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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.