



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

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ABSTRACT

Soil food webs respond to anthropogenic and natural environmental variables and gradients. We studied abundance, connectance (a measure of the trophic interactions within each channel), and diversity in three different channels of the soil food web, each comprised of a resource–consumer pair: the microbivore channel (microbes and their nematode grazers), the plant–herbivore channel (plants and plant-feeding nematodes), and the predator–prey channel (predatory nematodes and their nematode prey), and their associations with different gradients in a heterogeneous agricultural landscape that consisted of intensive row crop agriculture and grazed non-irrigated grasslands in central California. Samples were taken at three positions in relation to water channels: water's edge, bench above waterway, and the adjacent arable or grazed field. Nematode communities, phospholipid fatty acid (PLFA) biomarkers, and soil properties ($\text{NH}_4^+\text{-N}$, $\text{NO}_3^-\text{-N}$, total N, total C, pH, P, bulk density and soil texture) were measured, and riparian health ratings were scored. Environmental variables were obtained from publicly-available data sources (slope, elevation, available water capacity, erodability, hydraulic conductivity, exchangeable cation capacity, organic matter, clay and sand content and pH).

The abundance and richness in most food web components were higher in grazed grasslands than in intensive agricultural fields. Consumers contributed less than their resources to the abundance and richness of the community in all channels. The association between richness and abundance for each component was strongest for the lowest trophic links (microbes, as inferred by PLFA) and weakest for the highest (predatory nematodes). The trophic interactions for the predator–prey and plant–herbivore channels were greater in the grassland than in the cropland. Fields for crops or grazing supported more interactions than the water's edge in the plant–herbivore and microbivore channels. Connectance increased with the total richness of each community. Higher connectance within the microbivore and predator–prey soil food web channels were associated with soil $\text{NO}_3^-\text{-N}$ and elevation respectively, which served as surrogate indicators of high and low agricultural intensification.

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1. Introduction

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

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

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

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

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

The objectives of this paper were to: a) characterize the biotic composition of the assemblages comprising consumers and their resources in each of the three soil food web channels, b) study the relationship between richness and abundance of different functional groups of soil organisms, c) explore soil food web interactions

and connectance, d) study the influence of environmental variables on food web connectance, and e) draw inferences regarding the relationships between riparian health, land use, and food web properties.

2. Material and methods

2.1. Study site and sampling methods

The study area is a 150 km² landscape of Yolo County (CA, USA). The hilly rangeland in the west consists of grazed annual grasslands and oak savanna, while the flat croplands in the east are dominated by intensive agriculture (grains, vegetables, and alfalfa). Geographic Information System (GIS) data regarding soils, topography and vegetation across the landscape were used to systematically select 20 sites that captured a maximum level of landscape heterogeneity (Culman et al., 2010). At each site, a transect was established perpendicular to the waterway with sampling points at three distances from the water channel: i) Position A, in the agricultural field or the grazed pasture, 50 m from the water edge, ii) Position B, in the bench of the waterway, 5–10 m from the water edge, considered an intermediate environment between the agricultural and the riparian areas, and Position C, situated around 0.5 m from the edge of the waterway in the riparian corridor. Three soil cores (0–15 cm depth) were collected at each position 2 m apart. Thus, a total of 180 soil samples was collected (20 sites × 3 distances to water × 3 cores at each distance). Detailed descriptions of the study area and methodology used for selecting sampling sites are reported in Young-Mathews et al. (2010) and Culman et al. (2010).

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

2.2. Soil organisms

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

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

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

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