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RESEARCH ARTICLE

Biodiversity is associated with indicators of soil ecosystem functions over a landscape gradient of agricultural intensification

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Abstract Agricultural intensification has led to dramatic losses in biodiversity over the past several decades. Many studies have shown the effects of intensification on vegetation or soil communities at field or local scales. However, the functional significance of biodiversity may only appear at larger spatial and temporal scales, due to exchanges among local ecosystems throughout a landscape. To examine how patterns of biodiversity loss are reflected at larger spatial scales, plant and soil biodiversity and associated indicators of ecosystem functions were assessed in riparian areas over a 150 km^2 agricultural landscape in the Sacramento Valley of California. Publicly-available GIS data were first used to classify and select sites over the range of soils, topography and plant community types. Representative sites from the landscape were sampled for soil physiochemical properties, as well as microbial, nematode, and plant communities. Higher agricultural intensification, based on field and landscape indices, was negatively correlated with richness and diversity of plant and soil taxa, and was related to indicators of ecosystem functions, such as increased soil nitrate and phosphorus loading, decreased riparian health ratings, and lower soil carbon, soil microbial biomass and soil food web structure. Both field- and landscape-scale factors played important roles in the measured losses. The study area was composed of a wide array of soils, vegetation, and land management, indicating that the observed trends transcended site-specific conditions.

Keywords Agricultural intensification · Biodiversity loss · Riparian · Landscape classification · PLFA · Nematode · Soil biota · GIS · Aboveground–belowground diversity

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Introduction

Agricultural intensification has resulted in dramatic losses of biodiversity over the past several decades (Matson et al. 1997; Tscharntke et al. 2005). Declines in taxonomic richness have been reported across

gradients of agricultural intensification in both aboveground and belowground communities (Yeates and Bongers 1999; Eggleton et al. 2005; Attwood et al. 2008; Jangid et al. 2008; Yeates and Stirling 2008). Reductions in diversity have been associated with both field-scale factors (e.g., cultivation and application of mineral fertilizers; Neher et al. 2005; Minoshima et al. 2007) and landscape-scale factors (e.g., habitat fragmentation and heterogeneity of neighboring ecosystems; Tscharntke et al. 2005; Kleijn et al. 2009).

Most studies examining biodiversity and agricultural intensification have been limited to one or more biological communities at the field scale, where environmental factors can more easily be controlled. However, the functional significance of biodiversity may only appear at larger spatial and temporal scales, when spatial exchanges occur among local ecosystems throughout a landscape (Swift et al. 2004; Tscharntke et al. 2005). Recently a number of studies have examined aboveground diversity losses with intensification over agricultural landscapes (Billeter et al. 2008; Flynn et al. 2009; Kleijn et al. 2009), while others have reported changes in belowground community structure and diversity over landscapes (Eggleton et al. 2005; Guil et al. 2009). Quantitative relationships between aboveground and belowground diversity over landscape gradients of agricultural intensification have yet to be explored.

Studies at local scales have shown inconsistent relationships between diversity of plants and soil biota (Wardle et al. 1999; Zak et al. 2003; Waldrop et al. 2006). Aboveground and belowground biodiversity affect different ecosystem functions, and in turn, different ecosystem services of human value (Daily 1997). By studying the multifunctionality of agricultural landscapes, more species become implicated in overall functioning than at the field scale alone (Hector and Bagchi 2007; Jackson et al. 2007a, 2009). At the landscape level, however, measurements become logistically challenging to collect, and subject to high variability confounded by site-specific environmental factors (Neldner et al. 1995; Kleijn et al. 2009; Krishnaswamy et al. 2009). A necessary compromise can be to measure indicators of ecosystem functions (OECD 2003). For soils, some of these include soil carbon (C; an indicator of C retention; Arshad and Martin 2002), soil nitrate (an indicator of potential for fertilizer N movement and losses; Di and Cameron 2002; Wallenstein et al. 2006), nematode indices of soil food web structure (Ferris et al. 2001; Sánchez-Moreno and Ferris 2007), or riparian health ratings (an indicator of water filtration, sediment removal and wildlife habitats; Ward et al. 2003).

In this paper, we describe an approach to systematically select and sample sites along a landscape gradient of increasing agricultural intensification in order to examine relationships between aboveground and belowground diversity and indicators of ecosystem functions. The specific focus of this study was on riparian corridors and other waterways over a 150 km^2 landscape in California's Sacramento Valley, because of their important role in maintaining soil and water quality (Richardson et al. 2007). The objectives were to (i) devise a method to classify and sample riparian environments with Geographic Information Systems (GIS) where the range of landscape variability is captured, (ii) elucidate the relationships of aboveground diversity with belowground diversity over a landscape, and (iii) identify landscape-level patterns of soil and plant biodiversity and associated ecosystem functions as they relate to indices of agricultural intensification. A more detailed analysis of ecological relationships is given in Young-Mathews et al. (2010).

Materials and methods

Constructing GIS clusters

The study region is in western Yolo County, California and is composed of both extensive (grazed) and intensive (irrigated cropland) agroecosystems (Fig. 1). To the west, in the uplands of the Coast Range, grazed annual grassland and oak savanna predominate. To the east, irrigated crops (grains, vegetables, and alfalfa) occupy most of the area. Soils are represented by the following great groups as classified in the USDA-NRCS Soil Survey Geographic Database (SSURGO) database: Haploxeralfs, Chromoxererts (classified as Haploxererts in the recent version of Soil Taxonomy (Soil Survey Staff 2006)), Palexeralfs, Xerochrepts (now classified as Haploxerepts), and Xerorthents. Waterways occupy only 212.9 linear km in the entire landscape, and include natural creeks, sloughs, and irrigation canals.

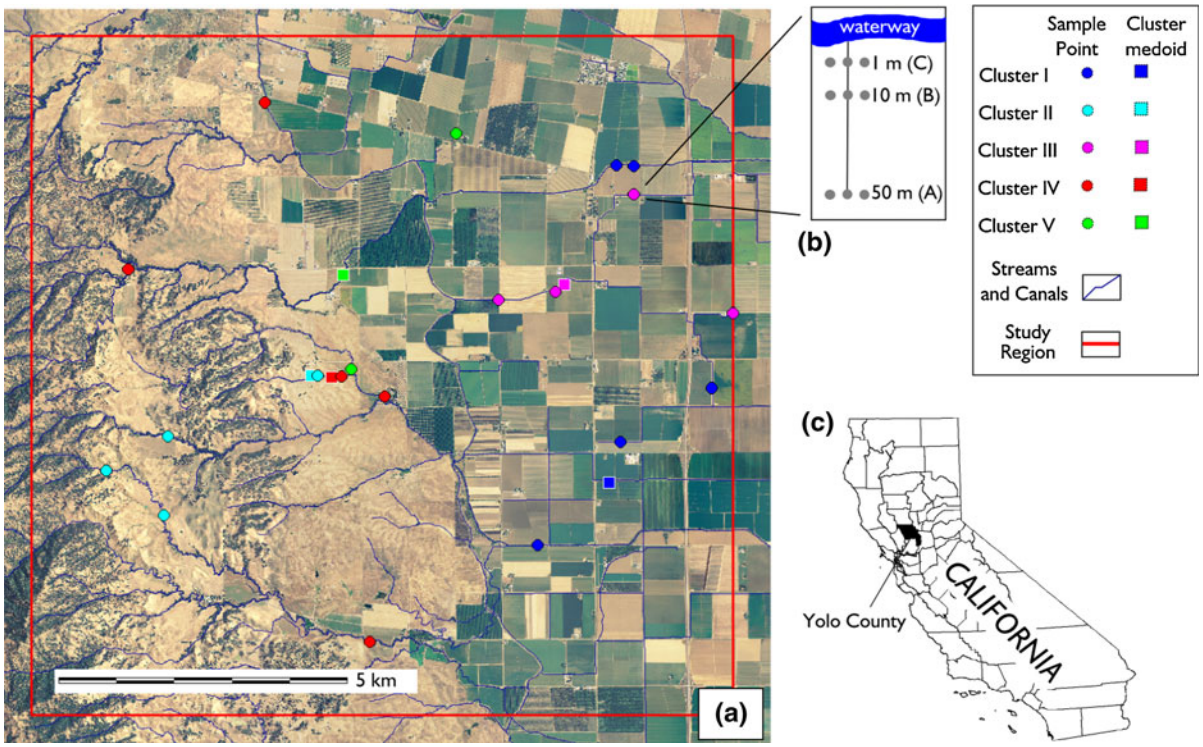

Fig. 1 **a** Map of study area in Yolo County, California, USA. *Circles* represent the 20 field sites with *colors* denoting the cluster (see legend). Sites representing cluster medoids are noted with a *box around the circle*. **b** Soil sampling scheme with positions A, B, and C at 50 m, 9–10 m, and 1 m from the waterway, respectively. **c** Study area in western Yolo County, California (Color figure online)

Site selection for field sampling reflected the large range of soils, vegetation, and agricultural management practices present in the landscape. To begin, a set of 2049 points within a 50 m buffer of all sloughs, canals, and streams was randomly selected over the 150 km^2 region. For each of these points, a GIS data layer stack was created with the values of 14 variables (8 continuous variables and 6 discrete factor variables) from publicly available sources (Table 1). The eight continuous variables were obtained from the SSURGO database, using the average of all horizons (weighted by horizon thickness) in the surface meter of the soil profile. The 6 discrete factor variables included presence of hydric soils in the map unit and the soil great group of the dominant component of the map unit, classification as a wetland by the National Wetlands Inventory, the land cover classification in both the National Land Cover Dataset (NLCD) and NOAA C-CAP land cover map inventories, and the presence and identity of natural vegetation, e.g., oak woodland, according to the California Department of Agriculture FRAP Multi-Source Land Cover map. These 14 variables were selected because they represent a broad range of landscape attributes that may affect biodiversity and ecosystem functions.

A distance matrix was constructed with these GIS data using Gower's dissimilarity algorithm (Gower 1971), using the *cluster* package in R (R Development Core Team 2008). This distance measure can measure continuous and discrete variables simultaneously. The distance matrix was then subjected to Partitioning Around Medoids (PAM), an algorithm similar to k-means clustering, which classifies samples into a pre-defined number of clusters (Kaufman and Rousseeuw 1990). After several iterations to classify the 2049 points on the landscape into clusters, PAM analysis with 5 clusters returned the best results yielding an average silhouette width (s_i) of 0.33. Cluster medoids, the most representative members of each cluster from the PAM analysis, varied widely in average soil and vegetation properties (Table 1).

Table 1 Medoid values of the 14 GIS variables for each cluster

Variable	Cluster I	Cluster II	Cluster III	Cluster IV	Cluster V
Clay content (%)	47.5	38.3	37.6	26.5	23.2
Silt content (%)	47.0	37.0	51.1	43.3	66.3
Organic matter content (%)	1.41	0.63	0.38	0.38	1.58
pH	7.5	8.0	7.5	6.9	7.2
Drainage class	4	5	5	5	5
Runoff class	5	6	4	5	3
Elevation (m)	46.7	85.5	55.7	79.4	66.0
Aspect (degrees)	87.7	275.1	113.3	101.1	169.5
Is hydric?	Yes	No	No	No	Yes
Is NWI wetland?	No	No	No	No	No
Soil great group	Chromoxererts	Chromoxererts	Xerochrepts	Haploxeralfs	Xerorthents
NLCD land cover	Small grains	Grasslands/ herbaceous	Row crops	Grasslands/ herbaceous	Small grains
C-CAP land cover	Deciduous forest	Evergreen forest	Deciduous forest	Evergreen forest	Deciduous forest
Oak type	Non-oak	Non-oak	Non-oak	Non-oak	Non-oak

Values were derived from the Partitioning Around Medoids analysis on the 2049 random riparian points over the study area. The specific sites of each cluster medoid are represented by squares in Fig. 1. Soil variables are from 0–100 cm depth

Site selection and experimental design

For field sampling, 20 sites were selected out of the 2049 possible points, by capturing the variability within each cluster. Every point was categorized into one of 5 intervals based on the silhouette distance from its cluster medoid: 0–20, 20–40, 40–60, 60–80, and 80–100%. One sampling site for each cluster was the cluster medoid (or closest accessible site). The other sites were chosen over the first four dissimilarity ranges, aiming to capture much of the variability within a cluster but omitting the most dissimilar points (80–100% range), because these did not match well with any one cluster.

Initially, 200 randomly selected sites were surveyed for suitable road access and landowner permission. Sites that did not meet both criteria were omitted. The proportion of the total points found in each cluster was multiplied by 20 sites, to give 5, 4, 4, 5 and 2 sampling sites for Clusters I to V, respectively (Fig. 1a). Since biological properties vary temporally, only 20 sites were logistically possible to sample and process given constraints imposed by seasonal changes.

Soil and vegetation sampling

Soil profile characterization and soil sampling took place from late-February to mid-March, 2007. At each of the 20 sampling sites, a 50-m transect was established perpendicular to the waterway, running from the edge of the water into the adjoining field. Three plots within each site were established along this transect at a distance of 1, 9–10 and 50 m from the water's edge (Fig. 1b). Thus, 60 plots in total were sampled over the study area. Soil pits were dug at each plot and two, 7.5 cm diameter soil cores were taken 2 m from the edge of the pit on either side (Fig. 1b). Soil was collected from four depth intervals (0–15, 15–45, 45–75, and 75–100 cm) at each core and from the pit (3 samples total for each position). Thus a total of 36 soil samples (3 cores, 3 positions, 4 depths) were sampled at each site, and were stored at 4°C until processing.

Vegetative sampling and riparian characterization were conducted at each site from May to June 2007 using the riparian greenline transect method (Winward 2000) to classify communities into the appropriate vegetation series (Sawyer and Keeler-Wolf 1995). Then more detailed relevés were made for each of the three soil pit locations at each site, producing cover class data for each species (CNPS Vegetation Committee 2000) for the 60 plots. The size of the relevé plots was 15–100 m^2 depending on the location, topography and vegetation. Physical characterization of watershed features was also performed along the reach according to a modified method for evaluating riparian/watershed health

(Ward et al. 2003), and is explained in more detail in Young-Mathews et al. (2010).

Soil analyses

Inorganic nitrogen (N) was extracted from moist soils according to Miranda et al. (2001) and analyzed colorimetrically for ammonium (NH_4^+) and nitrate (NO_3^-) concentrations. Two replicates per sample were run and averaged. Air-dried soil samples were ground and sieved through a 2 mm screen. Total N and C, pH, Olsen phosphorus (P), exchangeable cations (sodium (Na), potassium (K), magnesium (Mg), and calcium (Ca)), and extractable boron (B) were determined at the Division of Agriculture and Natural Resources Analytical Laboratory at the University of California at Davis (described at http://groups.ucanr.org/danranlab/Methods_of_Analyses545/). Particle size analysis was determined according to Eshel et al. (2004). Values for all soil chemical properties were determined for each sample and then averaged over the three cores.

Nematode and microbial communities were characterized from the surface soil samples (0–15 cm). PLFA biomarkers were extracted and analyzed following the protocol of Bossio et al. (1998), and biomarkers were classified into functional groups of actinomycetes, gram+, gram−, fungi, or unclassified (Bossio et al. 1998; Potthoff et al. 2006). Total PLFA peak abundance was used as a measure of microbial biomass. Nematodes were extracted from 100 g soil subsamples with sieving and Baermann funnels (Barker 1985). Nematodes were identified to genus or family and classified into functional guilds (Bongers and Bongers 1998) and 5 trophic groups: bacterial feeders, fungal feeders, plant-parasites and herbivores, predators, and omnivores (Yeates et al. 1993). The nematode Structure Index (SI, an indicator of soil food web length and connectance) was calculated to assess soil food web condition (Ferris et al. 2001). Most soil chemical and physical properties were performed on all 60 plots at each of the 4 depths in each of the 3 subsamples (720 samples total). PLFA and nematode communities were assessed at 0–15 cm depth in each of the 60 plots (60 samples total). For comparisons with soil biota, soil properties were averaged over the three subsamples either from the soil surface (0–15 cm) or with weighted averages of the four depths of the 0–100 cm profile.

Shannon diversity indices and taxonomic richness for PLFA, nematodes and vegetation communities were calculated with the *diversity* function in the *vegan* package in R. Values were constructed from the total abundance of taxa in the PLFA (70 biomarkers) and nematode (43 taxa) datasets, and from percent cover in the vegetation dataset (114 plant species).

Agricultural intensification index

To characterize the degree of agricultural intensification at each site, an index was created reflecting site management at the field scale, and neighboring site heterogeneity at the landscape scale. The agricultural intensification index was made up of 16 variables: 10 field-scale and 6 landscape-scale (Table 2). All variables were scaled from 0 to 1, with '0' representing 'low intensification' and '1' representing 'high intensification'. Field management variables were taken from farmer interviews and personal observation and were intended to capture major differences in the management of fields. Landscape variables were measured to capture major differences in landscape complexity and heterogeneity surrounding each sample plot. On aerial photographs that had been classified into one of 7 land use types (grassland, woodland, riparian area, cropland, orchard, developed or waterway), three concentric circles were overlaid on each of the 60 sampled plots, with radii of 100, 500, and 1000 m. The percentage of managed land and the land use heterogeneity were measured for each circle using GRASS GIS software (Table 2). An agricultural intensification index value was generated by summing all 16 scaled variables for all 60 plots. In addition, a second and third intensification index value was assigned to all plots based on the sum of the 10 field-scale variables only, and the sum of the 6 landscape-scale variables only.

Statistical analyses

Permutational multivariate analysis of variance (permANOVA) tested significance among the experimental factors (cluster type, position from waterway, and individual site (nested within cluster)) with microbial, nematode, and vegetation datasets. This test is analogous to multivariate ANOVA, but allows for a more ecologically appropriate distance measure

Table 2 Field and landscape variables included in agricultural intensification index

Variables	Scoring
Field management of the plot	
Land use	0 for grassland, 0.5 for orchard, 1 for cropland
Tilled in last 30 days	1 = yes, 0 = no
Irrigated in last 30 days	1 = yes, 0 = no
Planted in last 30 days	1 = yes, 0 = no
Woody species present	0 = yes, 1 = no
Organic or conventional	1 = conventional, 0 = organic
Evidence of riparian restoration	0 = yes, 1 = no
Evidence of channel disturbance	1 = yes, 0 = no
Tilled within last 2 years	1 = yes, 0 = no
Riparian health rating	Continuous scale from 0 to 1, based on Ward et al. (2003)
Landscape measurements (radii)	
Percent of managed land within 100 m	{Σ (area of cropland, orchard, developed)}/{total area within circle}
Percent of managed land within 500 m	
Percent of managed land within 1000 m	
Land use heterogeneity within 100 m	{Σ (number of land use types within circle)}/{7}
Land use heterogeneity within 500 m	
Land use heterogeneity within 1000 m	

See methods for specific details on variables and scoring

than Euclidean distance to be used (Anderson 2001). PerMANOVA analyses were performed in R with the *adonis* function in the *vegan* package with the default parameters. The proportion of variation that each factor contributed was calculated from the sum of squares. Total abundance data were used for microbial and nematode communities; percent cover data were used for plant communities. Multivariate homogeneity of group dispersions (Anderson 2006) was used to determine if the variance within a cluster differed from the other clusters within a biological community. This test is analogous to a univariate Levene's test, but allows for any distance measure to be used. The analysis was performed in R with the *betadisper* function in the *vegan* package, using the Bray-Curtis distance measure.

Pairwise comparisons of each group of biota and soil properties were performed with Mantel tests to test the null hypotheses that no relationship exists between two data matrices (Mantel 1967). Biota data used in the Mantel tests were the same as used with perMANOVA. Soil data included all field-measured parameters: moisture, total C, total N, NH_4^+, NO_3^-, Olsen P, Na, K, Mg, and Ca, B, pH, clay, silt, and sand. The test was performed in R with the *mantel* function in the *vegan* package. Bray-Curtis distance measures were used with all comparisons, except for comparisons made with the GIS dataset, which contained both continuous and categorical data, and thus Gower's distance measure was used.

Simple linear regression was used to test the relationships between i) agricultural intensification indices and diversity or richness measures of the three biological communities and ii) agricultural intensification and environmental properties. Simple correlations and partial correlation analyses were used to examine relationships between biological richness and environmental properties. Analyses were performed in R using the linear model function (*lm*) and correlation functions (*cor.test, pcor.test*).

Results and discussion

Selection and evaluation of clusters

In this study, the first step was to systematically classify this heterogeneous agricultural landscape so that the limited number of sampling sites would accurately reflect the range of variability found across the landscape. As described above, PAM analysis identified 5 general land types (i.e., clusters) using

GIS data (Table 1). Two main sets of land use types were identified: irrigated sites in the valley (Clusters I, III, V) and non-irrigated grazed grasslands and savannas in the uplands (Clusters II and IV).

The next step was to test whether the clusters determined by the 14 GIS variables reflected the structure of the biotic communities at the 20 sampling sites. PerMANOVA indicated that the amount of variance that each factor contributed was relatively consistent across each measured community (Table 3). Clustering was significant ($P < 0.001$) for PLFA, nematode and vegetation communities, accounting for 26.3, 17.3, and 14.6% of the respective total variation found in these datasets. The largest source of variance in all three communities came from the site * position(cluster) interactions followed by site(cluster) main effects, indicating that site-to-site variation was the strongest force in shaping all measured biological communities. The landscape clusters accounted for a subset of the total variance between sites, since field sites were systematically chosen so as to maximize the variability present within each cluster (i.e., selected across a range of varying similarity to each cluster medoid).

Similar within-cluster variance across all clusters in a biological community would suggest that the GIS-predicted clusters captured equal proportions of landscape heterogeneity. Homogeneity of multivariate dispersions analyses supported this, as clusters shared similar variability to one another for each biotic community (Fig. 2). Pairwise comparisons of group mean dispersions within each community showed no significant differences in PLFA and nematode communities. A significant difference was detected in the plant communities, between Clusters I and II ($P = 0.020$), but no other differences existed. Closer examination of vegetation communities between these clusters did not reveal striking differences; Cluster I simply had more total sites with lower average species richness than Cluster II, resulting in more variability. Based on this analysis, the sampling approach appears to have effectively obtained a relatively similar level of heterogeneity of soil and plant biota within each of the 5 clusters.

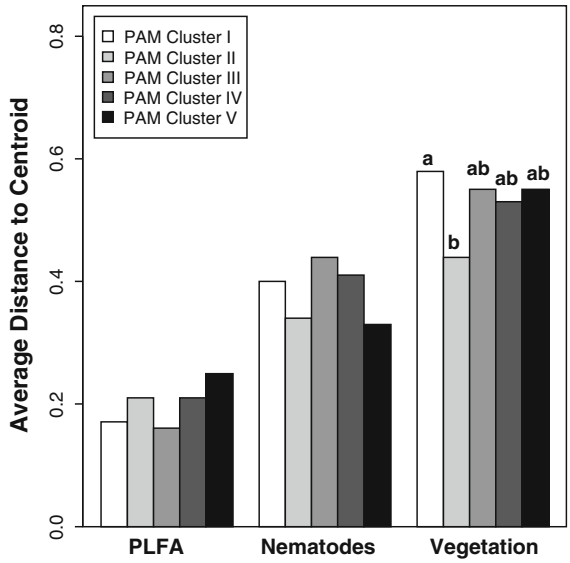

Fig. 2 Multivariate homogeneity of group dispersions among PFLA, nematodes and vegetation. Each *bar* within a community represents the average variance for that cluster in relation to the total variance within the community. Significant differences between clusters within a community were only found between Cluster I and II in vegetation

Table 3 R^2 values of each factor from perMANOVA of microbial, nematode, and plant communities[a]

Source	PLFA	Nematode	Vegetation
Cluster	0.263	0.173	0.146
Position	0.060	0.074	0.056
Site (cluster)	0.239	0.276	0.321
Cluster*position	0.090	0.115	0.102
Site*position (cluster)	0.348	0.362	0.376

[a] R^2 values represent the proportion of variation each factor contributes to the total variation in the dataset. All factors measured were significant at $\alpha = 0.01$

The increasing within-cluster variance from PLFA to nematode to vegetation communities (Fig. 2) may reflect a meaningful biological phenomenon, or merely a methodological artifact. Plants were identified to the species level, nematodes to the family/genus level, and the microbial community to the PLFA biomarker. This likely resulted in some degree of decreased variance in microbial and nematode communities, relative to plant communities. Regardless, perMANOVA and multivariate dispersion analyses suggested that the PAM clustering approach captured meaningful differences between these biological communities, and that variance across each cluster within a community was relatively constant.

Increased interest in examining ecological phenomena over larger spatial scales has led to a number of studies using GIS or remote sensing data to

classify a study area into smaller groups with similar attributes for the purposes of site selection (Danz et al. 2005; Krishnaswamy et al. 2009; Ruiz and Domon 2009). Here, the use of publicly-available GIS data and PAM analyses generated a systematic site selection process. This approach produced an assemblage of sites that represented an unbiased survey of the landscape, bringing rigor to a practice that can be done haphazardly, or based solely on plant communities or soil types. In reality, this study area is not defined by distinct clusters, but rather is a mosaic of soil types, biological communities and associated ecosystem services. Accordingly, the clustering approach served primarily as a tool for site selection, and the following ecological assessments were made in the context of a landscape mosaic without clusters.

Landscape properties

Sampled soil properties, soil biota and vegetation demonstrated large variation across the landscape in this study (Table 4). Ranges for soil properties such as total C, total N, and NO_3^-–N are consistent with values previously reported for an agricultural gradient in California (Steenwerth et al. 2006). Soil properties that varied the most across this landscape are typically associated with the high fertilizer use in irrigated croplands in the region. For example, NH_4^+–N, NO_3^-–N, P and K had coefficients of variation (CV) of 141.8, 64.7. 57.7, and 41.8, respectively (Table 4), and were all skewed right (data not shown).

Biological diversity and richness were relatively low given the fact that riparian ecosystems are noted for their high levels of plant diversity (Richardson et al. 2007), particularly in California's dry-summer, Mediterranean-type climate (Barbour et al. 1993). Shannon's diversity reached a maximum of 3.20, 2.47, and 3.05 for PLFA, nematodes, and vegetation, respectively. Biotic properties generally had much larger CV values than soil properties, indicating that these biological communities were more variable across the landscape and were only weakly linked to the measured soil properties (see Table 5).

Functional groups of biota showed far higher CV than measures of diversity and richness (Table 4). PLFA biomarkers showed about a 10-fold increase from lowest to highest values over the landscape for fungi, actinomycetes, and bacteria. In contrast, the range was >100-fold for nematode lower-level trophic level groups, and higher trophic levels were absent from many sites. For vegetation, annual grasses constituted the most abundant functional group, followed by woody perennials. The highest CV (>200) were for perennial forbs, grasses, legumes, and woody species, as well as annual legumes. These perennial plant taxa are mainly native species that have largely vanished from many disturbed grasslands, savannas and woodlands in California (Stromberg and Griffin 1996; Jackson et al. 2007b). Differences in community structure due to position from the stream edge were small relative to site differences (Table 3). Close examination of functional diversity is reported elsewhere (Young-Mathews et al. 2010) and suggests that specific traits and species interactions increase ecological functions in particular locations in the landscape.

Linking above- and belowground biota and soil properties

The relationships between aboveground and belowground communities were of particular interest to this study. The Mantel tests showed that most groups shared significant positive correlative structure, indicating linkages between most biological communities and soil properties (Table 5). PLFA were weakly related to nematodes and vegetation with the standardized Mantel statistics (analogous to correlation coefficients) of 0.11 and 0.08, respectively, indicating that microbial communities were more closely related to nematode communities than plant communities. Nematodes and vegetation shared the greatest correlative structure out of the three biological communities ($r = 0.24$). Microbial communities and nematode communities were correlated with the weighted average of the soil properties in the surface 100 cm (Table 5). Weaker correlative relationships with the soil properties in the surface 15 cm, where these communities were measured, are probably due to greater variability in soil properties compared to 0–100 cm (average distance to centroid in soil properties: 0–15 cm = 0.128, 0–100 cm = 0.112).

The relatively low standardized Mantel statistics indicates that although the three community datasets were related, the majority of structure in these data was not accounted for. In particular, greater trophic interactions would be expected to influence the structure of the microbial, nematode and vegetation communities,

Table 4 Soil and biotic properties sampled over the study area ($n = 60$)

	Range	Mean	Standard deviation	Coefficient of variation
Soil properties (0–15 cm)				
Soil total C (%)	0.48–2.42	1.01	0.39	38.2
Soil total N (%)	0.04-0.18	0.10	0.03	31.8
NO_3^-–N (μg g^{-1})	0.01–34.63	4.73	6.70	141.8
NH_4^+–N (μg g^{-1})	0.04–4.12	1.47	0.95	64.7
C:N ratio	6.35–14.15	9.93	1.73	17.5
Olsen P (μg g^{-1})	4.30–64.07	19.13	11.03	57.7
K (meq 100 g^{-1})	0.28–1.55	0.66	0.28	41.8
Ca (meq 100 g^{-1})	7.48–26.69	13.89	4.09	29.5
pH	5.47–8.17	7.09	0.67	9.5
Clay (%)	7.60–29.27	15.63	4.23	27.0
Silt (%)	30.12–68.78	52.82	8.56	16.2
Sand (%)	12.20–61.63	31.55	11.93	37.8
PLFA properties				
Diversity	2.95–3.20	3.09	0.06	1.9
Richness	30–57	38.63	5.77	14.9
Microbial biomass[a]	10.74–90.01	37.67	20.65	54.8
Functional group[a]				
Actinomycetes	0.74–5.25	2.20	1.08	48.9
$Gram^+$	2.46–17.81	7.73	4.02	52.0
$Gram^-$	1.31–14.67	5.54	3.04	54.8
Fungi	1.36–13.25	5.12	3.15	61.5
Unspecific	4.64–41.12	16.66	9.28	55.7
Nematode properties				
Diversity	1.14–2.47	1.82	0.29	15.7
Richness	7–30	15.79	4.26	27.0
Trophic group[b]				
Bacterivores	1.96–426.30	115.64	102.94	89.0
Fungivores	1.21–785.98	180.78	140.40	77.7
Plant feeders	1.13–552.29	121.01	107.41	88.8
Omnivores	0.00–116.67	26.23	25.78	98.3
Predators	0.00–9.61	0.71	1.66	235.2
Vegetation properties				
Diversity	0.00–3.05	1.28	0.60	47.0
Richness	1–35	10.17	6.25	61.4
Functional group[c]				
Annual forbs	0–40.5	10.12	11.47	113.4
Annual grasses	0–95.5	28.23	30.38	107.6
Annual legumes	0–23.0	2.08	4.22	203.2
Perennial forbs	0–45.0	3.37	7.33	217.6
Perennial grasses	0–53.0	4.53	9.26	204.5
Perennial legumes	0–20.0	1.48	4.12	278.0
Perennial woody	0–111.0	12.47	26.73	214.4

[a] PLFA microbial biomass and functional groups expressed as nmol g^{-1} soil

[b] Nematode trophic groups expressed as 100 nematodes g^{-1} soil

[c] Vegetation functional groups expressed as percent cover

Table 5 Standardized Mantel statistic (r) for pairwise comparison of groups[a]

	PLFA markers	Nematode taxa	Vegetation species	Soil properties (0–15 cm)	Soil properties (0–100 cm)
Nematode taxa	0.11**				
Vegetation species	0.08*	0.24***			
Soil properties (0–15 cm)	0.05	0.05	0.13***		
Soil properties (0–100 cm)	0.12*	0.08*	0.12**	0.76***	
GIS variables[b]	0.04	0.20***	0.12*	0.18***	0.18***

PLFA, nematode and vegetation groups are comprised of entire community dataset. Soil properties were measured in the field. GIS variables are a composite of the 14 data layers (Table 1) that were used as a basis for cluster analysis

[a] Mantel statistic is synonymous with a correlation coefficient. Significance levels: *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$

[b] All Mantel tests run with GIS used the Gower's distance measure, since the 14 GIS variables contained both continuous and categorical data. All other comparisons were based on Bray-Curtis distance

as has been previously reported (Zak et al. 2003; Waldrop et al. 2006). There are likely historical management effects, colonization events, or unmeasured site characteristics that have played an important role in determining community composition.

Correlation tests that compared diversity and richness measures between the three communities showed both positive and negative relationships. PLFA diversity and richness were positively correlated with nematode diversity and richness ($r = 0.320$, $P = 0.021$; $r = 0.334$, $P = 0.016$, respectively). PLFA diversity was negatively correlated with plant diversity ($r = -0.289$, $P = 0.036$) and PLFA richness was not significantly correlated with plant richness ($r = 0.180$, $P = 0.198$). Nematode diversity shared no relationship with plant diversity ($r = 0.065$, $P = 0.636$), but nematode richness was weakly correlated with plant species richness ($r = 0.238$, $P = 0.078$). Previous reports have shown aboveground and belowground diversity to be related either positively (Stephan et al. 2000), neutrally or idosyncratically correlated (Hedlund et al. 2003; De Deyn and Van der Putten 2005). Inconsistent relationships between plant, nematode and microbial diversity and richness were also reported from a previous farmscape study in this region of (Smukler et al. 2010). Our seemingly idiosyncratic results suggest that there may be different ecological controls acting to shape aboveground and belowground diversity. These mechanisms are typically complex and poorly understood (Wardle 2006). Despite significant positive relationships in overall community structure between all biological communities, as shown by Mantel tests (Table 5), these correlative structures were not always detectable in diversity measures and, in the case of PLFA and plant diversity, were negatively correlated.

Agricultural intensification and diversity

An overall consistent trend of decreasing biological diversity occurred with increasing agricultural intensification. The slopes of all regression lines were negative, and all but one was statistically significant (Fig. 3). There was no relationship between PLFA diversity and intensification; however PLFA richness was significantly reduced with intensification ($P = 0.005$; Fig. 3d). Both nematode diversity and richness were weakly, but significantly negatively related to intensification ($P = 0.044$, 0.024; Fig. 3b, e, respectively). Vegetation diversity and richness shared the strongest negative correlation with agricultural intensification out of the three communities (both, $P < 0.001$; Fig. 3c, f). These findings are consistent with other studies that have shown declines in plant, nematode and microbial richness with agricultural intensification (Billeter et al. 2008; Jangid et al. 2008; Yeates and Stirling 2008; Kleijn et al. 2009). This approach, however, has uniquely demonstrated concurrent declines in aboveground and belowground biodiversity due to agricultural intensification over a landscape.

Low abundance of rare PLFA biomarkers resulted in little difference in the Shannon diversity index between samples. PLFA richness was highly correlated with total PLFA abundance, a measure of microbial biomass ($P < 0.001$, $r = 0.932$), and total PLFA abundance was negatively related to agricultural intensification ($P < 0.001$, $r = -0.438$). Thus,

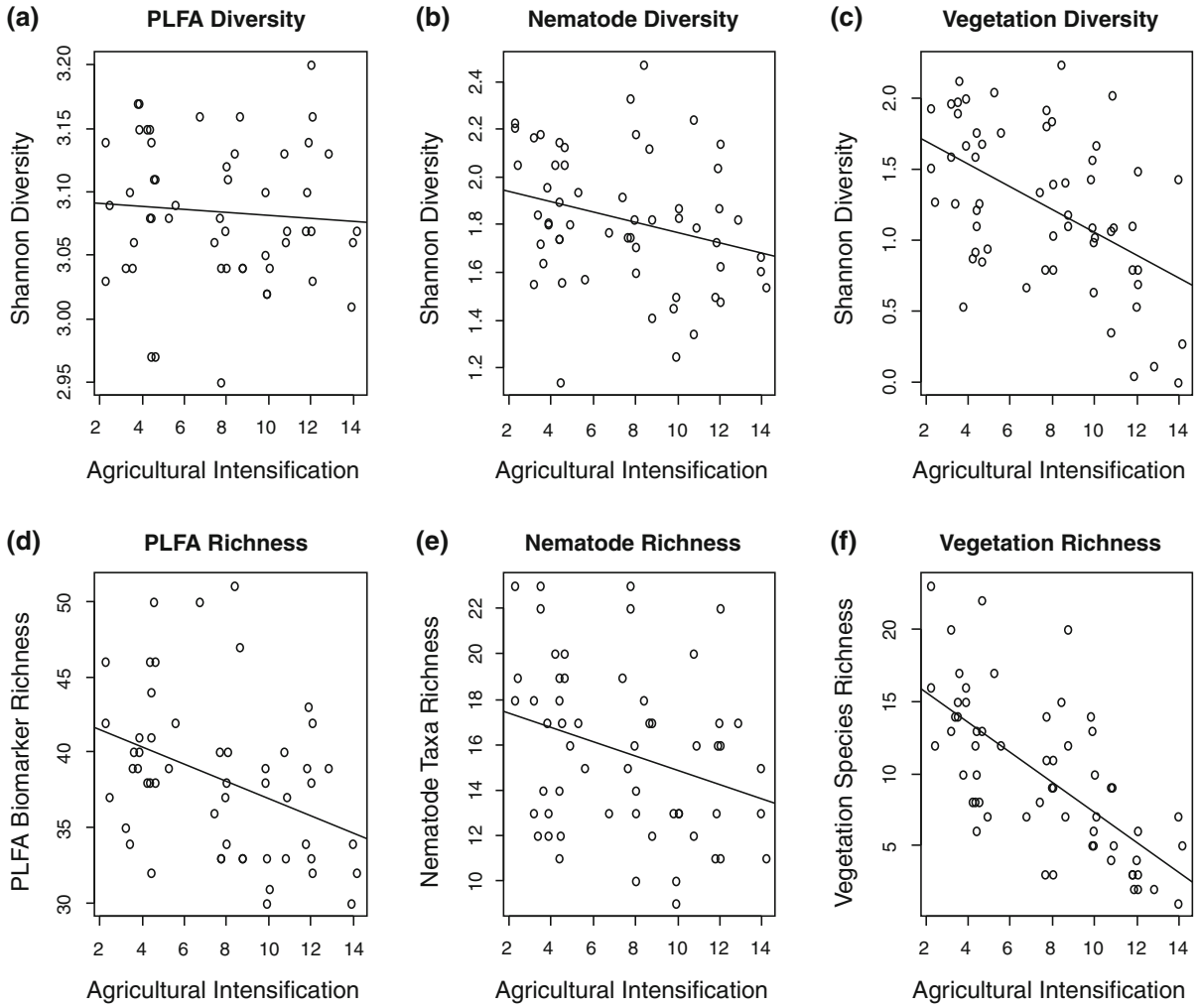

Fig. 3 The relationship between agricultural intensification and Shannon's diversity or taxonomic richness of PLFA, nematode and vegetation communities. Agricultural intensification was measured by both field-scale and landscape-scale variables. See Table 6 for R^2 and statistical significance

declines in PLFA richness may be driven by reductions in microbial biomass associated with agricultural intensification.

Both field-scale and landscape-scale variables for agricultural intensification played roles in the measured losses of diversity, but their relative importance differed according to biotic community (Table 6). Landscape variables accounted for more than three times as much variation as field variables with PLFA richness. Variation in nematode diversity and richness was explained nearly equally by field and landscape variables. Field variables explained losses in vegetation diversity and richness roughly twice as well as landscape variables. Other studies have shown that losses in diversity are associated with factors operating at both the field and landscape scale. For example, positive relationships between richness and landscape heterogeneity, or the percent of a landscape in semi-natural areas, have been found over a range of biotic communities (Atauri and de Lucio 2001; Steffan-Dewenter et al. 2002; Eggleton et al. 2005; Billeter et al. 2008). Likewise, field-scale factors such as N fertilization, tillage, and herbicide application have been linked to declines in plant and soil biota richness (Wedin and Tilman 1996; Yeates and Bongers 1999; Gough et al. 2000; Suding et al. 2005). As in other landscapes (Tscharntke et al. 2005; Billeter et al. 2008), mechanisms operating at

Table 6 R^2 values for linear regression model: diversity (or richness) vs. agricultural intensification index for each of the three biotic communities[a]

Community	Measure	Field + Landscape	Field[b]	Landscape[b]
PLFA	Diversity	0.006	0.000	0.042
	Richness	0.147 **	0.076*	0.256***
Nematode	Diversity	0.072*	0.065#	0.066#
	Richness	0.091*	0.081*	0.084*
Vegetation	Diversity	0.256***	0.294***	0.145**
	Richness	0.460***	0.502***	0.290***

The variables for the field-scale and landscape-scale agricultural intensification indices were regressed together and separately. The regressions for the relationship between biotic communities and the field + landscape scale agricultural intensification index are plotted in Fig. 3

[a] Significance levels: *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, # $P < 0.10$

[b] Table 2 outlines field and landscape variables

multiple scales appear to maintain overall biodiversity in this landscape, but PLFA, nematodes, and vegetation responded differently to field-scale management or landscape heterogeneity.

Associations between agricultural intensification, taxa richness and environmental properties

Linear regressions confirmed expected relationships between agricultural intensification and several key environmental properties (Fig. 4), that can be considered 'indicators' or 'proxies' of ecological function. Although these riparian areas occupy a small fraction of the landscape, they support important soil processes, such as filtering agricultural nutrients and pollutants, reducing eroded sediment from entering waterways, improving water quality, and providing reservoirs of biodiversity (Lovell and Sullivan 2006; Richardson et al. 2007). High levels of soil NO_3^- and P, which are of concern for water quality and reflect agricultural fertilization, are associated with considerable differences in aboveground and belowground biodiversity at the plot scale (Bardgett et al. 1999; Wassen et al. 2005; Clark and Tilman 2008; Treseder 2008). Greater soil NO_3^- and P levels were strongly associated with agricultural intensification ($P < 0.001$), indicating the strong correlation between intensification and increased nutrient load in riparian areas across the landscape (Fig. 4a, b).

For the riparian health rating, which is based on factors such as channel condition, access to floodplain, bank stability, riparian zone vegetation, and macroinvertebrate habitat (Ward et al. 2003), low values were associated with greater agricultural intensification values (Fig. 4c). Soil C reflects the total soil C pool, and microbial biomass reflects the labile, organic fraction of this pool. The structure index for nematode taxa provides an indicator of the complexity of the soil food web, and its pest- and disease-regulating capacity (Ferris et al. 2001). Soil C, microbial biomass, and structure index values decreased with intensification (Fig. 4d–f), suggesting that agricultural intensification diminishes soil C stock, and decreases overall soil food web abundance and complexity. These findings are consistent with field-scale studies in the region (Sánchez-Moreno et al. 2006; Minoshima et al. 2007), suggesting that similar ecological controls operate over larger scales.

The relationships between biodiversity and ecosystem functions are of primary interest in conservation today. These relationships are complex and can easily be confounded by human activity, making them even more opaque and difficult to understand. Our landscape study area was dominated by agricultural activity, which likely influenced both the biotic richness and the measured environmental properties. To assess the relationships between these three interacting components, we examined correlations between taxonomic richness and environmental properties both ignoring the effects of agricultural intensification (simple correlations) and controlling for the effects of agricultural intensification (partial correlations). Simple correlations indicated some consistency across the three measured biological communities (Table 7). Soil NO_3^- and P were both negatively

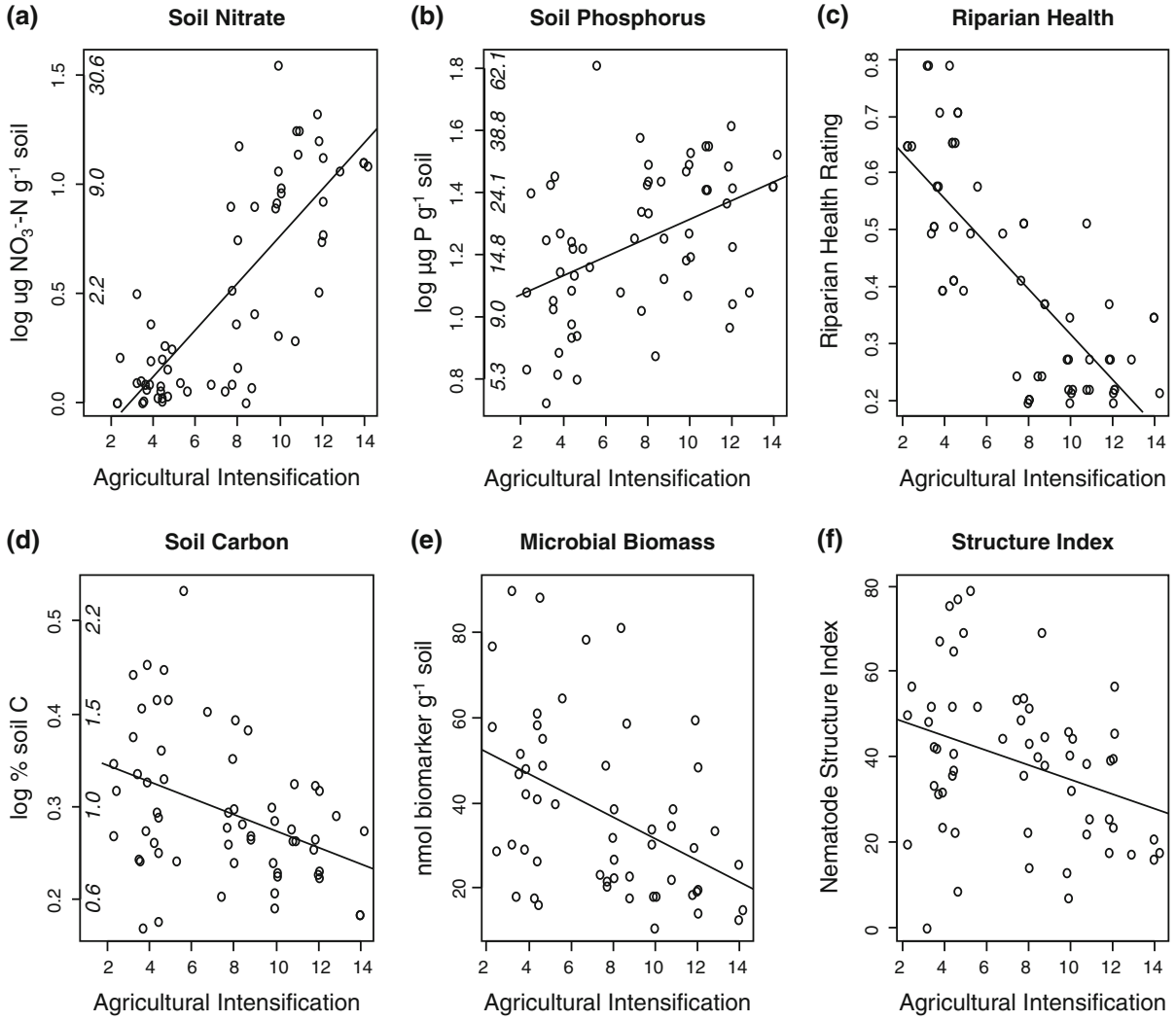

Fig. 4 The relationship between agricultural intensification and selected environmental properties based on linear regressions. Agricultural intensification was measured by both field and landscape variables. Respective R^2 and P values follow: soil nitrate (0.623, <0.001), soil phosphorous (0.194, <0.001), riparian health (0.581, <0.001), soil carbon (0.162, 0.001), microbial biomass (0.192, <0.001), nematode structure index (0.105, 0.013). *Italicized* numbers on the *y*-axis of panels **a**, **b**, and **d** indicate original backtransformed values for the log transformations

correlated with, and microbial biomass and riparian health were both positively correlated with diversity measures of every community. Other properties demonstrated more community-specific relationships (Table 7).

When the relationships between biotic richness and environmental properties were re-examined while holding the effects of intensification constant, the strength of the relationships were generally weaker but the magnitude of the effect varied greatly (Table 7). For example, when intensification was controlled for, soil NO_3^- and P remained negatively correlated with all three communities, except that the relationships to vegetation richness were no longer significant. In other words, agricultural intensification explained the majority of the negative relationship between vegetation richness and soil NO_3^- and P. This is likely attributable to the more direct intensive management of aboveground communities at high intensification sites, e.g., herbicides. Nematode and PLFA richness remained negatively correlated to soil NO_3^- even when accounting for intensification,

Table 7 Pearson's correlation coefficients between environmental properties at 0–15 cm depth and biotic richness, both ignoring influence of intensification (simple correlations) and controlling for influence of intensification (partial correlations)[a]

Property	Correlations ignoring intensification			Correlations controlling for intensification		
	PLFA richness	Nematode richness	Vegetation richness	PLFA richness	Nematode richness	Vegetation richness
Soil total C	0.546***	0.097	0.283*	0.458***	−0.042	−0.031
Soil total N	0.473***	−0.011	−0.082	0.466***	−0.054	−0.247#
Soil C:N ratio	0.114	0.124	0.617***	−0.112	−0.048	0.404***
Soil NO_3^-–N	−0.482***	−0.503***	−0.584***	−0.316*	−0.453***	−0.113
Soil Olsen P	−0.286*	−0.356**	−0.399**	−0.157	−0.273*	−0.163
Microbial biomass[b]	0.932***	0.341*	0.275*	0.919***	0.259#	−0.036
Nematode structure index	0.252.	0.437***	−0.040	0.151	0.373**	−0.378**
Riparian health	0.315*	0.421**	0.544***	0.044	0.309*	0.063

[a] Significance levels: *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$; # $P < 0.10$

[b] Microbial biomass was measured as total PLFA abundance

suggesting that soil biodiversity loss is associated with increased inputs of N fertilizer and its movement across the landscape. Agricultural intensification explained the majority of positive relationships with biotic richness and riparian health, reflecting the negative effects intensification has on the health of riparian areas. Overall intensification had the weakest effect on the relationships between PLFA richness and environmental properties (e.g., soil C, soil N, microbial biomass) and the strongest effect on relationships with vegetation richness (e.g., soil NO_3^-, soil P, nematode structure index, riparian health). Fully explaining these correlations demands more insight into ecological factors that shape species richness and trophic interactions in these ecosystems.

Conclusions

Numerous studies have shown that increased agricultural intensification leads to losses in aboveground and belowground biodiversity. However, to our knowledge this is one of the first studies that reports on the association between indicators of multiple ecosystem functions and aboveground and belowground diversity patterns over a landscape gradient of agricultural intensification. Despite the large amount of heterogeneity between sites, consistent patterns of declines in richness and diversity emerged, especially in nematodes and plants, with increasing intensification. These results show that the measured trends transcend site-specific variations, making them more robust than in studies operating at field scales alone.

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