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Biodiversity and multiple ecosystem functions in an organic farmscape

S.M. Smukler[a], S. Sánchez-Moreno[c], S.J. Fonte[d], H. Ferris[e], K. Klonsky[f], A.T. O'Geen[b], K.M. Scow[b], K.L. Steenwerth[g], L.E. Jackson[b,*]

[a] Tropical Agriculture Program, The Earth Institute at Columbia University, 61 Route 9W, Lamont Hall, Room 2H, Palisades, NY 10964-8000, USA
[b] Department of Land, Air and Water Resources, University of California, Davis, CA 95616, USA
[c] Unidad de Productos Fitosanitarios, Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria, Crta. Coruña km 7.5, Madrid 28040, Spain
[d] Department of Plant Sciences, University of California, Davis, CA 95616, USA
[e] Department of Nematology, University of California, Davis, CA 95616, USA
[f] Department of Agriculture and Resource Economics, University of California, Davis, CA 95616, USA
[g] USDA/ARS, Crops Pathology and Genetics Research Unit, Davis, CA 95616, USA

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ABSTRACT

To increase ecosystem services provided by their lands, farmers in the United States are managing non-production areas to create a more biodiverse set of habitats and greater landscape heterogeneity. Relatively little is known, however, of the actual environmental outcomes of this practice, termed 'farmscaping'. We inventoried communities of plant and soil organisms and monitored indicators of ecosystem functions in six distinct habitats of an organic farm in California's Central Valley to better understand the ecological costs and benefits of farmscaping. A riparian corridor, hedgerows, a system of drainage ditches, and tailwater ponds supported different plant life history/functional groups and greater native plant diversity than the two production fields. Differences were less pronounced for belowground organisms, i.e., nematode functional groups, microbial communities (based on phospholipid fatty acid (PLFA) analysis) and earthworm taxa. Partial ordination analysis showed that environmental variables, rather than spatial location, explained much of the distribution of soil and plant taxa across the farmscape. Riparian and hedgerow habitats with woody vegetation stored 18% of the farmscape's total carbon (C), despite occupying only 6% of the total area. Infiltration rates in the riparian corridor were >230% higher than those observed in the production fields, and concentrations of dissolved organic carbon (DOC) in soil solution were as much as 65% higher. The tailwater pond reduced total suspended solids in irrigation runoff by 97%. Drainage ditches had the highest N_2O-N emissions (mean values of 16.7 $\mu g\, m^{-2}\, h^{-1}$) and nitrate (NO_3^--N) leaching (12.1 $g\, m^{-2}\, year^{-1}$ at 75 cm depth). Emissions of N_2O-N and leaching of NO_3^--N were, however, quite low for all the habitats. Non-production habitats increased biodiversity (particularly plants) and specific ecosystem functions (e.g. water regulation and carbon storage). Extrapolating relative tradeoffs to the entire farmscape showed that greater habitat enhancement through farmscaping could increase both biodiversity and multiple ecosystem functions of agricultural lands with minor loss of production area.

1. Introduction

Management to provide multiple ecosystem services (e.g., food and fiber production, water and soil quality, and pest control) in agricultural landscapes requires an understanding of ecological functions (i.e., the processes that result in ecosystem services) (Adler et al., 2007; Bennett and Balvanera, 2007; Jordan et al., 2007). Ecological theory suggests that managing for biological diversity could improve ecological functions related to both agricultural production and environmental quality in agricultural landscapes, such as through a wider set of cultivars or crops (Bullock et al., 2001; Smukler et al., 2008), natural enemies of pests (Zehnder et al., 2007; Letourneau and Bothwell, 2008), more complex soil food webs to regulate nutrient cycling (Brussaard et al., 2007; Minoshima et al., 2007), and vegetated buffer zones to increase retention of C and other nutrients (Young-Mathews et al., 2010). In addition to management at the field level, more complex agricultural landscapes support higher biodiversity, resulting in increased ecosystem functions for pollination, pest control, or water quality (Gabriel et al., 2006; Tscharntke et al., 2008).

Most studies on biodiversity and ecosystem functions have been done at the plot level, often only considering a single ecosystem function and/or a single taxonomic unit of biodiversity (Balvanera et al., 2006). To understand multifunctionality, consideration of

* Corresponding author. Tel.: +1 530 754 9116; fax: +1 530 752 9659.
E-mail address: lejackson@ucdavis.edu (L.E. Jackson).

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species in a diversity of functional guilds is required (Hector and Bagchi, 2007; Gamfeldt et al., 2008), but few studies have occurred at scales broad enough to test this hypothesis (Bengtsson et al., 2003; Culman et al., in press). A mechanistic understanding of biodiversity and multifunctional relationships (Swift et al., 2004; Diaz et al., 2007) requires multi-scale, long-term research. As an initial approach, however, the focus can be placed on the associations and relationships of biodiversity inventories to ecological functions, which given sampling constraints, are often assessed by an indicator parameter rather than a quantitative flux (e.g. spot vs. continuous sampling of soil greenhouse gas emissions).

The farmscape, the land use system of a single farm, is an intermediate scale for studying biodiversity and ecosystem functions at the landscape level (Asteraki et al., 2004; Feehan et al., 2005). The farmscape unit allows for replicate plot level observations of some functions while serving as an indicator of ecological processes at larger scales (Herzog, 2005). Local experiences and farmer experimentation with biodiversity-based production systems exist in many farmscapes (Cardoso et al., 2001; Pacini et al., 2003; Harvey et al., 2005; Méndez et al., 2007; Henry et al., 2009). These approaches provide opportunities to analyze the relationship between the biodiversity of different sets of taxa, management and multiple ecosystem functions and show the tradeoffs that occur when some functions are provided at the expense of others. Understanding these tradeoffs will help prioritize biodiversity management options that are most likely to ensure long-term sustainability (Jackson et al., 2007).

In the United States, the term "farmscaping" has been adopted to refer to managing the farmed landscape for positive environmental outcomes (Imhoff, 2003). Farmscaping can enhance biodiversity and improve specific ecosystem functions. Hedgerows conserve plant biodiversity (Le Coeur et al., 2002), improve climate regulating services such as decreasing carbon dioxide (CO_2) and nitrous oxide (N_2O) emissions (Robertson et al., 2000; Falloon et al., 2004), increase carbon (C) storage (Follain et al., 2007), and increase water infiltration and quality (Caubel et al., 2003). Grassed waterways and tailwater ponds or wetlands can improve the water quality of effluent from agricultural lands (Braskerud, 2002; Jordan et al., 2003; Blanco-Canqui et al., 2004; O'Geen et al., 2007). Vegetated field margins can harbor insects that regulate pests or increase pollination (Olson and Wackers, 2007).

Farmscaping often involves planned biodiversity-based practices such as woody perennial plantings to increase associated diversity of birds (Vickery et al., 2002), mammals (Michel et al., 2007), and pollinators (Kremen et al., 2004). For belowground organisms, the relationship between farm habitats and biodiversity is more complex, because soil organisms are rarely planned components of biodiversity. Also, they perceive scale in different ways, depending on their size, movement, and mode of dispersal (Brussaard et al., 2007). The composition of soil microbial and faunal communities can be affected by management, particular plant functional groups (e.g. legumes, grasses, or woody perennials), or plant life history (e.g. native perennial vs. non-native annual species) (Hooper et al., 2000; Steenwerth et al., 2003; Broz et al., 2007; Sánchez-Moreno et al., 2008). Alternatively, there may be no link if restoration activities are recent, or if the setting is in a simplified landscape with little overall biodiversity (Wardle and van der Putten, 2002; Tscharntke et al., 2005; Wardle et al., 2006).

This case study examines how farmscaping may increase biodiversity and ecosystem functions related to soil and water quality in the various production and non-production habitats of an organic farm. Participatory research provided a way to focus on management practices that were considered important by the farmer and local agencies involved in biodiversity and natural resource conservation (Robins et al., 2002), i.e., riparian forest conservation, hedgerows of native shrubs, and vegetated tailwater ponds. Farmscaping practices with native perennial plant species were expected to result in greater biodiversity of plants, nematodes, and microbes (based on phospholipid fatty acid (PLFA) analysis which provides a profile or 'fingerprint' of specific groups and activities (Bossio et al., 1998; Ferris et al., 2004; Brussaard et al., 2007). In turn, higher biodiversity was expected to be associated with increased ecosystem functions related to crop production and environmental quality. Indicators of ecosystem functions were chosen that were

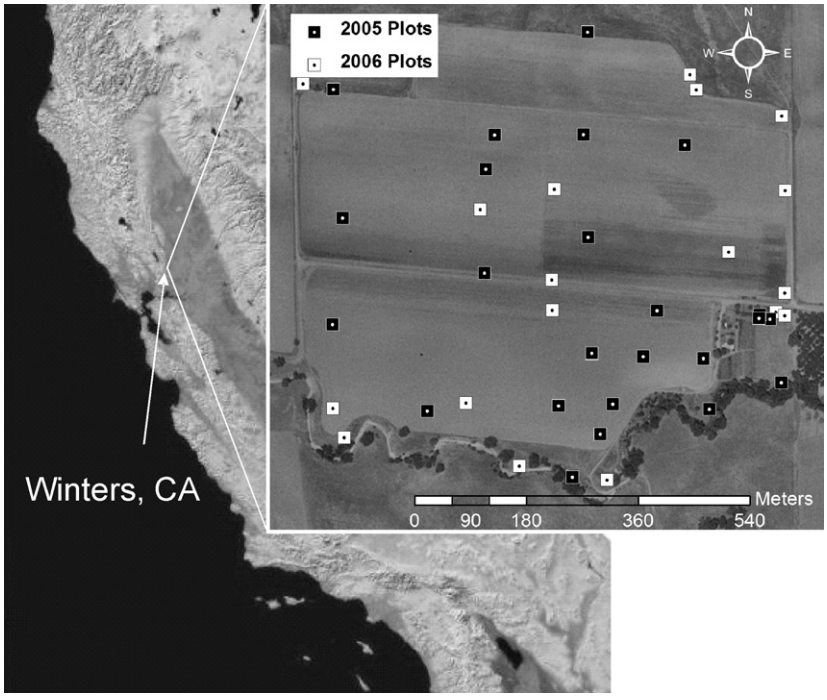

Fig. 1. Sampling map and location of the organic farm. The farm is located 5 km north of Winters, California, on the edge of the Central Valley. 42 plots were randomly stratified within six habitats across the 44 ha farmscape.

relevant to food provisioning services, soil and water quality regulating services, and supporting services to mitigate climate change (MA, 2005; Daily and Matson, 2008). Our specific objectives were to: (1) inventory the biodiversity of plant and soil organisms and the factors that contribute to their community assemblages across farm habitats; (2) monitor indicators of ecosystem functions in each of the habitats, such as periodic measurements of C stocks, soil CO_2 and N_2O emissions, nutrient availability, water infiltration, leaching, and sediment loss to waterways; and (3) identify potential tradeoffs in biodiversity and ecosystem function under putative management scenarios (e.g. hypothetical adoption of one or more farmscaping practices), by scaling results to the entire farmscape.

2. Materials and methods

2.1. Site description

The farmscape is located on an alluvial fan along the riparian corridor of Chickahominy Slough, 5 km north of Winters, California, USA, at the western edge of the Sacramento Valley (38°35′38.82″N, 122°0′45.47″W) at an elevation 72 m above sea level (Fig. 1). The farm has been in organic tomato and grain production since 1993. The Mediterranean-type climate has cool, wet winters and hot, dry summers. The average minimum and maximum air temperature between March, 2005, and April, 2007, was 8.7 and 23.6 °C, respectively. In the first year of the experiment (March 2005–April 2006), rainfall was high (863 mm), and the following year (April 2006–April 2007) was low (213 mm), compared to average precipitation (508 mm for the previous 5 years).

On the 44-ha farm, six distinct habitats were delineated with a handheld geographical position system (GPS) unit. Two habitats were dominated by perennial vegetation: a riparian corridor (2.48 ha) and hedgerows (0.16 ha) scattered around the fields (Fig. 1). The riparian forest on the edge of the farm is at least 80 years old as determined by aerial photos (Laval Company, 1937). As the entire farm is on a dissected alluvial fan, 10 m above the strongly incised stream channel, deposition of recent sediment is confined to the riparian corridor. Two production fields were to the north (26.5 ha) and south (14.7 ha) of a paved road in the center of the farm. Two habitats were related to irrigation, i.e., two tailwater ponds (0.06 ha) and several km of drainage ditches (0.02 ha) at the eastern edge of the fields.

The farm is mapped as a single soil type, a Tehama silt loam (fine-silty, mixed, superactive, thermic Typic Haploxeralfs; Soil Survey Staff, 2006). To confirm this classification, two soil profiles were excavated in both agricultural fields, and one soil profile in each of other the habitats, in the spring of 2005. Soil samples (approximately 1 kg) from each horizon were ground and analyzed for total C and nitrogen (N) with a combustion gas analyzer (Pella, 1990), and soil texture by laser diffraction (Eshel et al., 2004). Laboratory results and field descriptions of soil profiles were used to classify the soils (Soil Survey Staff, 2006).

2.2. Management of farm habitats

The woody non-cropped habitats (i.e., riparian corridor and hedgerows) received no management inputs. In these habitats, herbaceous plants are dead or dormant during the 6-month drought from late spring through early fall. The riparian corridor is remnant vegetation, with no history of planting of woody or herbaceous species. For the hedgerows, all the native shrubs and perennial grasses were planted in 1993, with no subsequent additions (see Appendix B). The hedgerows occur as isolated groups of shrubs scattered throughout the perimeter of the production fields. The understory is mowed along the perimeter of the hedgerows at least once each year.

The production fields are in alternate year rotation between oat and processing tomatoes. Compost (C:N ratio of 9.7) and cover crops are used as nutrient inputs. Tomato fields are laser leveled before preparing beds and subsequent field management consists of mechanical weeding/cultivation, manual weeding, a sulfur application if needed for disease, and furrow irrigations at intervals of about 10 days (see Smukler et al., in revision for more detail).

2.3. Spring inventory of biodiversity and soil properties

Plant and soil biodiversity and soil properties were inventoried in March of 2006 and 2007 to capture annual variation at the most uniformly active period of the year across all the sites. This is the warmest period of the rainy season, and irrigation has not begun, so the moisture regime was expected to be most similar across all farm habitats.

In both years, ArcGIS (ESRI, Inc., Redlands, CA, USA) was used to create a stratified random sample within each habitat type. The GPS sampling points ($n = 24$ in year 1 and $n = 18$ in year 2) served as the center of 16 m^2 plots. Within each plot, four 0.5 m × 0.5 m subplots were established in each cardinal direction randomly from the center at 0.5 m intervals.

Percent vegetation cover for each plot was recorded by species at each canopy layer, and herbaceous plants were clipped from each subplot, oven-dried at 60 °C, and composited before analysis. Plant species were classified into six broad functional groups: non-native legumes, non-native grasses, non-native forbs, native grasses, native forbs, and native woody-perennials (Appendix B). Soil cores were taken from each subplot at 0–15 cm and 15–30 cm depths, composited, and put on ice for transportation to the University of California, Davis, for analysis of nematodes, microbial communities based on PLFA analysis, and soil physicochemical properties (see below).

At the northwest corner of each plot a pit (30 cm × 30 cm × 25 cm deep) was rapidly excavated, and the soil was hand-sorted for earthworms. Specimens were transported back to the lab for cleaning, weighing, and identification of clitellate adults according to Schwert (1990).

An intact soil monolith (100 cm^2 × 15 cm deep) was excavated at this time from the edge of each pit and carefully placed in a sealed container and transported back to the laboratory for aggregate fractionation. Bulk density was determined at 0–6 cm, 9–15 cm, and 18–24 cm depths, using rings of 345 cm^3 volume to remove intact soil cores (Blake and Hartge, 1986).

2.4. Laboratory analysis for spring inventory of biodiversity and soil properties

Within 24 h, soil samples were homogenized in the laboratory on ice, and then separated into subsamples for biological and physiochemical analysis. Subsamples were stored at 4 °C for nematodes, and −20 °C for PLFA before extraction.

Nematodes were extracted using the sieving and Baermann funnel methodology (Barker et al., 1985). Nematodes were identified to genus and classified into five functional groups: bacterial feeders, fungal feeders, plant-parasites and herbivores, predators, and omnivores (Sánchez-Moreno et al., 2008). Phospholipid fatty acid (PLFA) extraction and analysis for microbial community composition followed the protocol of Bossio et al. (1998), and biomarkers were classified into functional groups of actinomycetes, gram+, gram−, fungi, or those that were unclassified (Bossio et al., 1998; Potthoff et al., 2006).

For plants, nematodes, and PLFA biomarkers, plot biodiversity was determined by richness (i.e. the total number of taxa) and by

the Shannon-Wiener diversity index (Shannon, 1948). It should be noted that the PLFA biomarkers are not directly equivalent to taxa, although some are characteristic of specific groups. The diversity across habitats was calculated as the number of unique taxa (or PLFA biomarkers) for each habitat (i.e. found only in that habitat) (Koleff et al., 2003).

Within 24 h, soil was analyzed for gravimetric moisture, and KCl-extractable ammonium (NH_4^+-N) and nitrate (NO_3^--N) colorimetrically (Foster, 1995; Miranda et al., 2001), or incubated anaerobically for 7 days to determine potentially mineralizable nitrogen (PMN) (Waring and Bremner, 1964). Microbial biomass carbon (MBC) was measured by fumigation extraction according to Vance et al. (1987), but with C analysis on a Dohrmann Phoenix 8000 UV-persulfate oxidation analyzer (Tekmar-Dohrmann, Cincinnati, OH).

Air-dried subsamples were analyzed for electrical conductivity (EC) (Rhoades, 1982), pH using a 1:1 ratio of soil to deionized water (USSL, 1954). Olsen phosphorus (P) was determined using the methods outlined by Olsen and Sommers (1982) and total C and N using a dynamic flash combustion system coupled with a gas chromatograph at the University of California Agriculture and Natural Resources (ANR) Analytical Laboratory. Vegetation samples were analyzed similarly for total C and N.

Intact soil monoliths were passed through an 8-mm sieve by gently breaking the soil clods by hand along natural fracture lines, then air dried. This soil was wet sieved into four fractions (Elliott, 1986): large aggregates (>2000 μm), small macroaggregates (250–2000 μm), microaggregates (53–250 μm), and the silt and clay fraction (<53 μm). A weighted average for the oven-dried soil mass of each fraction was calculated to obtain mean aggregate diameter, an indicator of aggregate stability (van Bavel, 1949).

2.5. Two-year assessment of indicators of ecological functions

Monitoring of indicators of ecological functions began immediately after the biodiversity inventory in March, 2005, and continued until April, 2007. Sampling took place in the same 16 m^2 plots for each habitat described above.

Gas emissions (CO_2-C and N_2O-N) from the soil surface were monitored on the ~13th day (+/− 2 days) of each month for the entire two-year period using closed chambers consisting of PVC collars that were pounded into the soil surface between 6 to 24 h before sampling and then removed to avoid disturbance by farming operations (Hutchinson and Livingston, 1993). Soil emissions were sampled from the production fields on the beds between plants, and in the ditches and tailwater ponds randomly within the plot when water was not present, or if present, within 6 cm of water's edge using a LI-COR 8100 fitted with a portable survey chamber 10 cm in diameter (LI-COR Biosciences, Lincoln, NE) and static closed chambers (Livingston and Hutchinson, 1995). The CO_2 samples taken by the LI-COR 8100 were analyzed in the field at 3-min intervals. One sample was taken from the closed chamber at 0 and 30 min with glass syringes and stored in over-pressurized vacutainers for <2 week. Concentrations of CO_2-C were determined using a gas chromatograph (GC) with a thermal conductivity detector (HP 5890, Hewlett Packard, Palo Alto, CA). Samples of CO_2-C from the two methods were treated as duplicates and reported as means. Analysis of N_2O was on a HP 6890 gas chromatograph (Hewlett Packard, Palo Alto, CA).

For sampling C stocks in woody plants, the 2.5 ha riparian corridor was stratified equally into six sampling areas, based on distance from the eastern edge of the farm. All hedgerow areas were sampled. Within each sampling area, all woody plants were sampled. Carbon stocks were categorized into six pools: standing live tree aboveground biomass, standing live tree belowground biomass, shrub and herbaceous understory aboveground biomass, standing dead trees, litter and duff, and soil (California Climate Action Registry, 2009). Biomass determinations for woody plants included stems, branches, leaves, and both live and dead roots in the case of trees, and coarse roots for shrubs (Cairns et al., 1997; California Climate Action Registry, 2009). Biomass for each tree was calculated using the allometric equations provided for C inventories of California forests (California Climate Action Registry, 2009) based on measuring the diameter at breast height (DBH) at 1.3 m above the ground. Belowground live tree root biomass was estimated using the equation developed by Cairns et al. (1997). Carbon was calculated as 50% of tree dry biomass (IPCC, 2006). For the one dead standing tree found on the farm, C was determined using the same methodology as live trees.

For C stored in all understory and hedgerow shrubs, biomass was calculated based on the shrub volume, which was estimated using the length of the longest diameter, its perpendicular length, and the shrub height (Appendix B). Allometric equations that relate shrub volume to total measured above- and below-ground biomass followed Cleary et al. (2008), but were based on sampled C content of leaves, wood, and roots for shrub species in the region.

In each subplot, litter (<2.5 cm) and duff was collected within a 30 cm diameter PVC ring. Dead downed branches up to 15 cm diameter were collected for the entire subplot. These materials were dried, weighed, chipped, ground, and analyzed for total C to determine surface litter and duff C pools. Soil C ($g\,m^{-2}$) was calculated for 0–15 cm depth using observed C concentrations and the mean of the bulk density measurements taken at 0–6 cm and 9–15 cm. For the 15–30 cm depth, bulk density taken at 18–24 cm depth was used.

Surface runoff was monitored for summer irrigation and winter storm events with ISCO 6700 (Teledyne Isco, Inc., Lincoln, NE) automated water samplers fitted with low-profile area flow velocity meters, and with targeted grab samples. Samplers were placed in four strategic locations on ditches and tailwater ponds to determine the influx and discharge of water and sediment into the tailwater pond, and the effectiveness of the tailwater pond to reduce sediment losses to the adjacent riparian habitat. During irrigation, 250 mL samples were taken every 4 h and composited daily. During storm events, autosamplers were programmed to capture initial flush of sediments accurately. Autosamplers initially were set to sample every 5 min for 30 min, then switched to sampling after every 1000 L of discharge. A total of 583 runoff samples were collected. Water samples were immediately put on ice, transported back to the laboratory and frozen. For thorough mixing of solids, a 50 mL subsample was pipetted while vortexed, then was suction-filtered through a 0.7 μm pore size glass fiber filter (GF75; Advantec, Tokyo, Japan). Total suspended solids (TSS) were calculated from differences in pre-filter and post-filter dry weights (Clesceri et al., 1998). Volatile suspended solids (VSS) were calculated from the difference in pre- and post-ignition filter weights. A separate subsample was analyzed for EC, pH, NH_4^+-N, NO_3^--N, (see above), dissolved reactive phosphate (DRP) colorimetrically (Murphy and Riley, 1958), and dissolved organic C (DOC) using a using a Dohrman DC-190 total organic C analyzer (Tekmar-Dohrmann, Cincinnati, OH).

Soil solute leaching was assessed in two ways: ceramic cup suction lysimeters (Soil Moisture Corp., Santa Barbara, CA) which were deployed in each randomized plot (Fig. 1) at a depth of 30 and 60 cm (Jackson, 2000), and anion exchange resin bags for cumulative NO_3^--N losses (Wyland and Jackson, 1993). Lysimeters were sampled weekly during periods when the soil was saturated (e.g. summer irrigation and the winter rainy season). Resin bags were set within a 7.62 cm diameter PVC ring, packed into a shelf dug into the side of the pit at 75 cm under an undisturbed soil profile. Bags

were collected in the spring and fall of the two years, and extracted with 2 M KCl for NO_3^--N analysis.

Cumulative infiltration rates were determined in single ring infiltrometers (25 cm dia.) that were pounded evenly into the soil to 20 cm depth. One reading was made per plot. Water was continuously added, and the rate of falling head was recorded for at least 30 min (Bouwer, 1986).

Tomato yields were sampled within 3 days before the farmer's harvest. To capture yield variability across the field, transects were oriented north-south of each main sampling plot (393 m in the North Field or 250 m in the South Field). Along each transect, a 1 m × 3 m sub-plot was established at 30-m intervals (five or nine sub-plots depending on the width of the field). At each sampling point, individual tomato plants were cut at the base and the fruit separated by hand. Biomass of fruits, tomato vegetative material, and weed biomass were weighed in the field (fresh weight) then subsampled and dried at 60 °C for 2 week, before grinding and analyzing for total C and N (see above).

2.6. Sampling design and statistical analysis

Due to the differences in relative size of the habitats, randomization inevitably resulted in some plots being closer together in particular habitats than in others (e.g., the largest distance between plots was 775 m, while the smallest distance was 22 m) creating a situation where pairs of locations could be more (positively autocorrelated) or less similar (negatively autocorrelated) than others.

Specific statistical approaches were used to address this potential spatial autocorrelation due to the uneven distribution of sampling units, which implies that standard assumptions of independence of random pairs could not be upheld (Legendre, 1993). When testing for differences in biodiversity or ecosystem function among habitats a mixed model ANOVA was employed that incorporated a spatial covariance structure. The *proc mixed* statement in SAS (SAS, 2003) combined with a power correlation function (*POW*) model enables spatial location to be used as a covariate. The *POW* model uses a one dimensional (1-D) isotropic power covariance term based on using the Universal Transverse Mercator (UTM) *X*, *Y* coordinates for each plot (Self and Liang, 1987; Wolfinger, 1993). This methodology has been tested against other spatial and non-spatial models in agricultural systems and is an effective way to deal with spatial covariance (Casanoves et al., 2005; Bajwa and Mozaffari, 2007). The *proc mixed* models were first run with all 42 sampling points (two years of data together) including *habitat*, *year*, and *year* × *habitat*, after checking for homogeneity of variance, and conducting log transformations if necessary. Graphs illustrate untransformed data. If there were no significant interactions between year and habitat, the two-year mean was reported. Otherwise, each year was analyzed separately and results are reported as year 1 (March 1, 2005–March 31, 2006) and year 2 (April 1, 2006–April 1, 2007).

To further explore the environmental variables that were important for species/taxa assemblages across the farmscape, Partial Canonical Correspondence Analysis (CCA), a method of partial (constrained) ordination analysis was employed (Legendre, 1993). The partial CCA concurrently uses ordination and regression to assess the relationship between variables, but also accounts for potential spatial autocorrelation by removing, through multiple linear regression, the effects of known or undesirable variables, called covariables, which in this case are spatial coordinates of each sampling point. A matrix of spatial covariables was developed as suggested by Borcard et al. (1992) using *x* and *y* (the difference of UTM coordinates of each plot from the UTM coordinate at the southeast corner of the farmscape) as variables for a cubic surface regression, that then is used to generate a best-fit equation for each type of biota (see Section 3):

$$f(x,y) = b_1x + b_2y + b_3x^2 + b_4xy + b_5y^2 + b_6x^3 + b_7x^2y + b_8xy^2 + b_9y^3.$$

For each species/taxa dataset, a CCA was run four times: with environmental variables only ('environmental'); with spatial variables based on the regression of UTM coordinates only ('spatial'); with environmental variables constrained by spatial covariables ('environmental variables partial'); and with spatial covariables constrained by environment ('spatial partial'). In the first two types of CCA runs, a forward selection process was used to identify those variables that were significant ($P < 0.05$) using a Monte Carlo permutations test run 499 times. Constraining each analysis by one set of explanatory variables (i.e. environmental or spatial) enabled the partitioning of the variation in species/taxa distribution into four classifications: environmental only, spatial and environmental, spatial only and unexplained variation. These partitions were calculated as follows, where the variation for each component is the sum of all canonical eigenvalues and the total inertia is the total variation of the model:

1. Environmental variation only	'environmental variable partial' × 100 total inertia
2. Spatially structured environmental variation	$\frac{\text{'environmental'} - \text{'environmental variable partial'} \times 100}{\text{total inertia}} = \frac{\text{'spatial'} - \text{'spatial partial'} \times 100}{\text{total inertia}}$
3. Spatial variation only	$\frac{\text{'spatial partial'} \times 100}{\text{total inertia}}$
4. Unexplained variation	1 − (the sum of the variation of 1–3)

The total inertia is measured by the chi-square statistic of the sample-by-taxa table divided by the table's total (ter Braak and Smilauer, 1998). The overall measure of the CCA fit is determined by dividing the sum of all canonical eigenvalues by the total inertia thus giving the percentage of total variance in the species/taxa dataset that is explained by the explanatory variables (ter Braak and Smilauer, 1998). This method was also used to calculate the proportion of the total inertia in the species/taxa data that is explained by each canonical axis. To test the significance of canonical axes an unrestricted Monte Carlo permutation was used. As these tests are not dependent on parametric distributional assumptions (Palmer, 1993), species/taxa data were not transformed, and environmental and spatial variables were simply standardized.

3. Results

3.1. Plant and soil biodiversity

Only 61 species of plants were observed across the entire farmscape. Each habitat had an average of only 11 plant species, with on average, more non-natives (8 species) than natives (3 species) (Table 1; Appendix B). The largest number of unique species was in the riparian corridor. The perennial habitats (i.e., the riparian corridor and hedgerow) had higher diversity of native plant species than the production fields, with the irrigation habitats intermediate. The Shannon-Wiener diversity index for native vegetation differed between years and by habitat. For native species richness, there was a year × habitat interaction. Non-native plant species were generally more abundant in the irrigation habitats, especially the tailwater pond, than elsewhere. Most of these species are annuals. The Shannon-Wiener diversity index for non-natives differed by habitat depending on year (Table 1). High cover of non-natives in the South Field was largely due to volunteer oats from previous crops (Fig. 2).

Table 1
Vegetation biodiversity by native, non-native, and all plant taxa.

		Shannon-Wiener diversity index			Species richness			Unique taxa[b]
		Native	Non-native[a]	All vegetation	Native	Non-native	All vegetation	
Year (*P* value)		<0.001	ns	ns	ns	0.013	ns	
Habitat (*P* value)		<0.0001	<0.0001	<0.0001	ns	<0.001	0.016	
Habitat × Year (*P* value)		ns	0.043	0.017	<0.01	ns	ns	
Habitat[c]	Year	$\bar{x} \pm$ SE	$\bar{x} \pm$ SE	$\bar{x} \pm$ SE	$\bar{x} \pm$ SE	$\bar{x} \pm$ SE	$\bar{x} \pm$ SE	Σ
Riparian Corridor	2005	0.24 ± 0.03a	0.29 ± 0.09	0.59 ± 0.11a	4 ± 1.2ab	6 ± 1.2bc	10 ± 1.5ab	10
	2006		0.23 ± 0.04yz	0.41 ± 0.03xy	3 ± 0.6x			
Hedgerows	2005	0.25 ± 0.05a	0.35 ± 0.07	0.68 ± 0.07a	5 ± 0.3a	10 ± 1.2ab	14 ± 1.1a	8
	2006		0.30 ± 0.02xyz	0.46 ± 0.01x	2 ± 0.6xy			
South Field	2005	0.04 ± 0.01bc	0.13 ± 0.01	0.18 ± 0.02b	2 ± 0.3b	7 ± 0.8b	10 ± 1.0ab	0
	2006		0.06 ± 0.02z	0.08 ± 0.01y	4 ± 0.0x			
North Field	2005	0.02 ± 0.01c	0.13 ± 0.02	0.16 ± 0.03b	2 ± 0.5b	6 ± 0.7c	8 ± 1.0b	0
	2006		0.32 ± 0.05xy	0.34 ± 0.05xy	3 ± 0.5x			
Tailwater Pond	2005	0.09 ± 0.03b	0.32 ± 0.14	0.42 ± 0.17ab	3 ± 0.9ab	11 ± 1.1a	13 ± 1.5ab	3
	2006		0.58 ± 0.13xy	0.65 ± 0.16x	1 ± 0.6y			
Ditches	2005	0.03 ± 0.01bc	0.34 ± 0.07	0.38 ± 0.07ab	3 ± 0.3ab	11 ± 1.5a	13 ± 1.5ab	3
	2006		0.45 ± 0.10xy	0.47 ± 0.11x	3 ± 0.3xy			
Farmscape[d]	2005–2006	0.10 ± 0.02	0.27 ± 0.03	0.37 ± 0.03	3 ± 0.2	8 ± 0.5	11 ± 0.6	61

[a] Non-native diversity was analyzed separately due to the habitat by year interactions but there were no significant differences in 2005.
[b] Unique taxa are found only in one habitat.
[c] Differences between habitats were compared using ANOVA. If there were significant interactions between habitat and year, the means and analysis of each year are shown separately. Different letters indicate significant differences using Tukey's Honestly Significant Difference Post Hoc test (abc for 2005 and xyz for 2006).
[d] Values for the farmscape are summed means of all habitats.

Considering total plant diversity (natives + non-natives), no habitat consistently had higher plant diversity across both years of sampling (Table 1). In 2005, diversity was highest in the perennial habitats, followed by the irrigation habitats, and then the production habitats. In the drier year, 2006, the irrigation habitats along with the hedgerow were the most diverse, and only the South Field had significantly lower values. Thus, total plant species richness was not a definitive measure for the differences in plant communities across the farmscape.

Plant cover tended to be higher in the habitats with woody perennials (Fig. 2), especially as compared to the ditches and tailwater ponds. Native woody perennials had higher cover in the riparian and hedgerow habitats (data not shown). The cover of various life history/functional groups of herbaceous plants (e.g., legumes,

Table 2
Indicators of belowground biodiversity for earthworms, nematodes, and microbial community biomarkers (PLFA).

		Earthworms			Nematodes			PLFA	
		Shannon-Wiener diversity index	Richness	Unique species[a]	Shannon-Wiener diversity index	Richness	Unique taxa[a]	Number of PLFA	Unique PLFA[a]
Year (*P* value)		<0.01	<0.01		ns	ns		<0.001	
Habitat (*P* value)		ns	ns		0.027	<0.01		<0.01	
Habitat × Year (*P* value)		0.021	0.017		ns	ns		ns	
Habitat[b]	Year	$\bar{x} \pm$ SE	$\bar{x} \pm$ SE	Σ	$\bar{x} \pm$ SE	$\bar{x} \pm$ SE	Σ	$\bar{x} \pm$ SE	Σ
Riparian Corridor	2005	0.05 ± 0.05b	1 ± 0.3abc	0	0.23 ± 0.01ab	15 ± 1.0a	4	43 ± 2.2	2
	2006	0.09 ± 0.09x	1 ± 0.6x	0					
Hedgerows	2005	0.30 ± 0.10ab	2 ± 0.3ab	0	0.22 ± 0.01b	15 ± 1.1a	2	43 ± 1.2	0
	2006	0.00 ± 0.00x	0 ± 0.3x	0					
South Field	2005	0.33 ± 0.02a	3 ± 0.2a	0	0.25 ± 0.00a	13 ± 1.1ab	2	45 ± 2.1a	10
	2006	0.00 ± 0.00x	0 ± 0.3x	0					
North Field	2005	0.20 ± 0.06b	2 ± 0.3ab	0	0.23 ± 0.00ab	13 ± 0.7ab	0	40 ± 0.8b	0
	2006	0.00 ± 0.00x	1 ± 0.3x	1					
Tailwater Pond	2005	0.09 ± 0.09ab	1 ± 0.7bc	0	0.23 ± 0.01ab	10 ± 1.2ab	1	40 ± 2.3b	1
	2006	0.10 ± 0.10x	1 ± 0.6x	0					
Ditches	2005	0.00 ± 0.00b	0 ± 0.0c	0	0.25 ± 0.01ab	11 ± 1.1b	0	41 ± 1.0	1
	2006	0.00 ± 0.00x	0 ± 0.3x	0					
Farmscape[c]	2005	0.19 ± 0.03	1 ± 0.3	4	0.24 ± 0.00ab	13 ± 1.0	37	42 ± 1.6	77
	2006	0.03 ± 0.02	1 ± 0.4						

[a] Unique earthworm species, nematode taxa, or PLFA are found only in one habitat.
[b] Differences between habitats were compared using ANOVA. If there were significant interactions between habitat and year the means and analysis of each year are shown separately. Different letters indicate significant differences using Tukey's Honestly Significant Difference Post Hoc test (abc in 2005 and xyz in 2006).
[c] Values for the farmscape are summed means of all habitats.

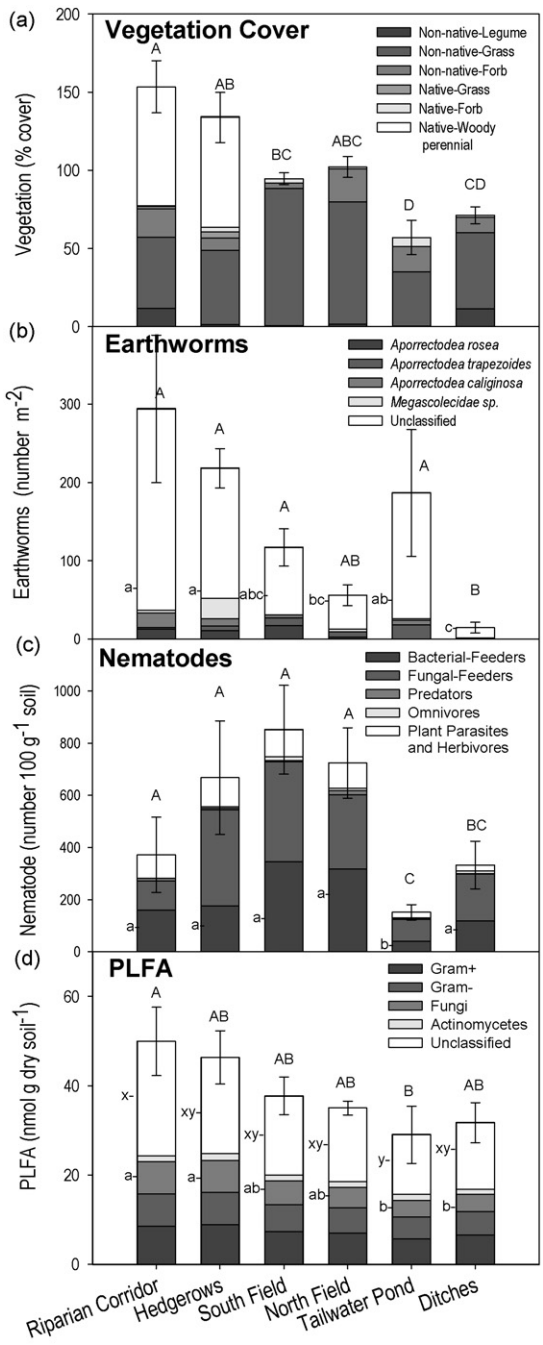

Fig. 2. Abundance of plant and soil taxa in each habitat. (a) Vegetation % cover classified by functional group; (b) earthworm species; (c) nematodes classified by functional group; and (d) microbial community composition classified by PLFA biomarker functional groups. Different letters indicate significant differences at $P < 0.05$, with upper case for totals and lower case for each group. Untransformed data are shown.

grasses, and forbs) was not significantly different among the habitats, and there was high interannual and spatial variation in cover and total herbaceous plant biomass within each habitat, especially for the annual plant species (data not shown).

Only four earthworm species were present; all were exotic species which predominate in disturbed agroecosystems throughout North America (Edwards et al., 1995): *Aporrectodea rosea, A. trapezoides, A. caliginosa*, and an unidentified species in the *Megascolecidae*. The two years of sampling differed for both species richness and Shannon-Wiener diversity index (Table 2). Habitats differed only in 2005: three of the four species were found in the South Field, compared to two in the hedgerows and North Field, one in the riparian corridor and tailwater pond, and none in the ditches. *A. rosea* was only found in the North Field. Earthworm abundance was highest in the riparian corridor, and lowest in the ditches (Fig. 2), but otherwise was not different across the habitats.

There were 37 different nematode taxa in the farmscape (Table 2; Fig. 2; Sánchez-Moreno et al., 2008). Richness of nematode taxa was similar in all habitats but tended to be greater in the riparian corridor. Hedgerows tended to be higher than the irrigation ditches, with the crop fields intermediate (Table 2). The Shannon-Wiener diversity index, however, was highest in the South Field and lowest in the hedgerows, where there were few but very abundant species/taxa. In the riparian corridor, there were four unique taxa found in no other habitats, compared to two in the hedgerows and South Field, one in the tailwater pond, and zero in the North Field and ditches. Total nematode abundance was higher in the riparian corridor, hedgerows, and the two production fields, compared to the tailwater pond and drainage ditch habitats (Fig. 2). Thus, abundance differed among the habitats, despite the lack of strong patterns in the diversity of nematode taxa.

The number of PLFA biomarkers was generally similar between perennial and production habitats, but in the tailwater pond there were fewer distinct PLFA, and lower total PLFA compared to the other habitats. A total of 77 different PLFA biomarkers were sampled across the entire farmscape at the 0–15 cm depth (Table 2). Higher numbers of PLFA biomarkers were observed in the South Field than the North Field and the tailwater pond. The South Field had 10 unique biomarkers, while the riparian corridor had only two, and the tailwater pond and drainage ditches had one. In both years, PLFA markers for unclassified, fungi, and total PLFA, a measure of microbial biomass, were highest in the riparian corridor and lowest in the tailwater pond, with the other habitats intermediate (Fig. 2). PLFA showed surprisingly little consistent difference in number, abundance, or unique biomarkers across habitats.

3.2. Soil profiles and properties

Soils in all habitats were classified the same at the subgroup level (Typic Haploxeralfs), with the exception of the tailwater ponds, which were classified as Aquic Haploxeralfs due to the redox depletions found in several horizons (data not shown). Each year's samples had similar soil texture across the habitats (Table 3), but as an artifact of sampling, the year*habitat interactions for sand and silt indicate a slight difference between years. Overall, this confirmed the assessment (Soil Survey Staff, 2006) that the entire farmscape had a very similar soil type and soil texture.

Soil moisture was similar among the habitats at the 0–15 cm depth during the biodiversity inventory periods in March of each year, with a mean of 0.26 g water g^{-1} dry soil. Sampling was intentionally conducted within a week of a rainfall event to minimize moisture differences among habitats and only the 15–30 cm depth of the tailwater pond had higher moisture content. Differences between other soil parameters were minor (Table 3). Bulk density was fairly similar across most of the habitats except for higher values in ditches than in the riparian corridor at 0–15 cm depth. Soil pH was not different among habitats at either depth. Electrical conductivity (EC) at 0–15 cm depth was low throughout the farmscape. Neither total N nor Olsen P differed among habitats. Aggregate stability, however, was significantly higher in the hedgerows than all other habitats.

All habitats had low concentrations of NO_3^--N and NH_4^+-N during the March biodiversity inventory periods, always $\leq$10 kg N ha^{-1} (Table 4). Soil NO_3^--N, NH_4^+-N, and PMN were generally highest in the perennial habitats. In 2006, the riparian corridor had higher NO_3^--N than any of the other habitats, but only at the 0–15 cm depth. For NH_4^+-N in 2005, highest values at 0–15 cm

Table 3
Soil physical and chemical properties at the 0–15 and 15–30 cm depths measured in March 2005 and March 2006[a].

	Depth (cm)	pH	EC ($\mu S\,cm^{-1}$)	Total N ($Mg\,ha^{-1}$)	Total C ($Mg\,ha^{-1}$)	Olsen-P ($\mu g\,g^{-1}$)	Sand (%)	Silt (%)	Clay (%)	Aggregates MWD[b] (μm)	Bulk density ($g\,cm^{-3}$)
Year (*P* Value)	0–15	ns	<0.001	<0.01	ns	ns	ns	ns	ns	ns	0.013
	15–30	<0.0001	<0.01	ns	ns	ns	0.036	<0.01	ns		0.022
Habitat (*P* Value)	0–15	ns	<0.01	ns	0.029	ns	ns	ns	ns	<0.0001	<0.01
	15–30	<0.0001	<0.01	ns	ns	ns	ns	ns	ns		<0.001
Habitat × year (*P* value)	0-15	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
	15–30	<0.0001	ns	ns	ns	ns	0.017	0.035	ns		<0.01
Habitat[c]		$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$
Riparian Corridor	0–15	7.50 ± 0.17	271.5 ± 33.5a	2.8 ± 0.5	32.3 ± 5.7a	44.6 ± 12.1	16.6 ± 8.3	65.5 ± 5.6	18.0 ± 3.7	1077 ± 141b	1.08 ± 0.06b
	15–30	7.30 ± 0.16	195.8 ± 21.6x	2.8 ± 0.4	26.8 ± 4.4	37.2 ± 12.6	8.5 ± 5.1	72.6 ± 3.6	18.9 ± 2.9		1.14 ± 0.06
Hedgerows	0–15	7.13 ± 0.07	166.7 ± 12.4b	2.7 ± 0.2	26.1 ± 2.1ab	28.2 ± 3.5	20.3 ± 7.0	64.4 ± 4.9	15.2 ± 2.4	2104 ± 182a	1.27 ± 0.03ab
	15–30	7.00 ± 0.04	110.9 ± 10.1y	2.3 ± 0.3	18.8 ± 2.4	15.7 ± 1.4	19.3 ± 5.8	66.3 ± 4.5	14.5 ± 2.8		1.40 ± 0.05
South Field	0–15	7.21 ± 0.04	138.4 ± 18.5b	2.5 ± 0.1	21.9 ± 1.3ab	33.7 ± 3.6	14.9 ± 3.9	70.7 ± 2.2	14.4 ± 2.0	965 ± 85b	1.20 ± 0.03ab
	15–30	7.23 ± 0.05	144.7 ± 8.5xy	2.6 ± 0.1	20.5 ± 1.1	28.3 ± 4.5	14.1 ± 4.8	67.1 ± 3.0	18.8 ± 2.1		1.33 ± 0.05
North Field	0–15	7.43 ± 0.09	120.2 ± 7.9b	2.5 ± 0.1	22.4 ± 1.0ab	31.4 ± 1.2	11.9 ± 3.2	72.6 ± 2.4	15.5 ± 1.7	982 ± 121b	1.31 ± 0.03a
	15–30	7.23 ± 0.10	123.4 ± 8.3y	2.6 ± 0.1	20.2 ± 0.6	28.9 ± 2.3	9.2 ± 3.0	74.2 ± 3.1	16.6 ± 1.8		1.37 ± 0.03
Tailwater Pond	0–15	7.24 ± 0.11	148.4 ± 11.1ab	2.3 ± 0.2	19.7 ± 2.2b	28.6 ± 5.1	8.1 ± 4.0	75.4 ± 2.3	16.6 ± 2.5	799 ± 144b	1.21 ± 0.10ab
	15–30	7.31 ± 0.12	163.5 ± 22.3xy	2.2 ± 0.2	17.8 ± 2.3	26.5 ± 6.0	5.9 ± 2.8	75.3 ± 1.3	18.8 ± 3.1		1.25 ± 0.10
Ditches	0–15	7.30 ± 0.08	133.7 ± 10.5b	2.5 ± 0.2	20.9 ± 2.0ab	44.9 ± 6.4	13.1 ± 4.1	70.0 ± 2.8	16.8 ± 1.3	899 ± 126b	1.35 ± 0.04a
	15–30	7.26 ± 0.12	130.0 ± 16.3y	2.9 ± 0.2	19.3 ± 1.6	38.0 ± 6.5	20.1 ± 7.0	66.5 ± 5.8	13.4 ± 1.3		1.50 ± 0.06

[a] The means of each year are analyzed together for each depth when there were no significant interactions between habitat and year.
[b] MWD refers to mean weight diameter of aggregates.
[c] Different letters indicate significant differences using Tukey's Honestly Significant Difference Post Hoc test, differentiating the habitats at 0–15 cm with abc and with xyz at the 15–30 cm depth.

Table 4
Mean soil nutrient indicators at the 0–15 cm and 15–30 cm depths measured in March 2005 and March 2006[a].

	Depth (cm)	NO_3^--N (kg ha^{-1})	NH_4^+-N (kg ha^{-1})	PMN[b] (μg g^{-1})	MBC[c] (μg g^{-1})
Year (*P* value)	0–15	<0.0001	<0.0001	ns	ns
	15–30	<0.01	ns	ns	<0.0001
Habitat (*P* value)	0–15	ns	<0.0001	<0.0001	<0.0001
	15–30	<0.01	<0.01	0.017	ns
Habitat × year (*P* value)	0–15	0.019	<0.0001	0.041	ns
	15–30	0.043	0.028	0.014	ns

Habitat[d]		2005 $\bar{x} \pm$ SE	2006 $\bar{x} \pm$ SE	2005 $\bar{x} \pm$ SE	2006 $\bar{x} \pm$ SE	2005 $\bar{x} \pm$ SE	2006 $\bar{x} \pm$ SE	2005–2006 $\bar{x} \pm$ SE
Riparian Corridor	0–15	5.5 ± 2.5	4.2 ± 1.3a	4.3 ± 1.0c	10.3 ± 0.5a	26.4 ± 12.2ab	83.4 ± 36.2a	380.1 ± 71.8a
	15–30	5.0 ± 1.5xy	1.8 ± 0.7	2.6 ± 0.7xyz	5.5 ± 0.6x	9.4 ± 4.3	24.3 ± 6.7x	138.4 ± 48.8
Hedgerows	0–15	3.2 ± 0.3	1.3 ± ±0.3b	8.4 ± 1.2a	6.1 ± 0.9	33.3 ± 9.5a	14.6 ± 4.4ab	273.9 ± 31.5a
	15–30	3.5 ± 0.5y	0.7 ± 0.2	4.6 ± 0.2x	3.3 ± 0.4x	17.3 ± 2.9	4.9 ± 1.1xy	140.1 ± 29.0
South Field	0–15	2.1 ± 0.2	0.4 ± 0.0b	2.7 ± 0.3c	2.7 ± 0.6	14.3 ± 2.8abc	7.8 ± 2.5b	242.3 ± 15.7ab
	15–30	2.9 ± 0.2y	0.4 ± 0.2	2.7 ± 0.3xyz	3.0 ± 1.6x	7.2 ± 2.4	4.9 ± 2.0x	201.2 ± 25.1
North Field	0–15	2.6 ± 0.2	0.6 ± 0.1b	4.3 ± 0.5c	5.0 ± 1.1b	15.2 ± 2.1abc	9.3 ± 0.8b	224.2 ± 7.9ab
	15–30	4.0 ± 1.0y	0.4 ± 0.2	1.9 ± 0.2xy	4.2 ± 0.9x	3.5 ± 1.0	24.5 ± 7.6x	184.7 ± 38.7
Tailwater Pond	0–15	2.2 ± 0.1	0.9 ± 0.3b	4.3 ± 0.8b	3.5 ± 0.9b	5.7 ± 2.9c	10.3 ± 5.8b	114.7 ± 25.2c
	15–30	4.2 ± 0.6xy	0.6 ± 0.1	3.2 ± 0.9xy	2.3 ± 0.5x	9.1 ± 8.9	2.8 ± 0.9y	119.5 ± 39.7
Ditches	0–15	5.0 ± 1.7	0.4 ± 0.2b	2.7 ± 1.4c	3.8 ± 1.6b	4.9 ± 2.1bc	4.9 ± 1.5b	129.0 ± 17.1bc
	15–30	15.4 ± 6.3x	0.4 ± 0.1	0.9 ± 0.2z	1.6 ± 0.7y	2.8 ± 1.6	9.1 ± 3.4x	127.0 ± 10.6

[a] The means of each year are analyzed together for each depth when there were no significant interactions between habitat and year.
[b] Potentially mineralizable N.
[c] Microbial biomass C.
[d] Different letters indicate significant differences using Tukey's Honestly Significant Difference Post Hoc test, differentiating the habitats at 0–15 cm with abc and with xyz at the 15–30 cm depth.

depth were in the hedgerows, with the lowest values in the ditches, and in 2006, the riparian corridor had higher NH_4^+-N than the North Field, tailwater pond, and ditch habitats. A few other differences occurred between habitats. For example, NO_3^--N at the lower depth (15–30 cm) was higher in the ditches than hedgerows, South Field, and North Field habitats in 2005. At 15–30 cm, NH_4^+-N was lowest in ditches. At the 15–30 cm depth, PMN was lowest in the tailwater pond, but only in 2006. Microbial biomass C was highest in the perennial habitats followed by the production habitats, with the lowest values in the irrigation habitats at the 0–15 cm depth, following the same general trends as inorganic N pools.

3.3. Species assemblages and relationship to environmental variables

The partial CCA analyses showed that environmental variables were much more important for determining the distribution of taxa (based on presence/absence data), than spatial location on the farmscape (Fig. 3). Environmental variables (e.g., surface litter, soil characteristics, and biota) accounted for 37.5, 51.4, 32.8, and 61.6% of the variation for distribution of plant species, earthworm species, nematode taxa, and PLFA biomarkers, respectively, across the farmscape. Spatial location was responsible for <12.5% of the variation, and this variation could be explained by a polynomial equation using *x,y* UTM coordinates that was unique to each group of biota (data not shown). The interaction of environmental + spatial variation varied considerably between types of taxa, and was far higher for the earthworms (28.8%) than for plants (1.5%), nematodes (6.1%), or PLFA (4.8%). For vegetation and nematode taxa, >50% of the variation was unexplained, indicating that the distribution of taxa was more complex than could be captured with our set of environmental indicators.

The next set of partial CCAs that were run for environmental variables constrained by spatial location as a covariate (i.e. spatial location is essentially removed from the analysis) showed that a unique set of environmental variables was related to the explained variation in distribution of taxa for each of the four different types of biota (Table 5). There were 10 to 18 environmental variables that were significant for each partial CCA for the first four axes.

Surface litter was an important environmental variable for explaining the distribution of taxa within each set of biota, but especially for nematodes (Table 5). Soil C also was a consistent factor explaining variation for all taxa and all partial CCA axes, but rarely with large effects. Soil infiltration rate and recent tillage were strongly associated with the variation in PLFA across the farmscape, and with plant species to some extent. Recent production of tomatoes explained some of the variation of earthworms and nematodes. Environmental variables related to soil N and P were of minor importance for determining the distribution of taxa across habitats; one exception was that soil NH_4^+-N was associated with

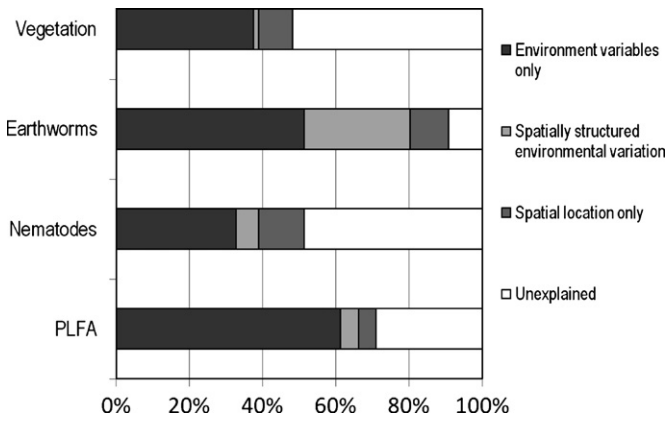

Fig. 3. Distribution of variation in the Partial Canonical Correspondence Analysis (CCA) for vegetation, earthworms, nematodes and PLFA biomarkers. Forward selection was used to identify the significant ($P < 0.05$) cubic surface regression to explain spatial data. See text for details.

Table 5
Coefficients of determination for Partial Canonical Correspondence Analysis (CCA) of environmental variables controlled for by spatial location covariates to explain the distribution of taxa[a].

Variable	Vegetation				Earthworms				Nematodes				Microbes (PLFA)			
	Axis 1	Axis 2	Axis 3	Axis 4	Axis 1	Axis 2	Axis 3	Axis 4	Axis 1	Axis 2	Axis 3	Axis 4	Axis 1	Axis 2	Axis 3	Axis 4
Cumulative Explained Variation (%)	32.0	50.3	63.3	72.6	51.1	71.5	86.7	100	25.1	46.1	63.0	76.2	30.0	52.2	64.2	73.8
Native Grass (% cover)	[b]	–	–	–	−0.31	−1.31	−0.24	0.19	ns[c]	ns	ns	ns	ns	ns	ns	ns
Native Forb (% cover)	–	–	–	–	0.59	−0.02	0.23	0.36	ns	ns	ns	ns	ns	ns	ns	ns
Native Woody Perennials (% cover)	–	–	–	–	−0.29	−1.04	0.84	−0.63	−0.87	−3.16	−0.63	1.61	0.80	0.97	1.02	−1.74
Non-native Forbs (% cover)	–	–	–	–	−0.16	0.00	0.81	0.31	ns	ns	ns	ns	ns	ns	ns	ns
Non-native Grass (% cover)	–	–	–	–	ns[c]	ns	ns	ns	3.11	1.98	5.64	−0.45	0.02	0.19	0.13	−0.17
Non-native Legume (% cover)	–	–	–	–	−0.43	−0.42	−0.52	0.44	−4.38	1.23	1.01	−0.24	ns	ns	ns	ns
Earthworms (biomass m^2)	ns	ns	ns	ns	–	–	–	–	ns	ns	ns	ns	0.16	−0.02	−0.70	0.41
PLFA Total (nmol g^{-1})	ns	ns	ns	ns	−0.12	−0.97	0.16	0.08	ns	ns	ns	ns	–	–	–	–
PLFA Unclassified (nmol g^{-1})[d]	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	–	–	–	–
PLFA Gram+ (nmol g^{-1})[e]	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	–	–	–	–
PLFA Gram− (nmol g^{-1})[f]	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	–	–	–	–
PLFA Fungi (nmol g^{-1})[g]	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	–	–	–	–
PLFA Actinomycetes (nmol g^{-1})[h]	ns	ns	ns	ns	ns	ns	ns	ns	5.08	−0.66	−1.58	−0.75	–	–	–	–
Nematodes Total (no. g^{-1})	0.01	0.66	−0.13	−0.02	1.37	−0.19	1.11	−0.58	–	–	–	–	1.47	−0.74	1.59	−2.61
Nematodes Bacterial Feeders (no. g^{-1})	ns	ns	ns	ns	ns	ns	ns	ns	–	–	–	–	−0.17	0.16	−0.04	1.86
Nematodes Fungal Feeders (no. g^{-1})	ns	ns	ns	ns	ns	ns	ns	ns	–	–	–	–	−0.66	0.79	−1.76	0.97
Nematodes Predators (no. g^{-1})	ns	ns	ns	ns	ns	ns	ns	ns	–	–	–	–	ns	ns	ns	ns
Nematodes Omnivores (no. g^{-1})	ns	ns	ns	ns	ns	ns	ns	ns	–	–	–	–	ns	ns	ns	ns
Nematodes Plant Parasites (no. g^{-1})	ns	ns	ns	ns	ns	ns	ns	ns	–	–	–	–	−0.52	−0.21	0.18	0.06
Soil Bulk Density (g cm^{-3})[a]	−0.03	0.42	−0.13	0.07	0.21	−0.37	0.03	−1.41	ns	ns	ns	ns	0.29	0.61	−0.72	−0.19
Soil Moisture (g H_2O g^{-1})	ns	ns	ns	ns	−0.46	−0.35	0.59	0.64	ns	ns	ns	ns	0.62	0.35	0.43	−0.03
Soil pH	ns	ns	ns	ns	−0.37	0.44	−0.41	−0.98	−4.04	−3.90	0.28	0.20	ns	ns	ns	ns
Soil EC (μS cm^{-1})	ns	ns	ns	ns	0.77	−0.57	1.30	−2.39	ns	ns	ns	ns	0.75	0.59	−0.71	0.22
Soil C (Mg ha^{-1})	0.07	−0.12	0.10	0.56	−0.70	1.10	−0.79	−0.46	−1.08	−0.67	4.00	0.74	0.02	−0.97	−0.23	−0.50
Soil Olsen-P (pg g)	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	0.12	0.21	0.77	0.09
Soil NCV-N (kg ha^{-1})	−0.08	0.42	0.14	−1.00	ns	ns	ns	ns	ns	ns	ns	ns	−0.17	0.13	−0.41	0.70
Soil NH_4^+-N (kg ha^{-1})	−0.18	−0.56	0.08	−0.38	ns	ns	ns	ns	0.94	−0.82	0.60	4.93	−0.04	0.29	0.23	0.05
Soil PMN (μg g^{-1})	0.05	0.37	0.09	−0.64	ns	ns	ns	ns	ns	ns	ns	ns	−0.38	−0.11	−0.16	−0.75
Soil % Silt	ns	ns	ns	ns	0.33	0.66	−0.59	−0.94	ns	ns	ns	ns	ns	ns	ns	ns
Soil % Clay	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Soil Aggregate MWD (μm)[i]	−0.12	0.12	−0.15	−0.43	ns	ns	ns	ns	−3.60	0.19	0.45	0.19	ns	ns	ns	ns
Soil Surface Litter (kg m^{-2})	0.97	0.42	−0.51	2.19	1.59	1.01	−1.97	1.69	0.42	3.18	−1.23	−0.46	0.14	−0.91	−1.60	2.18
Soil Infiltration Rate (cm min^{-1})	0.21	0.01	0.90	−0.10	ns	ns	ns	ns	ns	ns	ns	ns	−0.32	−0.03	0.23	−0.67
Previous year in tomato production	ns	ns	ns	ns	0.22	0.02	−0.07	0.67	−0.78	2.62	0.39	1.47	ns	ns	ns	ns
Tilled within 6 months	−0.11	0.35	0.36	1.59	ns	ns	ns	ns	ns	ns	ns	ns	0.92	0.41	−1.07	0.49

[a] Coefficients are only illustrated for variables that were significantly selected ($P < 0.05$) using a Monte Carlo permutation test.
[b] - indicates that the variable was not included in the analysis.
[c] ns indicates non-significant results.
[d] Unclassified 10:010:0 2OH, 12:0, i13:0,14:0, i15:1@5, i15:1f, i15:1g, unknown 14#503,15:0, i16:1h, 16:1w11c, 16:0, unknown 16#295, i17:1w5c, 15:0 3OH, 17:0, unknown i17:1,16:1 2OH, 10Me17:0,16:0 3OH, 18:0, i18:1h, unknown 18#715,10Me19:0, 20:2 w6,9c, 20:0, 20:4 co6,9,12,15c.
[e] Gram+i14:0, i15:0, a15:0, i16:0, a16:0, i17:0, a17:0,18:1w7t.
[f] Gram -16:1 w7t, 16:1 w7c, 17:1 w9c, cy17:0, cy19:0.
[g] Fungi 16:1w5c, 18:1w9c, 18:3 006c (6,9,12).
[h] Actinomycetes 10Me16:0,10me18:0.
[i] MWD refers to mean weight diameter of aggregates.

nematode diversity. Other soil properties were important for specific types of biota, e.g., a strong negative association with high pH for nematodes (e.g. *Psilenchus*). Soil moisture did not have a major effect on the distribution of any of the types of biota, confirming that the goal of sampling in the spring under fairly uniform moisture conditions had been achieved.

Furthermore, other biota were often more important than soil physical and chemical properties in explaining the distribution of taxa in the partial CCAs for environmental variables (Table 5). For earthworm variation, total nematodes were important along axis 1, and native grasses, woody perennials, and total PLFA along axis 2. Plant life history/functional groups present in the perennial habitats (e.g., native grasses and woody species) were associated with the earthworms, *A. caliginosa* and the unidentified species in the *Megascolecidae*. For the nematode partial CCA, trophic relationships were important in explaining variation (see Sánchez-Moreno et al. (2008) for details). Several fungal-feeding nematodes were associated strongly with the actinomycetes PLFA biomarkers (e.g., 10Me16:0, 10me18:0). Some plant-parasitic nematodes were associated with native forbs and previous tomato production (Sánchez-Moreno et al., 2008). Microbial communities, based on the PLFA partial CCA, were strongly explained by intertrophic relationships, such as total nematode biomass and presence/absence of native woody perennials.

The CCA of the life history/functional groups of plants, nematodes, and PLFA, and earthworm species (as function could not be determined), that was run concurrently with 17 soil and management variables, showed distinct separation between perennial, production, and irrigation habitats (data not shown). The first axis represented this sequential disturbance gradient and explained 37% of the variation. The second and third axes together accounted for 25% of the variation and were less useful in discerning patterns. This confirms that unexplained variation was high, as was observed for the partial CCAs (Fig. 3), indicating that unmeasured factors were important for the distribution of taxa for each group of biota across the farmscape.

3.4. Indicators of ecosystem functions

Total C storage (Mg C ha^{-1}) in soil and wood was greatest in the riparian corridor, largely due to woody biomass; it was twice that found in hedgerows, and more than three times that of the other habitats (Fig. 4). Total soil C at the 0–15 cm depth was 32.3 Mg ha^{-1} in the riparian corridor, higher than the tailwater pond (19.7 Mg ha^{-1}), but not significantly different from any of the other habitats (Table 3). No differences were found in total soil C at the 15–30 cm depth, which ranged from 17.8 to 26.9 Mg ha^{-1}.

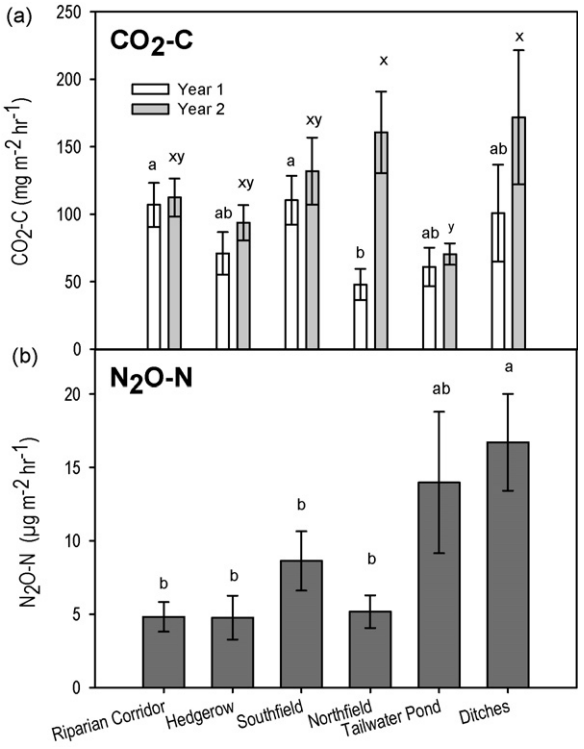

Fig. 5. Estimates of greenhouse gas emissions monitored in each of the six habitats with monthly spot measurements. (a) means for year 1 and 2 separately for carbon dioxide (CO_2-C) emissions; and (b) two-year mean of monthly nitrous oxide (N_2O-N) emissions. Different letters indicate significant differences at $P<0.05$. Graphs illustrating two years of data had significant year × habitat interactions ($P<0.05$), and thus years were analyzed separately. Untransformed data are shown.

Mean CO_2-C emissions for each year (monitored monthly with closed chambers and a LICOR 8100) provide a rough indicator of actual process rates, and differed among habitats (Fig. 5) (see Smukler et al., in revision for details). The highest emissions were observed in habitats that either had frequent wet-dry cycles (e.g.

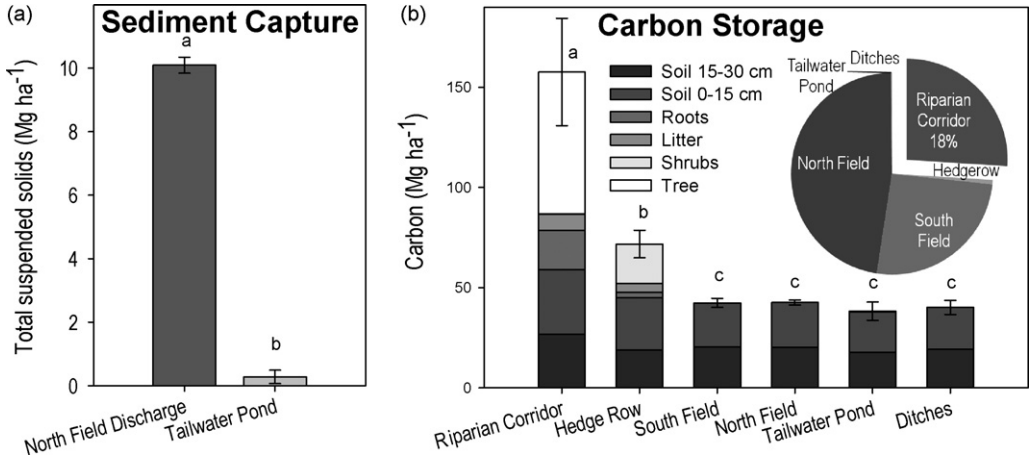

Fig. 4. Soil erosion and carbon stocks as two ecosystem functions of farmscaping. (a) Soil erosion from one season of summer irrigation captured by the tailwater pond; and (b) carbon storage (Mg ha^{-1}) for each habitat and its contribution to the total farmscape (44 ha) based on area of each habitat (given in %). The tree label refers to standing live tree biomass (aboveground), roots to standing live tree biomass (belowground), and the shrub label includes above- and belowground estimates for hedgerows and the riparian forest understory. The C in the one standing dead tree was negligible and not shown. Data for the tailwater pond, ditches and hedgerow are too small to be seen. Different letters indicate significant differences at $P<0.05$. Untransformed data are shown.

ditches, and after irrigation in year 1 in the South Field and year 2 the North Field), or high C stocks (e.g. the riparian corridor). The highest mean value observed for any month was in ditches in the spring of 2006, after the extremely wet winter (559 mg CO_2-C m^{-2} h^{-1}). In the spring of both years, CO_2-C emissions were >200 mg CO_2-C m^{-2} h^{-1} in the riparian corridor, and contributed to the high annual means, which were otherwise low for much of the year. The lowest average CO_2-C emissions were observed in the rainfed oats of the North Field.

Mean annual N_2O-N emissions monitored with closed chambers, again serving as a rough indicator of actual rates, were greatest in the irrigation habitats, but overall were very low for all the habitats (Fig. 5). For example, annual means from the ditches were two times greater than the production and perennial habitats, but were only 16.7 μg N_2O-N m^{-2} h^{-1} (data not shown). Emissions sometimes spiked considerably, and the highest observed monthly mean was in the tailwater pond in the fall, after production had ceased and the pond began to dry (92.8 μg N_2O-N m^{-2} h^{-1}). Mean annual N_2O-N emissions from the production fields and perennial habitats did not differ, and were consistently in the range of 4.8 to 8.6 μg N_2O-N m^{-2} h^{-1}.

Nitrogen losses in the form of leached NO_3^--N captured by the anion exchange resin bags were higher in the irrigation ditches in the second year than in any other habitat. NO_3^--N in the bags from the ditches was >20 times higher than for the two perennial habitats, and four times higher than those of the production habitats (Fig. 6). This large difference in leaching was not detected in the drier first year, when NO_3^--N leaching losses in the irrigation habitats were lower and more similar to other habitats.

Leachate DOC concentrations in lysimeters were highest in the perennial and production habitats. At 19.3 mg L^{-1}, mean DOC concentrations at 30-cm depth were highest in the riparian corridor, slightly higher than the hedgerow, South, and North Fields, and more than two times higher than the irrigation habitats. While similar patterns were observed for both depths in the first year, DOC did not differ at 60 cm depth in the second drier year.

There were large differences between habitats in surface water infiltration rates. The highest infiltration rates were in the riparian corridor, almost five times greater than the South Field, and >50 times greater than the tailwater pond and ditches, but not significantly different than the North Field or hedgerow habitats.

Tailwater return ponds were very effective at removing total suspended sediment from irrigation water. In the summer of 2006, average TSS and VSS removal efficiencies for the tailwater pond were 97% and 89%, respectively (Fig. 4). Mean NO_3^--N concentration, however, increased by 40% in pond effluent, and DOC concentration increased by 20%. The reduction in total load of TSS (kg ha^{-1}) was on average 35 times lower than influent loads (irrigation water discharging from the field) for the 9 irrigations. This amounted to a cumulative reduction for the entire season of 9.4 Mg ha^{-1}. Loads for VSS (kg ha^{-1}) were on average 12 times lower in the tailwater effluent than the influent, a reduction in concentration that amounted to 431 kg ha^{-1} for the season.

Tomato yields in the two years of the study varied greatly due to an outbreak of Southern Blight (*Sclerotium rolfsii*) in the first year. Yields were 15.7 ± 3.9 Mg ha^{-1} in the first year, and in the second year, when there was dramatically less disease, 50.0 ± 10.9 Mg ha^{-1}. For a detailed account of fruit quality, see Smukler et al. (in revision).

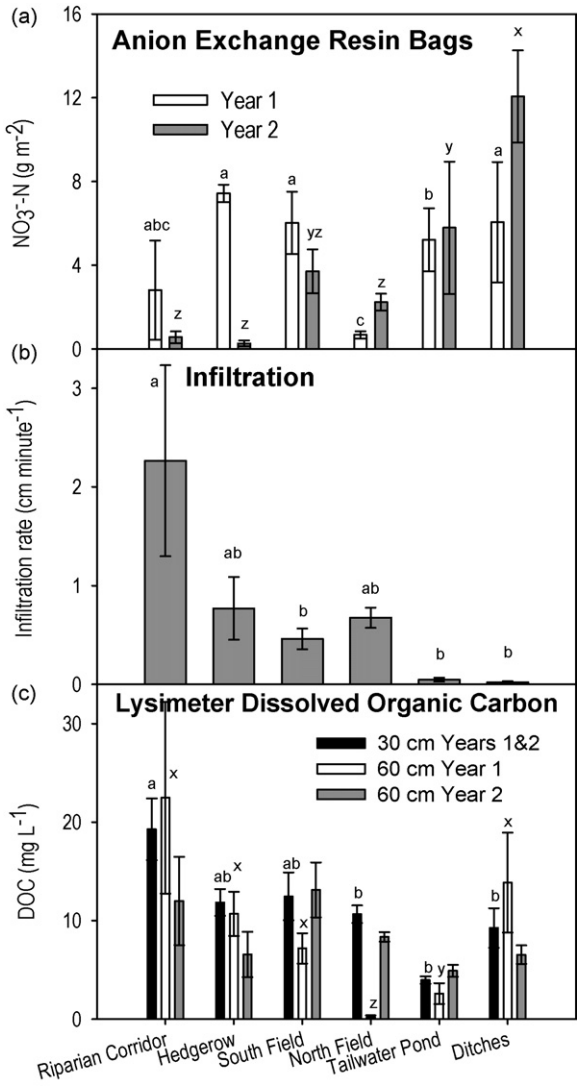

Fig. 6. Indicators of the water quality ecosystem function as monitored in the six habitats. (a) Means of year 1 and 2 of cumulative NO_3^--N collected in anion exchange resin bags; (b) infiltration rates; and (c) two-year means of weekly lysimeter solution concentrations of dissolved organic carbon (DOC) taken from 30 cm depth, and means for year 1 and 2 separately for solution from 60 cm depth. Different letters indicate significant differences at $P < 0.05$. Graphs illustrating two years of data had year × habitat interactions $P < 0.05$, and thus years were analyzed separately. Untransformed data are shown.

4. Discussion

In this study, farmscaping was associated with surprisingly small changes in plant and soil biodiversity. The low overall diversity may be due to the high connectivity of the habitats on the farm, past disturbance from intensive agriculture, possibly a scarcity of colonizing organisms from the surrounding landscape, uniformity of soils, and, most likely, a combination of these possibilities (see below). Large differences in some indicators of ecosystem functions among habitats appear to be associated with just a few species in a few functional groups (e.g. woody perennials that sequester C), and to the environmental conditions in the different habitats, which were managed in different ways. Thus, a few key species, along with biophysical characteristics of specific habitats, were more important than species richness in explaining ecosystem functions across the farm. Overall, farmscaping with hedgerows, riparian plants, and tailwater ponds increased environmental quality in a number of important ways via C storage, soil quality, surface water infiltration, and reduced sediment loss to the neighboring waterway. The future challenge is to find ways to further utilize biodiversity in this type of organic farmscape, with specific sets of ecosystem functions in mind, and to generate mechanisms to reward farmers and landowners for adopting such practices.

4.1. Research design

The farmscape in this study was selected for a number of reasons. It is a working farm which, of necessity, implements adaptive management practices. It is an organic farm, which is likely the best-case scenario for maximizing biodiversity (Drinkwater et al., 1995; Bossio et al., 1998; Hole et al., 2005). The farmscape also had a mature riparian forest, hedgerows, tailwater ponds, and was operated by an innovative farmer-cooperator, who plays a leadership role for farmers in the area. Finally, like many farms in California's Central Valley, the native woodlands at this site had been converted to highly intensive grain and vegetable production at the beginning of the last century.

Stratified random sampling was used to evaluate the contributions of the six habitats to the biodiversity and ecosystem function within this farmscape. Selecting a farmscape on a single soil type was an effort to increase statistical robustness. Effort was made to replicate and randomize, but a more robust design (e.g. a randomized complete block design) was not possible given the different configuration and size of the habitat types. For example, interspersing or randomizing mature riparian forests and tomato production areas was impossible within the same area. No other similar farms exist to serve as replications, but the results are still broadly relevant to other agricultural situations.

4.2. Plant biodiversity

We expected that farmscaping practices designed to increase biotic habitat along field margins would increase both landscape- and plot-level plant and soil biodiversity. In particular, we thought that an increase in plant diversity would increase belowground biodiversity (Hooper et al., 2000). However, comparison of undisturbed habitats dominated by woody perennial vegetation vs. the large fields under organic agricultural production and their connected irrigation habitats revealed surprisingly subtle differences in plant, and especially soil biodiversity.

Riparian habitat has elsewhere been shown to be important zone for maintaining landscape biodiversity (Naiman et al., 1993). Here, plots in the riparian habitat had an average of only 10 plant species, which is extremely low compared to the number of species (between 254 and 684) found in some wildland riparian zones in the mountains of nearby Oregon (Planty-Tabacchi et al., 1996). Published plant species lists of riparian forests in the Sacramento Valley are not complete inventories (*e.g.*, Harris, 1987), but undisturbed riparian vegetation is described as having some of the highest productivity and diversity of any California ecosystem due to the year-round water supply in this Mediterranean-type climate (Holstein, 1984; Barbour et al., 1993). In a floodplain above a continuously flooded zone (2–6 m above the water), undisturbed forests can have a complex architecture with typically five species of overstory trees, five species of shrubs, several vine species, and many annual and perennial herbs. Most (>90%) of the Central Valley's riparian forests, however, have been cleared and the soil has been disturbed; they are now relegated to narrow bands at the edge of stream channels (Barbour et al., 1993; Seavy et al., 2009), as observed here. The low number of plant species in the relatively small patches of perennial plant habitats in this farmscape may also be in part due to the simplicity of the surrounding landscape (Culman et al., in press). There may be a minimum threshold of complexity and connectivity required for a surrounding landscape to provide the colonization potential to maintain the biodiversity of these riparian forests (Tscharntke et al., 2005; Concepcion et al., 2008).

With fewer species present in an ecosystem or farmscape, small increases in biodiversity may become more important for ecosystem function than in higher diversity systems, as redundancy is less likely to occur (Naeem et al., 1994; Tilman and Downing, 1994). In fact, one of the major differences in ecosystem function between the habitats was C storage, due to a few species of woody perennials. These few species, found only in the riparian corridor and hedgerow habitats, were associated with higher soil infiltration rates, likely due to higher soil organic matter inputs, increased aggregate stability and absence of heavy traffic.

4.3. Soil biodiversity

Soil biodiversity, as indicated by the few groups of organisms studied, may be explained by a combination of environmental and intertrophic interactions. Earthworm diversity was consistently low across this farmscape, as is found for other nearby agricultural sites, including other organic farms (Fonte et al., 2009). Lack of tillage, less compaction, and high inputs of organic matter likely contribute to the higher abundance of earthworms in the perennial habitats (Curry et al., 2002; Chan and Barchia, 2007). Moreover, these habitats would be expected to provide both an abundant food source and a distinct litter layer that would help to conserve soil moisture and lessen temperature fluctuations, which promote earthworm growth and survival. Although ANOVA showed no differences among habitats, multivariate statistics indicated that both *A. caliginosa* and the *Megascolecid* spp. tended to be associated with the less-disturbed perennial habitats, while *A. trapezoides* was more prevalent in production habitats, possibly because it is more tolerant across a broader range of environmental stresses (Mele and Carter, 1999; Chan and Barchia, 2007). Earthworm taxa were more affected by spatial/environmental correlation than other soil organisms corroborating evidence for strong spatial aggregation in earthworm populations (Poier and Richter, 1992; Rossi and Lavelle, 1998). Thus more intensive sampling may be necessary to better assess the environmental and trophic factors controlling earthworm differences among habitats.

Multivariate analysis suggested that the abundance of earthworms is associated with other trophic groups, particularly nematodes. Low nematode survival rates due to earthworm gut transit have been reported (Monroy et al., 2008), and nematode populations have been drastically reduced by earthworms in a microcosm experiments (Räty and Huhta, 2003). In this study, the abundance of nematode functional groups were negatively associated with the earthworm, *A. caliginosa*, but were not significantly correlated with earthworm abundance in general (Table 5). Nematode functional groups instead were more correlated with actinomycete PLFA biomarkers and plant functional groups. One possible explanation for this relationship is that the nematode fungal feeders consumed fungi, opening a niche for competing actinomycetes. Alternatively, fewer bacterial feeding nematodes may be associated with higher actinomycete abundance (Wardle et al., 2006).

The lack of differences in nematode abundance and low diversity at the plot level among the perennial and crop production habitats was unexpected given the divergent forms of habitat management (Freckman and Ettema, 1993; Neher, 2001; Ou et al., 2005). Tillage was not a significant explanatory variable in the nematode partial CCA, but surface litter and pH correlations were large, suggesting that organic matter management may be more important than disturbance. A nearby study on a similar soil type showed that organic matter additions can increase the nematode abundance more rapidly than conversion to no-tillage (Minoshima et al., 2007). Many decades of prior intensive agriculture may have selected for nematodes that are resistant and resilient to tillage and intermittent moisture, and this may explain the very low species richness, i.e., 15 taxa in the cultivated fields. Across the entire farmscape, only 37 taxa were observed. Including the perennial plant habitats only slightly increased diversity. By contrast, in an extensive review, 15

to 82 taxa were reported for temperate cultivated ecosystems, and 13 to as many as 175 species for temperate broadleaved forests (Boag and Yeates, 1998).

Total PLFA in the production field plots were similar (~40 nmol g^{-1} soil) to those reported in a study across the State of California (Drenovsky et al., 2010). But, the mean number of PLFA observed per habitat (40–45) was in the middle of the range reported in the same study, from 30 in deserts to 55 in rice production systems. Overall, the 77 PLFA found across the entire farmscape is low, considering the potential diversity that exists in forested and agricultural ecosystems in California.

The low soil biodiversity within and among habitats may be a result of past or recurring disturbance, as well as lack of colonization potential from neighboring ecosystems. The production fields experience tillage, fluctuating water regimes, sporadic plant cover, and nutrient inputs, which constitute frequent and intensive disturbance. In the perennial habitats, disturbances consist of flooding in the riparian corridor, erosion from crop fields, or trampling of the hedgerows (i.e. farm workers often use the hedgerows for shade during the hot summers). It is also possible that the soil ecosystem is still recovering from the disturbance initiated by European settlers who arrived in the 1880s. At some point shortly thereafter, the alluvial valley was leveled for farming operations, the slough was deepened and bermed, and the undulating hills nearby were tilled and grazed, which inevitably resulted in the loss of topsoil (Vaught, 2007). Since these types of disturbance were nearly ubiquitous in the landscape with the widespread adoption of intensive agriculture, colonization may be limited by lack of nearby habitats with richer biodiversity.

4.4. Soil properties

Despite the apparent differences in habitat vegetation and management, soil properties were quite similar among all habitats. Even though higher plant biomass occurred in the riparian corridor, soil C was not significantly greater than in the production habitats. This may be related to the high inputs of organic material applied every year (> 15 Mg ha^{-1} of compost) to produce organic crops. Soil C (21.8 and 22.4 Mg C ha^{-1} at 0–15 cm depth in the South and North Field, respectively) was similar to fields under organic management at a nearby research station (22.8 Mg C ha^{-1}) (Kong et al., 2005). The long-term research station study reported much higher concentrations of soil C than conventional plots (16.1 Mg C ha^{-1}) indicating that substantial C can accumulate under organic management in a period of only 10–15 years.

Soil aggregate stability demonstrated the most pronounced differences for soil properties among habitats. Mean weight of diameter (MWD) values for the farm's production fields (0.9–1.0 mm) were similar to values for organic production at the nearby research station (0.3–1.2 mm, respectively, for conventional and organic fields) (Kong et al., 2005). Aggregate stability in the hedgerows (2.1 mm) was more than double that observed for the other farmscape habitats. These high values likely result from a combination of low disturbance, diverse types of plant litter, and the absence of mineral N fertilizers (Bronick and Lal, 2005). Curiously, despite a longer period of such conditions, the soils of the riparian corridor had lower aggregate stability than the hedgerow soils. This might be explained by more erosion on steeper slopes and deeper rooting systems than the hedgerow shrubs.

Some habitats were more homogenous in their soil properties than others (e.g. the high SE of Olsen P in the riparian corridor vs. other habitats). Variability in the riparian corridor is likely due to the interactions between topography, the influence of the ephemeral stream flow (deposition and erosion), and patchy plant community composition. The diversity of substrates from different life forms of plants, with different functional traits, in theory should result in a diversity of belowground soil organisms (Hooper et al., 2000; Wardle, 2006). But as mentioned above, the differences in plant species composition among habitats were not associated with concomitant difference in the belowground communities (Hooper et al., 2005).

4.5. Ecosystem functions

The C stocks in the mature riparian forest tree biomass far exceeded the storage of soil C (0–30 cm depth) in the production fields on a per ha basis. It should be noted, however, that these data for soil C at 0–30 cm depth underestimate the pool of soil C at 0–100 cm depth by about half, based on a survey of cropland and riparian corridor soils surrounding this project site (Young-Mathews et al., 2010). The estimated 70.8 Mg C ha^{-1} stored in aboveground woody biomass was lower than a pristine riparian forest in South Carolina Coastal plains (98.2 Mg C ha^{-1}) (Giese et al., 2003). It was, however, greater than the estimated potential 50 Mg C ha^{-1} for afforestation of marginal agricultural lands in the Midwest USA (Niu and Duiker, 2006). Including the estimates for soil, roots, litter and understory shrubs, the C stocks (157.7 Mg C ha^{-1}) in the small area of riparian forest (6%) represents a disproportionate amount of the total C stock (18%) measured within the farmscape (Fig. 4b). Hedgerows stored 1% of the total C in the farmscape. If soil data had been collected at 30–100 cm depth, these percentages would decrease, as would excluding C in leaves and in fine roots. Even so, woody perennials are an important pool of C storage in the farmscape.

Higher rates of CO_2-C emissions occurred during the rainy season in the late fall, winter, and early spring in the perennial habitats, while highest summer emissions occurred in the production habitats during the irrigated growing season. Despite the different seasonal emissions patterns, annual means were similar. N_2O-N emissions, however, were much larger in irrigation habitats. The highest flux observed on this farmscape (in the tailwater pond) was still an order of magnitude lower than what others have found in agricultural soils (Matson et al., 1998; Burger et al., 2005), probably due to the low level of mineral N in the production system (see Smukler et al., in revision). Higher rates of gas emissions found in ditches were likely a combination of two factors: (1) high influx of mineral N via the accumulation of water with high levels of dissolved N and deposition of N-rich eroded soil; and (2) frequent wetting cycles that saturated the soil during the warmest time of the year.

Although large quantities of sediment were lost in surface runoff from the production fields (see Smukler et al., in revision for details), most was captured by the tailwater pond (Fig. 4a). With no tailwater pond, this sediment would have discharged directly into the adjacent riparian corridor. And without a pump to return irrigation water to the field, DOC that accumulated in the pond would have discharged into the riparian zone.

The higher DOC concentrations in the soil solution in the perennial habitats compared to the fields were similar in range to concentrations found in a prairie vs. agriculture production study in Wisconsin (5 to 20 mg DOC L^{-1}) (Brye et al., 2001). Pore water NO_3^--N, measured in lysimeters and resin bags, was low relative to other studies. Infiltration rates were also high in the riparian corridor, similar to a study showing rates that were 6 times higher in the riparian buffer compared to corn and pasture (Bharati et al., 2002). High infiltration rates are an indicator of regulating services, as they prevent surface erosion and promote aquifer recharge, but are also likely to increase the loss of DOC by leaching and transport into the adjacent waterway, which is a concern for downstream water quality (Fujii et al., 1998).

The non-production habitats have little impact on the farm's food provisioning functions. Some local farmers are reluctant to

Table 6
Potential tradeoffs of yields, and indicators of biodiversity and ecosystem function as extrapolated from plot data to the farmscape for alternative management scenarios, and shown as the percent changes relative to values observed in this study (baseline data).

Biodiversity or ecosystem function indicator	Baseline data	Units of indicator	Farmscape management scenarios			
			Tomatoes only[a]	Tomatoes + Max. Hedgerows[b]	Tomatoes + Max. Perennials[c]	Tomatoes + Max. Perennials + Pond[d]
Food production: yield	22	Mg tomatoes ha^{-1} $year^{-1}$	4	−4	−9	−9
Water flow regulation: infiltration rates	0.7	cm min^{-1}	−15	−14	6	6
Climate regulation: mean emissions	71.9	mg CO_2 equivalent s m^{-2} h^{-1}	1	1	0	0
Carbon storage: total of 6 pools	49	Mg C ha^{-1}	−13	−10	8	8
Erosion regulation: sediment loss	0.1	Mg TSS ha^{-1} $year^{-1}$	−97	−97	−97	0
Water quality: nitrate leaching	26	kg NO_3^--N ha^{-1} $year^{-1}$	−6	−11	−3	−3
Earthworm diversity	4	Taxa farmscape^{-1}	0	0	0	0
Plant diversity	60	Species farmscape^{-1}	−62	−28	−12	0
Nematode diversity	37	Taxa farmscape^{-1}	−24	−14	−3	0
Microbial diversity	77	PLFA farmscape^{-1}	−10	−8	0	0

[a] 'Tomatoes only': maximizing tomato production to 100% of the 44 ha.
[b] 'Tomatoes + Max. Hedgerows': maximizing hedgerows by reducing the tomato production area by 6%.
[c] 'Tomatoes + Max. Perennials': maximizing both hedgerows and the riparian corridor (perennials) by reducing the tomato production area by 14%.
[d] 'Tomatoes + Max. Hedgerows + Pond': including a tailwater pond with maximized perennials in hedgerows and the riparian corridor.

establish plants in field margins because of concerns about limiting production and interfering with mechanical and chemical control of weeds (Brodt et al., 2008). The most problematic weed for tomato production in this area, *Convolvulus arvensis*, however, was only found in small quantities in the hedgerows and tailwater ponds.

Disease was by far the main cause of yield reduction. The unusually wet spring followed by high early summer temperatures resulted in ideal conditions for Southern blight. With very few organic management options to control disease, crop yields were far below conventional averages for the county (74.3 Mg ha^{-1}) in the first year. Prices, however, were unusually high for this harvest since the disease was widespread and late planting further increased the market demand for organic tomatoes. In the second year, yields exceeded county averages (80.1 Mg ha^{-1}).

4.6. Tradeoffs for land management

Tradeoffs are relevant to public policy that currently intervenes at the farmscape scale to promote sustainable farmland management through direct government payments, and cost-sharing (e.g. payments for agri-environmental schemes in Europe (European Commission, 2003) and the Environmental Quality Incentives Program in the USA (NRCS, 2008). These types of programs often promote biodiversity-based production practices such as using renewable resources, organic farming, or non-production practices such as the preservation and restoration of landscape and historical features such as hedgerows, ditches and woodlands (Marshall et al., 2006; Concepcion et al., 2008; Yano and Blandford, 2009). The adoption of these types of management practices without governmental assistance is assumed to incur a cost in terms of yield and/or economic returns (Lu et al., 2003; Steffan-Dewenter et al., 2007).

To explore potential tradeoffs in terms of relative difference in yields, and indicators of biodiversity and ecosystem services among farmscaping management options, we developed and contrasted four hypothetical scenarios that encompassed varying degrees of habitat enhancement (Table 6): (1) maximizing tomato production by assuming that 100% of the 44 ha farmscape was in a tomato oat rotation; (2) maximizing hedgerows by planting them on every available field edge thereby reducing the land in tomato production by 6%; (3) maximizing both hedgerows and the riparian corridor ('maximized perennials') by expanding the riparian corridor and planting hedgerows on all field edges, resulting in a 14% reduction of the land in tomato production; and (4) maximizing perennials in the farmscape and constructing a tailwater pond which would incur yet an additional 0.06 ha loss of production area. To scale up to the entire farmscape, means of the plot level data for key ecosystem functions from the two years were multiplied by the new area of land in each habitat type for each of these scenarios (Table 6). Assumptions were that species richness for each habitat was size-independent and farmscape richness was determined by sum of the number of unique taxa contributed by each habitat. Each scenario was then compared as a percentage of the maximum value of each of the four options vs. the baseline (that which was actually measured).

This exercise suggests that some ecosystem services provided by the farmscape as a whole would increase due to greater area of some types of habitats, while others would change minimally (Table 6). Expanding the riparian corridor and hedgerows by 6.2 ha, i.e., the 'maximized perennials and tailwater pond' scenario, would reduce tomato yields by 10% (using data from year two) and could slightly increase the amount of DOC lost from the farmscape. At the same time, the addition of more woody perennials and the tailwater pond would increase C stocks on the farm (e.g. an increase by 30% or 10 Mg ha^{-1}, assuming the same forest structure as currently exists), although it would take several decades before the C stocks were fully achieved. The increased area of riparian and hedgerow habitats could also improve surface water infiltration, and the addition of the tailwater pond plays a critical role in preventing soil and nutrient loss to the nearby waterway. There are a number of tradeoffs that were not included in the analysis but must be considered. For example, the tailwater pond requires dredging and redistribution of the soil across the field, entailing labor and fuel inputs and additional management costs.

A more complex crop and ecosystem model (Lowrance, 2000; Kirschbaum and Paul, 2002; Arnold, 2005) would show the time course and relative magnitude of management options more accurately. Estimates such as these, however, demonstrate the importance for developing reward mechanisms, e.g., payments for ecosystem services (PES) that could promote the adoption of alternative scenarios (Pascual and Perrings, 2007; Cowling et al., 2008) that increase food and fiber as well as improve environmental quality.

5. Conclusions

Farmscaping on a small proportion of an organic farm can support plant biodiversity and significantly improve ecosystem functions, even in agricultural landscapes with long-term disturbance and intensive production. However, farmscaping on a short time frame may not substantially affect belowground biodiversity, based on the groups of species/taxa studied here. Although

some taxa or functional groups were clearly associated with indicators of ecosystem functions, the mechanistic relationship between biodiversity, and most ecological functions and services remains unknown. A better understanding of these relationships may help farmers manage their lands for multiple ecosystem services sustainably.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.agee.2010.07.004.

Appendix B.

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