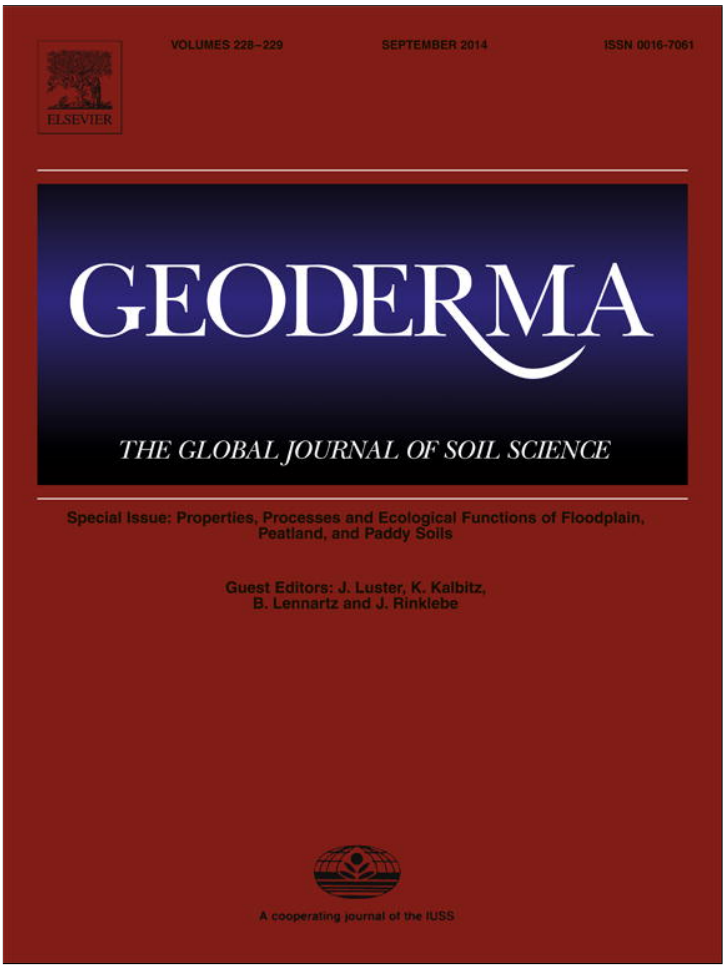

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Nematode food webs associated with native perennial plant species and soil nutrient pools in California riparian oak woodlands ☆

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ABSTRACT

The Coast Range mountains in California (CA), USA, may harbor remnant communities of soil biota that no longer occur in the intensively-managed agricultural valleys nearby. Relationships between nematode communities, riparian vegetation, soil carbon (C) and nitrogen (N) pools, and other soil properties were studied at a reserve managed for biodiversity conservation. Differences between riparian habitats were assessed using nematode community identification and metabolic footprint analysis (a method that evaluates ecosystem functioning based on nematode biomass). Nematode communities and metabolic footprints were compared across 12 riparian sites. Those from the sites with evergreen shrubs had high levels of predators but few prey while communities from under deciduous trees were more metabolically balanced, with high levels of both predators and prey. To examine how leaf functional traits affected nematode community structure, metabolic footprints, and soil C and N pools, a second study focused on two riparian woodland sites. Bacterivore and predator metabolic footprints increased with proximity to the creek-bank, where deciduous trees were prevalent. Leaf litter C:N ratio, soil C:N ratio, and the ratio of predators:prey also varied with plant functional traits. Both the complexity of the nematode communities and soil C storage were higher than in previous studies conducted along riparian corridors within intensive agriculture. In these relatively undisturbed areas, stream hydrology has created a patchy distribution of soil texture classes and woody plant species, which in turn, has resulted in diverse nematode assemblages and soil food webs associated with high levels of soil organic matter.

1. Introduction

Soil hydrologic processes in riparian corridors include water infiltration, as well as nutrient storage and redistribution and evapotranspiration by plants (Cooper et al., 1987; Gumiero et al., 2011; Hoffmann et al., 2012; Lowrance et al., 1983). Along the edges of waterways, soil physical and biological properties interact and influence biogeochemical processes such as nutrient cycling. For example, temperate riparian forests retain much more N than agricultural soils (Peterjohn and Correll, 1984) and restored wetlands effectively remove contaminants from agricultural runoff (O'Geen et al., 2010). Riparian corridors also harbor biodiversity and act as reservoirs from which organisms may disperse and colonize the managed ecosystems in the landscape, especially in seasonally dry climates (Bengtsson et al., 2003; Gonzalez et al., 2009).

Drought-adapted savanna and woodland occupy the upland Coast Range mountains above the intensively-managed and irrigated agricultural valleys of California (Barbour et al., 1993). Vegetation in these environments can be classified according to plant traits, reflecting adaptation to local environmental heterogeneity such as water availability (Cornwell and Ackerly, 2009). Remnant riparian ecosystems are more likely to occur in the upland areas since topography, soil quality, and lack of irrigation have constrained agricultural intensification. In the Central Valley of California, more than 95% of riparian, marsh, and river-delta wetlands have been converted to agricultural and urban use (Barbour et al., 1993). The remnant riparian ecosystems in the upland areas may provide useful conservation and restoration baselines for land management (Richardson et al., 2007). Of particular interest are creeks bordered by steep slopes, which discourage livestock access and human disturbance by roads and trails.

In a landscape study of riparian zones in intensively managed ecosystems in the California Sacramento Valley and Coast Range foothills, higher values of an agricultural intensification index were related to higher soil nitrate (NO_3^--N), less soil carbon (C) and nitrogen (N), and lower riparian health assessment scores (Culman et al., 2010; Young-Mathews et al., 2010). Across the landscape, soil microbial biomass, plant and nematode species diversity, and the number of PLFA biomarkers were negatively

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related to intensification. In contrast, higher riparian health scores were correlated with more ecologically complex nematode communities and higher woody C stocks (Young-Mathews et al., 2010).

Fluvial landforms influence riparian vegetation (Hupp and Bornette, 2003) and create localized microhabitats with different soil texture and other physical properties. Environmental heterogeneity is also affected by biotic processes, for example, nutrient uptake by riparian plants, their deposition of organic matter, and litter transformation by soil biota (Tabacchi et al., 2000). Past hydrology can indirectly affect tree species establishment, leading to legacy effects on soil properties. Meanwhile, the present soil conditions also affect litter accumulation, erosion, and organic matter movement into the current hydrological cycle. Studying hydrogeomorphic factors such as mineral particle size (Steiger et al., 2005) along with the distribution and litter quality of riparian woody plant species may help explain the heterogeneity of soil biota and nutrient pools in riparian corridors, and the implications for ecosystem functioning.

Since nematodes exploit many types of food sources and differ in their life history characteristics (Yeates et al., 1993), the metabolic activity of different functional groups provides an indication of the ecological structure and resource flow of the soil food web (Ferris, 2010; Sánchez-Moreno et al., 2009, 2011). For example, nematodes can be categorized from extreme *r* to extreme *K* strategists on a colonizer–persister (cp)[1] scale from 1 to 5 (Bongers and Ferris, 1999). Functional indices based on the relative abundance of nematodes can be calculated to describe the enrichment and structure characteristics of food webs, as well as the importance of fungal- and bacterial-mediated channels of decomposition (Ferris et al., 2001). The term, "enrichment", indicates the level of responsiveness of the food web to an increase in available resources, including the activity of primary detrital consumers. The term, "structure", indicates complex food webs with high connectance (Ferris et al., 2001). Ferris (2010) derived the nematode metabolic footprint as a metric of metabolic activity and ecosystem function based on estimated carbon utilization in nematode biomass production and respiration; this does not involve direct measurement of soil respiration (e.g., Ngao et al., 2012) or faunal biomass flux and distribution (e.g., Mulder et al., 2008). Nematode metabolic footprints use a taxon's cp group, body size as averaged from published morphometric parameters, and assumptions about C utilized in biomass production and respiration, to estimate the contribution of different groups of nematodes to various ecosystem functions (Ferris, 2010; Ferris et al., 2012).

In upland riparian corridors of the California Coast Range mountains, we hypothesized that nematode communities and their metabolic footprints would differ: 1) among sites with different plant community composition; and 2) according to leaf functional traits, soil C and N, and physical factors in the environment. The first study examined multiple sites across a landscape. Then, two riparian habitats with similar plant composition near separate creeks were studied in more detail to understand biotic relationships and their spatial distribution.

2. Materials and methods

2.1. Study region

The Audubon Bobcat Ranch Reserve (headquarters located at 38°31′57″N, 122 ° 02′18″W) is in western Yolo County, California, USA. It is a 2750 ha ranch within the Blue Ridge-Berryessa Natural Area, a 300,000 ha mix of private and public wildlands in the Coast Range mountains, which rise to the east of the irrigated croplands in the Sacramento Valley. The main vegetation types are oak savanna and oak woodland, with riparian woodland along the creeks. Several native deciduous and evergreen woody species occur close to these waterways, whereas the deciduous blue oak, *Quercus douglasii*, is the most important tree species above the waterway benches into the drier savanna and woodland ecosystems. Remnant native grasslands are dominated by a perennial bunchgrass, *Stipa pulchra* (purple needlegrass), and annual grasslands are mainly composed of non-native annual grasses and native forbs. The area has a Mediterranean climate with cool, wet winters and hot, dry summers; the mean annual rainfall is 57.9 cm, and maximum and minimum temperatures are 24.4 and 9.5 °C, respectively, in the nearest town (Winters, CA; Western Regional Climate Center, 2012). The ranch is grazed by cattle at low stocking rates and with careful attention to habitat protection and avoidance of overgrazing, and thus it provides a unique opportunity to test how soil food webs vary with soil properties under less disturbed conditions.

2.2. Comparison of nematode communities among riparian sites

To compare nematode communities and metabolic footprints between riparian habitats containing different plant communities, we sampled 12 sites at three locations within 25 m of the water's edge. The locations were chosen for their low disturbance and intact natural vegetation, based on the ranch managers' knowledge of the landscape (Table 1). Near the ranch headquarters (HQ location) at approximately 104 m elevation above sea level, remnant stands of bunchgrasses occur along Dry Creek, and three samples were taken in stands that differed in slope, and in the canopy cover of blue oak. A small spring higher in the hills (133 m elevation) was the second location (HILL location). Here, sampling occurred 2 m from the water's edge, in sites dominated by ferns and *Aesculus californica* (buckeye) or *Heteromeles arbutifolia* (toyon) in the canopy. The third location was in the canyon of Bray Creek (CYN location) along a 1 km-long reach of the riparian corridor at 106 to 143 m elevation. The seven sampling sites in Bray Creek differed in proximity to the water's edge, and in the occurrence of purple needlegrass, annual legumes, and deciduous and evergreen woody species. Two other samples are not presented here because they were highly affected by the creek-bank conditions; HQ4 was sedge-dominated in standing water, and CYN8 was very steep, eroded, and without herbaceous plants or litter.

One core was taken per sampling site (10 cm dia. × 10 cm deep) and slope and aspect were recorded for each sample. Global positioning system (GPS) point coordinates were entered into a geographic information system (GIS) so that soil type could be determined using the USDA-NRCS Soil Survey Geographic Database (SSURGO) (Soil Science Staff, 2006). Soils were classified as Haploxeralfs and Haploxererts (Soil Survey Staff, 2006). The dominant plant species in a 1 m^2 plot around the sample were noted. Air-dried soil samples were passed through a 2 mm sieve, then ground. particle size distribution was determined on a Beckman-Coulter LS-230 Particle Size Analyzer (Eshel et al., 2004). Total soil C was determined with an ECS 4010 CHNSO Analyzer. Nematodes were extracted from 350 g of field moist soil using a sieving and decanting Baermann funnel technique (modified from Barker, 1985). The total number of nematodes in each sample was counted and the first 200 encountered on a slide were identified. Most nematodes were identified to genus but some were identified to family (when identification was time consuming or taxonomically difficult, for example Tripylidae and Tylenchidae). Within such families, most genera have similar feeding groups/cp classifications and average biomass values can be used at the family level for metabolic footprint calculations. Nematode abundances were used to calculate enrichment and structure indices according to Ferris et al. (2001).

Metabolic footprints based on the size-dependent metabolic activity of different functional guilds of nematodes (Ferris, 2010) were calculated for each of the samples to provide an estimate of the contribution of the nematode assemblage to various functions related to C and nutrient

[1] Colonizer-persister (cp) scale: A 1–5 linear scale that assigns nematode taxa a value based on their *r* and *K* life history characteristics. For example, cp-1 nematodes have short generation times, small eggs, and high fecundity vs. cp-5 nematodes with the longest generation times, largest body sizes, lowest fecundity, and greatest sensitivity to disturbance. A letter may also be placed in front of the cp value to indicate the feeding group. See Appendix B for all feeding-cp group combinations.

Table 1
Characteristics of the sites sampled in the exploratory survey in three locations near creeks at the Bobcat Ranch in Yolo County, California, USA. For the vegetation, perennial bunchgrass refers to the occurrence of *Stipa pulchra* at the site. The soil sample from CYN2 was lost so no data (ND) is reported. Elev. = elevation above sea level. Fig. 1A or B indicates where the results of the nematode analyses are shown.

Location		Plants present at each site				Soil properties (0 to 10 cm depth)						Texture class	Fig.
ID	Distance to edge of water	Per. bunch grass	Annual legume	Deciduous trees/shrubs	Ever-green trees/shrubs	Total C (%)	Clay %	Silt %	Sand %	Elev. (m)	Soil type		
Headquarters (HQ)													
HQ1	≥5 m	X		X		3.7	6.0	32.4	61.6	104	PGL[a]	Silty Clay	1A
HQ2	≥5 m	X		X		4.7	4.2	34.5	61.3	101	PGL	Sandy loam	1A
HQ3	≥5 m	X		X		2.6	6.3	38.9	54.8	101	PGL	Sandy loam	1A
Hill slope spring (HILL)													
HILL1	2–5 m			X	X	2.7	13.5	58.4	28.1	133	PGL	Silt loam	1B
HILL2	2–5 m			X	X	2.5	5.6	40.9	53.5	133	PGL	Sandy loam	1B
Bray Canyon (CYN)													
CYN1	2–5 m				X	1.0	9.1	52.0	38.9	143	MR[b]	Silt loam	1B
CYN2	2–5 m				X	ND	ND	ND	ND	ND	ND	ND	1B
CYN3	2–5 m		X	X	X	0.8	8.1	56.7	35.2	125	MR	Silt loam	1A
CYN4	2–5 m		X	X	X	2.4	8.5	51.1	40.4	106	MR	Silt loam	1A
CYN5	≥5 m	X	X	X		3.2	9.7	43.6	46.7	122	MR	Loam	1A
CYN6	≥5 m	X		X	X	2.7	12.0	49.6	38.4	148	MR	Loam	1A
CYN7	≥5 m			X	X	2.5	7.6	50.9	41.5	153	MR	Silt loam	1B

[a] Positas gravelly loam.
[b] Millsholm rocky loam.

cycling. Using the nematode groups listed in Appendix A, different nematode metabolic footprints were calculated according to the following equation (Ferris, 2010):

$$F = \sum\left(N_t\left(0.1(W_t/M_t) + 0.273\left(W_t^{0.75}\right)\right)\right)$$

where N_t is the measured number of nematodes in each taxonomic group of interest (e.g., predators), and W_t is the estimated weight (in μg per individual). M_t is the (cp) classification of taxon t. For example, nematodes with low cp values indicate conditions where rapidly reproducing, small nematodes flourish, such as recently after resource addition or following a soil disturbance such as tillage (Bongers and Bongers, 1998). In contrast, high cp values indicate communities of less disturbance and greater resource conservation, where large bodied, slow reproducing nematodes such as predators are more common. In the second part of the equation, the weight of life-time C mineralized by each taxon is derived from the molecular weights of C and CO_2, as 12/44 or 0.273 of the mass of CO_2 evolved (Ferris, 2010).

The footprints of different nematode groups are summed to provide different metrics of ecosystem function. For example, the bacterial and fungal metabolic footprints are calculated from the bacterivore and fungivore nematode groups, and indicate the C entering the soil food webs through those respective channels. The enrichment footprint is calculated by summing those nematode groups that respond rapidly to enrichment (bacterivores with cp-1 and fungivores cp-2). A high enrichment metabolic footprint indicates greater C utilization at lower trophic levels, often as a response to nutrient addition. The structure metabolic footprint is calculated by summing those groups with higher cp values (cp-3, cp-4 and cp-5). A higher structure metabolic footprint indicates activity at higher trophic levels and the potential for suppression of opportunistic organisms and regulation of nutrient cycling.

The enrichment metabolic footprint and structure metabolic footprints can be visualized together graphically as the total area of the functional metabolic footprint (Fig. 1A and B), allowing for qualitative comparisons of nematode communities. In these graphs, the center of the rhomboid is the intersection of the structure and enrichment indices (Ferris et al., 2001). The width variables (x axis) are calculated as the structure index $-0.5F_s/k$ and the structure index $+0.5F_s/k$, where F_s is the sum of standardized C utilization by the taxa used in the structure metabolic footprint and k is a scalar term (constant across all samples) which can be adjusted to enable better visualization (Ferris, 2010). The height (y axis) coordinates are similarly plotted using the enrichment index and standardized C utilization for enrichment indicator taxa (F_e) and the same value for k. Thus, nematode communities can be compared in terms of their balance between resource enrichment and ecological structure.

2.3. Nematode communities and leaf functional traits

In order to examine how leaf functional traits affected nematode community structure, metabolic footprints, and soil C and N pools, the second experiment focused on two riparian woodland sites along seasonally dry creeks, each containing several shrub and tree species. The sites were chosen based on their close similarity in slope, aspect, plant species composition, and location in the same hydrological drainage system. The sites, separated by 460 m, both had southeast facing steep slopes (30 to 45°) and were located on Positas gravelly loam soil type (Soil Science Staff, 2006). The study area at each site was located 100 m along the waterway within 25 m of the creek edge. Plant communities were dominated by manzanita (*Arctostaphylos glandulosa*), toyon, and blue oak but also included some redbud (*Cercis occidentalis*). The cover of grasses and herbaceous plants was <20% at both sites.

Differences were observed between the two sites at the time of sampling. Site 1 had a slope of ~40°, terminating in a steep ravine, with no flowing water at the bottom. Some signs of animal disturbance, such as trails and footprints, were observed. Site 2 was more variable in slope, ranging from 30 to 45° and was heavily eroded in patches. The creek had flowing water and very little animal disturbance was observed.

Soil under the canopy of all individual woody shrubs and trees was sampled and locations were recorded as a GPS point. Woody plants were not sampled if trunks were adjacent to or intertwined with another species. If more than three individuals of the same species were growing together then two were randomly selected for sampling. The coordinates of each sample were mapped using a detailed digital elevation map (DEM) of each site, and a GIS was created. Samples were taken from 22 and 28 trees at site 1 and site 2, respectively. The distance of each sample from the creek edge was measured. Sampling areas (14 cm dia. × 7.5 cm deep) were designated on the downslope side of each shrub, half way between the edge of the canopy and the trunk. Litter was collected from the soil surface within this area and an intact soil core was taken in the center (7.5 cm dia. × 7.5 cm deep) after litter was removed. Then the remaining soil in the sampling area was also collected to 7.5 cm depth.

Soil microbial biomass C (MBC) was measured by fumigation extraction (Vance et al., 1987); field-moist soil was split into two portions (25 g for the fumigated and 25 g for the nonfumigated treatment), extracted with 60 mL of 0.5 M K_2SO_4, filtered, and analyzed on a Dohrmann Phoenix 8000 UV-Persulfate Oxidation Analyzer. Total MBC was measured by multiplying the flush of C by 2.64 (Vance et al., 1987). Nematodes were extracted and analyzed as described above from 350 g of soil taken from the larger PVC ring.

From the intact soil core, inorganic N was extracted from moist soil with 2 M KCl and analyzed colorimetrically for ammonium (NH_4^+-N) and nitrate (NO_3^--N) (Miranda et al., 2001). For pH and EC, soil was diluted at a 1:2 ratio with deionized water and measured with a pH/EC meter. Total soil C and N were measured as described above, as was litter C and N after drying samples at 60 °C and grinding. Particle size distribution analysis was performed as described above.

2.4. Data analysis

Non-metric multidimensional scaling (NMDS) was conducted to determine factors most highly associated with the nematode community composition in each soil sample. We used a Bray–Curtis distance measure for nematode relative abundance and metabolic footprint contribution for 13 cp/feeding group categories in R statistical software via the *meta*MDS function in the Vegan package (Oksanen et al., 2012). Correlations between the NMDS ordinations of nematode communities and soil variables were tested with loop permutations (999) in the *envfit* function in the Vegan package in R. The final stress value of the reported analysis was 0.24, suggesting some caution in interpretation of the results especially given the large sample size (Clarke, 1993).

Woody shrubs and trees were divided into three categories based on litter functional traits: evergreen leathery leaves (toyon), deciduous leaves (blue oak and redbud), and evergreen sclerophyllous leaves (manzanita and live oak, *Quercus wislizeni*). Sclerophyllous refers to small, hard leaves with a waxy cuticle, while leathery refers to slightly softer evergreen leaves. Relationships between soil biota and soil properties were examined by nonparametric Spearman's Rank Correlations (denoted by correlation coefficient Rho) and compared between plant categories by Kruskal–Wallis tests in SAS 9.1 software. In some cases, the natural log of nematode data was taken to obtain a normal distribution. To examine how soil biological data varied with soil texture, a Pearson's correlation coefficient (R) between each variable and particle size distribution from 0.04 to 2000 μm was plotted.

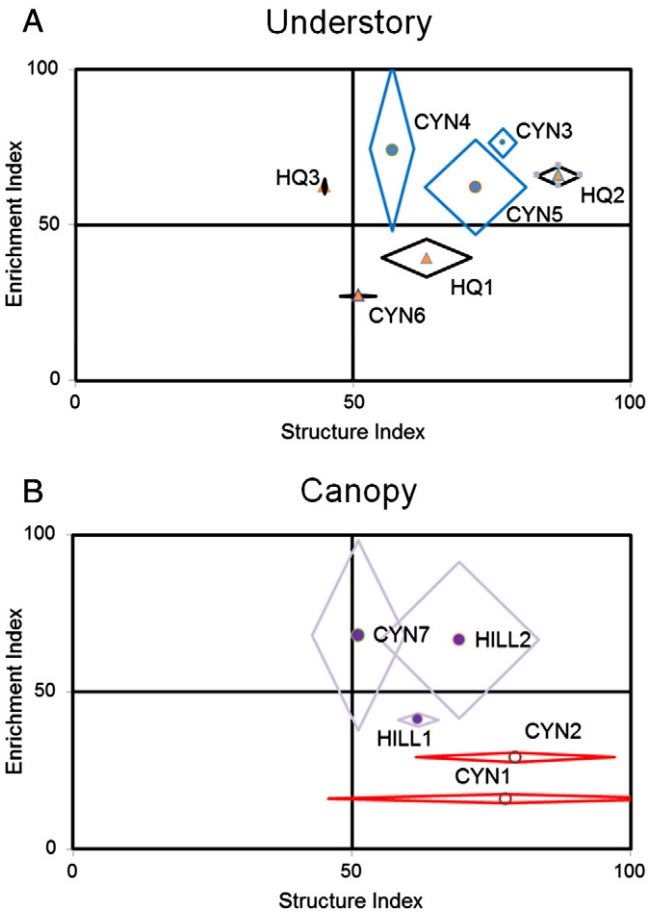

Fig. 1. Initial study of soil food web complexity. Total metabolic footprints for nematode assemblages from riparian woodlands of the Audubon Bobcat Ranch Reserve in Yolo County, California (USA) that were either dominated by A) understories according to the presence of the perennial bunchgrass, *Stipa pulchra* (triangles, black rhomboid) and annual legumes (circles, blue rhomboid); and B) canopies with evergreen (open circles, red rhomboid) vs. deciduous and evergreen trees and shrubs (closed circles, purple rhomboid). The area of the rhomboid represents the standardized units of C calculated to be utilized by the nematode community in biomass production and respiration; the vertical axis of each footprint rhomboid represents the enrichment footprint (indicating ecosystem processing of labile resources) and the horizontal axis the structure footprint (an indicator of food web complexity).

3. Results

3.1. Comparison of nematode communities among riparian sites

Two soil types and a range of soil textures were sampled, from sandy loam to silty clay, across the three exploratory locations along riparian corridors (Table 1). Woody trees and shrubs were present at all locations, but 8 locations had evergreen-leaved species, while deciduous species were present at 10 locations. The understory communities consisted of three general types: 1) grassland with the perennial, purple needlegrass, present (5 locations); 2) grassland with annual legumes present (three locations); and 3) grassland with annuals only, but no legumes (5 locations).

In the 12 samples, 26 nematode groups were found, spanning a range of feeding groups and cp life history categories (Appendices A and B). For exploring the general patterns of nematode diversity, we split the samples into groupings based on the presence of different types of plants: 1) sites where understories contained purple needlegrass and/or annual legumes (Fig. 1A; Table 1); and 2) sites where canopies contained either evergreen only vs. deciduous and evergreen trees and shrubs (Fig. 1B; Table 1).

In the comparison of understory effects on nematode communities, sites with the perennial purple needlegrass (HQ1, HQ2, HQ3, CYN5 and CYN6) were found in the middle right to upper right section of the biplot, indicating mid- to high enrichment and structure (Fig. 1A). The presence of annual legumes (CYN3, CYN4 and CYN5), however, was associated with higher enrichment despite the fact that the three sites were dissimilar in other ways. Their locations were either close (<5 m; CYN3 and CYN4) or far (≥5 m; CYN5) from the water's edge, and with either only deciduous (CYN5) or deciduous and evergreen canopies. The rhomboids showing total functional metabolic footprints were more balanced when legumes were present, while the perennial bunchgrass resulted in stronger effects of structure than enrichment, as shown by the more skewed shape along the x axis.

When considering the effect of different canopy types, nematode communities tended to differentiate according to the presence of evergreen only vs. deciduous and evergreen woody plants, and distance from the water's edge (Fig. 1B; Table 1). The sites with the highest structure and lowest enrichment indices (CYN1 and CYN2) were associated with evergreen shrubs, such as manzanita and toyon, and absence of deciduous trees and shrubs. Both of these sites were ≤5 m from the water's edge. A higher enrichment index was associated with presence of both deciduous and evergreen woody species (HILL1, HILL2 and CYN7). Note that we chose not to plot CYN3, CYN4 and CYN5 again in

Fig. 1B. These three sites all contained deciduous woody species, and Fig. 1A shows that they have higher enrichment and generally lower structure than the evergreen-dominated sites, CYN1 and CYN2, that are shown in Fig. 1B. When deciduous trees were present, the rhomboids of the metabolic footprints were more balanced in terms of both structure and enrichment, compared to the rhomboids under evergreen trees that were characterized more by structure than enrichment.

3.2. Two seasonally dry creeks: soil, nematode communities and shrub diversity

Given that the first study suggested strong effects of plant taxa on nematode metabolic footprints, the more detailed analysis of two creek sites focused on the relationship between leaf functional traits, nematode communities, and soil C and N pools. Soil properties were generally similar between sites, i.e., similar means for soil C in the top 7.5 cm depth (~3.5 mg C g^{-1} soil at both sites), C:N (20.5 and 18.6, respectively, for sites 1 and 2), and texture (51 and 50% sand, 42 and 43% silt, and 7 and 7% clay, respectively, for sites 1 and 2) (Table 2). Site 1, however, showed more variance in soil properties. At both sites, NH_4^+-N was low (≤3 μg g^{-1} soil) and NO_3^--N was often below the detection limit. For MBC, samples ranged from 376 to 2234 μg C g^{-1}, and was highly correlated with soil NH_4^+-N ($P < 0.01$, Rho = 0.669, df = 44), soil C ($P < 0.01$, Rho = 0.637, df = 44), and moisture ($P < 0.01$, Rho = 0.724, df = 44). MBC increased with sand content ($P = 0.044$, Rho = 0.302, df = 44) and decreased with pH ($P = 0.013$, Rho = −0.370, df = 44). The enrichment and structure indices were highly variable within both sites, reflecting high spatial heterogeneity in nematode groups (Table 2). The nematode structure index ranged from 9.6 to 85.7 at site 1 and 6.6 to 95.5 at site 2, and there were many high cp value predators such as *Aporcelaimus* and *Prionchulus* present.

Of the metabolic footprints calculated for different nematode groups, the bacterivore footprint was largest at both sites, followed by the predator footprint (Table 2). The fungivore metabolic footprint was less than 1/10 the bacterial footprint at both sites due to the lower abundance and lower biomass of fungal feeding nematodes. At site 1, closer proximity to the creek was associated with higher nematode structure footprint ($P < 0.01$, Rho = 0.620, df = 19), predator footprint ($P < 0.01$, Rho = 0.620, df = 19), bacterivore footprint ($P = 0.04$, Rho = 0.458, df = 19), and higher total metabolic footprint, which is the footprint of the complete nematode community regardless of trophic role ($P = 0.04$, Rho = 0.0521, df = 19). At site 2, the total abundance of omnivores increased with distance from creek ($P = 0.02$, Rho = 0.442, df = 26).

Nematode community composition was influenced by the leaf functional traits of the shrub canopy. For example, higher nematode predator:prey ratios were observed under shrubs with evergreen leathery leaves (toyon), compared to those with deciduous leaves (blue oak and redbud), or evergreen sclerophyllous leaves (manzanita and live oak) ($P = 0.02$, H = 8.3, df = 2). The structure index was higher under evergreen than deciduous trees at site 2 ($P = 0.01$, H = 2.35, df = 2).

Leaf litter and soil from under deciduous trees/shrubs had lower C:N ratios than under shrubs with either type of evergreen leaves (Fig. 2) while C:N ratios of soil and litter from evergreen leathery shrubs tended to be intermediate. Leaf C:N ratio was strongly correlated with soil C:N ratio ($P < 0.01$, Rho = 0.360, df = 45). Deciduous trees were more likely to grow along the creek-bank than other trees (Fig. 3) and overall, distance from the creek-bank was positively correlated with litter C:N ratio ($P = 0.014$, Rho = 0.360, df = 45).

Of the 27 taxa isolated (Table 3), the relative abundances of some individual nematode groups showed non-random distributions (Fig. 3a–c; for distribution maps of all groups see online appendix). For example, *Acrobeloides* and *Aphelenchoides* were common in almost all samples, while others, like *Prionchulus*, were typically only found under manzanita. Predators in the Tripylidae family were found closer to the creek-bank (predominantly under oaks) while omnivores in the Qudsianematidae tended to occur farther away from the creek-bank.

Functional groups of nematodes varied with soil properties. For example, the metabolic footprint of fungal-feeding nematodes (cp-2) was

Table 2
Soil properties and nematode community indices in the 0 to 7.5 cm depth of the soil profile at two riparian woodland sites at Audubon Bobcat Ranch Reserve in Yolo County, California (USA). Mean and standard deviation (SD).

Soil or nematode variable	Riparian Site 1	Riparian Site 2	Riparian Site 1		Riparian Site 2	
	Range	Range	Mean	SD	Mean	SD
pH	7.19–8.32	6.25–8.42	7.7	0.3	7.6	0.5
EC (uS cm^{-2})	42.2–253.0	47.9–268	100.1	52.8	113	49.4
MBC (μg C g^{-1})	385.4–2233.9	375.9–1944.1	865.1	431.6	945.1	430.6
Nitrogen (mg g^{-1})	0.08–0.41	0.06–0.44	0.2	0.1	0.2	0.1
Carbon (mg g^{-1})	1.1–11.4	0.8–8.5	3.8	2.5	3.2	1.8
C:N	12.8–35.9	12.6–29.9	20.5	6.8	18.6	4.5
NH_4^+-N (μg g^{-1})	1.6–5.4	1.2–6.3	3.0	0.9	3.4	1.3
NO_3^--N (μg g^{-1})	0–0.52	0–0.49	0.1	0.1	0.0	0.1
Moisture (%)	0.17–0.89	0.25–0.64	0.4	0.1	0.4	0.1
Clay (%)	2.9–17.1	4.2–9.1	7.2	3.6	6.8	1.3
Silt (%)	22.1–62.2	30.2–54.7	41.6	9.8	43.2	5.7
Sand (%)	20.7–74.9	38.4–65.4	51.2	13.2	50	6.5
Nematode indices						
Enrichment	14.6–88.2	30.9–87.9	51.9	20.3	50.5	13.2
Structure	9.6–85.7	6.6–95.5	43.6	17.9	47.0	18.8
Nematode metabolic footprints (μg C g^{-1})						
Bacterivore	0.1–9.3	0.0–3.7	1.1	2.0	0.7	0.9
Fungivore	0.0–0.1	0.0–2.2	0.0	0.0	0.1	0.1
Herbivore	0.0–0.3	0.0–2.7	0.1	0.1	0.2	0.5
Predator	0.0–1.8	0.0–2.1	0.3	0.4	0.5	0.6
Enrichment	0.1–9.4	0.0–3.6	1.0	2.0	0.7	0.8
Structure	0.0–1.8	0.0–2.1	0.3	0.4	0.5	0.6
Total	0.2–9.9	0.1–4.2	1.5	2.1	1.5	1.1

Table 3
Nematode taxa isolated from two riparian woodland sites at the Audubon Bobcat Ranch Reserve in Yolo County, California (USA) and their associated feeding groups, life history colonizer persister (cp) values, and average metabolic footprint (the standardized units of C calculated to be utilized in biomass production and respiration) for the two riparian sites surveyed. b = bacterivore, f = fungivore, h = herbivore, o = omnivore, p = predator.

Taxa	Feeding group	Cp value	Site 1 Metabolic footprint (μg C/100 g soil)	Site 2 Metabolic footprint (μg C/100 g soil)
Panagrolaimus	b	1	2.36	1.42
Rhabditidae	b	1	94.25	53.04
Acrobeles	b	2	0.00	0.15
Acrobeloides	b	2	8.53	6.32
Cephalobidae	b	2	1.03	6.05
Monhysteridae	b	2	0.86	0.35
Plectidae	b	2	2.90	1.23
Wilsonema	b	2	0.04	0.07
Prismatolaimus	b	3	0.63	1.84
Aphelenchoides	f	2	3.82	4.76
Aphelenchus	f	2	0.20	0.44
Aprutides	f	2	0.13	0.74
Tylencholaimus	f	4	0.02	0.85
Paratylenchus	h	2	0.00	9.29
Tylenchidae	h	2	6.46	11.51
Pratylenchus	h	3	0.02	0.02
Tylenchorhynchus	h	3	0.43	0.90
Dorylaimidae	o	4	0.59	0.39
Qudsianemtaidae	o	4	1.77	6.59
Thonus	o	4	3.16	2.79
Mircodorylaimus	o	4	1.35	1.89
Mesodorylaimus	o	5	0.53	0.00
Prodorylaimus	o	5	0.00	1.35
Tripylidae	p	3	2.85	1.56
Eudorylaimus	p	4	2.88	1.88
Prionchulus	p	4	16.86	16.25
Aporcelaimus	p	5	10.25	21.17

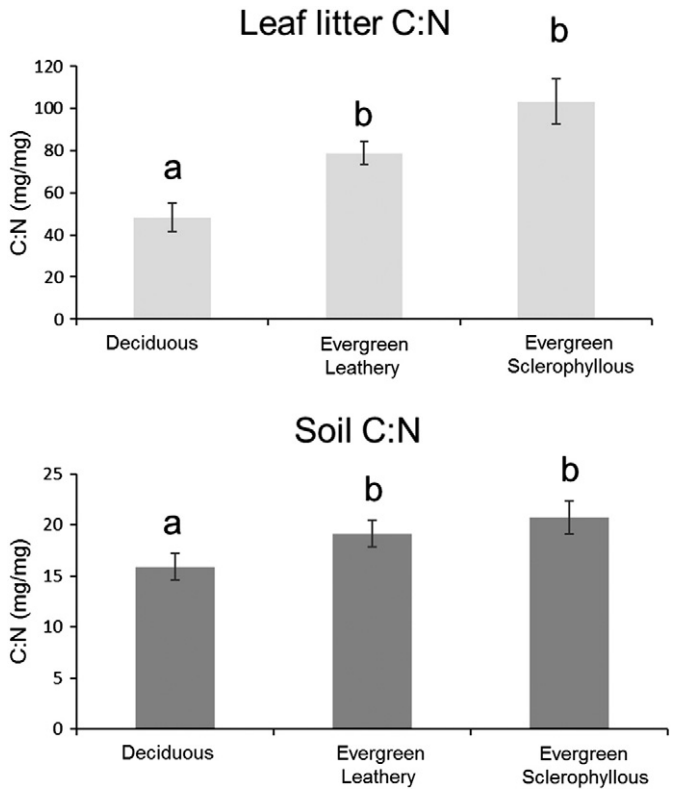

Fig. 2. C:N ratios of leaf litter and soil sampled (0 to 7.5 cm depth) under woody shrubs of different functional leaf traits at two seasonally dry creek sites at the Audubon Bobcat Ranch Reserve in Yolo County, California (USA). Bars are standard errors of the mean. Columns with different letters are significantly different ($P < 0.05$). Plants in the deciduous category included *Quercus douglasii* (blue oak) and *Cercis occidentalis* (redbud); evergreen leathery category, *Heteromeles arbutifolia* (toyon); and evergreen sclerophyllous category, *Arctostaphylos glandulosa* (manzanita) and *Quercus wizlizenii* (live oak).

negatively correlated with pH ($P = 0.034$, Rho $= -0.313$, df $= 45$). The root feeding genus, *Tylenchorhynchus* (cp-3), was negatively correlated with MBC ($P < 0.01$, Rho $= -0.413$, df $= 44$). Many groups including bacterivores, fungivores, herbivores and omnivores also showed a positive relationship with the percentage of very fine sand (fungivores (cp-2): $P < 0.01$, Rho $= 0.442$; bacterivores (cp-2): $P = 0.092$, Rho $= 0.251$; herbivores (cp-3): $P = 0.031$, Rho $= 0.317$; omnivores (cp-4): $P = 0.07$, Rho $= 0.270$, df $= 45$). Metabolic footprints based on each nematode functional group also varied substantially with particle size (Fig. 4). For example, the bacterivore and fungivore metabolic footprints increased with the content of fine and very fine sand, and this pattern was shared by omnivores (cp-4). Some predators (cp-4, mostly *Prionchulus*) were associated with very coarse sand, while others (cp-5, *Aporcelaimus*) were more associated with silt. These relationships may be partially influenced by plant species' preferences for soil texture. Manzanita, a sclerophyllous species, was growing in soil that was higher in sand ($P = 0.03$, $H = 3.71$, df $= 2$) and lower in silt ($P = 0.02$) than toyon and was also the preferred habitat of *Prionchulus*. Blue oak tended to grow in soils with a higher percentage of very fine clay (<1 μm), compared to toyon and manzanita ($P = 0.09$, $H = 2.53$, df $= 2$).

Nonmetric multidimensional scaling analyses revealed complex relationships between nematode and plant functional groups and soil properties (Fig. 5). When samples from both sites were analyzed together, the five environmental factors that best explained variation in the nematode functional groups were moisture NH_4^+-N ($P = 0.06$), ($P = 0.09$), MBC ($P = 0.09$), soil C ($P = 0.10$) and soil N ($P = 0.13$). These factors covaried and together related inversely to silt and clay content. At site 1, higher soil C and N was associated with bacterivores (cp-1) and plant taxa with evergreen leathery leaves. Based on ordination scores, total soil N at site 1 influenced the nematode community ($P = 0.043$), especially bacterivores. At site 2, high litter C:N was associated with fungivores (cp-2). Deciduous woody plants showed a preference for higher clay content while evergreen sclerophyllous plants were on soils with higher C:N. Based on ordination scores, both soil moisture ($P = 0.034$) and litter C:N ($P = 0.054$) affected

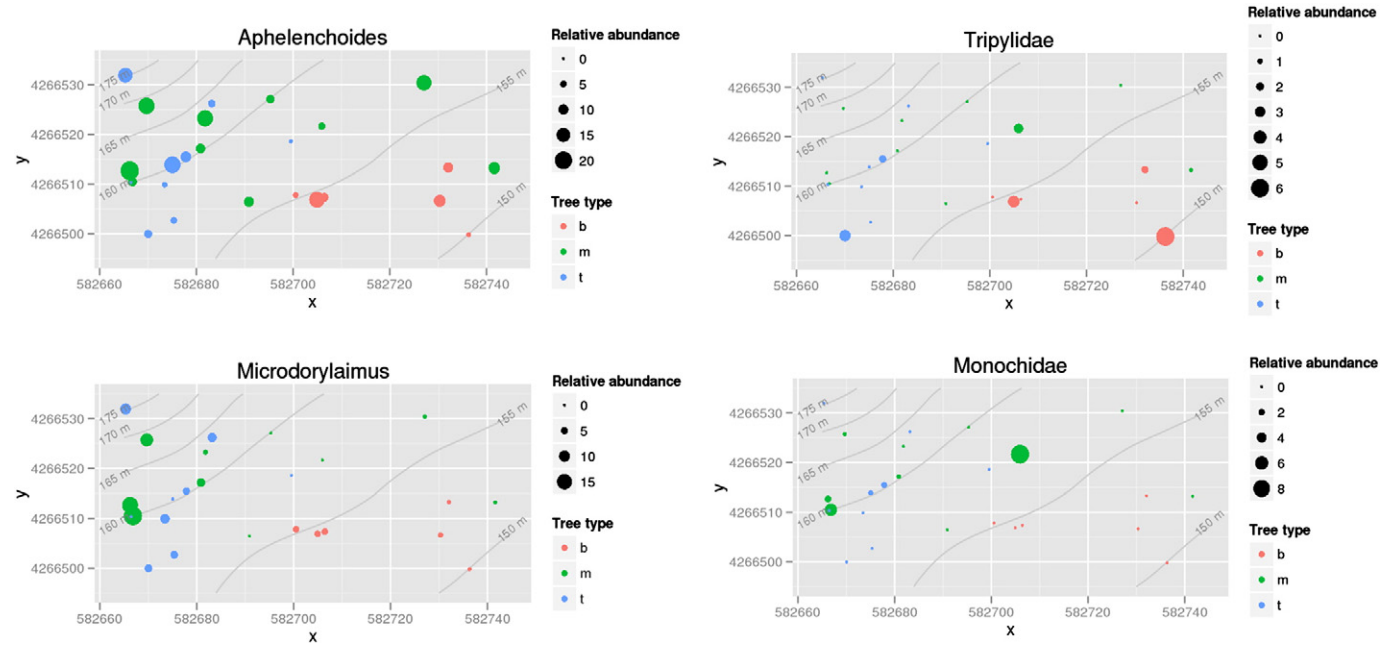

Fig. 3. Relative abundances of selected nematode groups from the 27 taxa monitored at riparian site two at the Audubon Bobcat Ranch Reserve in California (USA). The size of the circle increases with the relative abundance (the percentage each group contributes to the total nematode community). The x and y axes are Universal Transversal Mercator (UTM) coordinates and contour lines created using a digital elevation map. The creek-bank is situated along the lowest of the contour lines (at approximately 150 m elevation) at the bottom of the hill in the lower right corner of each graph. Tree type b = blue oak, m = manzanita, t = toyon. *Apelenchoides* genus = fungal feeder (cp-2), Tripylidae = predator (cp-3), *Mircodorylaimus* genus = omnivore (cp-4) and Mononchidae (*Prionchulus*) = predators (cp-4).

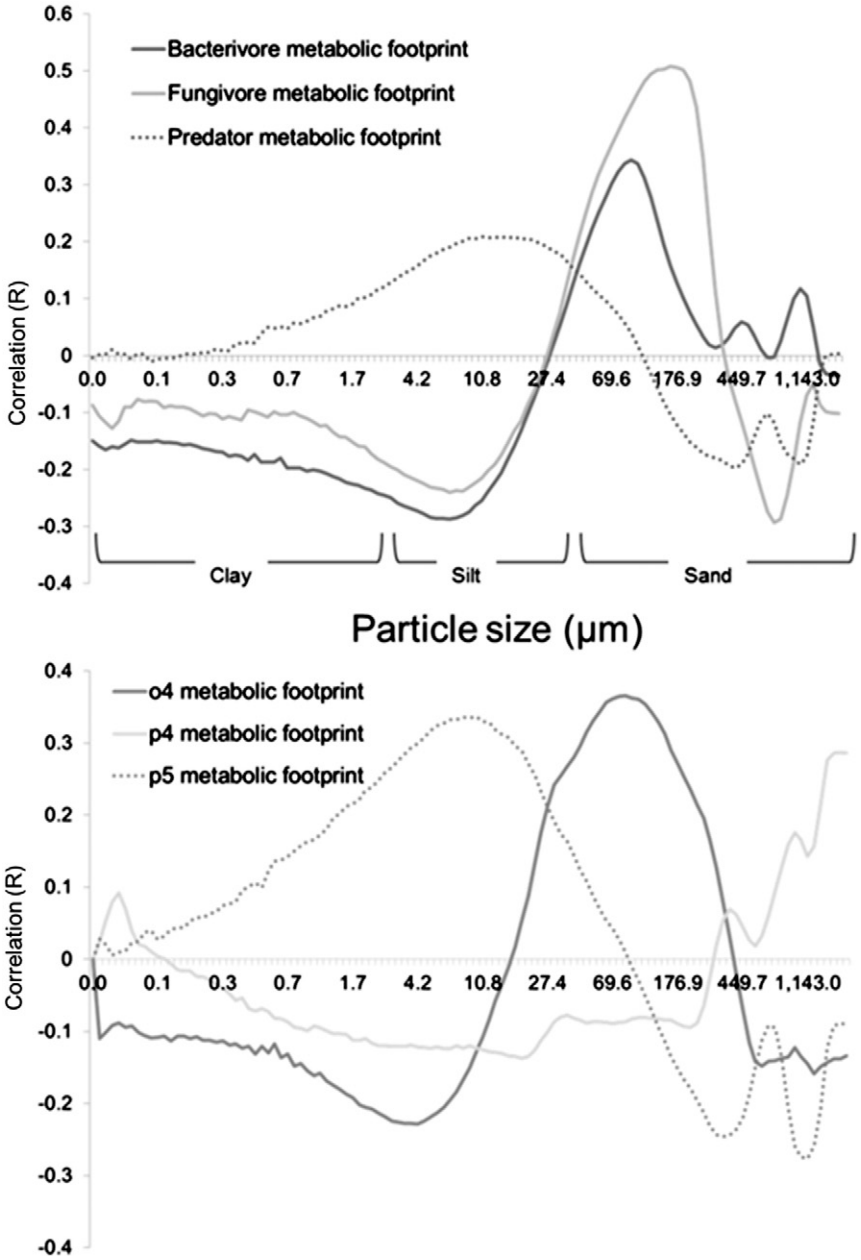

Fig. 4. Pearson's R correlation of particle size spectra against nematode metabolic footprints and functional groups of nematode predators and omnivores, with data combined for the two riparian sites at the Audubon Bobcat Ranch Reserve in California (USA), where the x axis is particle size and y axis is the strength of the correlation coefficient. Clay = 0.04 to 2.0 μm; Silt = 2.2 to 47.9 μm; Sand = 52.6 to 2000 μm.

nematode functional group composition at site 2, with high litter C:N associated with fungivores (cp-2), bacterivores (cp-2), and omnivores (cp-4).

4. Discussion

In a previous study in a nearby agricultural landscape at lower elevations, Culman et al. (2010) found that the structure and complexity of nematode food webs was weak and declined with increasing agricultural intensification. This led us to wonder if soil food web diversity was inherently low, even in remnant natural ecosystems, possibly due to stress from the long summer drought in California's Mediterranean climate. Or alternatively, decades of soil disturbance by cultivation and grazing may have greatly reduced higher trophic level nematodes, and thereby their functional significance in retaining nutrients, sequestering C, and increasing the benefits from soil organic matter (Brussaard, 2012; Mulder et al., 2011; Schmidt et al., 2011). The results of the current study suggest that the latter explanation is likely, since the relatively undisturbed ecosystems of Bobcat Ranch support complex communities of nematodes and higher C pools than are found in the nearby soils under intensive agriculture (Culman et al., 2010; Minoshima et al., 2007; Sánchez-Moreno et al., 2006, 2008; Smukler et al., 2010).

The first study on different types of riparian habitats showed high nematode structure metabolic footprints at many sites, indicating complex ecological communities with many trophic connections. Our functional footprint values were also much higher than levels measured in intensively grazed and crop ecosystems in the lowlands a few kilometers away (Ferris, 2010). In the two riparian woodland sites at Bobcat Ranch, the bacterial metabolic footprint increased with proximity to the creek, in line with the findings of Briar et al. (2012), who found that bacterial feeding nematodes predominated near the bank of restored creek channels. The higher structure metabolic footprints found near the creek are also in agreement with data from Ferris (2010), who

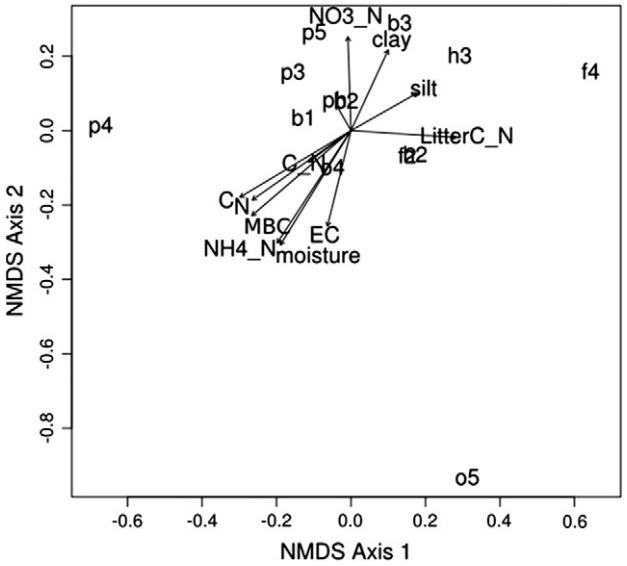

Fig. 5. Nonmetric multidimensional scaling analyses of soil nematode communities from two riparian woodland sites at the Audubon Bobcat Ranch Research Reserve in California (USA) and their relationship to properties of soil and leaf litter. Refer to text and Table 3 for descriptions of the nematode colonizer persister (cp) groups.

using the data from Culman et al. (2010), found greater nematode structure indices closer to the creek in less disturbed rangeland sites, but no difference in more disturbed riparian sites in row-crop agriculture. Omnivores and predators were rare in riparian corridors of row-crop agriculture, and increased to a small extent in the less disturbed grazed uplands (Young-Matthews et al., 2010), but such nematodes were present in all but one of the Bobcat Ranch samples. These included generalist predators such as *Prionchulus*, as well as specialists such as *Aporcelaimus*, a predator of oligochaetes.

The survey of plant community types in the first study provided a basis for hypothesizing that leaf functional traits of woody plants affect the structure of nematode communities. Graphing the functional metabolic footprint as a rhomboid allowed a qualitative comparison of nematode communities in terms of their balance between the enrichment metabolic footprint (y axis) and structure metabolic footprint (x axis) (Ferris, 2010). As the rhomboid figures became more square-like, the area of the functional metabolic footprint increased, suggesting that the available resources (such as nutrients and C) in the ecosystem (enrichment) were sufficient to support higher trophic level predators (structure). The rhomboids under evergreen shrubs, such as manzanita and toyon, were particularly skewed in their y axis coordinates, indicating high levels of predatory nematodes compared to bacterial and fungal feeders. Those from the sites with deciduous trees were more metabolically balanced, with high levels of both predators and prey, while those with legumes were more skewed towards resource enrichment. Thus, the different types and combinations of detrital resources provided by the plant community may not only increase the complexity of the nematode community (Wardle et al., 2006), but its ecological functions as well.

Nematode communities and metabolic footprints varied with leaf functional traits perhaps because hydrology in these riparian ecosystems directly or indirectly affected tree establishment (Harris, 1999; Zentner, 1997), which, in turn, affected litter and soil C:N ratios. Plant traits such as C:N ratio can affect decomposition rates and carbon cycling (Cornwell et al., 2008). Nematode communities and their associated ecosystem functions may, therefore, be a product of interactions of physical soil characteristics such as particle size (affecting soil moisture and water infiltration), and chemical factors such as leaf litter C:N ratio and soil N content that are mediated by biota (Mulder et al., 2012). For example, bacterivore nematode activity increased with proximity to the creek-bank, perhaps due to increased seasonal water availability (Sohlenius, 1985) or the prevalence of deciduous trees with more degradable leaf litter that provides more nutrients. The predator metabolic footprint showed a similar trend, perhaps responding to the distribution of bacterial feeders, the most abundant prey nematodes in these soils.

Nematode communities and metabolic footprints varied with soil physical properties such as particle size, perhaps because nematodes do not move very well in pores with diameters much larger than their body width (Jones et al., 1969). Across both riparian woodland sites, the metabolic footprints of several functional groups of nematodes (bacterivores cp-2, fungivores cp-2, herbivores cp-3, omnivores cp-4) showed a positive Spearman's Rank Correlation relationship with fine sand content. This was confirmed when particle size was viewed as a continuum (Fig. 4), and the bacterivore and fungivore metabolic footprints increased with the content of fine and very fine sand; this pattern was also mirrored by omnivores (cp-4). We found that across the larger landscape of the first study, omnivores in the Qudsianematidae (cp-4, most commonly the very small *Microdorylaimus*, 0.3–0.8 mm) were strongly associated with very fine sand. In contrast, at the two creek sites, larger bodied predatory nematodes (cp-4, mainly *Eudorylaimus* and *Prionchulus*, ~2 mm) were more common in soils with very coarse sand, perhaps because the larger pore size facilitated their movement (Fujimoto et al., 2010). In a nearby agricultural soil, larger aggregates (>1000 μm) contained larger pore sizes and more nematodes per g^{-1} soil than small aggregates (250–1000 μm) (Briar et al., 2011). In other grassland soils, nematode biomass also closely correlated with the volume of pores typical of sandy soils (Hassink et al., 1993).

Mineral particle sizes (and their interaction with soil water) can provide different habitat opportunities for soil organisms, affecting the rates of organic matter decomposition (Strong et al., 2004) as well as N and C mineralization (Hassink et al., 1993). Soil organic matter also mineralizes more rapidly in sandy soils than in clay soils (Verberne et al., 1990), possibly due to greater activity of soil biota. Such food web interactions by microbiota can increase C and N mineralization rates (Ingham et al., 1985; Savin et al., 2001) with increases in N mineralization reported to be up to 30% (Verhoef and Brussaard, 1990). Increased C and N availability due to nematodes grazing on microbes may also explain why, in our study, MBC was positively related to total sand content.

4.1. Conclusions

The results of this study provide encouraging evidence that reservoirs of soil biodiversity exist in remnant undisturbed ecosystems, and are indeed associated with ecological functions related to soil C and N cycling and retention. The success of reinstating such populations in disturbed ecosystems may be unlikely due to relationships between litter C:N and soil C that have created microenvironments for biota over long periods of time. Even after 7 years, restoration seemed to hardly affect nematode communities, possibly due to plant and litter effects or the slow rate of nematode recolonization (Briar et al., 2012). This study does illustrate the value of mature vegetation, however. Since native woody plants such as manzanita and toyon support high soil C pools and complex soil communities, plantings of these species could promote nutrient retention, an important goal in working landscapes (Gumiero et al., 2011). Further exploring how soil communities interact with organo-mineral complexes may also increase our ability to predict, and enhance ecosystem functioning in both managed and unmanaged ecosystems.

Acknowledgments

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Appendix A. Nematode feeding groups, life history colonizer persister (cp) values, individual biomass from published literature and calculated metabolic footprint (in μg C) per individual based on equations in Ferris (2010), from a survey of 12 riparian habitats at Audubon Bobcat Ranch Reserve in Yolo County, California (USA). b = bacterivore, f = fungivore, h = herbivore, o = omnivore, p = predator

Nematode taxa	Feeding group	cp value	Individual nematode biomass (μg)	Metabolic footprint (μg C per individual)
Panagrolaimus	b	1	0.68	0.27
Rhabditidae	b	1	6.80	1.83
Acrobeles	b	2	0.63	0.23
Acrobeloides	b	2	0.15	0.07
Cephalobidae	b	2	0.37	0.15
Monhysteridae	b	2	0.43	0.17
Plectidae	b	2	0.89	0.29
Wilsonema	b	2	0.05	0.03
Chromadorida	b	3	0.54	0.19
Chronogaster	b	3	0.35	0.14
Prismatolaimus	b	3	0.65	0.22
Alaimus	b	4	0.53	0.18
Aphelenchoides	f	2	0.17	0.08
Aphelenchus	f	2	0.24	0.10
Aprutides	f	2	0.06	0.04
Ditylenchus	f	2	0.59	0.21
Leptonchidae	f	4	1.07	0.31
Tylencholaimus	f	4	0.54	0.19
Paratylenchus	h	2	0.06	0.04
Tylenchidae	h	2	0.15	0.07
Helicotylenchus	h	3	0.37	0.14
Hemicriconemoides	h	3	1.00	0.31
Pratylenchus	h	3	0.13	0.07
Tylenchorhynchus	h	3	0.18	0.08
Longidorella	h	4	0.52	0.18
Trichodorus	h	4	0.74	0.24
Belondiridae	h	5	2.62	0.61
Xiphinema	h	5	4.89	1.00
Dorylaimidae	o	4	7.46	1.42
Dorylaimus	o	4	53.68	6.76
Epidorylaimus	o	4	1.42	0.39
Qudsianematidae	o	4	2.00	0.51
Mesodorylaimus	o	5	1.68	0.44
Prodorylaimus	o	5	6.35	1.22
Thornenematidae	o	5	1.25	0.35
Tripylidae	p	3	2.50	0.63
Eudorylaimus	p	4	3.60	0.80
Monochidae	p	4	3.99	0.87
Prionchulus	p	4	10.58	1.87
Aporcelaimus	p	5	83.13	9.18
Nygolaimidae	p	5	5.39	1.07

Appendix B. Metabolic footprints (μg C 100 g^{-1} soil) for nematode functional groups collected from different habitats at Audubon Bobcat Ranch Reserve in Yolo County, California (USA). Letters denote feeding groups (b = bacterivore, f = fungivore, h = herbivore, o = omnivore, p = predator) and numbers the classification on a life history colonizer persister (cp) scale with cp-1 being life histories of extreme colonizers vs. cp-5 extreme persisters

Site	b1	b2	b3	f2	f4	h2	h3	h4	h5	o4	o5	p3	p4	p5
HQ1	31.5	20.6	9.0	2.2	4.4	5.7	2.1	0	2.1	20.6	3.6	6.7	9.3	0
HQ2	17.8	1.4	0.2	0.4	2.9	1.8	0.3	0	0	6.8	0.5	0	1.27	0
HQ3	12.9	1.1	1.0	0.8	0.7	1.4	0.1	0	0	0	0	0	0	0
HILL1	91.0	81.0	1.1	0.8	1.8	5.8	0.7	0	0	7.6	1.7	0	9.3	0
HILL2	137.0	15.0	6.1	6.7	1.1	10.4	0.9	0.6	0	50.1	0	1.9	22.2	3.3
CYN1	69.0	24.2	0.8	0.0	9.1	3.5	0.2	0.7	2.3	38.5	1.6	0	0	139
CYN2	0	23.4	8.1	1.9	12.2	13.4	0	6.5	0	43.0	15.9	13.8	13.7	0
CYN3	27.0	1.3	0.6	0.1	0.3	0.8	0	0	0.9	1.9	0.7	0	10.3	0
CYN4	147.7	6.1	0	7.0	6.0	9.4	0	0	0	9.6	2.8	0	5.2	0
CYN5	81.2	9.5	0	7.2	12.1	7.5	0.2	1.1	0	21.3	3.4	0	17.4	0
CYN6	0	11.2	1.5	0.7	0	2.6	0.2	0.4	0	4.6	0	0	13.4	0
CYN7	167.8	20.7	0	10.6	1.3	6.7	0	0	0	21.6	8.0	2.2	13.2	3.8

Appendix C. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.geoderma.2013.07.021.

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