Abundance, diversity and connectance of soil food web channels along environmental gradients in an agricultural landscape

Sara Sánchez-Moreno [a,*], Howard Ferris [b], Anna Young-Mathews [c], Steven W. Culman [c], Louise E. Jackson [c]

[a] Unidad de Productos Fitosanitarios, DTEVPF, Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria, Ctra. Coruña km 7.5, 28040 Madrid, Spain
[b] Department of Nematology, One Shields Avenue, University of California, Davis, CA 95616, USA
[c] Department of Land, Air and Water Resources, One Shields Avenue, University of California, Davis, CA 95616, USA

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ABSTRACT

Soil food webs respond to anthropogenic and natural environmental variables and gradients. We studied abundance, connectance (a measure of the trophic interactions within each channel), and diversity in three different channels of the soil food web, each comprised of a resource-consumer pair: the micro-bivore channel (microbes and their nematode grazers), the plant–herbivore channel (plants and plant-feeding nematodes), and the predator–prey channel (predatory nematodes and their nematode prey), and their associations with different gradients in a heterogeneous agricultural landscape that consisted of intensive row crop agriculture and grazed non-irrigated grasslands in central California. Samples were taken at three positions in relation to water channels: water's edge, bench above waterway, and the adjacent arable or grazed field. Nematode communities, phospholipid fatty acid (PLFA) biomarkers, and soil properties (NH_4^+-N, NO_3^--N, total N, total C, pH, P, bulk density and soil texture) were measured, and riparian health ratings were scored. Environmental variables were obtained from publicly-available data sources (slope, elevation, available water capacity, erodability, hydraulic conductivity, exchangeable cation capacity, organic matter, clay and sand content and pH).

The abundance and richness in most food web components were higher in grazed grasslands than in intensive agricultural fields. Consumers contributed less than their resources to the abundance and richness of the community in all channels. The association between richness and abundance for each component was strongest for the lowest trophic links (microbes, as inferred by PLFA) and weakest for the highest (predatory nematodes). The trophic interactions for the predator–prey and plant–herbivore channels were greater in the grassland than in the cropland. Fields for crops or grazing supported more interactions than the water's edge in the plant–herbivore and microbivore channels. Connectance increased with the total richness of each community. Higher connectance within the microbivore and predator–prey soil food web channels were associated with soil NO_3^--N and elevation respectively, which served as surrogate indicators of high and low agricultural intensification.

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1. Introduction

A central goal of food web ecology is to generalize from observed patterns among food web diversity and functioning. Due to the myriad direct and indirect trophic interactions among organisms in the soil food web (predator–prey, herbivore–plant, root exudates–microbial communities), compartmentalization of the soil food web into separate functional units is necessary for examining patterns of the relationships between diversity and functioning.

Distinct carbon and energy channels are broadly recognized (Moore et al., 2005), and some authors postulate that the maintenance of the heterogeneity in such channels is critical to maintain ecosystem stability (Rooney et al., 2006). Soil food web organisms examined in this study included microbes, nematodes, and plants, which were categorized into three main food web channels, that is, into three main trophic associations comprised of organisms linked by direct trophic interactions accounting for the main fluxes of carbon through the web: 1) the *microbivore channel*, in which C flows from microbes to their nematode grazers, the most important animal grazers of soil bacteria; 2) the *plant–herbivore channel*, in which C flows directly from plants via plant-feeding nematodes, and 3) the *predator–prey channel*, in which C flows from micro-bivore nematodes to their nematode predators. Although it is

* Corresponding author. Tel.: +34 913478710; fax: +34 913471479.
E-mail address: sarasm@inia.es (S. Sánchez-Moreno).

a common practice to separate bacterial and fungal energy channels (Moore et al., 2005; Holtkamp et al., 2008), which do have distinctive characteristics (Ruess and Ferris, 2004), we have aggregated the two as soil microbes and their nematode grazers (Ferris et al., 2001). Indeed, the two compartments are closely related; bacteria and bacterial-feeding nematodes may affect the functioning of soil fungi (Nieminen and Setälä, 2001), while the presence of fungi may strongly affect the dynamics of bacterial-feeding nematodes and their bacterial food source (Nieminen, 2009). Although in general nematode grazing on microbes decreases the pool of grazed organisms, nematode bacterivore activity may stimulate bacterial growth (Ingham et al., 1985). In a similar way, weak root infections of herbivore nematodes may increase nutrient availability to plants (Yeates et al., 1999). Carbon flow through the channels may be indirectly inferred by counting organisms, determining biomass, estimating C (Ingham et al., 1985; Ferris, 2010), or by direct techniques such as labeling with radioactive isotopes (Yeates et al., 1999, Albers et al., 2006).

Food web connectance, a metric of food web complexity, is generally measured by field observations, e.g., by sampling plants and their associated plant-feeding and pollinator arthropods (Macfadyen et al., 2009; Basilio et al., 2006). Although different experimental approaches have been used to elucidate trophic habits of soil organisms (Bjørnlund and Rønn, 2008; Lundgren et al., 2009), direct observations of who eats whom among micro and mesofauna inhabiting natural soils are difficult, if not impossible, to perform with currently available technology because of the small scale and nature of the soil matrix. Separating food web channels in the soil system may also be difficult due to a lack of trophic specialization (Gunn and Cherret, 1993). In this paper, connectance among soil food web organisms was calculated as the total sum of all possible interactions among them, assuming that all taxa in each channel may interact (in this case any organism in the resource group may be eaten by any organism in the consumer group). Specificities exist in all channels (for example, microbivore nematodes may prefer certain species of bacteria or fungi (Newsham et al., 2004), or plant-feeding nematodes are specific to their plant hosts), but less specificity may exist for most soil organisms. Some authors state that larger communities are more poorly connected than smaller ones (Fonseca et al., 2005; Basilio et al., 2006; Beckerman et al., 2006; Banašek-Richter et al., 2009), while other suggest that connectance is independent of richness (Fox and McGrady-Steed, 2002). Few studies dealing with soil food web connectance have considered feedbacks between organisms and environmental variables (Bagdassarian et al., 2007).

Riparian areas, associated with natural waterways and constructed irrigation channels, provide many ecological functions related to water quality, soil conservation, terrestrial and aquatic wildlife, and environmental aesthetics (Fernald et al., 2007). In previous papers we reported greater plant diversity and C storage associated with riparian areas (Young-Mathews et al., 2010) and negative correlations between agricultural intensification, plant and soil diversity, and indicators of ecological functions related to soil quality (Culman et al., 2010). This data set included the composition of the three soil food web channels in two land use types (i.e., grazed, hilly annual grasslands and flat intensive croplands) at 20 sites selected to represent a wide range of abiotic (soil type, slope, elevation, etc.) and biotic (plant cover) factors (Culman et al., 2010). Distance from the water channel was included to provide another environmental gradient.

The objectives of this paper were to: a) characterize the biotic composition of the assemblages comprising consumers and their resources in each of the three soil food web channels, b) study the relationship between richness and abundance of different functional groups of soil organisms, c) explore soil food web interactions and connectance, d) study the influence of environmental variables on food web connectance, and e) draw inferences regarding the relationships between riparian health, land use, and food web properties.

2. Material and methods

2.1. Study site and sampling methods

The study area is a 150 km^2 landscape of Yolo County (CA, USA). The hilly rangeland in the west consists of grazed annual grasslands and oak savanna, while the flat croplands in the east are dominated by intensive agriculture (grains, vegetables, and alfalfa). Geographic Information System (GIS) data regarding soils, topography and vegetation across the landscape were used to systematically select 20 sites that captured a maximum level of landscape heterogeneity (Culman et al., 2010). At each site, a transect was established perpendicular to the waterway with sampling points at three distances from the water channel: i) Position A, in the agricultural field or the grazed pasture, 50 m from the water edge, ii) Position B, in the bench of the waterway, 5–10 m from the water edge, considered an intermediate environment between the agricultural and the riparian areas, and Position C, situated around 0.5 m from the edge of the waterway in the riparian corridor. Three soil cores (0–15 cm depth) were collected at each position 2 m apart. Thus, a total of 180 soil samples was collected (20 sites × 3 distances to water × 3 cores at each distance). Detailed descriptions of the study area and methodology used for selecting sampling sites are reported in Young-Mathews et al. (2010) and Culman et al. (2010).

Soil was sampled between late March and mid April 2007. Riparian health was assessed visually by the riparian health rating, a continuous scale that ranges from 0 to 100% based on channel condition, access to the floodplain, bank stability, extent of natural riparian zone vegetation, macroinvertebrate habitat, pool variability, and pool substrate (Ward et al., 2003), which was determined for each of the 20 sampling sites (Young-Mathews et al., 2010).

2.2. Soil organisms

Nematodes were extracted and identified from the 180 samples collected (20 sites × 3 positions × 3 cores). Phospholipid fatty acids (PLFA) and plants were only indentified from 60 samples (20 sites × 3 positions). Nematode data from three cores were averaged when necessary to relate with PLFA and plant data.

Composition and abundance of the microbial community were estimated by quantifying and identifying PLFA biomarkers, which were extracted from moist soil samples according to Bossio and Scow (1998). Total lipids were extracted from a 5 g sample using a chloroform–methanol extraction and PLFA purified, quantified and identified using a Hewlett Packard 6890. Identified PLFA included markers from gram+ and gram− bacteria, fungi, microeukaryote, actinomycetes, and protozoa, as well as unidentified PLFA. Richness of PLFA was calculated as the number of different PLFA detected per sample, and abundance was expressed as μg per 100 g dry soil. Recent studies state the limitations of the use of PLFA to assess soil microbial diversity (Frostegård et al., 2010), but since no better approximation was available to infer microbial diversity, PLFA were used to assess soil microbial diversity in our study.

Nematodes were extracted using a modification of sieving and Baermann funnels. The total number of nematodes was counted in each sample under a stereoscope (50×) and 200 individuals were identified to genus/family level in a microscope. Nematode taxa were assigned to trophic groups (Yeates et al., 1993) and functional guilds (Bongers and Bongers, 1998). Abundance (N) and richness (S) were expressed as number of individuals or taxa per 100 g dry soil.

Composition, abundance and taxa richness of the selected organisms were studied in three different C flow channels of the soil food web across the landscape: (1) the plant–herbivore channel was studied by identifying plants and genera of herbivore nematodes, (2) the microbivore channel was studied using PLFA markers as a proxy for the abundance and richness of microflora in the soil and by identifying genera of microbivore nematodes, and, (3) the predator–prey channel was analyzed by identifying predatory nematodes (genera and families) and their main food source, microbivore nematodes. Each channel, thus, is comprised of a group of consumers and their main resources. Since many plant-feeding nematodes are endoparasitic and live within root tissue, with only transient free-living stages, they were not considered to be a usual food source for predatory nematodes, and thus were excluded from the predator–prey nematode combinations. Predatory nematodes included both strictly predator and omnivore nematodes (sensu Yeates et al., 1993). Trophic habits were assumed to be constant for the whole life cycle of each nematode genus or family.

Taxa richness and organism abundance were used as the primary measures for each carbon channel of the soil food web. In each channel the best available approximation for richness and abundance was used. Plants were identified to species level and taxa richness expressed as number of species per sampling site. Since no data of actual abundance of each plant species was available, mean cover (%) was used as a measure of plant abundance at each sampling site. Plant diversity was measured around the three positions located at three different distances from the water edge. A complete list of the plant species found in the study area is provided in Young-Mathews et al. (2010).

2.3. Soil properties

Soil properties were measured in the same soil samples from which nematodes were extracted (180 samples). Soil was extracted with 2 N KCl solution, and analyzed colorimetrically for NH_4^+-N and NO_3^--N on a Genesys 10VIS spectrophotometer. Total N, total C, pH, and P were analyzed by the Department of Agriculture and Natural Resources Analytical Laboratories at UC Davis. Methods of analysis are described at http://danranlab.ucdavis.edu. Bulk density was measured in intact soil cores by dividing the dry mass (oven dried at 105 °C) of the soil by the volume of the ring used to collect the samples (Blake and Hartge, 1986). Particle size was measured in air-dried samples crushed and sieved through a 2 mm screen. Particle size analysis was performed on 0.4 g sub-samples dispersed with hexametaphosphate and read on a Coulter LS-230 Particle Size Analyzer.

Ten environmental variables (pH, slope, elevation, clay, sand, available water capacity, erodability, hydraulic conductivity, exchangeable cation capacity, and organic matter) were obtained from publicly-available databases for each sampling site using GPS coordinates, and integrated in a GIS (Culman et al., 2010).

2.4. Statistical analyses

This study comprised one continuous and two discrete gradients, the riparian health rating comprised the continuous gradient (Young-Mathews et al., 2010), while land use (nine of the sample sites were located in the rangeland and eleven in the cropland) and the three different distances from the water's edge (positions A, B, and C) were the two discrete gradients.

To assess differences in richness and abundances of soil organisms between land use types and among positions, one-way ANOVAs were used, and Tukey-tests were used as post-hocs when necessary. Simple regression was used to relate diversity and abundance with riparian health scores, and to compare richness, diversity, abundance, and connectance among them.

Connectance is often calculated as the ratio between the number of actual and the number of possible interspecies interactions (Pimm, 1984), or the number of detected links expressed as a proportion of the total possible number of links in the community (Beckerman et al., 2006). Due to the lack of accurate knowledge of trophic habits of soil organisms, together with their small size and the difficulty in observing direct contact between them, connectance was inferred in each channel as co-occurrence of consumers and their resources. The number of potential interactions among them was calculated as $A \times B$, where A and B are the number of taxa in the consumer (A) and the resource (B) groups of organisms of each channel (Fonseca and John, 1996). The number of potential interactions was calculated at each of the sixty points (20 sites × 3 positions). Realized interactions were calculated in the same way at each soil sample taken at each position from the waterway (see Section 2.1). Connectance (C) was then calculated as the ratio of realized to potential interactions. Thus, both potential and realized interactions were inferred as co-occurrence matrices. An example of the calculations of potential and realized interactions is shown in Fig. 1. Since $A \times B$ depends on the taxa richness of each component, and since different taxonomic levels were used in the identifications of soil organisms in each channel, connectance could not be compared among food web channels.

To infer whether smaller communities are more or less richly connected than larger communities, the slope of the regression between the numbers of realized versus potential interactions was used. The residuals of such regression represent the number of realized interactions relative to the number of possible interactions, a parameter independent of the total richness of the community, which may be used as a connectance index that may relate to other environmental variables (Fonseca and John, 1996).

To study the relationships between the richness of the components of each channel and the total richness of the community (all the organisms in one channel), we used the allometry approach of Fonseca and John (1996). Linear regressions of the richness of each of the two components of each channel against the total channel size (total number of species in each channel) were used to measure the rate (the slope of the regression, b) at which both components increase when total richness increases, and the rate of change of richness in one channel with respect to the other. When $b = 1$, both components contribute to the total richness of the channel similarly (isometry); when $b > 1$ or $b < 1$ the contributions are uneven (positive or negative allometry). The residuals of the regression of the richness of each pair of components were used to test whether the proportion of both components changes across the three types of gradients (position with respect to the water edge, land use type and riparian health rating).
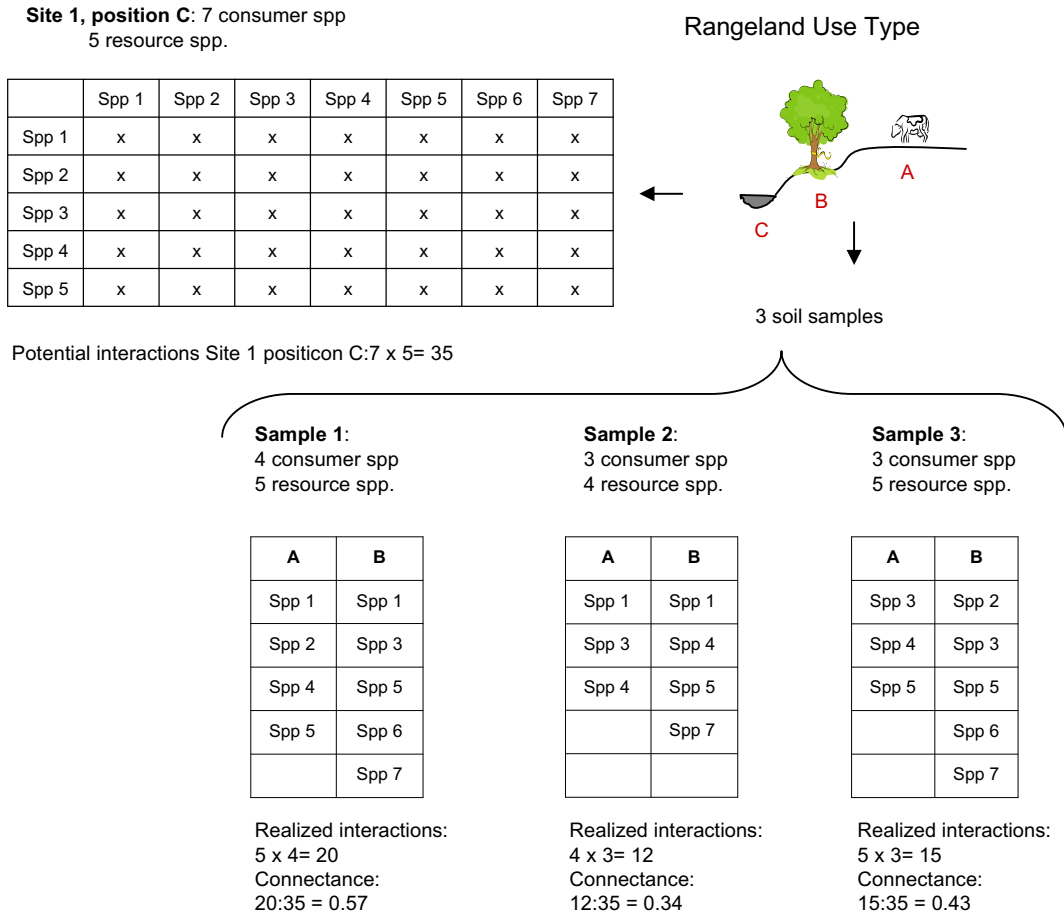
To relate connectance in each channel with soil properties measured in soil samples (NH_4^+-N, NO_3^--N, total N and C, bulk density, sand and clay content, P, and pH) and with environmental variables from publicly-available databases (slope, elevation, water holding capacity, erodability, hydraulic conductivity, exchangeable cation capacity, organic matter, clay and sand content and pH), two canonical correspondence analyses (CCA) were used.

All variables were log-transformed before analysis to achieve normality. All analyses were performed with STATISTICA software (StatSoft, 1996).

3. Results

3.1. Characterizations of soil food web channels

Forty-seven PLFA microbial biomarkers were identified across the study area. There were 41 nematode taxa (37 genera and 4 families) identified across all soil samples, 19 of which were

Site 1, position C: 7 consumer spp
5 resource spp.

Rangeland Use Type

	Spp 1	Spp 2	Spp 3	Spp 4	Spp 5	Spp 6	Spp 7
Spp 1	x	x	x	x	x	x	x
Spp 2	x	x	x	x	x	x	x
Spp 3	x	x	x	x	x	x	x
Spp 4	x	x	x	x	x	x	x
Spp 5	x	x	x	x	x	x	x

Potential interactions Site 1 positicon C:7 x 5= 35

3 soil samples

Sample 1:
4 consumer spp
5 resource spp.

A	B
Spp 1	Spp 1
Spp 2	Spp 3
Spp 4	Spp 5
Spp 5	Spp 6
	Spp 7

Realized interactions:
5 x 4= 20
Connectance:
20:35 = 0.57

Sample 2:
3 consumer spp
4 resource spp.

A	B
Spp 1	Spp 1
Spp 3	Spp 4
Spp 4	Spp 5
	Spp 7

Realized interactions:
4 x 3= 12
Connectance:
12:35 = 0.34

Sample 3:
3 consumer spp
5 resource spp.

A	B
Spp 3	Spp 2
Spp 4	Spp 3
Spp 5	Spp 5
	Spp 6
	Spp 7

Realized interactions:
5 x 3= 15
Connectance:
15:35 = 0.43

Fig. 1. Example of calculations of interactions and connectance. The amount of potential interactions per site was calculated as the number of consumer spp (A) by the number of resource spp (B) in each channel. Realized interactions were calculated in the same way for each soil sample, and connectance was calculated as the ratio realized (interactions in each soil sample) to potential (interactions in the whole position) interactions.

microbial-feeding, 14 herbivores, and 8 predators. Vegetation across the landscape included 144 plant species (details on vegetation composition can be found in Young-Mathews et al., 2010).

The abundance and richness of organisms in each channel differed between the rangeland and the cropland (Table 1). Abundance and richness of all groups, other than microbial-feeding nematodes, were significantly higher in the rangeland that in the cropland. Abundances of PLFA and microbivore and predator nematodes were significantly greater in position A (agricultural field or grazed pasture) than in position C (water edge), with intermediate values in position B (bench of the waterway), while the pattern for plant richness was opposite (Table 1). Abundance of PLFA, herbivore nematodes and plants, and taxa richness of herbivore nematodes, increased significantly with riparian health rating scores (Table 1). Four such significant relationships illustrate the higher riparian health scores of the rangeland sites (Fig. 2). No significant effects of the interaction between land use type

Table 1
Abundance and richness of PLFA, microbivore nematodes (Nem. BaFu), predatory nematodes (Nem. Pred.), herbivore and plant−parasitic nematodes (Nem. Pp), and plants in the two different zones of the study area, rangeland (Range) and cropland (Crop), and at different positions ($A = 50$ m, $B = 5−10$ m, and $C = 0.5$ m from the water edge). Regression coefficients and significance are shown using the riparian health rating as predictor of richness and abundance.

		Land use type		Position			Riparian health	
		Range	Crop	A	B	C	r^2	p
Abundance	PLFA	44.05**a** ± 3.95	25.22**b** ± 2.19**	39.27**a** ± 4.47	37.09**ab** ± 4.31	25.33**b** ± 3.67**	0.35	0.005**
	Nem. BaFu	341.94**a** ± 45.37	413.70**a** ± 52.49ns	511.70**a** ± 55.68	372.26**ab** ± 64.33	240.92**b** ± 45.21**	0.00	0.790ns
	Nem. Pred.	20.56**a** ± 4.91	13.39**b** ± 4.46**	26.77**a** ± 7.06	13.80**ab** ± 4.37	8.85**b** ± 4.50**	0.16	0.080ns
	Nem. Pp.	163.89**a** ± 22.19	50.76**b** ± 19.12**	131.94**a** ± 30.87	117.42**a** ± 31.13	59.89**a** ± 17.90ns	0.47	<0.001**
	Plants	82.13**a** ± 8.43	45.15**b** ± 7.56**	46.35**a** ± 7.38	75.74**a** ± 12.00	67.00**a** ± 11.47ns	0.33	0.008**
Richness	PLFA	35.93**a** ± 0.87	32.37**b** ± 0.67**	34.85**a** ± 1.08	35.05**a** ± 0.96	32.11**a** ± 0.90ns	0.23	0.030**
	Nem. BaFu	8.42**a** ± 0.49	9.12**a** ± 0.55ns	9.22**a** ± 0.49	9.33**a** ± 0.71	7.74**a** ± 0.68ns	0.01	0.700ns
	Nem. Pred.	1.41**a** ± 0.15	0.70**b** ± 0.13**	1.17**a** ± 0.18	1.00**a** ± 0.21	0.93**a** ± 0.18ns	0.06	0.300ns
	Nem. Pp.	3.63**a** ± 0.28	2.73**b** ± 0.37**	2.85**a** ± 0.33	3.26**a** ± 0.38	3.39**a** ± 0.55ns	0.48	<0.001**
	Plants	13.74**a** ± 1.27	7.87**b** ± 0.91**	6.60**a** ± 0.78	11.26**b** ± 1.05	14.50**b** ± 1.92**	0.20	0.050ns

** means significant differences ($p < 0.05$) between rangeland and cropland or among A, B, and C. ns = not significant. See methods for explanation on abundance and richness measurements for different organisms.
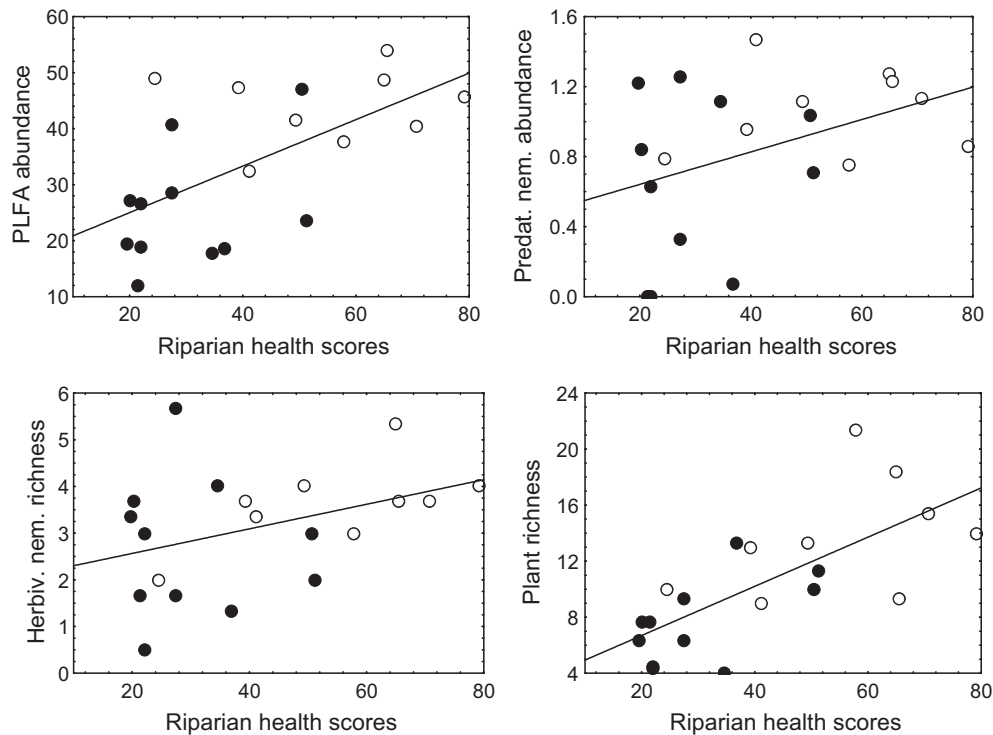
Fig. 2. Abundance of PLFA, abundance of predatory nematodes, plant richness and herbivore nematode richness response to the riparian health scores. For statistics, see Table 1. Dark circles: cropland; white circles: rangeland.

(rangeland or cropland) and position from the water's edge were detected (data not shown).

### 3.2. Abundance and richness in soil food web channels

The slope of the regressions of both the abundance and richness of consumers and their resources revealed that consumers were always less abundant and rich than their resources in all carbon channels (linear regression slope b between −0.15 and 0.78, Fig. 3). Abundances and richness of each pair of components in the microbivore channel tend to be higher in rangeland than cropland locations (Fig. 3a and d), but were only significant for PLFA (Table 1). The abundance of plant-feeding nematodes and plant cover were also significantly related (Fig. 3c), as were the richness of microbial-feeding nematodes and PLFA (Fig. 3d). The ratio of the abundances of PLFA and microbivore nematodes was significantly higher in the rangeland ($p < 0.05$, data not shown). In contrast, the ratio of plant cover to plant-feeding nematode abundances was significantly higher in the cropland ($p < 0.05$, data not shown), while the same ratio for the predator–prey channel significantly increased with riparian health score ($p < 0.05$, data not shown). The ratio of resource to consumer richness was significantly higher in the cropland than in the rangeland for the predator–prey channel ($p < 0.05$, data not shown). This ratio was significantly lower in position A (agricultural soil) than in position C (waterway soil) for the plant–herbivore channel ($p < 0.05$, data not shown).

A set of regressions was used to explore how richness and abundance are related to each other in different channels. The regressions of abundance against richness were always positive and significant and the relationships were strongest at the lowest trophic level (microbes as indicated by PLFA), and weakest at the highest link (predatory nematodes) (Table 2). When comparing the contribution of taxa (expressed by the slope, b) of resource and

consumer organisms in each channel, we found that the contribution of nematode grazers, plants, and microbivore nematodes were greater than that of PLFA, herbivore nematodes and predatory nematodes in the microbivore, plant–herbivore, and predator–prey channels, respectively (Table 2). The residuals of such regressions provide a connectance index independent of the channel richness. That index did not significantly vary with the riparian health rating (Table 2) or among positions ($p > 0.05$, data not shown). Only residuals of the predator–prey channel significantly varied between land use types, with rangeland greater than cropland ($p = 0.02$; data not shown).

3.3. Soil food web interactions and connectance

The number of interactions realized in each channel always depended on the total richness, with the highest value in the microbivore channel ($r^2 = 0.70$, $p < 0.001$), and lowest in the predator–prey channel ($r^2 = 0.16$, $p < 0.001$) (Table 3). Respectively, these are the channels with highest and lowest number of realized interactions per taxa (7.16 and 0.86 respectively, data not shown). The slopes (b) of the regressions of the number of realized against potential interactions (Table 3) show that to increase realized interactions at the smaller scale, more potential interactions are required at the larger scale in the predator–prey channel compared to the other channels. The number of realized interactions was affected by riparian health scores in the predator–prey and the plant–herbivore channels (Table 3). Also, there were differences between the rangeland and the cropland for those channels (Table 4). Realized interactions differed among positions for the microbivore and plant–herbivore channel (Table 4). Connectance was significantly higher in the cropland than in the rangeland in the plant–herbivore channel, and higher in the rangeland than in the cropland for the prey-predator channel (Table 4).
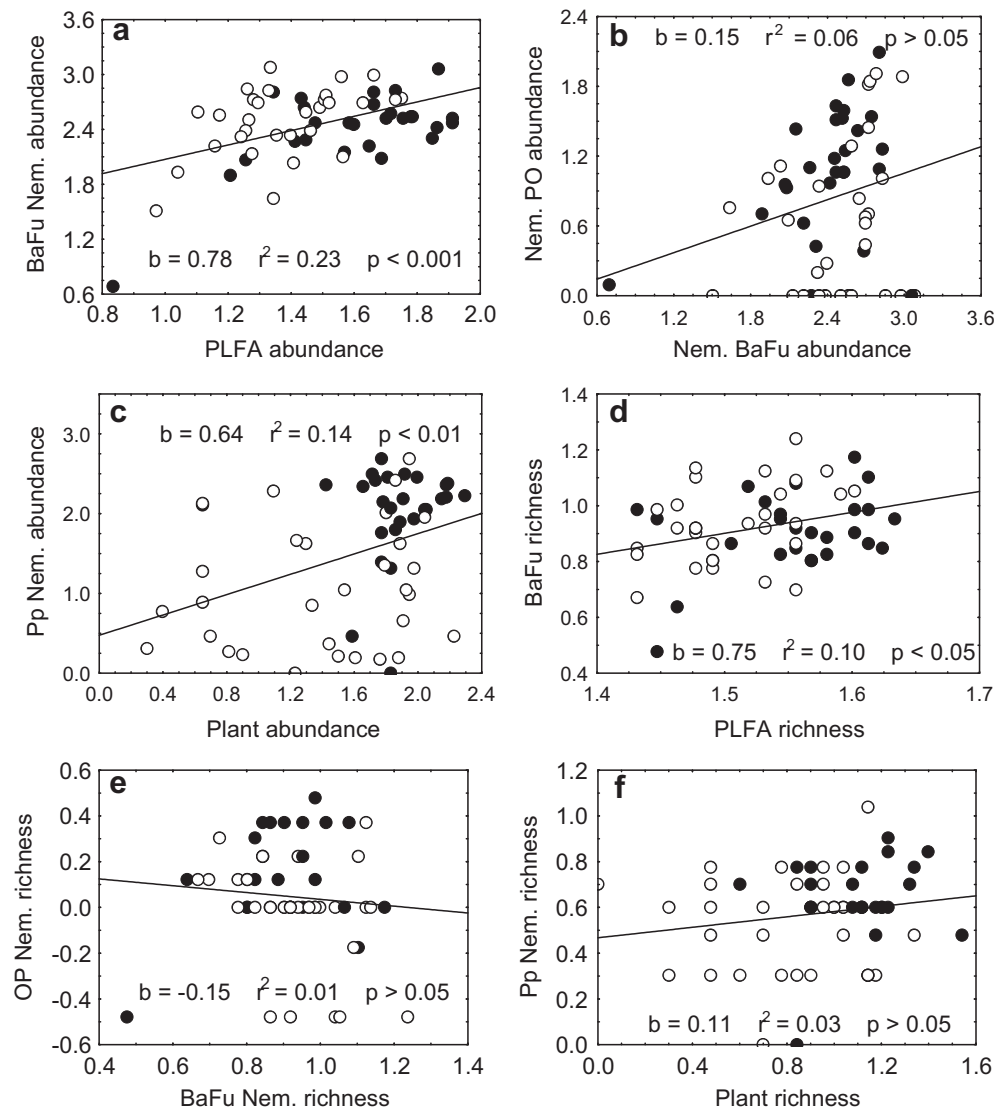
Fig. 3. Relationships between components of each channel; abundance of PLFA and their nematode grazers (BaFu) (a), of microbivore nematodes (BaFu) and their nematode predators (PO) (b), and of plants and herbivore nematodes (Nem. Pp) (c), and relationships between richness of the same pairs of consumer-resource (d–f). Dark circles: cropland; white circles: rangeland. Variables were log-transformed prior to analysis.

3.4. Associations with soil and environmental properties

Two canonical analyses were performed to explore associations between food web connectance and soil and environmental properties in the three different soil food web channels. The first analysis related connectance with a set of soil properties measured in the field (Fig. 4a). The first two roots extracted 14 and 5% of the variance of the soil properties and 33 and 31% of the variance of the ratios. Higher connectance in the nematode predator–prey channel was positively associated with the rangeland, and with total soil C, N and, negatively, with NO_3^--N. Connectance in the microbivore channel was associated, although only slightly, with NO_3^--N, and otherwise was little related to soil properties. Finally, connectance in the plant–herbivore channel was associated with P and higher clay content.

The second analysis (Fig. 4b) showed associations between connectance and soil properties extracted from GIS databases. The first two roots extracted 14% and 12% of the variance of the environmental properties and 33% and 34% of the variance of the ratios. Connectance

in the nematode predator–prey channel was associated with higher elevation and slope, and, very slightly with higher sand content. In the plant–herbivore channel, it was associated with soil organic matter. Connectance in the microbivore channel was associated with water holding capacity, erodability and hydraulic conductivity.

Soil NO_3^--N content, associated with agricultural intensification due to high fertilization inputs, was the measured chemical property with the strongest influence on the richness of organisms in each channel. The residuals of the regressions of abundance against richness in each channel, an indicator of the abundance of organisms independent of richness, showed that soil NO_3^--N was significantly associated with four out of five functional groups of organisms included in this study (Fig. 5), although coefficients were low (≤ 0.14). Regressions indicated negative relationships between the abundance of predatory nematodes, plants, and herbivore nematodes with the amount of NO_3^--N in the soil. Only bacterivore nematodes presented a positive relationship with NO_3^--N, while the abundance of PLFA was the only functional group that did not show a relationship with NO_3^--N.

Table 2
Linear regression analyses of richness against abundance (No., number of nematodes, plant cover and amounts of PLFA) of each group of organisms (I) and of richness (taxa richness for nematodes, species richness for plants, and identity of PLFA) of each group against the total richness in its channel, richness of the consumer against richness of the resource, and residuals of such regression against riparian health scores (II: microbivore channel, III: prey–predator channel, and IV: plant–herbivore channel). a is the constant, b is the slope, r^2 is the regression coefficient, and p is the probability of each regression. See Table 1 for other abbreviations.

Dependent var.	Independent var.	a	b	r^2	p
I) Richness PLFA	No. PLFA	1.24	0.20	0.73	<0.001**
Richness Nem. BaFu	No. Nem. BaFu	0.27	0.27	0.59	<0.001**
Richness Nem. Pred.	No. Nem. Pred.	−0.10	0.17	0.23	<0.001**
Richness Nem. Pp	No. Nem. Pp	−0.15	0.26	0.42	<0.001**
Richness Plants	No. Plants	0.27	0.41	0.46	<0.001**
II) Richness PLFA	Total Microb. richness	0.15	0.85	0.79	<0.001**
Richness Nem. BaFu	Total Microb. richness	−1.73	1.63	0.48	<0.001**
Richness Nem. BaFu	Richness PLFA	−0.22	0.75	0.10	0.02**
Nem BaFu/ PLFA (residuals)	Riparian health	0.00	0.00	0.00	0.92ns
III) Richness Nem. BaFu	Total Pred–prey. richness	−0.09	1.04	0.91	<0.001**
Richness Nem. Pred.	Total Pred–prey. richness	−0.16	0.22	0.01	0.37ns
Richness Nem. Pred.	Richness Nem. BaFu	0.18	−0.15	0.01	0.51ns
Nem OP/ Nem. BaFu (residuals)	Riparian health	−0.11	0.00	0.07	0.27ns
IV) Richness Nem. Pp	Total Plant richness	0.39	0.18	0.06	0.07ns
Richness Plants	Total Plant richness	−0.19	1.09	0.92	<0.001**
Richness Nem. Pp	Richness Plants	0.47	0.11	0.03	0.21ns
Nem. Pp/ Plants (residuals)	Riparian health	−0.12	0.00	0.12	0.14ns

** means statistical significance at $p < 0.05$. ns = not significant.

4. Discussion

Abundance and richness of soil organisms clearly responded to the main land use types within this landscape; abundance and richness of PLFA, plants, predatory and omnivore nematodes, and herbivore and plant–parasitic nematodes were higher in the rangeland than in the intensively-managed cropland. The only functional group that did not present such differences, microbial-feeding nematodes, are "basal" organisms (sensu Ferris et al., 2001) often resistant to environmental perturbations and with generalist ecological traits that may make them unresponsive to such gradients in comparison with other soil organisms. They clearly responded, however, to the gradient of proximity to waterways; abundance of PLFA, microbial-feeding nematodes, and predatory nematodes were higher in the agricultural and pasture fields than near the water edge. The abundance of these organisms

Table 3
Linear regression analysis of the relationships between realized interactions (Real. Int.) and richness (Tot. Richness), potential interactions (Pot. Int.) and riparian health scores in the microbivore (I), prey–predator (II) and plant–herbivore (III) channels. a is the constant, b is the slope, r^2 is the regression coefficient and p is the probability of each regression.

Dependent variable	Independent variable	a	b	r^2	p
I) Real. Int. Microb.	Tot. richness Microb.	−3.04	5.36	0.70	<0.001**
Real. Int. Microb.	Pot. Int. Microb.	−0.50	1.00	0.80	<0.001**
Real. Int. Microb.	Riparian health	5.08	0.17	0.05	0.33ns
II) Real. Int. Pred–prey.	Tot. richness Pred–prey.	−0.67	1.51	0.16	<0.01**
Real. Int. Pred–prey.	Pot. Int. Pred–prey.	−0.01	0.75	0.91	<0.001**
Real. Int. Pred–prey.	Riparian health	−0.99	0.49	0.30	<0.05**
III) Real. Int. Plant	Tot. richness Plant	−0.01	3.02	0.56	<0.001**
Real. Int. Plant	Pot. Int. Plant	−1.62	1.06	0.41	<0.001**
Real. Int. Plant	Riparian health	−1.93	1.37	0.51	<0.001**

** means statistical significance at $p < 0.05$. ns = not significant.

in the proximity of waterways was positively related to riparian health scores, showing that preservation of undisturbed river banks actually increases the abundance of such soil organisms. As expected, higher plant richness was also associated with riparian health, which was not associated to the richness of other organisms. Higher abundances of PLFA and microbial-feeding organisms in agricultural fields compared to riparian edge and bench soils may be due to the effect of fertilization (Ruess et al., 2002; Vestergård, 2004) and intermittent incorporation of plant residues with tillage (Sánchez-Moreno et al., 2006). On the contrary, higher abundances of predatory nematodes, generally sensitive to soil perturbation, in agricultural fields were not expected. Low abundances of nematode predators in the riparian areas have already been reported (Culman et al., 2010). Their absence or low abundances within this landscape may be due to the long history of perturbation of this region, which also decreased plant diversity (Young-Mathews et al., 2010). In a previous study performed in an organic farm within the same area, predatory and omnivore nematodes were also scarce in an on-farm riparian area (Sánchez-Moreno et al., 2008).

The prevalence of omnivore nematodes in the predator group may explain their abundance in the agriculture and grazed fields. Omnivory is a prevalent trophic habit in soil invertebrates (Gunn and Cherret, 1993), and previous experiments have shown that the application of manure to an agricultural field may increase the abundance of omnivore nematodes (Villenave et al., 2004). At the same time, higher abundances of prey in cropped and grazed fields compared to riparian areas may have favored the maintenance of higher abundances of predators. High abundances of organisms in the microbivore channel and of higher trophic links are in agreement with observations of higher metabolic footprints of both groups of organisms further from the channel edge (Ferris, 2010). Our results indicated that higher rates of C supply inferred by Ferris (2010) in agricultural and grazed fields compared to the riparian areas within this landscape supported higher abundances of organisms in three functional groups of the soil food web (microbes, microbivores, and their predators).

Greater richness in lower compared to higher trophic levels is a common pattern in food webs. In agreement with this pattern, consumer organisms always contributed with less individuals and taxa to its channel than the resource organisms. Resource organisms in the microbivore and the plant–herbivore channel were more abundant and diverse in the cropland than in the rangeland. In the predator–prey channel, abundance of prey was associated with rangeland sites, while higher richness was associated with the cropland. Since higher trophic levels are in general sensitive to perturbation and tend to disappear when the ecosystem is disturbed (Bongers and Bongers, 1998), less diversity was expected in cropped fields. However, this was only true for strictly predatory nematodes, which were less diverse than their prey in the cropland. In experimental food webs, Long et al. (2006) found that more diverse communities contain more biomass than less diverse ones, which is at least partially confirmed by our results. Abundance and richness were always significantly correlated, and the correlation was strongest in the lowest trophic links and weakest in the highest.

Our results indicate that the greater the richness of organisms in an area, the greater the number of interactions that will exist at a given point. Since connectance is always calculated from number of taxa or trophic links (see for example Banašek-Richter et al., 2009, and Gross et al., 2009), certain circularity is assumed when analyzing the relationships between richness and connectance. However, dependence between both parameters varies in an idiosyncratic way. This relationship was strongest in the microbivore channel in our study area. The realized interactions at a site likely

Table 4
Mean number of realized interactions (Real. Int.) and connectance among links in different carbon channels in the two land use zones of the study area (Range = rangeland, Crop = cropland), and at different distances from waterways (A,B,C).

	Land use type		Position		
	Range	Crop	A	B	C
Real. Int. Microb.	313.59**a** ± 20.99	313.77**a** ± 23.53ns	352.27**a** ± 30.99	331.83**a** ± 22.91	251.65**b** ± 21.48**
Real. Int. Pred−prey.	11.91**a** ± 1.47	6.24**b** ± 1.32**	10.42**a** ± 1.55	8.75**a** ± 2.04	7.46**a** ± 1.88ns
Real. Int. Plant	49.59**a** ± 6.33	20.63**b** ± 4.50**	18.45**a** ± 3.17	35.21**ab** ± 5.76	51.11**b** ± 10.28**
Connectance Microb.	0.61**a** ± 0.03	0.63**a** ± 0.02ns	0.67**a** ± 0.02	0.59**a** ± 0.04	0.59**a** ± 0.02ns
Connectance Pred−prey.	0.45**a** ± 0.04	0.26**b** ± 0.05ns	0.39**a** ± 0.05	0.37**a** ± 0.07	0.29**a** ± 0.06ns
Connectance Plant	0.03**a** ± 0.00	0.04**b** ± 0.01**	0.04**a** ± 0.01	0.04**a** ± 0.00	0.04**a** ± 0.00ns

** means significant differences at $p < 0.05$; different letters show significant post-hoc differences between groups. ns = not significant.

depend on the potential interactions that exist within the larger habitat. They also depend on the degree of specificity of the trophic relationships among the organisms; it is likely that there is less specificity, and thus more potential interactions, between species in the microbivore channel (composed of thousands of species of microbes and dozens of species of microbivore nematodes) than in the predator−prey channel (probably composed of tens of species in each functional group). For the plant−herbivore and the predator−prey channels the realized interactions were positively affected by the riparian health score and also associated with taxa richness. When the effect of taxa richness was not considered, connectance within each channel was independent of the riparian health scores. In the predator−prey channel, higher connectance and riparian health scores were associated with the rangeland suggesting a negative effect of intensive agriculture on soil food web


connectance. Although the amount of realized interactions between plant and herbivores was greater in the rangeland than in the cropland, connectance showed the opposite trend, indicating that cropping does not increase the amount of interactions but increase the fraction of them which become realized. The number of realized interactions in the microbivore channel was greatest in the cropped or grazed position on the gradient from the waterway, probably due to the influence of chemical fertilizers, manure, and tillage.

Of the channels included in this study, the microbivore channel may be considered the fastest energy channel, since opportunistic nematode grazers have life cycles around ten days, compared with plant-feeding nematodes, which have life cycles of a few weeks, and with predatory and omnivore nematodes, which comprise the slowest channel and may have life cycles of several months. Differences between fast and slow channels (Rooney et al., 2006) seem to extend to other attributes of food web connectance; the fast microbivore channel exhibited the strongest relationship between abundance and richness, the strongest dependence of the realized interactions on the richness of the community, and had the greatest number of realized interactions per species and the highest connectance. This fast channel appears to be composed of a highly structured community, with strong interactions among components. Such inferences agree with reports that show that the nematode community strongly affects the composition (De Mesel et al., 2004) and biomass (Fu et al., 2005) of bacterial communities.

In allometric studies focused on the autoecological relationship between mass and abundance, Mulder et al. (2009) concluded that the environment regulates web topology. The low percentage of explanation obtained in canonical analyses in this study may be an effect of the high coefficients of variation of biological properties across the landscape, which were only partially related to the measured soil properties (Culman et al., 2010). Most components of the soil fauna, for example bacteria and bacterial-feeding nematodes, tend to aggregate around resources, resulting in patchy distributions (Blanc et al., 2006). As stated by Kaspari and Weiser (2007), the world becomes an increasingly rugose place for smaller individuals.

The relationship between connectance and different soil and environmental properties suggested that higher total N, C, and soil pH were associated with sandy soils, in which connectance in the predator−prey and the microbivore channels was high. The levels of NO_3^--N and P, indicators of agricultural intensification, were negatively correlated with biological diversity (Culman et al., 2010) and with riparian health rating scores (Young-Mathews et al., 2010), but were positively, if only slightly, correlated with connectance in the plant−herbivore channel.

When landscape-scale properties were taken into account, slope and elevation were the variables more related to the connectance in the predator−prey channel. Such variables may be considered surrogate indicators for lack of perturbation, which agrees with previous observations in which both total nematode abundance
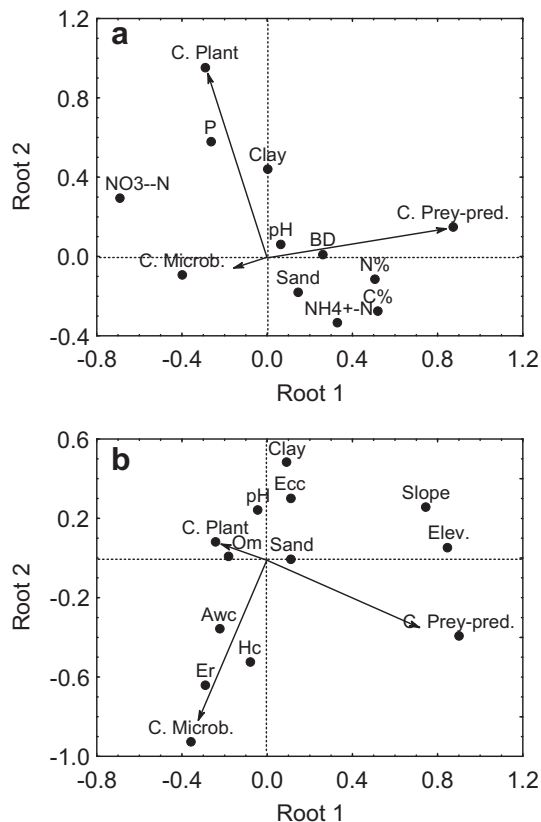
Fig. 4. Canonical analysis of correspondence, showing the associations among connectance (C) for each channel and soil properties measured in the field (a) (NH_4^+-N, NO_3^--N, N%, C%, BD, pH, Clay, Sand, P), and macroenvironmental variables extracted from a GIS (b) (pH, Slope, Elevation, Clay, Sand, Awc = Available water capacity, Er = erodability, Hc = hydraulic conductivity, Ecc = Exchangeable cation capacity, Om = organic matter).
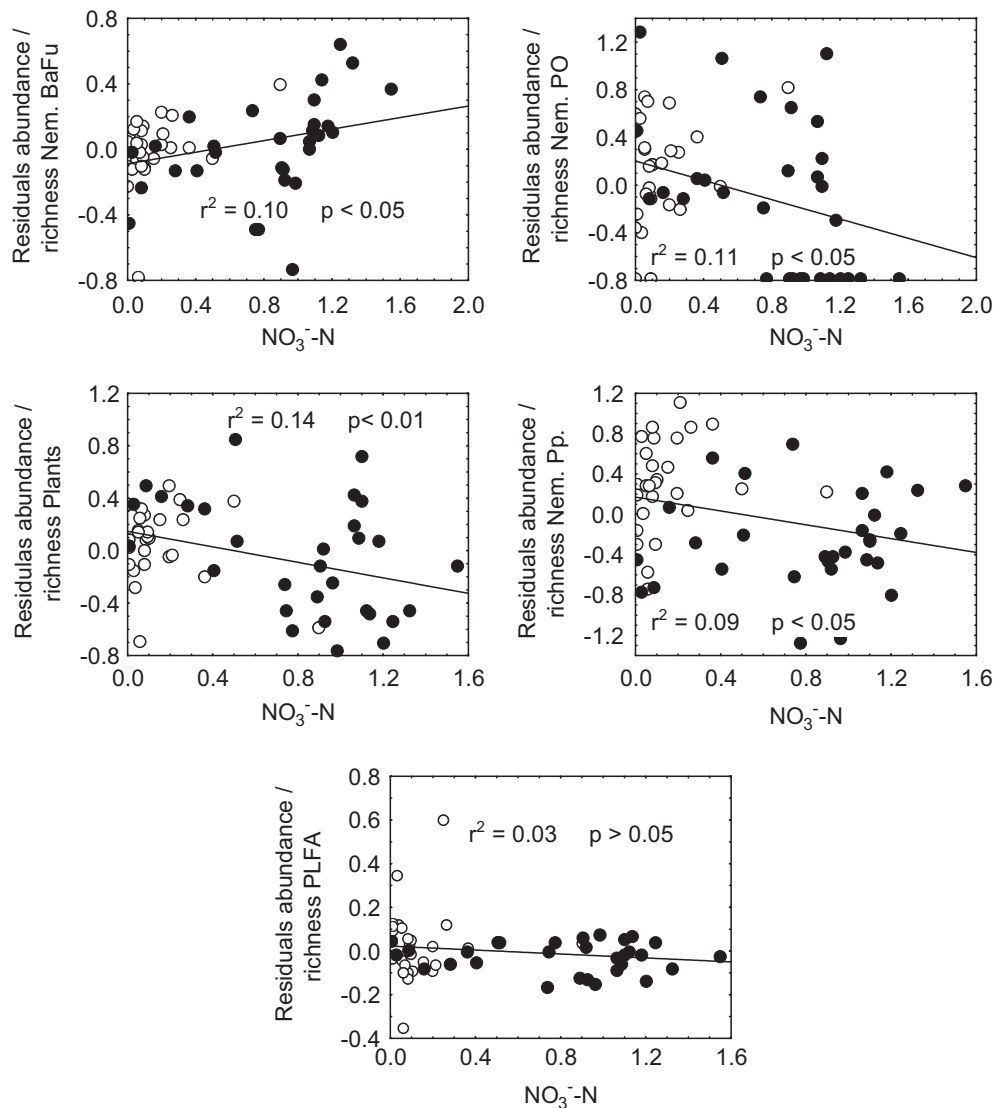
Fig. 5. Regression results of the residuals of the regressions between abundance and richness of each group of organisms versus soil NO_3^--N. See Table 1 for abbreviations. R = rangeland, C = cropland.

and richness were negatively related to intensification (Culman et al., 2010). Abundances of three of the functional groups (predatory nematodes, plants, and herbivore nematodes) were negatively correlated with soil NO_3^--N, a situation that is clearly associated with the cropland land use type. In this landscape, soil NO_3^--N may be considered as a surrogate indicator of agricultural disturbance, generally including tillage, use of pesticides and chemical fertilizers.

5. Conclusions

Considering carbon flux channels in the soil food web as independent functional units provided clear patterns of soil food web complexity in relation to land use and habitat characteristics. Richness and abundance were always correlated, and consumers always contributed less, both in abundance and in richness, to total abundance and richness of the channel. At the landscape scale, maintenance of diverse patchy populations may favor more inter-actions at a given site, especially for the lowest trophic links, probably due to their lower trophic specificity. Higher connectance and more trophic interactions were associated with lower

disturbance and higher riparian health, except in the microbivore channel, in which higher channel connectivity was associated with the cropland area probably due to several factors related to intensive management. Soil and landscape variables that served as indicators of soil food web connectance were the amount of soil NO_3^--N for the microbivore channel, and elevation for the predator–prey channels, apparently because they serve as surrogates of high and low agricultural intensification, respectively.

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