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# Nematode community responses to a moisture gradient and grazing along a restored riparian corridor

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ABSTRACT

Nematode assemblages were assessed to infer soil functions along a stream channel restored with native vegetation in a California on-farm study. Samples were taken at three distances from the water at six sites along the stream channel. Sites represented differences in grazing management and vegetation type. Bacterivorous nematodes, dominated by r-strategists, c–p 1 and 2 (colonizer–persister) categories, were in greater abundance in the ungrazed than the grazed sites. Among the fungivores, c–p 2 were abundant in the ungrazed sites and at positions closest to the water's edge, while only one genus, c–p 4 *Tylencholaimus*, was more abundant at the top of the stream bank and in grazed sites. The stream edge had greater abundance of bacterivores than the drier uppermost soil. Nematode faunal analysis suggests that bacterial decomposition channels predominated near the water while fungal channels predominated in drier locations. Higher aboveground herbaceous plant biomass in the ungrazed sites and closer to the water might have contributed to greater abundance of c–p 1 and 2 bacterivores. Overall, nematode communities were not strongly affected by the restoration, possibly due to dampened effects on soil properties after seven years, lack of colonization from other riparian areas, and/or insufficient time for the restored plant communities to shape nematode communities.



## 1. Introduction

Riparian corridors support important ecological functions and acts as an interface between terrestrial and aquatic environments [31]. They are recognized as functionally unique ecosystems and have become a major focus in the restoration and management of landscapes [32]. An ongoing goal of land managers is to improve the conditions of disturbed riparian corridors [44]. Floodplains formed in riparian zones are valuable for their complex wildlife habitats and are productive areas for agricultural activities such as livestock grazing [32]. However, exploitation of riparian areas for animal grazing often results in a wide range of ecological effects, including soil degradation and loss of biodiversity [9,32].

Livestock grazing can indirectly influence belowground communities through effects on plant communities, on litter mass and quality, and through nutrient deposition [5]. Likewise, soil fauna, such as nematodes, exert considerable influence on energy and nutrient transfers, especially in undisturbed ecosystems [27]. Nematodes influence rates of carbon and nitrogen flux through grazing on microbes, plant roots, fungi and by predation on other biota; they play essential roles in ecosystem functioning [18,20,28]. Nematodes represent many trophic components of the soil food web [55] and are sensitive to changes in environmental conditions [7,11,39,51]. Their faunal assessment can provide unique insights into soil biological processes [45]. Further, nematode faunal analysis, based on the relative weighted abundance of colonizer–persister (c–p) guilds, provides a representation of the probable conditions of the soil food web [19].

Impacts of livestock grazing on nematode communities vary according to geographic region, climatic factors, soil type, plant species composition and type of livestock animal [4,23,26,52,54]. Riparian corridors may have special importance for sustaining highly diverse nematode assemblages in summer-dry climates. Since nematodes require a constant film of moisture for their movement and other activities in the soil [29], and moisture gradients can affect nematode communities and their ecosystem functions [42,49]. Riparian areas can be corridors and reservoirs for biodiversity during dry periods [30], but little is known about the effects of animal grazing on the belowground nematode community which can be used to evaluate ecosystem restoration strategies.

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We investigated the composition of the nematode assemblages in soil of different habitats along a stream channel on a farm in the Central Valley of California. The habitats differed according to degree of soil movement, the grazing pressure of goats, and the survival of native plant species established seven years prior to sampling in 2008. Our objective was to examine the effects of aboveground grazing in a riparian corridor on nematode diversity and community structure, and on plant communities. Nematode assemblages were analyzed to test the following hypotheses: a) nematode diversity is greater in ungrazed than in grazed sites; b) among deteriovores, bacterivores predominate in the moist soils at the stream edge, whereas fungivores predominate in the drier soils at the top of the bank; c) nematode abundance is greater in the more mesic soils at the edge of the stream than in the drier soils at the top of the bank and d) differences in plant communities between restored and unrestored habitats affect the soil nematode communities.

## 2. Materials and methods

### 2.1. Study site description

The study site was located on Union School Slough of western Yolo County, CA, USA (38.596°N and 121.849°W). The site is characterized by intensively irrigated with mild winters and dry summers that permit year-round biological activity near perennial stream edges but not on stream banks. The mean annual air temperature is 15 °C and mean annual precipitation, falling predominantly in winter months, is 44 cm. In 2000–2001, 400 m of Union School Slough was graded to create a 4 m wide floodplain bench on the western bank, which was subsequently re-vegetated with a mixture of native perennial grasses, sedges, forbs, shrubs and trees. Winter-spring grazing of sheep and goats in approximately half of the restored section began in 2005, with about 14 animals/ha, while the other half was fenced to exclude grazing. The soil in the study area is mapped as Hillgate loam, (a fine, montmorillonitic, thermic Typic Palexeralf).

Six different sampling sites (S1–S6) were evaluated in the study, oriented in a North–South direction along the slough. Sites 1–3 were within the grazed area, while sites 4–5 were not. Sites 1–5 were in the restoration zone while site 6 was unrestored and ungrazed. Important soil properties of the different sites are shown in Table 1.

**Table 1**
Site descriptors and mean soil properties: % soil particle fractions, gravimetric water content (GWC), mineral-N ($NH_4^+$–N and $NO_3^-$–N), microbial biomass carbon (MBC) and aboveground plant biomass of herbaceous species measured at sites 1–6 and shown as means for three samplings.

| Site | | | | | | |
|---|---|---|---|---|---|---|
| Site properties | 1 | 2 | 3 | 4 | 5 | 6 |
| Grazed | Yes | Yes | Yes | No | No | – |
| Soil properties | | | | | | |
| Clay (%) | 13.7 | 14.8 | 15.7 | 14.7 | 13.7 | 15.7 |
| Silt (%) | 41.2 | 52.2 | 50.0 | 50.3 | 42.3 | 46.2 |
| Sand (%) | 45.7 | 32.7 | 34.1 | 35.0 | 44.5 | 38.3 |
| GWC | 0.20 | 0.24 | 0.18 | 0.21 | 0.23 | 0.21 |
| $NH_4^+$–N (μg/g) | 1.70 | 2.00 | 1.12 | 2.29 | 2.49 | 3.07 |
| $NO_3^-$–N (μg/g) | 0.81 | 0.49 | 0.47 | 1.52 | 0.64 | 1.35 |
| Total N (%) | 0.08 | 0.10 | 0.08 | 0.08 | 0.09 | 0.08 |
| Total C (%) | 0.78 | 1.05 | 0.83 | 0.89 | 1.09 | 0.90 |
| MBC (μg/g) | 198.2 | 247.0 | 161.8 | 295.2 | 372.0 | 329.5 |
| Plant biomass[a] (kg $m^{-2}$) | 0.49 | 0.94 | 0.90 | 0.98 | 1.20 | 0.66 |

Sites 1–5 riparian restoration zone; Site 6 unrestored riparian.
[a] Mean aboveground herbaceous biomass collected from 0.5 × 0.25 m plots.

### 2.2. Soil sampling

Soil sampling for nematodes and soil properties was performed three times during the winter and spring rainy season, on December 11–14, 2007, March 17, 2008 and April 21, 2008. Soil cores (7.5 cm diam.) were taken at three positions on the stream bank: 1) the lower slope within 0.5 m of the edge of the stream ('lower'), 2) the middle of the floodplain bench ('mid'), and 3) the upper bank of the floodplain slope ('upper'). Three replicated cores about 2 m apart were taken at 0–30 cm depth at each position. Thus, nine samples were collected from each site on each sampling date, each of which was analyzed separately.

### 2.3. Analysis of soil properties

Samples of moist soil were analyzed for inorganic N by KCl extraction and colorimetric determination using a modification of Miranda et al. [38] for nitrate ($NO_3^-$–N) and Forster [22] for ammonium ($NH_4^+$–N). Gravimetric water content was determined after oven drying at 105 °C. Microbial biomass carbon (MBC) was determined by chloroform fumigation followed by $K_2SO_4$ extraction using a $k_C$ -factor of 2.64 [10,53]. Total C and N of the <2 mm fraction were measured by combustion on a 4010 Elemental Combustion System, Costech Analytical Technologies, Inc., Valencia, CA [40]. Soil particle size distribution of this fraction was measured using a Coulter LS-230 particle size analyzer [Beckman and Coulter Inc., Miami, FL; [15]].

### 2.4. Vegetation and aboveground plant biomass analysis

In May 2008, vegetation was characterized at each of the three positions on the stream bank at each site. Vegetation was surveyed with Braun-Blanquet style relevé plots of 10–50 $m^2$, which included compiling a species list and visually estimating percent cover (according to seven cover categories) for each species (CNPS Vegetation Committee 2000). Plants were identified in the field according to description by Hickman [25] and DiTomaso and Healy [14], or by taxonomist Ellen Dean at the Tucker Herbarium at the UC Davis.

Aboveground herbaceous plant biomass was clipped from 0.25 m × 0.5 m plots at each sampling location on October 23–26, 2007, April 1–3, 2008 and May 5–7, 2008. Samples were oven-dried at 60 °C and total dry weight was calculated on a kg $m^{-2}$ basis.

### 2.5. Nematode analyses

Nematodes were extracted from a subsample of 200 g of soil in the first and 300 g in the second and third sampling dates using a modified sieving and Baermann funnel technique [6]. Nematode counts were expressed as number of nematodes per 100 g dry soil weight. The total number of nematodes in each sample was counted under a microscope at 50×magnification and the first 200 individuals were identified at 100–400×to genus or family level. Nematode biomass was calculated for individual nematode taxa following Andrássy [2] and then summed to get the total biomass according to taxa abundance in a sample. Nematode taxa were assigned to trophic [55] and c–p groups [8]. Given the uncertain trophic habit of the nematodes in the family Tylenchidae [21,41,56], half of nematodes from this family were considered fungal feeders and the other half plant-feeders. Shannon's diversity index [$H'$, [48]] was calculated and the soil food web indices and the soil food web indices including Enrichment Index (EI which indicates the prevalence of bacterial decomposition pathways), Channel Index (CI, which indicates the prevalence of fungal decomposition), Structure Index (SI which indicates soil food web length and connectance), and Basal

Index (BI which indicates depleted and stressed soil food webs) were used to assess soil food web condition [19].

### 2.6. Statistical analyses

Since our experimental design was essentially pre-determined and randomization was not possible due to linearity of the stream channel, we used a general linear mixed model to examine the effects of sampling date, grazing, and position on the stream bank. We used the coordinates of each soil core to define the spatial relationship of samples and modeled the residuals to account for the lack of spatial independence in *PROC GLIMMIX* [46]. Tukey Kramer mean comparison was used to compare the three positions on the stream bank. Site 6 was the only unrestored site and was therefore excluded from the statistical analysis; only mean values were reported to show a baseline comparison. Spearman's rank correlation analysis was performed on pooled data from all sampling dates to determine the relationships of nematode trophic groups with soil properties and aboveground plant biomass. An alpha level of 0.05 was used for all tests.

Permutational multivariate analysis of variance (PerMANOVA) was performed to test for significant effects among the experimental factors (sampling date, grazing effect, position from waterway, and site) on the nematode and vegetation community structure. This test was analogous to multivariate ANOVA, but allows for a more ecologically appropriate distance measure than Euclidean distance [1]. PerMANOVA analyses were performed in "R" [43] with the *adonis* function in the *vegan* package with the default parameters. Total taxa abundance was used for nematode communities; percent cover data were used for plant communities. A Mantel test [35] was used to test the null hypothesis that no relationship exists between the nematode and vegetation communities. The test was performed in "R" with the *mantel* function in the *vegan* package with a Bray–Curtis distance measure.

Nonmetric multidimensional scaling (NMS) was used to examine the relationships in vegetation and nematode communities among unrestored, grazed and ungrazed sites. NMS analyses with the Bray–Curtis distance measure were performed on percent cover and abundance data for vegetation species and nematode taxa, respectively. NMS analyses were performed in R via the *metaMDS* function in the *vegan* package with default parameters. The final stress values of the reported figures were 15.2 (vegetation) and 13.0 (nematodes).

## 3. Results

### 3.1. Nematode and plant taxa at individual sites

Nematode genera found in the soil samples collected form the study site are reported in Table 2. A total of 42, 43, 45, 45, 44 and 46 nematode taxa, at either genus or family level, were recorded in samples from sites 1 through 6, respectively.

Of the 68 plant species identified, most of them were ruderal, of which 47 were non-natives, and only a third were natives planted during the restoration (14 herbaceous and seven woody species). Despite the relatively short length of stream included in this study, each sampling site differed in the predominant vegetation species present along the channel edge [47]: sedge, Bulrush-cattail, cattail, creeping ryegrass, narrow-leaf willow, and California annual grassland series for sites 1–6, respectively.

### 3.2. Nematode and plant assemblages

Permutational multivariate analysis of variance (perMANOVA) showed that all factors in the experimental design (date, position, grazing, and site) significantly affected nematode community structure (Table 3). When all dates were analyzed simultaneously, the effects of the factors were highly significant, but collectively they only explained about one quarter of the variance in the nematode community. Sampling date had the greatest effect on nematode community structure (8.4%), followed by position on the stream bank (7%), site (5.1%), and grazing (4.7%). When analyzed separately by date, perMANOVA revealed relatively similar trends with factors at each sampling date (Table 3). Position on the stream

**Table 2**
Mean nematodes/100 g dry weight soil averaged across three sampling dates in sites 1–6. Ba: bacterivores; F: fungivores; O: omnivores; Pr: predatory; Pf: plant-feeders; the associated numbers are the colonizer–persister scale group.

| Nematode genera (C–p Value) | Sites | | | | | | Nematode genera (C–p Value) | Sites | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | | 1 | 2 | 3 | 4 | 5 | 6 |
| *Rhabditis* (Ba-1) | 5.4 | 3.9 | 2.0 | 13.1 | 23.0 | 7.7 | *Tylencholaimus* (Fu-4) | 40.6 | 27.5 | 99.4 | 24.0 | 19.3 | 35.7 |
| Dauerlarvae (Ba-1) | 1.0 | 2.4 | 0.6 | 10.3 | 4.3 | 1.4 | *Mononchus* (P-4) | 0.0 | 0.0 | 0.4 | 0.3 | 0.2 | 0.4 |
| *Mesorhabditis* (Ba-1) | 1.1 | 0.7 | 0.2 | 1.7 | 4.5 | 0.9 | *Mylonchulus* (P-4) | 0.5 | 0.3 | 3.4 | 0.8 | 0.6 | 1.1 |
| *Rhabdolaimus* (Ba-1) | 0.2 | 0.1 | 0.3 | 2.1 | 1.0 | 0.4 | *Labronema* (P-4) | 0.3 | 0.2 | 0.3 | 0.8 | 0.1 | 0.2 |
| *Panagrolaimus* (Ba-1) | 8.7 | 12.2 | 4.1 | 31.0 | 50.0 | 22.0 | *Discolaimus* (P-5) | 0.0 | 0.1 | 0.2 | 0.4 | 0.0 | 0.0 |
| *Monhystera* (Ba-1) | 1.7 | 3.5 | 2.7 | 8.6 | 2.1 | 1.7 | *Pungentus* (O-4) | 0.0 | 0.1 | 0.4 | 0.0 | 0.1 | 0.3 |
| *Diplogasteroides* (Ba-1) | 0.9 | 0.0 | 0.3 | 0.3 | 4.2 | 0.5 | Quadsianematidae (O-4) | 0.0 | 0.0 | 0.8 | 0.6 | 0.2 | 1.0 |
| *Achromadora* (Ba-1) | 0.0 | 0.0 | 0.1 | 0.0 | 0.0 | 0.1 | *Eudorylaimus* (O-4) | 5.5 | 3.0 | 14.2 | 5.6 | 3.4 | 5.3 |
| *Acrobeloides* (Ba-2) | 52.6 | 66.7 | 41.0 | 84.1 | 52.4 | 77.2 | Other dorylaimids (O-4) | 1.4 | 3.3 | 2.4 | 2.9 | 1.0 | 0.7 |
| *Acrobeles* (Ba-2) | 0.5 | 0.3 | 0.0 | 0.3 | 0.2 | 0.1 | *Mesodorylaimus* (O-5) | 7.7 | 8.1 | 6.4 | 18.9 | 18.4 | 4.4 |
| *Cephalobus* (Ba-2) | 8.2 | 6.2 | 3.7 | 6.2 | 9.5 | 8.0 | Aporcelaimidae (O-5) | 0.8 | 1.2 | 0.8 | 3.1 | 0.7 | 1.4 |
| *Eucephalobus* (Ba-2) | 1.8 | 3.0 | 1.5 | 6.2 | 4.7 | 4.2 | *Dorylaimus* (O-5) | 0.8 | 0.8 | 0.6 | 0.9 | 0.7 | 0.3 |
| *Chiloplacus* (Ba-2) | 0.6 | 0.4 | 0.6 | 1.4 | 0.5 | 1.0 | *Prodorylaimus* (O-5) | 0.7 | 3.7 | 0.4 | 1.4 | 1.1 | 0.4 |
| *Teratocephalus* (Ba-2) | 0.1 | 0.8 | 0.0 | 0.1 | 0.5 | 0.6 | *Tylenchus* (Pf/Fu-2) | 78.0 | 87.4 | 114.3 | 72.1 | 53.5 | 92.3 |
| *Plectus* (Ba-2) | 2.0 | 5.1 | 5.7 | 11.3 | 17.1 | 3.6 | *Filenchus* (Pf/Fu-2) | 59.9 | 92.4 | 67.5 | 60.8 | 45.1 | 70.3 |
| *Wilsonema* (Ba-2) | 0.0 | 0.3 | 0.0 | 0.5 | 0.1 | 1.1 | *Paratylenchus* (Pf-2) | 0.7 | 1.6 | 2.9 | 1.7 | 1.9 | 3.0 |
| *Prismatolaimus* (Ba-3) | 1.4 | 0.8 | 1.5 | 4.9 | 0.8 | 2.9 | *Gracilacus* (Pf-2) | 4.9 | 1.5 | 3.1 | 32.8 | 2.7 | 0.4 |
| *Alaimus* (Ba-4) | 0.2 | 0.3 | 0.1 | 0.1 | 0.0 | 0.3 | *Pratylenchus* (Pf-3) | 59.3 | 83.1 | 44.7 | 106.6 | 24.8 | 23.9 |
| *Aphelenchoides* (Fu-2) | 21.2 | 25.8 | 15.4 | 32.4 | 55.5 | 30.2 | *Hoplolaimus* (Pf-3) | 0.1 | 0.9 | 0.3 | 0.6 | 0.4 | 0.3 |
| *Aphelenchus* (Fu-2) | 23.8 | 18.6 | 30.9 | 22.5 | 18.0 | 21.6 | *Helicotylenchus* (Pf-3) | 18.5 | 8.4 | 11.2 | 28.0 | 22.2 | 1.7 |
| *Aprutides* (Fu-2) | 0.7 | 0.8 | 1.4 | 1.3 | 1.0 | 2.6 | *Tylenchorhynchus*(Pf-3) | 20.4 | 7.1 | 5.1 | 8.6 | 5.9 | 4.2 |
| *Ditylenchus* (Fu-2) | 2.7 | 4.3 | 1.2 | 14.6 | 22.1 | 2.9 | *Hoplotylus* (Pf-2) | 0.2 | 0.9 | 0.4 | 0.3 | 0.9 | 1.1 |
| *Psilenchus* (Fu-2) | 3.8 | 11.4 | 2.3 | 6.3 | 3.7 | 9.9 | *Criconemoides* (Pf-3) | 0.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Ecphyadophora* (Fu-2) | 0.0 | 0.0 | 0.4 | 0.0 | 0.0 | 0.4 | *Xiphinema* (Pf-5) | 0.1 | 0.8 | 0.3 | 0.2 | 4.9 | 0.6 |
| *Diptherophora* (Fu-3) | 0.3 | 0.1 | 0.2 | 0.1 | 0.1 | 0.0 | | | | | | | |

**Table 3**
Nematode and vegetation community perMANOVA values showing the percent that each factor contributed to the total variation in the dataset. Each column reflects separate perMANOVA analyses performed either on the entire dataset or on datasets subset by date.

| | Nematodes | | | | Vegetation |
|---|---|---|---|---|---|
| Source | All Dates | Dec '07 | Mar '08 | Apr '08 | May '08 |
| Main Effects | | | | | |
| Date | 8.4 *** | – | – | – | – |
| Position | 7.0 *** | 11.8 *** | 13.9 *** | 14.1 *** | 23.7 ** |
| Grazing | 4.7 *** | 2.8 | 7.9 *** | 9.2 *** | 21.4 ** |
| Site | 5.1 *** | 10.5 * | 10.5 ** | 8.3 | 22.6 * |
| Residuals | 74.8 | 74.9 | 67.7 | 68.4 | 32.3 |

Significance levels: $P < 0.001$ = '***'; $< 0.01$ = '**'; $< 0.05$ = '*'; $< 0.10$ = '.'

bank affected nematode community throughout all 3 sampling dates. The effects of position on the stream bank and sheep and goat grazing on the nematode community structure grew stronger with each subsequent sampling, while the site effects diminished over time.

PerMANOVA revealed vegetation community structure was strongly shaped by the characteristics at each of the sites (position on the stream bank, presence or absence of grazing, as well as site itself) than was the structure of nematode communities (Table 3). Position on the stream bank (23.7%), grazing (21.4%) and site differences (22.6%) were all significant drivers of plant communities, and together these factors explained approximately two-thirds of the variance found in those data. Even though experimental design factors affected plant communities to a greater extent than nematodes communities, a Mantel's test revealed a positive correlation between plant and nematode communities ($r = 0.490$; $P < 0.001$).

### 3.3. Effect of grazing

Bacterivorous nematode taxa (c–p 1, c–p 2, total) were less abundant in the grazed than the ungrazed sampling sites (Table 4). *Tylencholaimus*, a c–p 4 fungivorous nematode genus, was in greater abundance in the grazed than ungrazed sites ($P = 0.04$), while differences among sites for c–p 2 and total fungivores were not significant ($P > 0.05$). Grazed and ungrazed sites did not differ in the abundance of plant-feeders or in the sum of omnivores and predators.

Enrichment Index (EI) ($P < 0.001$) and Shannon diversity ($P = 0.004$) were significantly lower, while Channel Index (CI) was higher ($P < 0.001$) in the grazed than the ungrazed sites (Table 5). There was no significant effect ($P > 0.05$) of grazing on Structure Index (SI) and Basal Index (BI). Nematode biomass was significantly lower ($P = 0.04$) in grazed than ungrazed sites. Plant biomass was significantly higher ($P = 0.002$) in the ungrazed than the grazed sites.

### 3.4. Effect of position on the stream bank

Soil samples collected closer to the edge of the stream (lower position) had greater total abundance of bacterivores, dominated by c–p 1 and 2 guilds, than positions higher on the banks (Table 4). The c–p 4 fungivore, *Tylencholaimus*, was greater in abundance at the upper position, farthest from the water, while the effect of position was not significant on c–p 2 and total fungivores. High c–p value predatory and omnivorous nematodes were significantly more abundant at the mid and lower than the upper position. Total plant-feeders, dominated by the c–p 3 group, mainly consisting of the endoparasitic genus *Pratylenchus*, were significantly more abundant at the mid and lower than the upper position (Table 4).

EI was highest at the lower position, indicating greater activity in organic matter decomposition pathways mediated by bacteria (Table 5). SI was higher at the mid than the lower position, indicating greater food web structure at this location. CI was significantly higher at the upper than the lower position, indicating greater reliance on fungal decomposition pathways further from the stream. Nematode taxa diversity was higher at the lower position than the mid position and intermediate in the upper position. Basal Index (BI) and total nematode biomass did not differ among positions.

**Table 4**
Effect of grazing, position from waterway, sampling date and interactions between factors on abundance of nematodes 100 $g^{-1}$ in each guild.

| Factor | Bacterivores | | | | Fungivores | | | Om + Pr | Plant-feeders | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | c–p 1 | c–p 2 | c–p 3 | Total | c–p 2 | c–p 4 | Total | Total | c–p 2 | c–p 3 | Total |
| *Grazing*[b] | | | | | | | | | | | |
| Grazed | 17 ± 2b[a] | 67 ± 5b | 1 ± 0 | 86 ± 16b | 138 ± 16 | 56 ± 9a | 194 ± 20 | 21 ± 3 | 89 ± 10 | 87 ± 10 | 176 ± 14 |
| Ungrazed | 76 ± 14a | 100 ± 7a | 3 ± 1 | 178 ± 28a | 147 ± 18 | 22 ± 4b | 168 ± 18 | 29 ± 6 | 78 ± 12 | 99 ± 15 | 180 ± 20 |
| *Position*[c] | | | | | | | | | | | |
| Upper | 16 ± 2b | 77 ± 7ab | 2 ± 1 | 95 ± 8b | 135 ± 12 | 60 ± 12a | 195 ± 22 | 16 ± 2b | 88 ± 11 | 52 ± 8b | 140 ± 13b |
| Mid | 33 ± 7b | 73 ± 7b | 1 ± 0 | 108 ± 11b | 129 ± 16 | 39 ± 8 ab | 169 ± 18 | 28 ± 5a | 69 ± 10 | 126 ± 20a | 197 ± 22a |
| Lower | 72 ± 16a | 91 ± 9a | 3 ± 1 | 166 ± 23a | 160 ± 30 | 27 ± 8b | 188 ± 31 | 29 ± 6a | 97 ± 19 | 97 ± 13ab | 196 ± 23a |
| *Type III tests of fixed effects-P values* | | | | | | | | | | | |
| Grazing (G) | <0.001 | 0.03 | ns | <0.001 | ns | 0.04 | ns | ns | ns | ns | ns |
| Position (P) | <0.001 | 0.04 | ns | <0.001 | ns | 0.03 | ns | 0.01 | ns | 0.001 | 0.05 |
| Sampling time (T) | 0.01 | ns | ns | ns | 0.001 | ns | 0.004 | 0.01 | 0.03 | ns | ns |
| G × P | <0.001 | ns | ns | 0.001 | ns | ns | ns | 0.01 | ns | ns | ns |
| G × T | 0.01 | ns | ns | ns | ns | ns | ns | ns | ns | ns | ns |
| P × T | <0.001 | 0.002 | ns | 0.001 | ns | ns | ns | 0.03 | ns | ns | ns |

[a] Values shown are the average across three sampling times (±SE).
[b] Grazed restored (sites 1–3) vs. ungrazed restored (sites 4–5).
[c] Different letters indicate significant differences between the positions determined by Tukey Kramer mean comparison test at $P < 0.05$. Om + Pr: omnivores and predatory; ns: non-significant.

**Table 5**
Effect of grazing, position from stream channel, time of sampling and interactions between the factors at the riparian restoration study area on nematode community indices and nematode biomass.

| Factor | EI | SI | CI | BI | $H'$ | Nematode biomass (μg/100 g dry soil) |
|---|---|---|---|---|---|---|
| *Grazing*[b] | | | | | | |
| Grazed | 50 ± 1b[a] | 50 ± 2 | 68 ± 2a | 32 ± 1 | 2.12 ± 0.02b | 557 ± 68b |
| Ungrazed | 58 ± 2a | 41 ± 2 | 45 ± 3b | 31 ± 1 | 2.30 ± 0.04a | 831 ± 138a |
| *Position*[c] | | | | | | |
| Upper | 49 ± 1c | 49 ± 3ab | 68 ± 3a | 33 ± 1 | 2.20 ± 0.03ab | 581 ± 82 |
| Mid | 53 ± 2b | 50 ± 3a | 59 ± 4ab | 30 ± 2 | 2.10 ± 0.04b | 659 ± 143 |
| Lower | 57 ± 2a | 40 ± 3b | 50 ± 4b | 32 ± 2 | 2.28 ± 0.04a | 759 ± 128 |
| *Type III tests of fixed effects-P values* | | | | | | |
| Grazing (G) | <0.001 | ns | <0.001 | ns | 0.004 | 0.04 |
| Position (P) | <0.001 | <0.001 | <0.001 | ns | 0.001 | ns |
| Sampling time (T) | <0.001 | ns | <0.001 | ns | ns | <0.001 |
| G × P | 0.01 | ns | ns | ns | ns | 0.02 |
| G × T | 0.001 | ns | 0.03 | ns | 0.03 | ns |
| P × T | 0.002 | ns | <0.001 | ns | ns | ns |
| Site 6 (Unrestored) | 53 ± 2 | 39 ± 4 | 56 ± 4 | 35 ± 2 | 2.24 ± 0.04 | 466 ± 73 |

[a] Values shown are the average across three sampling times (±SE).
[b] Grazed restored (sites 1–3) vs. ungrazed restored (sites 4–5).
[c] Different letters indicate significant differences among the positions determined by Tukey Kramer mean comparison test at $P < 0.05$ level. EI: Enrichment index, SI: Structure index; CI: Channel index; BI: Basal index; $H'$: Shannon diversity index; ns: non-significant.

### 3.5. Relationship of nematodes with soil properties and plant biomass

Bacterivore abundance was positively correlated with gravimetric water content GWC ($r = 0.28$; $P = 0.001$), total soil N ($r = 0.34$; $P < 0.001$) and C ($r = 0.34$; $P < 0.001$) and MBC ($r = 0.36$; $P < 0.001$). Fungivores abundance was negatively correlated with GWC ($r = -0.28$; $P = 0.001$). Both nematode biomass ($r = 0.17$; $P = 0.05$) and total abundance ($r = 0.15$; $P = 0.07$) tended toward a positive correlation with MBC. Neither nematode total abundance nor biomass was correlated with plant biomass.

### 3.6. Unrestored communities

Nonmetric multidimensional scaling (NMS) analyses revealed some apparent differences in biotic communities among unrestored and restored plots (Fig. 1). The vegetation communities in unrestored sites (circles in Fig. 1 a) grouped apart from those in restored sites, appearing to be more similar to those in grazed, restored sites (triangles) than ungrazed, restored sites (squares). However, the nematode communities in the unrestored plots did not separate distinctly from the grazed, restored or ungrazed, restored sites, but rather seemed to share similarities with both grazed and ungrazed communities (Fig. 1b). Permutational MANOVA confirmed the relationships revealed with NMS analyses, when the unrestored site (site 6) was included in the model to test the effects of restoration, grazing and position on nematode and vegetation communities. In the vegetation communities, grazing accounted for 16.7% of variation, while the differences between restored (sites 1–5) and the unrestored site accounted for 11.6% of the total variation ($P < 0.001$) for both factors. In the nematode communities, grazing accounted for 8.0% ($P < 0.001$) and restoration accounted for 3.0% ($P = 0.045$) of the total variation. Although restoration affected both the nematode and plant communities, the magnitude of the effect on vegetation was nearly four times greater than the effect on nematodes.

## 4. Discussion

The abundance and diversity of nematodes in the restored area was comparable to other studies conducted in undisturbed riparian wetlands [16,17]. Seven years after the riparian zone of Union

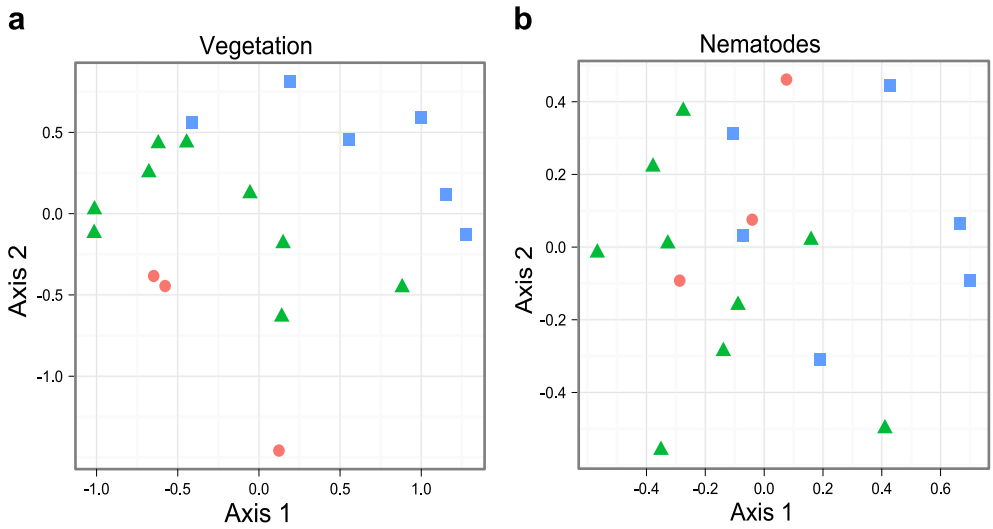


**Fig. 1.** NMS analyses of a) vegetation and b) nematode communities showing the relationship between unrestored sites (circles) and restored, grazed (triangles) and restored, ungrazed sites (squares). Nematode communities and vegetation were sampled in April and May 2008, respectively.

School Slough was graded and restored with native vegetation, differences in nematode assemblages reflected the impact of grazing, and position on the stream bank. However, no clear distinction in the nematode community was observed between the restored and unrestored sites.

### 4.1. Effect of livestock grazing and disturbance due to restoration

In the present study, livestock grazing was associated with lower abundances of the dominant trophic group bacterivorous nematodes. Stanton [52] observed a decrease in bacterivore nematodes as a result of reduction in belowground root biomass and root exudations, which was likely a function of reduction in aboveground plant biomass due to clipping. Although root biomass was not measured, reduction in aboveground plant biomass may have similarly impacted the root system in our study results. An increase in bacterivores in response to grazing has been primarily attributed to a greater microbial populations resulting from addition of organic matter by the grazing animals [4,23,26] or to root mortality due to loss of aboveground plant biomass thereby fueling carbon availability which supports greater microbial activity [36]. Therefore, the reduction in bacterivores in the present study seems to be because sheep and goats may not have added enough organic matter to the soil, while the decrease in the aboveground plant biomass likely reduced root biomass. A positive correlation of bacterivores with MBC further suggested that lower abundance of bacterivores in the grazed sites was likely the result of reduction of both above and belowground plant biomass. Apart from this, indirect effects of animal grazing on soil conditions such as change in soil temperature and soil moisture [52], may also affect the belowground communities.

Although there were no significant effects of grazing on absolute abundance of fungivores, higher CI values indicated slow fungal decomposition channels in the grazed sites. In addition, feeding habits of nematodes in the Tylenchidae probably vary; as an aggregate they are considered either root hair or fungal feeders [41,55]. In our study, c–p 2 Tylenchidae, predominantly *Tylenchus* and *Filenchus*, were marginally more abundant in the grazed sites, lending more weight to the inference of fungal-dominated decomposition in those sites. Further, the lower values of EI in the grazed sites reflected the low abundance of enrichment opportunist c–p 1 bacterivores, indicating soil food web condition to be less enriched [19]. Overall, the grazed sites exhibited a soil food web with depleted conditions and greater contribution of fungal decomposition pathways.

Grazing had no effect on the abundance of high c–p value (3–5) omnivores and predatory nematodes, but SI was higher in the grazed than the ungrazed sites. A major contribution to the SI was provided by the c–p 4 genus *Tylencholaimus* in the grazed sites. However, this genus is reported to be sensitive to chemical disturbance [51], acidified hog manure [34] and mechanical disturbance to the soil [24]. Why grazing appeared to have a positive effect on a high c–p value nematode like *Tylencholaimus* in our study results is worthy of further study in relation to its life history (*r* vs. *K*) attributes. Coincidentally, Clausi and Vinciguerra [12] observed rapid increase in the abundance of *Tylencholaimus* in response to forest clear-cuts.

Grazing by sheep and goat reduced nematode diversity compared to the ungrazed sites. Possibly ungrazed sites assured a better vegetation cover and greater supply of nutrients and food sources for maintenance of diverse group of nematodes compared to the grazed sites. Zolda [58] found similar reduction in nematode diversity due to horse grazing on steep grassland. However, Zolda [58] observed that nematode diversity may also be influenced by the individual site characteristics.

The plant community of the unrestored site was distinct from those in the restored sites, sharing more in common with grazed, restored than with ungrazed, restored sites (Fig. 1a). The nematode communities in the unrestored sites were significantly different than those in the restored sites ($P = 0.045$), but these relationships were much weaker than in plant communities (Fig. 1b; $r^2 = 3.0\%$), indicating the relatively weak effect that restoration had on the soil nematodes. This finding suggests two possible phenomena. First, nematode communities in general may be more strongly shaped by grazing, than by differing plant taxa due to restoration. Alternatively, the weak effect of restoration on soil nematodes could be due to a lack of sufficient recovery time since the disturbance of the floodplain restoration. Differences in belowground communities among restored and unrestored sites may only be apparent after many years of restoration, even though plant communities have been changed [33]. Nematodes may be slow to colonize newly restored areas, especially when the landscape is fragmented by intensive agriculture. The nearest stand of riparian forest is over 2 km distant from the study area. Previous studies in the area also noticed a lack of effects of management on the nematode communities, potentially due to distance from other sites with more complex food webs [13,37,57]. This second hypothesis, i.e., that nematode communities are much slower to recover after restoration than vegetation, has dramatic implications for soil biodiversity loss and ecosystem recovery after degradation. Continued monitoring of these sites should help determine if restored plant communities play a larger role in shaping nematode communities in restored sites.

### 4.2. Effect of position on stream bank on nematode communities

High soil moisture favors bacterivore nematodes [50], while fungivores are more abundant in drier soil conditions [3]. In this study, total bacterivores, predominantly c–p 1 and 2 were more abundant close to the edge of the stream. Among the fungivores, c–p 4 (*Tylencholaimus*) was favored by the drier soil at the upper position on the bank, while there were no clear moisture affiliations for the c–p 2 fungivores (mainly *Aphelenchoides* and *Aphelenchus*), indicating that all taxa within the trophic group might not respond to edaphic factors in the same way. Nevertheless, the EI and CI values indicated predominance of bacterial decomposition at the lower position and fungal decomposition channels in the upper position, further from the stream edge. Plant-feeders, on the other hand, were in greater numbers at the mid position on the floodplain bench, and were less abundant at the other two positions, possibly reflecting favorable moisture conditions and plant hosts in that location.

### 4.3. Conclusions

Our data support the following hypotheses: a) nematode diversity is greater in the ungrazed than in the grazed sites, b) bacterial-feeding nematodes predominate among detritivores in the wet soils at the stream edge, and c) nematode abundance is greater in the more mesic soils at the edge of the stream than in the drier soils at the top of the bank. Restoration of native vegetation has had little effect on nematode community composition as yet, possibly due to slow changes in soil properties, heterogeneity in plant species establishment, or lack of colonization of soil fauna from other riparian areas in this fragmented agricultural landscape.

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