coefficient is $P < 0.05$.

Table 4
Averages (±S.E.) of physical–chemical properties, suppressiveness, trophic group abundances and food web indices in the microcosm experiment

	NH_4^+	NO_3^-	Tardi.	pH	Sup. Ab.	EI	SI	CI	BI	N	S	Ba	Fu	Pp	O	P
C																
T0	2.7 ± 0.4	4.7 ± 0.6	6.8 ± 4.0	6.1 ± 0.0	87.7 ± 8.8	39.7 ± 14.9	18.1 ± 12.9	25.8 ± 8.9	55.7 ± 16.9	36.5 ± 16.6	6.8 ± 2.8	14.1 ± 4.5	9.6 ± 4.7	10.2 ± 5.1	2.1 ± 2.1	0.5 ± 0.5
T1	4.7 ± 1.7	9.8 ± 3.3	4.0 ± 1.6	6 ± 0.1	75.0 ± 19.1	53.4 ± 1.8	29.0 ± 15.5	**72.1 ± 7.5**	37.1 ± 5.6	42.1 ± 14.3	11.3 ± 0.8	5.2 ± 1.2	24.1 ± 10.1	10.9 ± 5.1	0.3 ± 0.2	1.5 ± 1.1
T2	8.5 ± 2.1	**12.3 ± 3.3**	2.5 ± 0.9	6.2 ± 0.1	77.2 ± 2.8	51.5 ± 3.1	25.2 ± 5.2	**63.5 ± 6.4**	41.4 ± 2.5	**139.7 ± 17.8**	10.3 ± 1.0	36.0 ± 11.9	**55.8 ± 10.1**	**42.6 ± 4.6**	4.8 ± 2.8	0.3 ± 0.3
T3	6.3 ± 2.0	4.6 ± 0.1	3.0 ± 0.4	6.0 ± 0.0	75.7 ± 6.5	42.6 ± 3.8	22.0 ± 6.3	**86.4 ± 6.4**	48.2 ± 0.6	**184.2 ± 48.7**	9.0 ± 1.2	60.4 ± 30.1	**73.8 ± 19.2**	**42.6 ± 4.7**	7.4 ± 3.1	0.0 ± 0.0
AN																
T0	4.2 ± 0.3	5.3 ± 1.4	2.3 ± 0.8	5.0 ± 0.1	88.9 ± 4.1	55.3 ± 2.9	49.9 ± 5.0	40.5 ± 10.8	30.4 ± 2.0	157.5 ± 39.9	10.8 ± 1.6	58.3 ± 21.3	40.4 ± 12.2	40.0 ± 12.3	17.0 ± 7.0	1.8 ± 1.1
T1	**17.3 ± 1.5**	**13.1 ± 1.9**	0.3 ± 0.3	4.7 ± 0.1	56.6 ± 22.3	56.4 ± 7.89	51.3 ± 9.4	43.3 ± 19.0	28.5 ± 5.9	136.6 ± 39.8	10.0 ± 2.0	50.2 ± 17.7	53.4 ± 25.2	18.3 ± 6.9	7.8 ± 4.3	6.9 ± 3.0
T2	**17.6 ± 2.0**	16.2 ± 2.8	1.0 ± 0.4	**5.3 ± 0.0**	78.2 ± 4.8	44.4 ± 9.2	29.9 ± 10.4	29.7 ± 14.3	41.1 ± 4.4	**53.5 ± 9.8**	7.5 ± 0.9	36.0 ± 9.1	**6.5 ± 1.5**	**6.2 ± 1.7**	**3.8 ± 1.5**	0.8 ± 0.3
T3	**19.2 ± 5.2**	5.0 ± 1.9	0.3 ± 0.3	4.9 ± 0.0	**51.9 ± 9.8**	46.4 ± 3.0	31.9 ± 9.1	24.8 ± 5.2	42.7 ± 5.3	76.2 ± 6.3	10.3 ± 1.3	52.8 ± 4.2	**11.1 ± 1.8**	**6.2 ± 1.7**	4.0 ± 2.0	2.2 ± 0.9
CN																
T0	3.9 ± 0.4	7.5 ± 5.1	3.5 ± 2.3	5.4 ± 0.2	77.9 ± 7.1	56.8 ± 7.1	8.5 ± 8.5	26.8 ± 9.5	42.3 ± 7.8	95.9 ± 27.0	8.8 ± 1.4	39.2 ± 16.1	19.9 ± 3.6	35.7 ± 19.3	1.1 ± 1.1	0.0 ± 0.0
T1	**8.7 ± 0.7**	17.7 ± 2.1	1.5 ± 0.3	5.2 ± 0.2	59.4 ± 8.1	40.1 ± 8.3	20.1 ± 7.0	48.8 ± 18.2	51.4 ± 6.2	71.6 ± 26.5	10.0 ± 1.8	40.0 ± 17.7	19.9 ± 6.6	10.5 ± 2.7	1.2 ± 0.8	0.0 ± 0.0
T2	**10.4 ± 0.6**	19.9 ± 2.2	2.3 ± 0.8	5.5 ± 0.2	87.6 ± 2.9	50.6 ± 4.67	33.1 ± 11.7	57.2 ± 15.3	40.3 ± 6.7	127.7 ± 42.4	10.3 ± 1.4	62.4 ± 21.1	35.1 ± 12.5	24.9 ± 9.8	2.6 ± 1.0	2.7 ± 1.6
T3	**11.2 ± 2.3**	3.3 ± 0.7	1.5 ± 0.7	5.4 ± 0.1	71.6 ± 8.8	46.0 ± 5.5	14.5 ± 10.4	57.9 ± 18.4	50.0 ± 7.6	167.0 ± 61.5	10.3 ± 1.3	69.0 ± 9.0	69.4 ± 47.7	24.6 ± 9.5	3.1 ± 1.9	1.0 ± 0.6
D																
T0	3.1 ± 0.6	2.9 ± 0.5	3.0 ± 2.0	5.6 ± 0.3	88.3 ± 5.1	55.0 ± 8.0	31.6 ± 6.9	34.6 ± 22.2	35.0 ± 4.4	141.1 ± 53.6	10.8 ± 0.8	72.9 ± 29.8	30.4 ± 10.2	28.4 ± 10.6	6.7 ± 5.2	2.6 ± 1.6
T1	5.9 ± 1.4	9.3 ± 5.5	1.5 ± 0.7	5.5 ± 0.3	−20.1 ± 65.7	53.9 ± 4.45	19.8 ± 6.1	43.8 ± 12.7	41.0 ± 4.0	97.1 ± 31.6	10.8 ± 2.0	39.0 ± 23.6	37.2 ± 13.5	19.2 ± 6.1	1.0 ± 0.8	0.6 ± 0.4
T2	**8.3 ± 1.5**	7.5 ± 2.4	2.3 ± 0.8	5.7 ± 0.2	84.3 ± 0.8	46.9 ± 3.6	25.4 ± 7.4	45.5 ± 11.7	45.3 ± 5.2	94.0 ± 20.9	9.0 ± 0.7	40.5 ± 3.0	27.4 ± 12.9	20.1 ± 8.4	5.7 ± 2.9	0.0 ± 0.0
T3	10.2 ± 3.4	2.9 ± 0.7	2.0 ± 0.4	5.6 ± 0.3	**66.6 ± 5.3**	56.5 ± 11.23	31.2 ± 6.0	48.8 ± 22.3	35.9 ± 9.0	91.4 ± 16.3	9.8 ± 1.4	41.0 ± 10.2	25.6 ± 9.9	20.7 ± 8.4	2.6 ± 0.5	1.6 ± 0.9
S																
T0	6 ± 1.3	7.5 ± 3.5	6.3 ± 1.9	5.5 ± 0.2	81.3 ± 11.01	56.9 ± 2.3	23.3 ± 7.8	22.1 ± 6.7	38.4 ± 3.9	102.9 ± 44.1	9.8 ± 2.7	55.2 ± 22.8	24.3 ± 11.9	19.5 ± 7.5	3.6 ± 2.5	0.4 ± 0.4
T1	7.6 ± 1.0	8.7 ± 3.3	2.3 ± 1.6	5.5 ± 0.2	79.7 ± 6.45	53.2 ± 5.45	16.1 ± 7.45	54.9 ± 20.6	43.5 ± 5.9	106.5 ± 51.6	10.0 ± 2.0	18.8 ± 10.9	59.7 ± 37.1	26.4 ± 16.4	1.3 ± 0.8	0.3 ± 0.3
T2	9.9 ± 2.5	7.4 ± 2.6	5.5 ± 2.1	5.6 ± 0.2	87.5 ± 6.3	47.2 ± 3.4	23.9 ± 5.2	80.1 ± 11.7	45.4 ± 3.7	127.2 ± 43.4	7.3 ± 1.4	38.7 ± 12.3	49.5 ± 17.9	33.8 ± 13.8	4.6 ± 2.7	0.0 ± 0.0
T3	15.2 ± 4.7	3.8 ± 1.0	7.5 ± 6.5	5.5 ± 0.3	66.2 ± 10.7	57.4 ± 3.2	24.4 ± 10.3	45.8 ± 17.9	36.7 ± 3.1	129.2 ± 23.2	10.0 ± 0.4	45.7 ± 17.0	46.3 ± 18.3	33.8 ± 13.8	3.3 ± 2.3	0.0 ± 0.0
T																
T0	3.4 ± 0.3	9.4 ± 3.6	7.5 ± 1.8	5.8 ± 0.0	95.9 ± 3.0	44.0 ± 16.3	10.7 ± 10.7	24.4 ± 12.3	27.3 ± 10.8	32.6 ± 11.7	5.0 ± 1.8	18.2 ± 9.0	6.4 ± 3.0	7.7 ± 3.6	0.2 ± 0.2	0.0 ± 0.0
T1	**6.8 ± 0.3**	4 ± 0.6	2.3 ± 1.9	5.8 ± 0.0	85.4 ± 7.7	36.4 ± 12.5	0.0 ± 0.0	55.0 ± 21.2	62.2 ± 13.2	17.6 ± 7.6	6.3 ± 2.5	4.2 ± 0.6	9.9 ± 6.0	3.4 ± 1.6	0.1 ± 0.1	0.0 ± 0.0
T2	10.6 ± 2.0	26.1 ± 20.4	4.3 ± 1.9	5.9 ± 0.1	84.4 ± 7.0	51.4 ± 3.4	0.0 ± 0.0	58.6 ± 21.0	47.0 ± 3.2	19.5 ± 2.1	3.8 ± 0.5	3.5 ± 1.2	8.8 ± 0.9	6.9 ± 0.7	0.3 ± 0.3	0.0 ± 0.0
T3	**14.1 ± 1.6**	1.6 ± 0.2	0.3 ± 0.3	5.9 ± 0.0	**20.5 ± 7.2**	56.3 ± 4.6	16.1 ± 5.7	43.6 ± 18.1	38.7 ± 3.4	48.3 ± 10.7	7.3 ± 0.3	12.7 ± 2.6	27.3 ± 9.3	6.9 ± 0.7	1.4 ± 0.7	0.0 ± 0.0
Time					$P < 0.001$	ns	ns	$P < 0.001$	ns	ns	ns	$P < 0.05$	ns	ns	ns	ns
Treatment					ns	ns	$P < 0.01$	ns	ns	$P < 0.01$	$P < 0.01$	ns	ns	$P < 0.05$	$P < 0.05$	$P < 0.05$
pH					$P < 0.01$	ns	ns	ns	ns	ns	ns	$P < 0.05$	ns	ns	ns	ns
Tardigrades					ns	ns	ns	$P < 0.05$	ns	ns	ns	$P < 0.05$	ns	ns	ns	ns

Levels of significance of the univariate effects of independent on dependent variables are shown in the bottom rows.
Bold numbers indicate differences between T1, T2 or T3 and the control (T0) ($P < 0.05$).
C: Control, AN: ammonium nitrate, CN: calcium nitrate, D: diuron, S: Simazine, T: tillage.

nitrate at T1 (10 days after the treatments were applied). Significant increases in NH_4^+ were also detected in the diuron treatment at T2 and in tilled samples at T1 and T3.

The CI tended to increase between T0 and T1 in all the treatments, although only significantly in the control series, indicating a slow shift from bacterial- to fungal-mediated decomposition as readily-decomposed resources decreased. The SI did not vary significantly in any treatment but tended to be lowest in the microcosms that received simulated tillage, indicating little effect of treatments on higher trophic level organisms. In the control microcosms, number of nematodes increased with time, especially between T1 and T2, primarily reflected in the increase of fungal- and plant-feeding nematodes. Even though the variance was very high, ammonium nitrate produced a decrease in the number of fungal feeders that was not seen in any other treatment. In the ammonium treatment, total number of nematodes decreased significantly at T2.

The main effects of treatment and time on the analyzed variables were both highly significant ($P < 0.01$), but the interaction treatment × time was not significant. The univariate analyses of each dependent variable indicate that treatment was the independent variable that affected the greatest number of index descriptors (Table 4).

A second GLM analysis was done using NH_4^+ and NO_3^- as dependent variables of food web structure. Trophic group abundances and food web indices, together with time and treatments, were used as categorical or continuous predictors of soil nitrogen concentration. Soil nitrogen was strongly dependent on nematodes abundance; all the trophic groups were significant predictors ($F > 6.9$, $P < 0.05$) of soil NH_4^+. EI and CI were good predictors of NO_3^- ($F > 7.0$, $P < 0.05$) and were, respectively, negatively and positively related to it). Time affected both NH_4^+ and NO_3^- ($F > 12.6$, $P < 0.001$), while treatments modified only soil NH_4^+ ($F = 8.24$, $P < 0.001$) concentration.

3.4. Effects of disturbance on the suppressiveness service of the food web

Soil suppressiveness was negatively correlated with number of living nematodes (excluding *M. incognita*, $r = -0.34$, $P < 0.05$); more *M. incognita* juveniles survived when nematode abundance was high. Defaunated and non-defaunated soil samples suppressed, respectively, 65.0% and 90.9% of the inoculated *Meloidogyne* juveniles. The presence of the soil food web in the non-defaunated samples increased soil suppression by 74% compared to defaunated samples ($P < 0.0001$, two groups ANOVA). By T3 (30 days after the application of the treatments), suppressiveness was significantly reduced by ammonium nitrate, diuron and tillage (Table 4).

Across all four exposure periods, suppressiveness was also negatively related to number of bacterial feeders ($r = -0.36$, $P < 0.05$) and number of fungal feeders

Table 5
Spearman rank order correlation coefficients of relationships between absolute soil suppressiveness and the soil food web[a] at time intervals after treatment application ($n = 96$, all the samples from the microcosm experiment)

	T0	T1	T2	T3
NH_4^+	−0.20	−0.38	−0.30	**−0.52**
NO_3^-	0.10	−0.35	**−0.43**	0.34
pH	**0.44**	**0.58**	0.26	0.34
EI	−0.06	−0.03	0.14	−0.26
SI	−0.34	−0.26	−0.39	0.11
CI	0.18	−0.22	**0.43**	0.32
BI	−0.08	0.08	0.07	0.29
N	**−0.62**	**−0.71**	−0.25	**0.51**
S	**−0.51**	0.12	−0.22	0.28
Ba Ab.	**−0.55**	**−0.63**	−0.33	0.15
Fu Ab.	**−0.54**	**−0.55**	0.00	**0.42**
Pp Ab.	**−0.58**	**−0.65**	−0.08	**0.58**
O Ab.	**−0.55**	−0.14	**−0.52**	0.32
P Ab.	−0.33	−0.13	−0.30	0.06

[a] Bold numbers indicate significant relationships ($P < 0.05$).

($r = -0.25$, $P < 0.05$), suggesting that efficiency of predation is a density-dependent function. It was also related to pH ($r = 0.27$, $P < 0.05$) and NH_4^+ ($r = -0.53$, $P < 0.05$).

The relationship between suppressiveness and the soil food web changed across time due to the effects of the treatments applied to the soil (Table 5). At T0, before treatments were applied, suppressiveness was related to nematode numbers, soil pH and taxa richness, in accordance with the density-dependent relationship suggested above. At T1 and T2, some of the relationship of suppressiveness to numbers of nematodes disappeared due, probably, to direct treatments on the mortality rate of the target nematode (*M. incognita*) and the survival rates of the other nematodes, but were again detectable at T3.

3.5. Effect of time

Only samples from the woodland in June, and samples collected in October and processed immediately upon return from the field (T0, October), were used to perform the comparisons. Samples treated with herbicides, fertilizers and tillage were omitted from the comparison analysis to avoid the treatment effects.

NH_4^+ varied significantly from June to October, while pH and NO_3^- did not change (Table 2). Total numbers of nematodes and trophic group abundances significantly decreased in October. Structure Index and taxa richness were significantly reduced in October, while BI increased. Suppressiveness, both absolute and relative, increased significantly in October (Table 2). Suppressiveness was negatively related to abundances of all trophic groups, number of nematodes, taxa richness and EI (Table 6). NH_4^+ was positively related to predator abundance and SI, and negatively related to fungal feeders, plant parasites, CI and BI. NO_3^- was positively related to fungal feeders, plant

Table 6
Spearman rank order coefficients correlations between variables[a] measured in samples from the woodland site (June and October)

	Sup. Rel.	Sup. Abs.	pH	NH_4^+	NO_3^-	O Rel.	P Rel.
Ba Rel.	**−0.62**	**−0.70**	0.04	−0.18	0.23	**0.47**	**0.26**
Fu Rel.	**−0.53**	**−0.73**	0.00	**−0.34**	**0.30**	**0.55**	0.21
Pp Rel.	**−0.51**	**−0.56**	−0.19	**−0.31**	**0.34**	**0.45**	0.12
O Rel.	**−0.31**	**−0.41**	−0.15	0.21	0.00	1.00	**0.49**
P Rel.	−0.16	**−0.30**	−0.02	**0.39**	−0.13	**0.49**	1.00
S	**−0.39**	**−0.51**	0.04	0.23	0.03	**0.66**	**0.55**
EI	**−0.33**	**−0.27**	−0.01	−0.04	0.14	−0.01	0.16
SI	−0.17	−0.16	−0.05	**0.38**	−0.24	**0.78**	**0.58**
CI	0.07	−0.10	−0.05	**−0.31**	0.08	**0.29**	−0.10
BI	0.09	0.09	0.05	**−0.30**	0.03	**−0.38**	**−0.47**
N	**−0.56**	**−0.73**	−0.06	−0.23	**0.28**	**0.60**	**0.29**
Sup. Rel.	1.00	**0.74**	−0.14	0.21	−0.25	**−0.31**	−0.16
Sup. Abs.	**0.74**	1.00	−0.14	0.26	**−0.30**	**−0.41**	**−0.30**
pH	−0.14	−0.14	1.00	−0.17	0.12	−0.15	−0.02
NH_4^+	0.21	0.26	−0.17	1.00	−0.20	0.21	**0.39**
NO_3^-	−0.25	**−0.30**	0.12	−0.20	1.00	0.00	−0.13

[a] Bold numbers indicate significant relationships ($P < 0.05$).

parasites and total number of nematodes, and negatively related to suppressiveness.

4. Discussion

4.1. Nematode faunal composition

As expected, taxa richness was lower in the vineyard than in the woodland, indicative of a decrease in faunal diversity due to agricultural intensification. The 11 taxa were found only in woodland samples included representatives of all the trophic groups. Sensitivity to disturbance is dependent on the life cycle characteristics of the nematode taxa (Tenuta and Ferris, 2004), but we were unable to find a relationship between trophic habit or life cycle and the presence or absence of nematode taxa in the vineyard. Some taxa usually considered sensitive to perturbation were present in the vineyard, including *Odontolaimus* and Aporcelaimidae. However, consistent with other reports, *Wilsonema*, *Achromadora*, *Prionchulus* and *Panagrolaimus*, described as sensitive to tillage by Fiscus and Neher (2002), were present in greater abundance in the woodland. In contrast, some nematodes described as sensitive to chemicals and nutrients (Fiscus and Neher, 2002), including *Mesorhabditis* and *Aphelenchus*, were more abundant in the vineyard.

4.2. Soil suppressiveness and food web dynamics

Although dafaunated soil did not seem to be a favorable environment for the introduced *M. incognita*, soil suppressiveness to Meloidogyne juveniles was greater in the non-dafaunated samples. The lack of roots in the microcosms, and thus the lack of available food, may explain these relatively low survival rates over the 5-day incubation period. However, juveniles of this genus, under the conditions of the current experiment, are known to remain active and infective to plants for up to 30 days (Van Gundy et al., 1967; Ferris et al., 1982).

Most predatory nematodes have long life cycles and are sensitive to environmental perturbations. Although scarce, nematodes like *Discolaimus*, *Tripyla* and *Prionchulus* were more abundant in the natural area than in the vineyard. The differences in the nematode faunal composition between the areas indicate a more structured soil food web in the woodland, with more abundant organisms in the higher trophic levels and greater connectance, which was more suppressive to introduced *M. incognita* juveniles. *Meloidogyne incognita* juveniles are reported to be, under experimental conditions, a preferred prey for predatory nematodes (Khan et al., 1995; Bilgrami et al., 2005). The relative abundance of omnivores and predators may have determined the total number of nematodes in the community; when predators and omnivores were abundant, there were fewer lower trophic level nematodes. Thus, we infer that predator and omnivore nematodes, together with the other regulatory components of the soil food web, may reduce abundance of other nematodes. Top-down regulation of microbial- and plant-feeding nematodes by predators has been observed in other studies (Yeates and Wardle, 1996; Khan and Kim, 2005).

Nonetheless, soil suppressiveness was not directly related to the absolute abundance of predator or omnivore nematodes but did correlate with the SI and with the relative abundance of predators and omnivores. Both the SI and the relative abundance of predators and omnivores are indicators of the length and connectance of the soil food web and dependent on the ratios among functional guilds rather than on the total number of individuals in the community. Additionally, total nematode abundance was inversely correlated with suppressiveness and with relative abundance of predators and omnivores. Our results thus suggest that the

number of prey available for each predator, and not the absolute abundance of organisms in the higher trophic levels, determines the effectiveness of top-down suppression of plant parasites.

Although causal effects are difficult to infer from field data, our results suggest that the relationship between predators and plant–parasitic nematodes follows the well-known density-dependent function describing relationships between predator and prey (Bilgrami et al., 2005; Bilgrami and Gaugler, 2005). When many prey are available, the predation pressure on the target nematode is weaker, while when few prey are accessible, the intensity of the predation on the target nematode is stronger. The SI indicates higher connectance in the food web; the presence of predators and omnivores that feed on the lower trophic links (microbivore nematodes, plant feeders, bacteria and protozoa) and may also reflect other soil organisms with activities and sensitivities similar to those of the predator and omnivore nematodes (Ferris et al., 2001). Predator and omnivore nematodes can play a role in regulation of lower soil food web levels when they are sufficiently abundant. Khan and Kim (2005) proved experimentally that the predatory nematode *Mononchoides fortidens* can reduce root-knot nematode galls and plant damage. Agricultural fields with poorly structured soil food webs that contained few predatory nematodes did not effectively suppress plant parasites in several of our preliminary experiments (unpublished).

The number of nematodes at lower trophic levels (plant, fungal and bacterial feeders) was negatively correlated with predator and omnivore nematodes expressed as number of taxa or as number of functional guilds ($r = -0.41$ and -0.45, respectively, $P < 0.05$). Functional guild diversity may contribute to the resilience of the system, increasing the range of functional roles performed by the organisms in the community and thus improving the chance of recovery after an environmental perturbation. It also may provide complementarity of service due to the increase of a diversity of organisms with similar functional attributes or niche preference (Ferris, 2005).

4.3. Effects of management

Treatments simulating agricultural practices affected the abundance of several nematode taxa. Clearly, agricultural practices in the vineyard affected the soil food web, particularly the abundance of higher trophic levels and the capacity for suppressing plant-feeding nematodes. The disappearance of higher trophic levels and the subsequent effect of increased lower trophic levels, due to the lack of predation and to the effects of enrichment in bacterial biomass, have been reported before (Wardle et al., 1995). Our results, however, showed minor changes in the nematode community due to experimental perturbation. Even in the long-term, herbicides seem to have little direct effect on nematode abundance (Ishibashi et al., 1983; Wardle et al., 1995; Salminen et al., 1996; Sturz and

Kimpinski, 1999). Indirect effects of herbicides on nematode communities are probably mediated by plant and rhizosphere conditions in the long term. Other agricultural practices, such as mulch amendments, could be more important in altering the nematode community (Porazinska et al., 1999; Forge et al., 2001). Even though tillage can reduce nematode number and alter abundance of trophic groups (Wardle, 1995; Lenz and Eisembeis, 2000), we did not detect any change in nematode community structure due to the simulated tillage treatment in these experiments.

The presence of tardigrades in October samples affected the nematode community, and probably the interpretation of our results. The effect of tardigrades on the nematode community and in soil suppression will be reported in a further paper.

4.4. Soil food web

Univariate effects are difficult to infer from field data, so relationships between trophic structure and soil food web services are usually studied in microcosm with simple
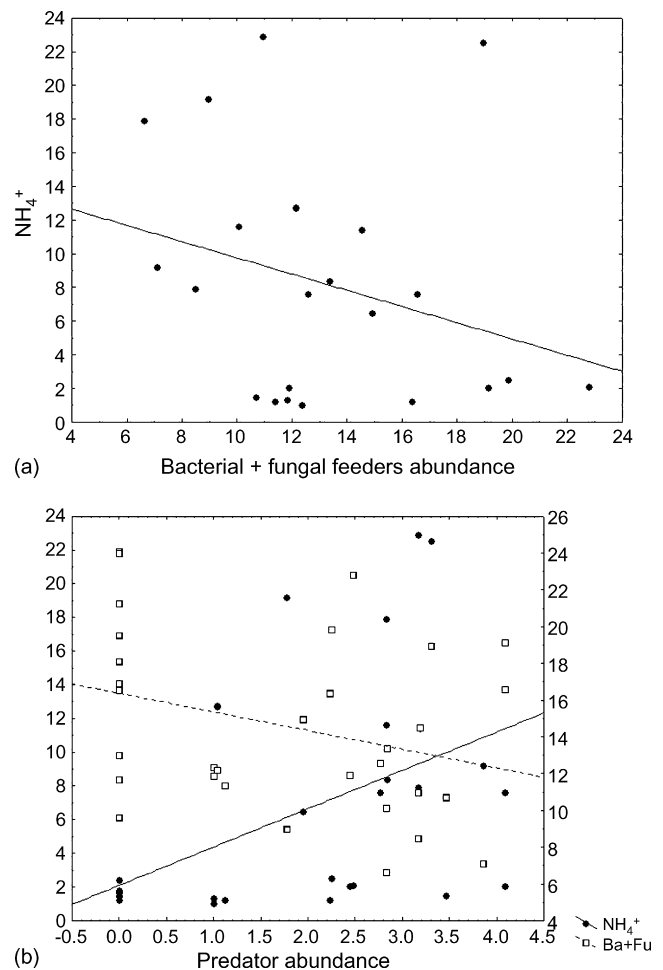

(a)

(b)

Fig. 4. Relationship between abundance of microbial feeders and NH_4^+ soil content (a) and relationship between predator abundance with NH_4^+ soil concentration and abundance of microbial feeders (b).

food webs (Mikola and Setälä, 1998; Laakso and Setälä, 1999; Postma-Blaauw et al., 2005). However, our field data agree with general expectations derived from food web theory which predicts changes in the primary decomposer community when predators affect intermediate consumers (Carpenter et al., 1985). Lower levels of NH_4^+ were correlated with higher abundances of microbial grazers, and lower abundances of microbial grazers were correlated with high predator abundance (Fig. 4). In agricultural fields, high levels of N are often associated with microbial grazers due to the positive effects of bacterial and fungal feeders on immobilized resources (Ingham et al., 1985; Ferris et al., 2004). In the present data, however, the positive relationship between predator and omnivore abundances and NH_4^+ might be interpreted as a trophic cascade effect of predators on microbes through decrease in bacterial and fungal feeding nematodes. In some previous studies, there was no correlation between nitrogen mineralization and higher nematode trophic links (Forge and Simard, 2001; Villenave et al., 2004), but the introduction of predators into the soil food web can change microbial activity with no change in microbial abundance (Laakso and Setälä, 1999; Zelenev et al., 2004) and relationships between predator nematodes and bacterial biomass have been observed (Wardle and Yeates, 1993). It can also be argued that nematode excretion contributes to soil NH_4^+ (Bouwman et al., 1994) but we did not find positive correlations between soil NH_4^+ and total number of nematodes or abundance of any other trophic group other than predators and omnivores.

Plant- and fungal-feeding nematodes were negatively associated with NH_4^+ and positively associated with NO_3^-. Plant and fungal feeders were more abundant in the vineyard, while they were less abundant, probably due to predation pressure, in the woodland, where NH_4^+ is more abundant than NO_3^-. Previous studies (Villenave et al., 2004) also found positive relationships between abundance of fungal feeders and NH_4^+ in potted soil treated with manure. Significant relationship between the EI and soil nitrogen have been observed (Ferris and Matute, 2003; Ferris et al., 2004) but not in this study.

Whether different levels of the soil food web are bottom-up or top-down regulated is still unclear, and both processes probably act together on each soil food web link. Lack of agreement in different studies regarding ecosystem services in relation to soil food web structure might lie in the relative balances of bottom-up and top-down forces. Our results suggest that where primary resources are abundant, the growth rate of microbial populations exceeds the feeding rates of microbial grazers and mineralization services are unchanged by reductions in those grazers. Where primary resources are limited, predation on the microbial grazers allows greater microbial abundance and higher mineralization rates. Further experiments and observations in natural areas of low enrichment are necessary to confirm this hypothesis.

5. Conclusions

At least some level of soil disturbance is necessary in agricultural production systems. For development of sustainable practices, it is important to know the acceptable degree of disturbance that will maintain desired ecosystem functions while preserving both productivity and soil health; that is, the equilibrium point between soil disturbance and conservation of ecosystem services. Our data suggest that predator and omnivore nematodes, as components of the higher trophic levels of the soil food web, may play an important role in regulating plant-feeding nematode populations, particularly where bottom-up resources are restricted, for example in our woodland area where plant growth and activity are limited by seasonality of rainfall, but further studies are needed to determine temporal changes in the driving factors of these trophic interactions. Agricultural management and other disturbances reduce the abundance of predators and the ecosystem services provided by them. Even if predatory nematodes are not effective biological control tools for suppressing plant-feeding nematodes (Yeates and Wardle, 1996), increasing the abundance of predator and omnivore nematodes and, coincidentally, similar functional guilds of other organisms, can have a regulatory effect on lower trophic levels, including plant feeders. Although the general principles are emerging, further research is necessary to develop site-specific strategies for managing the soil food web to optimize agricultural production and soil functioning.

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