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Relationships between labile soil organic matter and nematode communities in a California oak woodland

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Summary – Labile soil organic matter (SOM) is an important energy source for below-ground ecosystems but the association of labile SOM and nematode communities is poorly characterised. In this study, soil nematode communities and nematode-derived indices of ecosystem function were characterised and related to SOM lability in an undisturbed riparian woodland (California, USA). SOM lability was assessed by microbial biomass C (MBC), permanganate-oxidisable C (POXC), extractable organic C (EOC), and diffuse reflectance infrared Fourier transform (DRIFT) spectroscopy. The channel index, which measures the ratio of bacterial-feeding to fungal-feeding nematodes in cp groups 1 and 2, respectively, decreased with labile C fractions and aliphatic C-H enrichment (infrared absorbance at 2920 cm^{-1}) but increased with aromatic C=C enrichment (1620 cm^{-1}) and index of decomposition (2930:1620 cm^{-1}), as did the nematode structure index. These results indicate that nematode communities respond to variation in labile C fractions and SOM composition across a heterogeneous natural landscape, which may reflect observed differences in SOM lability among woody plant species.

Keywords – diffuse reflectance infrared Fourier transform spectroscopy, ecosystem, extractable organic C, free-living nematodes, microbial biomass, permanganate-oxidisable C.

In detrital food webs, microbial community composition depends largely on the quality of the soil organic matter (SOM), which can affect rates of decomposition (Grandy & Neff, 2008), nutrient mineralisation (Erhagen *et al.*, 2013) and, consequently, below-ground ecosystem function (Meier & Bowman, 2008). For example, bacteria are more likely to consume readily decomposable resources with low C:N ratios (Dilly & Irmler, 1998), whereas fungi are favoured by higher C:N ratios (Grosso *et al.*, 2016) and may be better adapted to degrading processed and/or recalcitrant SOM enriched in polyaromatic compounds (Rosenbrock *et al.*, 1995; Frankland, 1998; Leonowicz *et al.*, 2001; Scheu *et al.*, 2005; Rineau *et al.*, 2012; Mäkelä *et al.*, 2015). These differences in microbial communities are reflected in bacterial- and fungal-feeding nematodes that respond rapidly to the abundance of their prey. The role of nematodes in modulating organic matter decomposition and turnover makes them a sensitive indicator of reciprocal above- and below-ground ecosystem processes (Wardle *et al.*, 2004; Wright & Coleman, 2000; Culman *et al.*, 2010).

The ability of nematodes to exploit many types of food sources combined with their diverse life history strategies makes them key indicators of ecological structure (Yeates *et al.*, 1993; Ferris, 2010; Sánchez-Moreno *et al.*, 2009, 2011) as well as resource enrichment and processing (Bongers, 1990; Ferris & Matute, 2003; Ferris & Bongers, 2006; Briar *et al.*, 2007; Chauvin *et al.*, 2015). The life history strategies of nematodes can be categorised from extreme r to extreme K strategists on a coloniser-persister (cp) scale from 1 to 5 (Bongers & Ferris, 1999). Combined with the relative abundance of nematodes of different feeding groups, cp values can be used to calculate function indices to describe the enrichment and structure characteristics of food webs, and also to compare whether decomposition is proceeding through more fungal- or bacterial-mediated channels (Ferris *et al.*, 2001). For example, during primary succession following resource addition, rapidly reproducing, opportunistic bacterial-feeding nematodes with low cp values ($cp < 1$) often predominate (Ferris *et al.*, 1996; Bongers & Ferris, 1999; Ferris & Bongers, 2006; Steel *et al.*, 2010), re-

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sulting in high enrichment indices (EI). Enrichment indices >50 signal more nitrogen (N)-enriched communities responding to nutrient addition. With further decomposition, fungal feeders such as the Aphelenchidae (cp 2) become more common (Bouwman & Zwart, 1994; Niles & Freckman, 1998). These changes would be reflected in the channel index (CI), which measures the ratio of bacterial to fungal feeders in the cp groups most likely to respond to changes in food availability (cp 1 and 2, respectively). Through time, as the soil community becomes more mature, predatory nematodes proliferate, as well as larger bodied, more slowly reproducing, bacterial and fungal feeders with higher cp values. This is reflected in the structure index (SI), which increases as communities become more complex (Ferris *et al.*, 2001).

Linking SOM fractions of differing lability and structural composition with nematode communities can lead to a better understanding of how SOM decomposes and is stabilised (Liang & Balser, 2011; Schmidt *et al.*, 2011). Labile C fractions offer measures of readily available resources that form the basis of soil food webs. For example, extractable organic C (EOC) is generally considered a highly labile fraction because aqueous solubility is a determinant of bioavailability (Marschner & Kalbitz, 2003). Intermediate in turnover is microbial biomass carbon (MBC), which is largely responsible for nutrient mineralisation and is a highly sensitive indicator of SOM dynamics (Sparling, 1992; Dalal, 1998; Liang & Balser, 2011). Permanganate-oxidisable carbon (POXC) represents a labile fraction that is related to MBC (Blair *et al.*, 1995; Culman *et al.*, 2012), implicated in nutrient mineralisation (Culman *et al.*, 2013), and serves as an early indicator of changes in SOM cycling (Panettieri *et al.*, 2014, 2015; Plaza-Bonilla *et al.*, 2014).

Diffuse reflectance infrared Fourier transform (DRIFT) spectroscopy offers a more detailed characterisation of the organic functional groups that compose SOM (Essington, 2004), such as aliphatic C-H, aromatic C=C, carboxyl C=O and amide C=O. These functional groups influence the ability of SOM to decompose and mineralise (Calderón *et al.*, 2011a; Erhagen *et al.*, 2013), are implicated in labile SOM fractions (Margenot *et al.*, 2015), and reflect microbial processing (Ernakovich *et al.*, 2015). DRIFT indices that compare the relative composition of functional groups can be useful to assess the lability of SOM (Parikh *et al.*, 2014). For example, the absorbance ratios of aromatic C=C and aliphatic C-H represent the degree of SOM decomposition and are strongly related to labile SOM fractions and indicators of microbiological activity (Hsu & Lo, 1999; Calderón *et al.*, 2011b; Demyan *et al.*, 2012; Giacometti *et al.*, 2013; Veum *et al.*, 2014; Margenot *et al.*, 2015). Additionally, because DRIFT spectroscopy is sensitive to the organic bonds that compose substrates fed on by microbes, it can potentially link SOM dynamics with nematode communities. DRIFT absorbance of organic bonds in the near-infrared region (10 000-4000 cm^{-1}) has been used previously to predict nematode abundance and diversity (Barthès *et al.*, 2011). However, absorbance in the mid-infrared (4000-400 cm^{-1}) offers a potentially more sensitive analysis of SOM composition because organic bonds exhibit fundamental vibrations in this region, whereas only some bonds exhibit overtones in the near-infrared (Parikh *et al.*, 2014).

Though relationships between nematode food webs and SOM dynamics have been considered in both high-input and perennial agricultural systems (Ferris *et al.*, 1996), less is known about these relationships in unmanaged ecosystems. In the Coast Range mountains of California, USA, diverse nematode assemblages were positively associated with SOM concentration, and differed with litter functional traits of nearby riparian woody plant species (Hodson *et al.*, 2014). In these communities, differences in the litter quality of woody plant species may have caused differences in SOM chemical quality, contributing to the heterogeneity of soil biota and nematode derived indices of ecosystem function. Here, we explore in more detail the relationship of nematode communities with SOM lability to improve understanding of what drives community assembly in undisturbed ecosystems. Nematode communities, labile C fractions and DRIFT spectra of soils were measured across a landscape encompassing native tree and shrub species on a hillslope in the California Coast Range. Specifically, we sought to: *i*) assess the relationship between nematode communities and labile SOM fractions (POXC, MBC, EOC); *ii*) using DRIFT spectroscopy, characterise how nematode communities vary with (a) known specific markers of SOM lability and (b) additional absorbance bands throughout the mid-infrared (4000-400 cm^{-1}) region; and *iii*) evaluate the influence of woody plant species on nematode communities and labile SOM.

We hypothesised that nematode feeding preferences and life history characteristics would be influenced by SOM lability, with more bacterial-feeding nematodes in soils with greater labile SOM and more fungal-feeding and predatory nematodes in soils with less labile SOM. Furthermore, we expected a significant effect of tree species on SOM lability and nematode communities.

Materials and methods

Site description and soil sampling

The study was conducted at the Audubon Bobcat Ranch Reserve (38°31′57″N, 122°02′18″W, western Yolo County, CA, USA) in the Blue Ridge-Berryessa Natural Area of the Coast Range mountains. The main vegetation types in this protected area are oak savanna and oak woodland, with riparian woodland along the creeks. The area has a Mediterranean type climate with cool, wet winters and hot, dry summers. Mean annual precipitation in the form of rain is 579 mm, and average maximum and minimum temperatures are 24.4 and 9.5°C, respectively (Western Regional Climate Center, 2012).

Soil samples were collected at two riparian woodland sites near seasonally dry creeks dominated by species such *Quercus douglasii* (blue oak), *Q. wizlizenii* (live oak), *Heteromeles arbutifolia* (toyon), *Cercis occidentalis* (redbud) and *Arctostaphylos glandulosa* (manzanita). The two sites, separated by 460 m, had similar slopes (30-45°), aspect and plant species composition, and were located on Positas gravelly loam soil series (fine, smectitic, thermic Mollic Palexeralfs; Soil Science Staff, 2006). Samples sites were additionally selected for their low disturbance and intact natural vegetation (Hodson *et al.*, 2014). Sampling was performed on 29 March 2011 since soils were still moist from spring rains during this time. Within each site, soil was sampled from under all trees and shrubs within a defined area, 100 m along the creek and 25 m from the waterway. Woody plants were not sampled if trunks were intertwined with another species. If more than three individuals of the same species were growing together, two were randomly selected for sampling. Under each tree or shrub, the litter was removed and one soil core taken on the downslope side, halfway between the edge of the canopy and the trunk (n = 50, 7.5 cm diam. × 7.5 cm depth). Sampling soil from this location was used to standardise between different sized trees and woody shrubs, so that all related primarily to the root zone of the plant. Soil samples were kept on ice and then refrigerated (4°C) until processing.

Soil characterisations

Inorganic N was extracted from moist soils with 2 mol l^{-1} KCl and analysed colorimetrically for ammonium (NH_4^+) and nitrate (NO_3^-) (Foster, 1995; Miranda *et al.*, 2001). For additional analyses, soils were air-dried and ground to pass through a 2 mm sieve. Soil pH was determined on air-dried samples using a 1:2.5 soil/water (m/v) ratio. Soil particle size distribution was determined by laser diffraction (LS-230 Particle Size Analyzer, Beckman-Coulter) as described by Eshel (2004) and size fractions were calculated for clay (<2 μm), silt (2-50 μm), and sand (50-2000 μm). Total soil C and N was determined with an ECS 4010 CHNSO Elemental Analyzer (Valencia).

Nematode characterisations

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. Nematode abundances were used to calculate Enrichment, Channel, and Structure indices according to Ferris *et al.* (2001) and feeding classifications determined according to Yeates *et al.* (1993). Cp groups were categorised according to Bongers (1990) and Bongers *et al.* (1995). Whilst nematodes in the family Tylenchidae have been classified mostly as epidermal root feeders (Yeates *et al.*, 1993), some genera feed on fungi (Okada *et al.*, 2002, 2005; Okada & Kadota, 2003). Therefore, in calculating nematode indices, the abundance of Tylenchidae was split, with half categorised as root herbivores (cp2) and half as fungivores (cp2).

SOM fractions

Microbial biomass C (MBC) and extractable organic C (EOC)

Field-moist soil was used in determination of microbial biomass C (MBC) by the chloroform fumigation extraction method (Vance *et al.*, 1987). Plant roots were removed prior to analysis and organic C in fumigated and non-fumigated samples was extracted by 0.5 mol l^{-1} K_2SO_4 (Ros *et al.*, 2009) and quantified using a Dohrmann Phoenix 8000 UV-persulfate oxidation analyzer (Tekmar-Dohrmann). The labile fraction of extractable organic C (EOC) was obtained from non-fumigated samples. MBC was estimated as the difference between organic C in fumigated and non-fumigated samples. No correction factors were applied. Insufficient soil was collected for MBC and EOC under the two redbud trees sampled.

Permangate-oxidisable C (POXC)

Potassium permanganate was used in the same manner as for the determination of active C, or permanganate-

oxidisable C (POXC), based on Weil (2003) and modified by Culman (2012). Briefly, 2.50 g soil was oxidised with 0.02 mol l^{-1} $KMnO_4$ with 2 min shaking followed by 10 min incubation. Non-reduced Mn^{7+} was quantified by colorimetry (550 nm) and POXC (μg (g soil)$^{-1}$) was calculated as described by Culman (2012):

$$\mu\text{g POXC (g soil)}^{-1} = \left(0.02\ \text{mol l}^{-1} - (a + b \times \text{abs})\right) \times \left(9 \times 10^6\ \mu\text{g C mol}^{-1}\right) \times \left(\frac{0.02\ \text{l}}{m}\right),$$

where 0.02 mol l^{-1} is the initial concentration of permanganate (Mn^{7+}), a is the intercept of the standard curve, b is the slope of the standard curve, abs is the sample absorbance, 9×10^6 μg C mol^{-1} is assumed stoichiometry of C oxidation and reduction of Mn^{7+} to Mn^{2+}, 0.02 l is the volume of 0.2 mol l^{-1} $KMnO_4$ solution, and m is the mass of air-dried soil (g).

Diffuse reflectance infrared Fourier transform (DRIFT) spectroscopy

DRIFT spectra were collected on neat soil samples (*i.e.*, no dilution with potassium bromide) (Parikh *et al.*, 2014). Soils were loaded into an aluminium well and surface smoothed using a razor. Absorbance spectra were corrected against a solid aluminium blank in ambient air as the background using a Nicolet 6700 spectrometer (Thermo Scientific) with a deuterated triglycine sulfate (DTGS) detector diffuse reflectance accessory (Pike AutoDIFF, Pike Technologies). Spectra were calculated as the mean of 400 scans across 4000-600 cm^{-1} at 4 cm^{-1} resolution. For each sample, replicate spectra (n = 3) were collected on separate soil samples and averaged. To enable comparison of relative absorbance, absorbance intensity at each wave number was normalised to the mean of total absorbance across 4000-600 cm^{-1}.

Absorbance areas were calculated for two bands used for assessing SOM composition in bulk soil DRIFT spectra using a tangential baseline method described elsewhere (Smidt *et al.*, 2002; Demyan *et al.*, 2012; Giacometti *et al.*, 2013): aliphatic C-H at 3010-2810 cm^{-1} and aromatic C=C and ketone and quinone C=O and/or COO^- at 1660-1580 cm^{-1}. Absorbance at these two bands includes mineral contributions, but the similar soil mineralogy enables absorbance differences to be attributable to organic functional groups (Verchot *et al.*, 2011; Demyan *et al.*, 2012). As a measure of SOM lability, the humification index (HI) was calculated as the ratio of absorbance areas of aromatic C=C, ketone and quinone C=O, and/or amide C=O at 1660-1580 cm^{-1} to aliphatic C-H at 3010-2810 cm^{-1} (Inbar *et al.*, 1989; Hsu & Lo, 1999; Demyan *et al.*, 2012).

Statistical analyses

Kruskal-Wallace tests were used to compare soil characteristics and nematodes communities both between sites and between plant species. Since there were no statistically significant differences between the sites, they were pooled and analysed together. Relationships between nematode indices of ecosystem function, soil C fractions and DRIFT absorbance bands and humification index (HI) were assessed using Spearman Rank correlations. Whilst all plant species were included in correlations, comparisons focused on those with sufficient sample sizes for analysis: toyon, blue oak and manzanita. All statistical analyses were performed using the statistical program R (v 3.1.1; R Core Team, 2014).

Results

Soil C fractions

There were minor differences in labile SOM fractions by tree species (Table 1), and POXC was generally higher under blue oak, manzanita and redbud than live oak and toyon. Across tree sites, POXC was the largest labile C fraction in soil (mean 826 μg C g^{-1}) and showed less variability (1140-358 μg C g^{-1}; CV = 0.32) than MBC (CV = 0.47) and EOC (CV = 0.61) (Table S1). EOC

Table 1. Labile soil organic matter fractions under different tree and shrub species at riparian woodland sites at the Audubon Bobcat Ranch Reserve in Yolo, County, CA, USA, along with their standard errors (SE).

Species	n	MBC		POXC		EOC	
		Mean	SE	Mean	SE	Mean	SE
Blue oak	12	374	148	906	198	131	77
Live oak	4	83	24	684	145	113	52
Manzanita	16	360	174	867	278	147	104
Redbud	2	nd	nd	881	226	nd	nd
Toyon	12	327	187	732	329	141	83

All values are in μg g^{-1}. No statistically significant differences were detected between tree species. MBC = microbial biomass C; POXC = permanganate-oxidisable C; EOC = extractable organic C; nd = not determined.

ranged from 360-30 μg C g^{-1}, and was the smallest fraction with a mean of 138 μg C g^{-1}, whereas total MBC represented a mean of 341 μg C g^{-1} and exhibited greatest variation (846-142 μg C g^{-1}) (Table S1). Similar trends occurred when C fractions were expressed as a proportion of total soil C. POXC represented a mean of 2.78% of total C, whereas EOC represented a mean, six-fold smaller, proportion of 0.43%.

SOIL NEMATODE COMMUNITIES

Nematode taxa identified (Table 2) comprised communities that were highly variable. Whilst there were no significant differences in any nematode indices between the two sites, within each site communities under individual trees and shrubs could have very different ecological structures and enrichment responses due to differences in the abundance of certain species (Fig. 1). For example, while some soils had very high numbers of predators such as *Aporcelaimus* and *Prionchulus*, others were dominated by bacterial feeders such as *Mesorhabditis* and *Acrobeloides*. This resulted in structure indices varying from 6.6 to 95.5, with a mean and standard error of 45.4 $\pm$ 2.7 and enrichment indices varying from 14.6 to 88.2 with a mean of 50.6 $\pm$ 2.5 (Table 3). Individual tree species did not greatly influence community indices, although toyons and manzanitas tended to support communities that were more highly structured (Fig. 1).

Table 2. Average abundances of nematode taxa isolated from surface soils (0-7.5 cm) in riparian woodland at the Audubon Bobcat Ranch Reserve in Yolo County, CA, USA, and their associated feeding group, life history coloniser-persister (cp) values and abundance per 350 ml soil sample.

Taxon	Feeding group	cp	Abundance (350 ml soil)$^{-1}$
Panagrolaimus	b	1	14.4
Mesorhabditis	b	1	85.1
Acrobeles	b	2	0.9
Acrobeloides	b	2	218.2
Cephalobidae	b	2	64.4
Monhysteridae	b	2	7.9
Plectidae	b	2	15.4
Wilsonema	b	2	3.8
Prismatolaimus	b	3	14.3
Dauer	b	1	21.0
Aphelenchoides	f	2	117.8
Aphelenchus	f	2	6.6
Aprutides	f	2	32.6
Tylencholaimus	f	4	5.5
Paratylenchus	h	2	244.4
Tylenchidae	h	2	289.2
Pratylenchus	h	3	0.9
Tylenchorhynchus	h	3	20.0
Longidorella	h	4	0.3
Dorylaimidae	o	4	0.8
Qudsianematidae	o	4	20.5
Thonus	o	4	12.6
Microdorylaimus	o	4	43.0
Mesodorylaimus	o	5	0.6
Prodorylaimus	o	5	1.4
Tripylidae	p	3	8.0
Eudorylaimus	p	4	6.8
Prionchulus	p	4	18.9
Aporcelaimus	p	5	4.1

Nematode communities and indices of ecosystem function varied with the concentrations of labile C fractions. For example, the channel index decreased with MBC (rho $= -0.34$, $P = 0.02$), EOC (rho $= -0.34$, $P = 0.02$), and POXC (rho $= -0.35$, $P = 0.02$), indicating lower proportions of opportunistic fungal feeders in cp group 2 and a higher proportion of bacterial feeders in cp group 1. The total abundance of fungal-feeding nematodes also decreased with EOC (rho $= -0.31$, $P = 0.04$) and the relative proportion of bacterial-feeding nematodes in the community increased (rho $= 0.26$, $P = 0.08$).

DRIFT SPECTROSCOPY AND BANDS CORRESPONDING TO ORGANIC FUNCTIONAL GROUPS

Relative absorbance of bands representing organic functional groups that constitute SOM differed among soils according to trees species and life history strategies (Table 4). For example, blue oaks (with deciduous leaves) occurred at sites with higher relative absorbance of aliphatic C-H at 2920 cm^{-1} in soils compared to toyons (with evergreen leathery leaves) ($\chi^2 = 3.63$, $P = 0.06$). Soils under blue oaks also had a lower humification index than toyons, indicating SOM of greater decomposability ($\chi^2 = 5.6$, $P = 0.02$), and lower absorbance at the band area centred at 1620 ($\chi^2 = 5.6$, $P < 0.01$).

The relative band areas corresponding to specific SOM functional groups and the humification index varied with soil biochemical properties indicating nutrient availability and food resources available to nematodes. For example, absorbance of aliphatic C-H at 2920 cm^{-1}, considered to represent labile SOM, increased with labile C fractions and soil fertility measures such as MBC (rho $= 0.55$, $P < 0.01$), POXC (rho $= 0.80$, $P < 0.01$), EOC (rho $= 0.80$, $P < 0.01$), as well as EC (rho $= 0.4$, $P < 0.01$), total N (rho $= 0.80$, $P < 0.01$), NH_4^+-N (rho $= 0.55$,

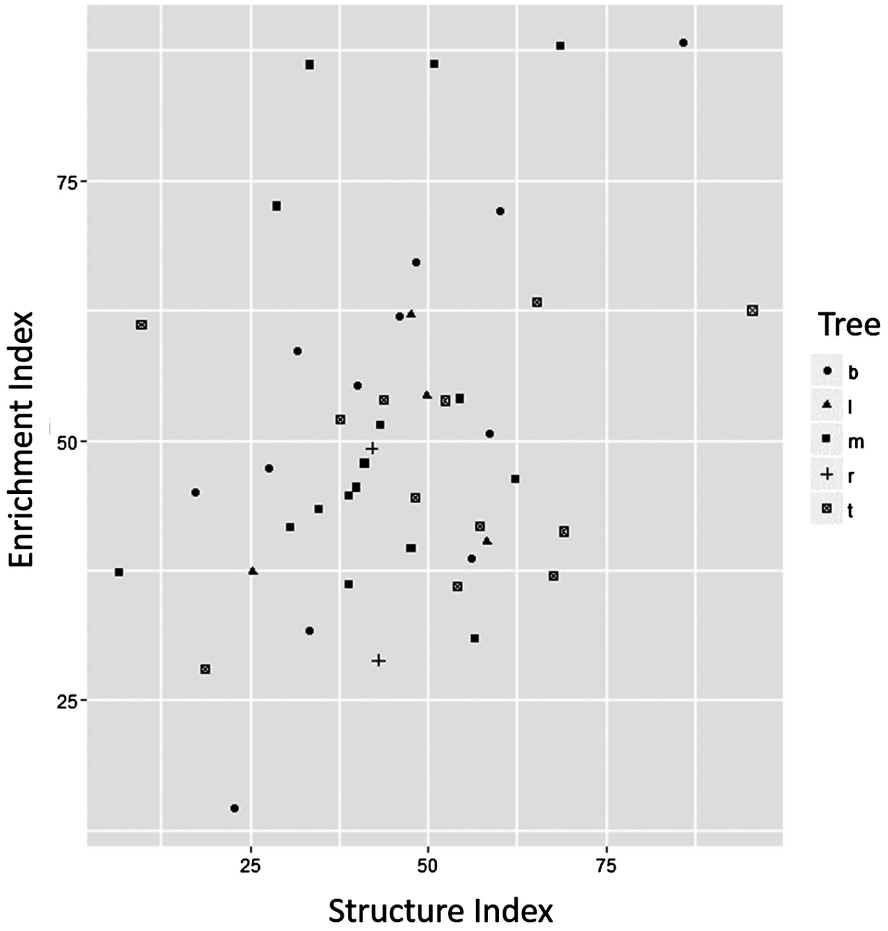

Fig. 1. Nematode food web analysis of taxa isolated from surface soils (0-7.5 cm) in riparian woodland at the Audubon Bobcat Ranch Reserve in Yolo County, CA, USA. Communities with enrichment indices (EI) over 50 are considered more N-enriched, whilst those with structure indices over 50% are either mature or maturing. Symbols represent different tree species, circle = blue oak, triangle = live oak, square = manzanita, x = redbud, and circle within a square = toyon.

Table 3. Properties of the nematode communities isolated from surface soils (0-7.5 cm) in riparian woodland at the Audubon Bobcat Ranch Reserve in Yolo County, CA, USA.

	Mean	SE
Enrichment Index	50.64	2.5
Structure Index	45.41	2.7
Channel Index	54.48	4.2
Total nematodes	1279	260
Species Richness	12.23	0.36

$P < 0.01$) and total C (rho = 0.9, $P < 0.01$). These same properties were negatively related to aromatic C=C and/or ketone C=O and amide C=O (1660-1580 cm^{-1}), and to the humification index (1620 cm^{-1}:2930 cm^{-1}), which can indicate more decomposed organic matter.

Interrelationships of SOM fraction and functional group composition with nematode indices

Several nematode indices of ecosystem function exhibited a relationship with band areas corresponding to specific SOM functional groups. For example, the channel index decreased with the relative absorbance of aliphatic C-H (3010-2800 cm^{-1}, rho = -0.32, $P < 0.03$) but increased with the relative absorbance of relatively recalcitrant aromatic C=C and/or ketone C=O and amide C=O (1660-1580 cm^{-1}, rho = 0.31, $P < 0.04$), and with the

Table 4. Average band areas corresponding to specific soil organic matter functional groups under different tree and shrub species at riparian woodland sites at the Audubon Bobcat Ranch Reserve in Yolo County, CA, USA.

Species	n	Aromatic C=C (1620 cm^{-1})		Aliphatic C-H (2920 cm^{-1})		HI (1620 cm^{-1}: 2920 cm^{-1})	
		Mean	SE	Mean	SE	Mean	SE
Blue oak	12	1.77a	0.1	1.54a	0.3	1.71a	0.4
Live oak	4	2.13ab	0.2	0.82ab	0.2	3.53ab	1.6
Manzanita	16	2.15ab	0.1	1.28ab	0.2	4.69ab	2.8
Redbud	2	2.50ab	0.6	1.07ab	0.7	3.32ab	2.8
Toyon	12	2.57b	0.2	0.98b	0.3	7.99b	3.1

The band area centred at 1620 cm^{-1} ranges from 1660-1580 cm^{-1} and measures the ratio of aromatic C=C, with potential amide C=O contributions. The band centred at 2920 cm^{-1} ranges from 3010-2810 cm^{-1} and corresponds to absorbances of aliphatic C-H. The humification index, or HI, is the ratio of two band areas (1620 cm^{-1}:2930 cm^{-1}) and increases with the degree of decomposition. Letters differentiate Kruskal Wallace test results with $P < 0.05$.

Table 5. Spearman Rank correlation coefficients (rho) between nematode indices and average band areas corresponding to specific SOM functional groups.

Nematode index	Aromatic C=C (1620 cm^{-1})	Aliphatic C-H (2920 cm^{-1})	HI (1620 cm^{-1}: 2920 cm^{-1})
EI	−0.12	0.14	−0.11
SI	0.28*	0.02	0.06
CI	0.36**	−0.30**	0.33**
Bacterial metabolic footprint	−0.22	0.03	−0.09
Fungal metabolic footprint	−0.03	−0.04	0.02
Herbivore metabolic footprint	0.08	−0.11	0.11
Predator metabolic footprint	0.1	0.07	0.10
Enrichment metabolic footprint	−0.21	0.02	−0.10
Structure metabolic footprint	0.07	−0.08	0.10
Metabolic footprint predator:prey	0.34**	0.01	0.08

The band area centred at 1620 cm^{-1} ranges from 1660-1580 cm^{-1} and measures the ratio of aromatic C=C, with potential amide COO^{-} contributions. The band centred at 2920 cm^{-1} ranges from 3010-2810 cm^{-1} and relates to absorbances of aliphatic C-H. The humification index, or HI, is the ratio of two band areas (1620 cm^{-1}:2930 cm^{-1}) and increases with the degree of decomposition. $^{*}P < 0.10$; $^{**}P < 0.05$.

humification index (rho = 0.36, $P = 0.01$). The structure index, a measure of the trophic complexity of the nematode community, also increased with relative absorbance at 1660-1580 cm^{-1} (rho = 0.38, $P < 0.01$). The nematode enrichment index dropped at this absorbance precipitously, although the effect was not statistically significant (rho = −0.01, $P = 0.9$). Correlation coefficients between nematode indices and average band areas corresponding to specific functional groups are summarised in Table 5.

In the PCA of nematode indices and SOM functional groups (Fig. 2), axis 1 explained 48.6% of the variation and divided the variables into two categories. Along axis 1, variables involved in labile SOM grouped tightly together on one side including POXC, EOC and the intensity of the band area centred at 2920 cm^{-1}, which relates to absorbances of aliphatic C-H. In the opposite direction, grouped variables signified more processed organic matter as assessed by the increase in HI and intensity of the band area at 1620 cm^{-1}, which reflects aromatic C=C albeit with potential amide C=O contributions. The nematode channel index was also associated with these variables. The vectors for the nematode structure and enrichment indices were somewhat intermediate between these two groups, although they plotted more towards variables involved in labile SOM.

Individual nematode taxa showed more variation in their responses to band areas associated with SOM functional groups. The percentage of free living nematodes

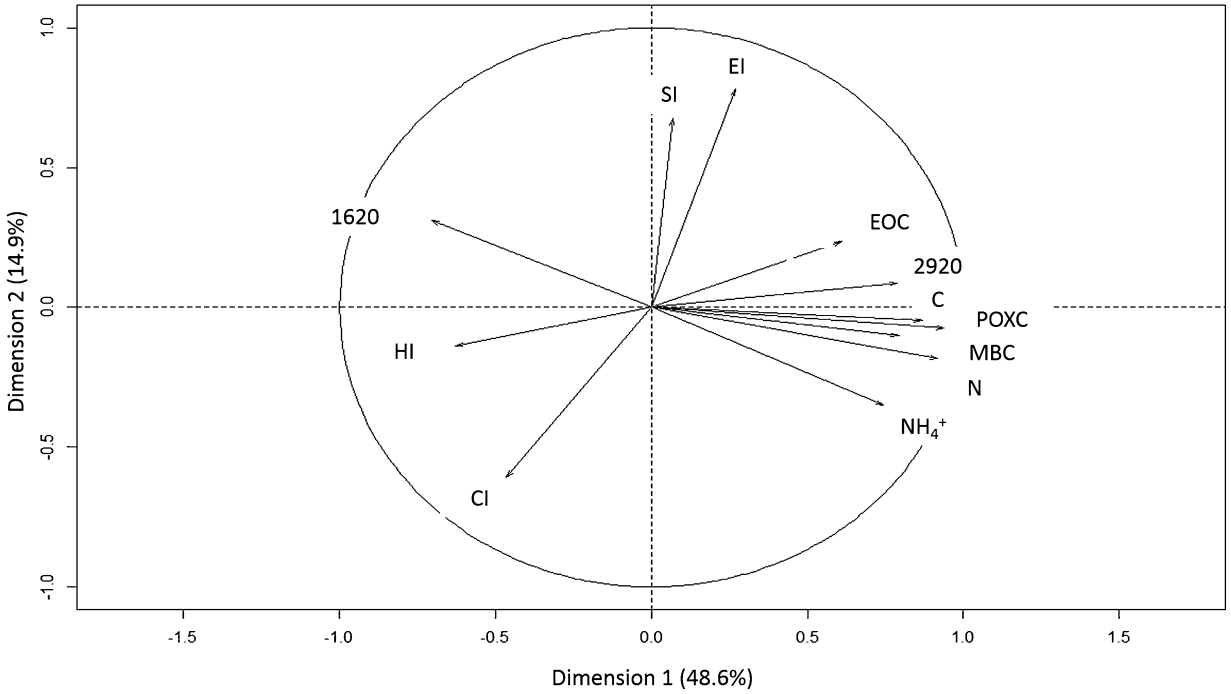

Fig. 2. Principle components analysis of nematode indices, carbon pools and average band areas corresponding to specific soil organic matter (SOM) functional groups. CI = Nematode Channel Index, SI = Nematode Structure Index, EI = Nematode Enrichment Index. The band area centred at 1620 cm^{-1} ranges from 1660-1580 cm^{-1} and corresponds to aromatic C=C,with potential contributions from amide C=O. The band centred at 2920 cm^{-1} ranges from 3010-2810 cm^{-1} and corresponds to aliphatic C-H. The humification index, or HI, is the ratio of two band areas (1620 cm^{-1}:2930 cm^{-1}) and increases with the degree of decomposition.

in cp group 1 (*Panagrolaimus* and *Mesorhabditis*) decreased with the relative absorbance of relatively recalcitrant aromatic C=C and/or ketone C=O and amide C=O (rho = −0.35, $P = 0.01$), as did bacterial feeders in the genus *Prismatolaimus* (cp 3; rho = −0.35, $P = 0.01$). *Prismatolaimus* also increased with aliphatic C-H (rho = 0.25, $P = 0.08$), but decreased with the humification index (rho = −0.28, $P = 0.06$). By contrast, the relative abundance of *Panagrolaimus* decreased with aliphatic C-H (rho = −0.34, $P = 0.02$) and increased with the humification index (rho = 0.32, $P = 0.03$). *Wilsonema* also increased with the humification index (cp 2, rho = 0.28, $P = 0.05$) and also with the relative absorbance of relatively recalcitrant aromatic C=C and/or ketone C=O and amide C=O (1660-1580 cm^{-1}, rho = 0.36, $P = 0.01$).

Additional analyses of absorbances revealed further relationships with nematode communities. The bands were identified by correlation analysis between nematode indices and absorbance intensity of DRIFT spectra (4000-600 cm^{-1}) and are shown in Figure 3. It was found that the channel index decreased with absorbances corresponding to aliphatic C-H at 2923 cm^{-1} (rho = −0.39, $P = 0.01$), quartz Si-O at 2050-1800 cm^{-1} (rho = −0.39, $P < 0.01$ at 2923 cm^{-1}), and aromatic C=C and/or potentially amide C-N (rho = −0.38, $P < 0.01$). The relative abundance of the otherwise common genus, *Acrobeloides*, was also inversely associated with absorbance at 1575 cm^{-1} (rho = −0.31, $P < 0.04$). The channel index correlated with absorbance at 1283 cm^{-1} (rho = 0.4, $P < 0.01$) corresponding to phenol C-O, and the correlation of structure index also slightly increased with absorbance at this frequency (rho = 0.22, $P = 0.15$). Higher structure indices also correlated with polysaccharide C-O and/or silicate Si-O at 1000-1100 cm^{-1} (rho = 0.38, $P < 0.01$ at 1281 cm^{-1}).

Discussion

SOM LABILITY AND NEMATODES

While many studies have examined the trophic roles of nematodes, few have directly related their communities

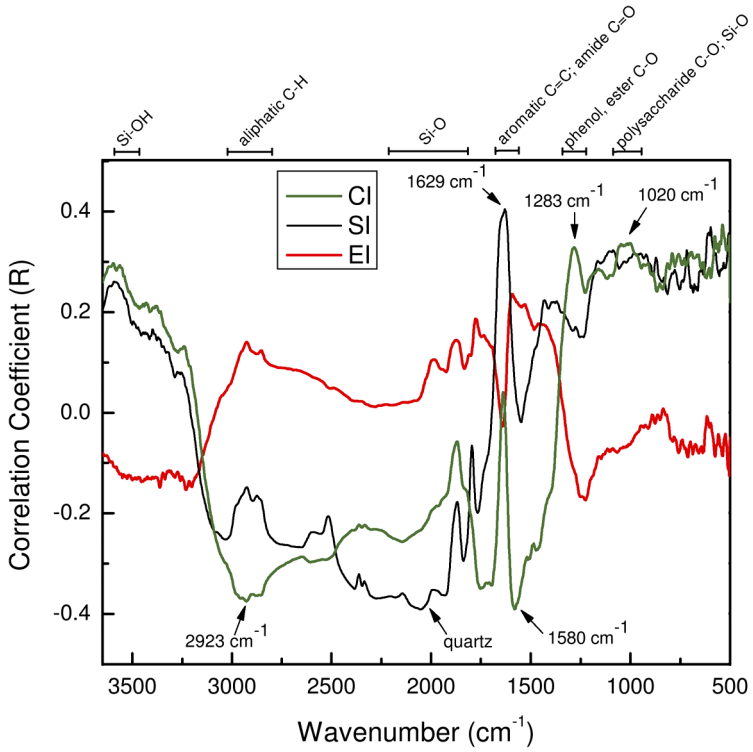

Fig. 3. Correlation coefficient (Pearson R) between nematode indices and absorbance of surface soils (n = 50) measured by diffuse reflectance infrared Fourier transform (DRIFT) spectroscopy. SI = nematode Structure Index, which increases with the proportion of predators and indicates more mature communities. CI = nematode Channel Index, which measures the ratio of fungal feeders to bacterial-feeders in the population in cp groups 1 and 2, respectively. Soil samples (0-7.5 cm depth) are from undisturbed riparian woodland at the Audubon Bobcat Ranch Reserve in Yolo County, CA, USA. This figure is published in colour in the online edition of this journal, which can be accessed *via* http://booksandjournals.brillonline.com/content/journals/15685411.

to SOM pools and composition. In this study of an undisturbed ecosystem, nematode feeding groups and indices of ecosystem function related with labile soil C fractions and DRIFT measures of SOM composition. For example, POXC was negatively correlated with the channel index, suggesting that POXC is a resource pool that is not preferred by fungal-feeders. This is consistent with the preference of fungal feeders for more processed resources (Ferris & Matute, 2003; Ruess and Ferris, 2004; Steel *et al.*, 2010) and increases in bacterial feeders with readily decomposable resources such as compost feedstocks (Steel *et al.*, 2010) and cover crops (DuPont *et al.*, 2010).

The relationships between nematode groups and DRIFT characterisation of SOM composition were somewhat consistent with the hypothesis that fungal feeders and predators are more common in soils with lower SOM lability. The SI increased with relatively recalcitrant aromatic C=C and/or ketone C=O and amide C=O and also with phenols. With more labile aliphatic C-H enrichment, the CI decreased and the relative abundance of bacterial-feeding *Prismatolaimus* increased. In this study, relative absorbance of aliphatic C-H at 2920 cm^{-1} strongly correlated with labile fractions such as MBC and POXC, agreeing with previous findings (Calderon *et al.*, 2011, 2015; Giacometti *et al.*, 2013; Veum *et al.*, 2014; Margenot *et al.*, 2015). By contrast, the CI increased with DRIFT indicators of more processed SOM (*i.e.*, increased humification index). This may reflect development of more structurally complex, fungal-based, communities under conditions of less labile, more processed SOM.

While we expected to find more bacterial feeding nematodes in soils with greater labile SOM, the effects of functional groups on the EI were very weak. Slight dips were seen in the EI with chemically recalcitrant organic functional groups at 1620 cm^{-1} but in general, the effect

of SOM on the EI was not as pronounced as other indices. It could be that the effects of SOM functional groups on bacterial feeders were masked by spatial effects, such as proximity to the creek bank (Hodson *et al.*, 2014) and also the preferences of individual taxa for different tree species. For example, while *Prismatolaimus* was slightly more common under deciduous blue oaks, *Wilsonema* was most common under trees with evergreen leathery leaves, like toyon and manzanita. By contrast, *Panagrolaimus* and *Mesorhabditis* both had patchy distributions and seemed to show no preference for individual tree species.

Nematodes and infrared spectroscopy

This study is the first to apply infrared spectroscopy to relate absorbance of soil samples in the mid-infrared region to nematode communities. Relationships between mid-infrared spectra absorbance and nematode groups reflected absorbance of SOM as well as minerals. Nematode biomass may have directly contributed to organic functional group absorbances, but the small proportion of organic matter and even smaller proportion of nematode biomass in soil samples means observed correlations were most likely indirect rather than by direct detection of nematodes. This is in contrast to *in vitro* studies in which FTIR spectroscopy of pure nematode samples can be used to classify individual nematodes by detecting taxa-specific organic functional group composition of organs (Ami *et al.*, 2004; San-Blas *et al.*, 2011), and can even detect metabolic changes within a single specimen (Sheng *et al.*, 2016). In soils, the minor component of nematodes necessitates chemometric analyses to elucidate potential contribution of nematode biomass to absorbances. For example, Barthès *et al.* (2011) evaluated the potential of near-infrared spectra with multivariate modelling to predict nematode groups in agricultural soils. Their prediction models highlighted absorbances that corresponded to organic bonds present in nematode biomass and in SOM (*e.g.*, cellulose). Specific absorbances contributed differently to predictions of different trophic groups. For example, aliphatic C-H associated with bacterial feeders, aliphatic and aromatic C-H with fungal feeders, and amide C=O and C-N with herbivores (Barthès *et al.*, 2011).

Although our study focused on a different spectral region, it is in agreement with the finding by Barthès *et al.* (2011) that feeding groups associated differently with DRIFT indices of SOM decomposability. In this study, correlations were found between absorbances attributable to organic functional groups and nematode indices, while Barthès *et al.* (2011) found correlations only with individual nematode feeding groups. These differences may reflect land use, as the soils assessed by Barthès *et al.* (2011) came from agricultural fields whereas those surveyed in this study came from a likely more heterogeneous and natural landscape that encompassed greater variability in SOM and nematode community complexity.

Possible role of tree species, litter and SOM

Variation in carbon pools and SOM lability could be partly explained by woody plant species, supporting the hypothesised link between above-ground litter quality and below-ground ecosystem function. These findings support previous investigations of the effect of tree individuals and species on soil ecosystem function in Mediterranean wooded grasslands. This has been conceptualised as 'islands of fertility'; for example, in blue oak (*Q. douglasii*) grasslands, where soil nutrient uptake and surface deposition *via* litter results in a concentration of nutrients in soils underlying individual trees (Dahlgren *et al.*, 2003). In a cork oak (*Q. suber*) grassland, litter deposition and surface coverage by individual trees led to +50% increases in soil C and greater diversity of collembola (Rossetti *et al.*, 2015). The authors interpreted tree above-ground input of organic matter (*i.e.*, litter) as linking the tree-soil-biodiversity system. Tree species may also produce below-ground influences on SOM by root exudates and by influencing underlying vegetation, such as grass species. In a comparison of perennial grasslands and annual croplands, differences in total and labile soil C that tracked with nematode community structures were attributed to below-ground differences in vegetation, namely greater root biomass in grassland (Culman *et al.*, 2010).

While the results of the current analysis focused on SOM, previous analysis of nematode communities in relation to tree species found higher nematode predator: prey ratios under toyon compared to more deciduous species and manzanita (Hodson *et al.*, 2014). SOM lability may be driving the distribution of predatory nematodes, with concentrated populations occurring in soils with less labile SOM. Toyons have evergreen leathery leaves of lower decomposability, and in this landscape SOM under toyons had a significantly higher humification index compared to soils under blue oak, consistent with previous findings of greater SOM recalcitrance from tannin-rich litter of evergreens (Northup *et al.*, 1995). We hypothesise that the low nutritional quality of toyon leaves, combined with their nearly constant supply, could result in a build-up of complex nematode communities with high numbers of predators and omnivores.

The abundance of leaf litter could also create microhabitats more conducive to complex communities. In toyon-dominated communities, labile C would be rapidly decomposed by the food web, a scenario supported by the higher humification index in soils under toyon. By contrast, the aliphatic C-H enrichment and a lower humification index of SOM under the deciduous species of blue oaks could reflect the pulse in OM during oak leaf drop, which is relatively concentrated to a shorter time period in the autumn. While sampling in the current study was restricted to one time point, more detailed monitoring of nematode communities and SOM chemical functional groups over time could confirm not only the feeding preferences of individual taxa, but also their roles in decomposition and carbon cycling.

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Table S1. Labile soil organic matter (SOM) fractions from surface soils (0-15 cm) in the Coast Range, CA, USA, determined as microbial biomass carbon (MBC), extractable organic carbon (EOC), and potassium permanganate oxidisable carbon (POXC).

Fraction	Total (μg C (g soil)$^{-1}$)			Proportion of soil C (%)		
	Mean	Range	CV	Mean	Range	CV
MBC	341	142-846	0.47	1.14	0.35-1.89	0.36
EOC	138	30-360	0.61	0.43	0.10-1.05	0.49
POXC	826	358-1440	0.32	2.78	1.26-4.87	0.30

CV = coefficient of variation.