



# Field-scale habitat complexity enhances avian conservation and avian-mediated pest-control services in an intensive agricultural crop



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## ABSTRACT

The relationship between on-farm avian conservation measures and the potential provisioning of pest-control services by birds is poorly understood in intensive agricultural landscapes, especially in temperate regions. We used an exclusion experiment to test the effects of field- and landscape-scale habitat complexity on avian-provisioned pest-control services and assessed avian abundance and diversity across 32 conventional alfalfa (*Medicago sativa*) fields in winter and early spring in California. Alfalfa is a key forage crop around the world and is grown on approximately 30 million hectares globally each year. Bird foraging reduced the abundance of the most significant insect pests of alfalfa by over 33%. The presence of complex edge habitat (presence of at least two trees >1.5 m) led to higher avian abundance within fields, which in turn led to reduced pest insect populations at sampling points close to the field edge. Fields with complex edge habitat also harbored nearly three times as many bird species as those with simple edge habitat. The distance from the nearest riparian habitat, a measure of landscape diversity, did not affect bird abundance or diversity in winter alfalfa fields, which may be related to the homogenous landscape in which our study was based. Our results show that relatively simple conservation measures in intensively managed farming landscapes, such as planting small trees along a field edge, can result in increased abundance and diversity of over-wintering birds, with direct benefits to farmers through increased avian-mediated pest-control services.

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## 1. Introduction

Dramatic loss of biodiversity globally has been primarily driven by large-scale loss of natural habitats (Pimm et al., 1995), much which has been a result of agricultural land conversion. Nearly 40% of terrestrial land is devoted to agriculture (Foley et al., 2011) and escalating expansion and intensification of farming practices to produce more food for a growing human population has been linked to continuing biodiversity declines (Geiger et al., 2010; Green et al., 2005; Sala et al., 2000). For example, agriculture has been characterized as the “greatest extinction threat to birds” (Green et al., 2005).

Given the scale of biodiversity loss, it is increasingly recognized that conservation of biodiversity cannot be achieved solely through protected reserve systems (Fahrig 2001; Chazdon et al., 2009). Thus, there have been calls for the expansion of biodiversity

conservation beyond the reserve system (e.g. Chazdon et al., 2009) and particularly into agricultural landscapes (Scherr and McNeely, 2008). There is also increasing recognition that human populations rely on the ecosystem services provided by biodiversity, such as biological control of crop pests (Losey and Vaughan, 2006; Perrings et al., 2006; Tilman et al., 2002). Thus, designing or restoring agroecosystems that are capable of conserving biodiversity may also enable farmers to take advantage of functional natural diversity that provides ecosystem services at the farm and landscape levels and, as a result, benefit both people and nature (Cumming and Spiesman, 2006; Perrings et al., 2006; Power, 2010; Tscharrntke et al., 2007).

Compared with more diverse agroecosystems that incorporate diverse cropping systems and non-crop habitat, and which typically characterize developing world agricultural landscapes and smallholder systems, intensively farmed and simple monoculture landscapes support lower biodiversity and receive fewer ecosystem services (Foley et al., 2005; Power, 2010; Tscharrntke et al., 2005). Wildlife-friendly farming practices, including maintaining refugia habitat, restoring natural habitat along field

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margins, and reducing chemical inputs and diversifying crop types, have been suggested as a way to preserve wildlife populations in farming areas (e.g. Donald and Evans, 2006; Fahrig et al., 2011; Quinn et al., 2014). Large-scale, long-term conservation programs in farmland are rare, but programs such as the European Union's agri-environmental schemes and the U.S. Farm Bill's conservation programs have shown that such practices can be effective for conservation, although they often do not benefit rare species (e.g. Kleijn et al., 2015), and the effects of such schemes on ecosystem-services for farmers are rarely measured (Batáry et al., 2015).

Birds are often targets of conservation actions, particularly in agricultural landscapes (e.g. Vickery et al., 2004) in part because they have declined dramatically in these systems, can respond positively to improved management, and are easily measured indicators of ecosystem health (Gardali et al., 2006). The complexity of field-edge and landscape-scale habitats has been shown to increase bird diversity in a number of European and tropical systems (Batáry et al., 2011; Kellermann et al., 2008; Vickery et al., 2004), suggesting such actions could be effective for bird conservation. Also, at broader scales, the proportion of natural and semi-natural habitat in the landscape in which a field is embedded can influence the efficacy of increasing field-edge habitat for bird diversity (Batáry et al., 2011; Quinn et al., 2012). Unfortunately, there have been few examples from temperate North America (but see Jobin et al., 2001; Quinn et al., 2012) or intensively cultivated landscapes that can be used to evaluate the potential for bird- or broader biodiversity-conservation benefits of similar practices.

Pest-control services provided to US farmers by beneficial insects are estimated to be worth \$4.5 billion per year (Losey and

Vaughan, 2006), however very few studies have quantified pest-control services provided by birds. Landscape complexity and the presence of natural habitats has been shown to influence avian-mediated pest-control services in coffee agroforestry (e.g. Johnson et al., 2009; Karp et al., 2013; Railsback and Johnson, 2014) and management to encourage diverse bird assemblages have been shown to be beneficial for both avian conservation and invertebrate pest management (reviewed in Wenny et al., 2011). However, most of these studies have been conducted at a small scale (1–4 sites), in non-intensive systems, and in predominantly tropical agroforestry systems such as coffee and cacao (e.g. Johnson et al., 2010; Karp et al., 2013; Kellermann et al., 2008; Railsback and Johnson, 2014). We therefore have few comparable figures for the value of birds as natural enemies of agricultural pests, especially within intensive temperate and Mediterranean agricultural systems. With 21% of avian species at risk of extinction, the ecosystem services provided by birds are likely to decrease in the coming decades; a fact that will only be appreciated after the decline of each species (Sekercioglu et al., 2004).

In this study, we sought to address the potential for birds as significant contributors to pest control in an intensively cultivated crop in North America and to quantify how these potential pest control services vary with implementation of farm-scale practices to improve habitat for birds. We conducted exclusion experiments in 32 fields representing a gradient of both local- and landscape-scale habitat complexity in alfalfa (*Medicago sativa*, also known as lucerne) to quantify the abundance of key invertebrate pests in the presence and absence of potential bird predation. Alfalfa is grown on approximately 30 million hectares globally each year (Yuegao and Cash, 2009). North America is currently the top-producing

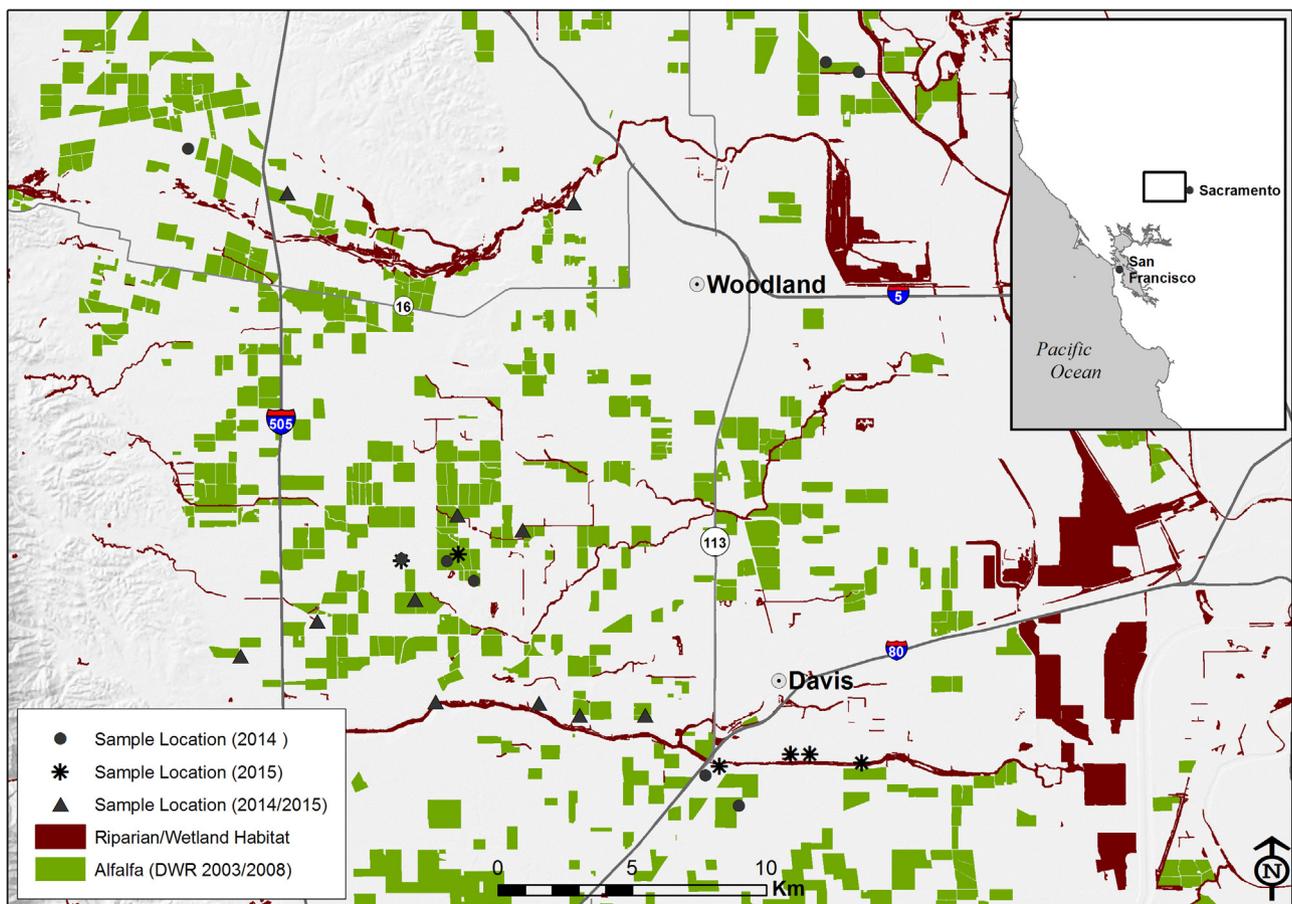


Fig. 1. Map showing experiment locations and locations of riparian habitat.

region for alfalfa, but as dairy industries expand in regions such as China, alfalfa production is also expected to grow (Yuegao and Cash, 2009). Alfalfa is one of the highest acreage crops in California and has come under public scrutiny recently because of its high water use. However, alfalfa also provides important habitat for imperiled open-country birds, such as the Swainson's hawk (*Buteo swainsoni*; Swolgaard et al., 2008) and long-billed curlew (*Numenius americanus*; Shuford et al., 2013). Also, the value of this habitat for a diversity of overwintering migrant and resident birds has thus far not been evaluated. Our two primary aims in the present study were to quantify 1) whether avian-mediated pest-control services exist in alfalfa and, if so, how habitat management affects pest-control, and 2) the potential of alfalfa to provide overwintering habitat for birds. This information will be of importance for landowners, policy-makers, and conservation professionals seeking to design land-use policies based on a better understanding of the role of birds in agricultural landscapes.

## 2. Methods

### 2.1. Study area/crop

California's Central Valley runs 724 km north-south and covers a total of 10.9 million hectares (26.9 million acres). It is one of the most productive agricultural landscapes in the world, producing over 25% of the fresh produce consumed in the United States (USDA, 2015), and valued at over \$45 billion (USD) per year. Over 95% of the Central Valley's riparian and wetland ecosystems have been replaced by highly intensive agriculture and urban development (Frayer et al., 1989; Katibah, 1984), with remnant native habitat existing only in fragmented and isolated patches. Nevertheless, some native biodiversity in this region persists despite the highly anthropogenic landscape (Dybala et al., 2015).

Each year, alfalfa is grown for hay production on between 323,750 and 404,690 ha (800,000–1 million acres) across California, producing over 5.8 million short tons valued at \$1.2 billion/year in 2013 (USDA, 2015), 70% of which is grown in the Central Valley. Alfalfa is a perennial crop generally grown for 3–5 consecutive years as part of a roughly seven-year rotation with row crops on fields in our study area. In winter, alfalfa grows from a low, dormant stage starting around mid-January to reach full-height by mid-April, at which point it is cut, dried, and baled. Following this initial slow growth period, alfalfa grows quickly after the first cutting and is subsequently cut and harvested approximately every four weeks over the spring and summer

months. Alfalfa is attacked by two species of nearly identical invasive weevil species prior to the first cutting: the alfalfa weevil (*Hypera postica*) and the Egyptian alfalfa weevil (*Hypera brunneipennis*). Weevil damage is common and growers frequently utilize at least one pesticide spray during winter to control weevil damage (Godfrey et al., 2005), contributing to increased scrutiny of alfalfa as a source of chemical contamination of waterways (Long et al., 2002).

We conducted this experiment on 32 farm fields in partnership with five private farm managers. Growers provided maps of their alfalfa fields along with information on field edge habitat, field age and growing methods used, and we combined this information with remote-sensing aerial imagery to examine field- and landscape-scale natural habitat characteristics. We made field selections to create a balance of fields with both complex and simple field edge habitat (see below for definitions) and at varying distances from natural habitat, which in our study area consists mainly of remnant and restored riparian areas (Fig. 1). Each sample year, fields were separated by an average of  $2.46 \text{ km} \pm 0.39 \text{ km}$  (min 700 m), and ranged in size from 10 to 50 ha. Since this experiment was conducted within conventional fields (i.e. non-organic fields) we had to control for the impacts of insecticide sprays. Growers participating in the study supplied the date, product applied, and rate of active ingredients applied per acre for all spray events during the study. Since very similar compounds and application rates were used for all of our experimental fields, but the date of sprays varied, we included the days since the most recent insecticide spray in our analyses.

### 2.2. Exclusion experiments

Exclusion experiments were set up perpendicular to the center point of a 200-m transect along the focal edge of each field which was used to assess bird diversity and abundance (see below). The transect for each field was roughly centered halfway along the field's edge or, if habitat present did not run the entire field length, the transect was centered halfway along that habitat. We completed our field experiments between January and March in both 2014 (19 fields) and 2015 (14 fields), with nine fields common across years. Exlosures prevent large vertebrates from accessing areas of a crop without hindering access by invertebrates. A minimum of two exclosures were set up in each field: one approximately 5 m from the edge of the field (to avoid overly patchy areas of growth at the immediate edge of many fields) and one 55 m from the edge of the field. Each exclosure was paired with

**Table 1**

Habitat categories used for each study site, and variable used in analyses for weevil abundance, avian species richness, and avian abundance.

Category	Variables measured	Use in analyses
Edge Habitat	Edge Habitat: Field edge closest to exclosures has two or more trees or shrubs with an average height greater than 1.5 m. Simple Edge: Field edge closest to exclosures has less than two trees or shrubs with an average height greater than 1.5 m.	Categorical variable presence of edge habitat, otherwise considered "Simple Edge".
Edge Habitat Complexity	<i>Height</i> —mean from visually-estimated canopy height at five points along 200 m transect on field edge. <i>Width</i> —mean estimated canopy width measured from five points along 200 m transect using aerial imagery of the area. <i>Canopy Layers</i> —mean from five points along 200 m transect, at each point the total number of canopy layers present within six categories chosen to represent the variety of vegetation observed at our sites was counted, including low grasses, medium grasses, shrubs, small trees, and tall trees (0–20 cm, 21–50 cm, 51 cm–1 m, 1.1–5 m, 5.1–10 m, >10 m). Sites could therefore have a maximum of six canopy layers.	Continuous variables combined in a Principle Components Analysis to account for collinearity.
Distance to Riparian Habitat	Mean distance from each 10 m cell within a 50 m buffer of the avian abundance transect center points to the nearest riparian habitat as classified. Habitat was defined as riparian if it had one of the following classifications: Native Riparian (CA DWR, 2003, 2008); Blue Oak Woodland, Valley Foothill Riparian; Fresh Emergent Wetland; Saline Emergent Wetland; and Valley Foothill Riparian (Geographic Information Center, 2009).	Continuous variable used to predict weevil densities, bird abundance and species richness.

an adjacent control area of the same size, which was approximately 2 m from the treatment. The experiment included a total of 76 enclosure/control pairs across the 32 fields over two years. Enclosures were 1.22 m long  $\times$  1.52 m wide  $\times$  0.91 m high (4 ft  $\times$  5 ft  $\times$  3 ft) and constructed of  $\frac{3}{4}$  in. PVC-pipe, nylon bird-netting (2 cm mesh), and chicken-wire (2.54 cm mesh). We designed the enclosures in consultation with growers to accommodate for normal tractor and spray use in fields and so that the enclosures could be easily removed and replaced by farm workers if necessary. All experiments were carried out in accordance with the University of California's Institutional Animal Care and Use Committee approved protocol #18033.

In both seasons, we harvested the alfalfa from within our enclosures and controls within approximately one week of final field harvest by the farmer in order to quantify the density of weevils per kilogram of harvested alfalfa. By expressing weevil numbers as a function of yield, we controlled for inter-field variability in alfalfa plant density and height. Enclosure and control samples were always taken at the same time. We harvested from within our enclosure and control areas by cutting the alfalfa to 1-in. above ground-level inside of quadrats (0.91  $\times$  1.22 m in 2014, 0.5  $\times$  0.5 m in 2015) using hand-scissors and placing the alfalfa top-first into large bags or containers, discarding any weed plants that were harvested. To count weevils, we weighed each sample of alfalfa, placed it into a large bin fitted with a lid (45 cm  $\times$  55 cm  $\times$  330 cm), shook it violently 30 times, then struck all of the alfalfa plants against the side of the container to dislodge weevils from the plants and into the bottom of the bin. Remaining leaves and stems in the bin were then passed through a series of three progressively smaller-sized soil sieves to separate out the weevils, which were then counted. We did not attempt to distinguish between the two nearly identical species of weevil.

### 2.3. Habitat complexity

For each site, we measured three levels of habitat complexity for the edge nearest the exclusion experiments and along which we ran our bird surveys: 1) Presence of "Edge Habitat" consisting of two or more trees or shrubs with an average height greater than 1.5 m along the 200 m transect used for our bird abundance counts, all other sites were considered "Simple Edge"; 2) A continuous measure of "Edge Habitat Complexity", measured by estimating the height, width and number of canopy layers at five points along a 200-m transect at the edge of each field; and 3) The distance to the nearest riparian habitat (Table 1). The edge with the greatest habitat complexity was always chosen for sampling. Examples of sites with complex edges include fields that bordered directly onto dense riparian habitat, field edges with purposefully planted hedgerows of native trees and shrubs, and field edges with treelines of mature valley oak (*Quercus lobata*). Sites with simple edges included fields with unmanaged herbaceous or grassy vegetation, and fields with 'clean' borders lacking in any vegetation such as dirt roads. Distance to riparian habitat was used as a landscape-scale habitat variable because in our study area, riparian areas represent the last patches of natural habitat remaining (CA DWR, 2003, 2008; Geographic Information Center, 2009), and are a vital resource for overwintering birds (Dybala et al., 2015). To calculate the distance to riparian area, we used ArcGIS 10.1 (ESRI, 2010) to create a distance raster that encompassed the entire study area by using the Euclidean distance algorithm. We used the riparian vegetation GIS dataset (Table 1) as the 'source' input for the algorithm and set the output grid cell size to 10 m. Each field's transect center point was then buffered by 50 m, and we calculated the distance from each grid cell within the buffer to the nearest riparian vegetation polygon. The mean distance for all cells within each buffer was calculated as the distance value for each field.

### 2.4. Bird surveys

We conducted two bird surveys in late winter/early spring (February 16–April 9) of 2014 (19 fields) and 2015 (16 fields) to quantify both bird abundance and diversity and to evaluate the potential role that birds play in consuming pest insects during each season. Note that two fields that had bird surveys completed in 2015 did not have final alfalfa counts completed because alfalfa was harvested in those fields before data could be collected on weevils. All bird counts were conducted by trained observers and timed to coincide with the middle of the growing and weevil-pest season. All counts were conducted between dawn and 10 am and were not conducted in very cold ( $<3^{\circ}\text{C}$ ) or very hot weather ( $>24^{\circ}\text{C}$ ), in high winds or heavy precipitation. Counts were also cancelled or abandoned if there were any farm workers or machinery in our focal field or if the field was sprayed in the previous 48 h. We conducted two counts on each field visit: one to quantify the birds utilizing the edge habitat alongside the field, and one to quantify the birds utilizing the field interior. These methods provide relative values for comparing inter-site bird communities. To count birds utilizing edge habitat, observers walked a 200 m transect carefully counting all birds seen or heard within the 20 m of the field edge, but not within the field itself. To count birds utilizing the field interior, observers returned to the mid-point of the transect, allowed five minutes for birds to settle, and then conducted a 10-min. modified area search (Ralph et al., 1993) by walking 50 m into the field to flush birds and scanning the field for bird activity, recording all birds observed within the field. We used different methods for the edge and interior transects to maximize our detection of birds utilizing each type of habitat. Because of the differences in transect length and count methods, our bird counts allow us to compare the inter-site relative abundance and richness of birds utilizing edge habitat, and to compare the inter-site relative abundance and richness of birds utilizing fields; not to compare between edge and field data within sites.

### 2.5. Analyses

Because the variables describing "edge habitat complexity" (height, width, and number of vegetation layers) are highly correlated, we used a Principle Components Analysis to reduce these into two orthogonal axes that explained over 94% of the variance among them. The two axes, PC1 and PC2, were included as predictor variables in our candidate models for both weevil densities and bird abundance and richness.

To analyze our data on the number of weevils counted per kg of alfalfa, we used a generalized linear mixed model with a Poisson error and a log-link function to analyze the impact of our exclusion treatment, bird abundance, species richness, distance to nearest riparian habitat, and edge and field-scale complexity. To account for our hierarchical design, we included site nested within year as random effects in our models. This avoided treating multiple samples taken within each site and within each year of the study as being independent of one another. We used a square-root transformation on our response variables to meet model assumptions.

To analyze our bird count data, because conducting two counts per season is likely to underestimate both the species richness and abundance of birds, we used the maximum number of individuals of each species observed on either visit to calculate avian abundance and total species richness for each site. We ran separate models for each of our bird variables (species richness and abundance) and for the edge and field bird counts to determine the effects of habitat complexity on birds. We included the presence or absence of edge habitat, the two PCA axes describing edge-habitat complexity, and the distance to nearest riparian habitat in our full

models. For species richness, we used generalized linear mixed effects models with Poisson errors. For avian abundance, we first log-transformed our data to meet model assumptions, and then ran linear mixed effects models.

For all of our statistical analyses, we used the lme4 package (Bates et al., 2008) for the generalized- and linear-mixed effects models in R (version 3.1.2; R Core team 2014). We simplified the maximal models by removing interactions, then main effects, until no further reduction in residual deviance (measured using Akaike's Information Criterion) was obtained. For all analyses, we considered candidate models with  $\Delta AIC \leq 2$  and chose the most parsimonious model. Results are presented  $\pm$  one standard error of the mean.

### 3. Results

#### 3.1. Pest control by birds

The most parsimonious model for predicting the number of weevils present per kilogram of alfalfa included the effect of bird exclusion, and an interaction between the distance of sampling points from the edge of the field and the abundance of birds within the field (Table 2). Other variables not supported by the model included the distance of the field from the nearest natural habitat, edge habitat complexity (PC1 and PC2), the number of days since the most recent insecticide spray, avian richness at the field edge and interior, and avian abundance at the field edge (Table 2).

The best supported model therefore predicted that areas of alfalfa fields birds could access and forage in had 33.56% fewer weevils per kg of alfalfa than areas of alfalfa from which birds were excluded ( $Z = 2.97$ ,  $p = 0.003$ ). Holding all other variables constant, we estimated weevil abundance at the edges of fields (5m) to be  $35.19 \pm 1.81$  weevils<sup>-1kg</sup> in areas birds could access and  $52.95 \pm 1.15$  weevils<sup>-1kg</sup> within exclosures. In the field interior, weevil abundance was estimated to be  $12.53 \pm 1.55$  weevils<sup>-1kg</sup> in areas birds could access, whereas areas that birds could not access had  $18.86 \pm 1.78$  weevils<sup>-1kg</sup>. In both exclosures and controls, at the field edge the number of weevils declined as avian abundance increased ( $Z = -3.37$ ,  $p < 0.001$ ), whereas within the field interior, the number of weevils increased as avian abundance within the field increased ( $Z = -2.85$ ,  $p = 0.004$ ; Fig. 2).

#### 3.2. Avian abundance and richness

Along field edges, sites with edge habitat had higher relative species richness ( $13.62 \pm 1.1$  species) compared to sites with simple edges ( $4.98 \pm 1.2$  species,  $Z = -5.09$ ,  $p < 0.001$ ; Table 3), and increasing edge habitat complexity also led to increased relative

species richness (PC1:  $Z = -2.84$ ,  $p < 0.01$ , Fig. 3). While the best-fit model for relative avian diversity at the field edge included only presence of edge habitat and the PCA axis for habitat complexity, the next best-fitted model also incorporated distance to riparian habitat in predicting avian diversity (Table 3) but this variable explained very little variance ( $p = 0.17$ ). The best-fit model for relative avian abundance along the field edge included just the categorical variable for edge habitat complexity and predicted that sites with complex edges had a greater relative abundance of birds ( $67.09 \pm 1.17$  birds) compared to sites with simple edges ( $17.31 \pm 1.25$  birds,  $t = -6.03$ ,  $p < 0.001$ ; Table 3). A model containing both PC1 and the categorical habitat complexity variable was the second most parsimonious model ( $\Delta AIC$  of 2.08; Table 3) for predicting relative avian abundance along the field edges, but the PC1 variable explained very little additional variance ( $p = 0.14$ ).

Within field interiors, the most parsimonious model for relative avian species richness included just the categorical variables for edge habitat (Table 3) and predicted that relative bird diversity was higher for sites with edge habitat ( $6.10 \pm 1.22$  species) compared to sites with simple edges ( $4.42 \pm 1.15$  species,  $Z = -2.22$ ,  $p = 0.03$ ; Table 3). Alternate candidate models included PC1 (Table 3) and suggested that relative avian richness increased with edge complexity, but PC1 was nonsignificant in these models ( $p = 0.09$ ). Similarly, the presence or absence of complex habitat was the most important predictor of relative avian abundance within fields (Table 3). Fields with edge habitat ( $32.11 \pm 1.18$ ) had a greater relative abundance of birds utilizing field interiors compared to fields with simple edges ( $19.82 \pm 1.27$ ,  $t = -2.044$ ,  $p = 0.05$ ).

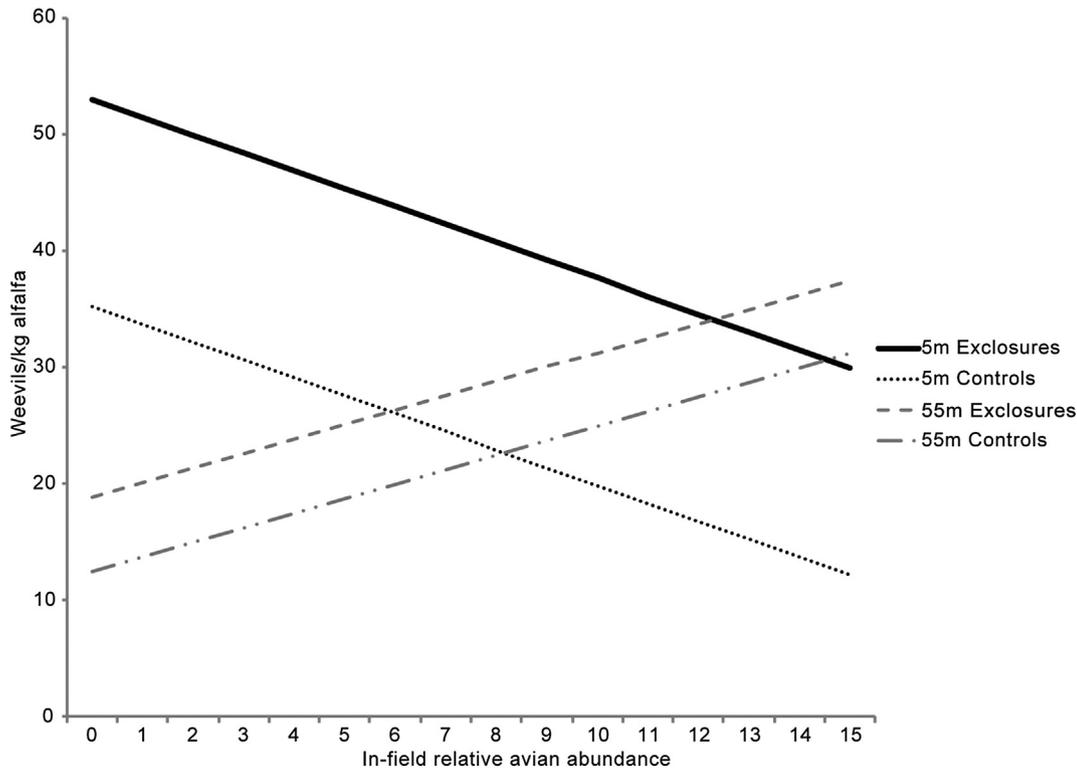
Across all sites, a total of 74 different bird species were identified along field edges, and 36 species were observed utilizing field interiors, however note that our methods for counting birds along field edges differed from our methods within fields, so these values are not directly comparable. There was considerable variation in the relative abundance of different bird species. Savannah sparrows (*Passerculus sandwichensis*) were the most abundant bird observed in our counts at both the field edge and within the field, relative to counts for other species (Fig. 4). Red-winged blackbirds (*Agelaius phoeniceus*) were also common, but were more abundant at sites with edge habitat (Fig. 4). Ten of the 14 most common birds observed at our sites consume insect material as all or part of their diets during the winter (Fig. 4; De Graaf et al., 1985; Judd, 1901).

#### 3.3. Exclosure performance

Two of the winter 2014 alfalfa fields had populations of Northern Pacific tree frogs (*Pseudacris regilla*) which likely accessed

**Table 2**  
The ten best-fit models predicting weevil densities in alfalfa, testing the effects of bird exclosures, distance of sampling point from the field edge, field-scale habitat complexity (PC1, PC2), distance to nearest riparian habitat, time since an insecticide spray, and avian abundance/richness.

Model Terms	AIC	$\Delta$ AIC	log-likelihood	df	$w_i$
~(Exclosures + Avian field abundance + factor(distance from field edge))^2	768.4	0	-374.18	10	0.31
~Exclosures + Avian field abundance $\times$ factor(distance from field edge) + Exclosures: factor(distance from field edge)	768.9	0.5	-375.5	9	0.24
~Exclosures + Avian field abundance $\times$ factor(distance from field edge)	769.1	0.7	-376.56	8	0.22
~(Exclosures + Avian field abundance + factor(distance from field edge))^2 + Distance to riparian	770.4	2	-374.12	11	0.12
~(Exclosures + Avian field abundance + factor(distance from field edge))^2 + Distance to riparian + Days since insect spray	772.4	4	-374.18	12	0.04
~Exclosures + Avian field abundance	773.6	5.2	-380.82	6	0.02
~(Exclosures + Avian field abundance + factor(distance from field edge))^2 + Distance to riparian + Days since insect spray + Simple/Complex	773.9	5.5	-373.97	13	0.02
~Exclosures + Avian field abundance + Distance to riparian	775.6	7.2	-380.8	7	0.01
~(Exclosures + Avian field abundance + factor(distance from field edge))^2 + Distance to riparian + Days since insect spray + Simple/Complex + PC1	775.9	7.5	-373.93	14	0.01
~(Exclosures + Avian field abundance + factor(distance from field edge))^2 + Distance to riparian + Days since insect spray + Simple/Complex + PC1 + PC2	777.7	9.3	-373.86	15	0.00



**Fig. 2.** Estimates from a GLMM for the effects of bird exclosures and in-field avian abundance on the mean number of weevils/kg of harvested alfalfa. Bird exclosures were positioned close to field edges (“5m Exclosures”) and within fields (“55m Exclosures”).

**Table 3**

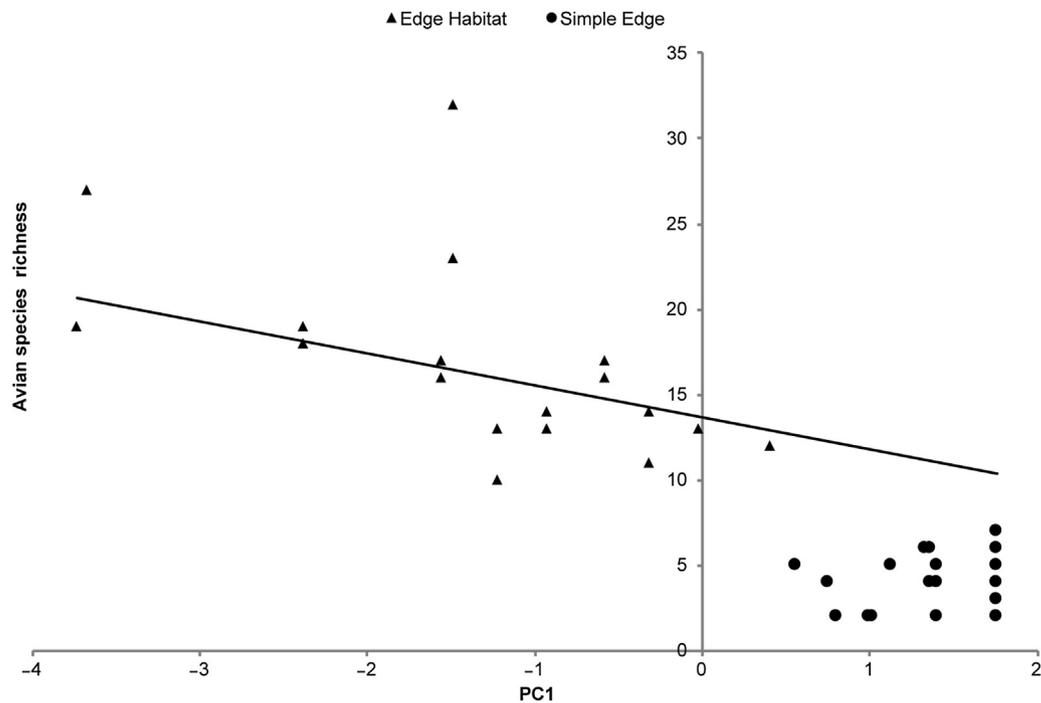
Model selection for the 4 avian models predicting the effects of habitat on avian abundance and species richness both within alfalfa fields and along field edges, the most parsimonious models ( $\Delta AIC \leq 2$ ) are shown in bold for each set of models.

Model Terms	Species Richness (GLMM* with Poisson errors)					Abundance (Log-transformed, LMM*)					
	AIC	$\Delta$ AIC	log-likelihood	df	$w_i$	AIC	$\Delta$ AIC	log-likelihood	df	$w_i$	
Within-Field	Null model	163.30	3.00	-78.60	3	0.12	<b>84.54</b>	<b>0.69</b>	<b>-38.27</b>	<b>4</b>	<b>0.41</b>
	Complex/Simple	<b>160.30</b>	<b>0.00</b>	<b>-76.10</b>	<b>4</b>	<b>0.52</b>	<b>83.84</b>	<b>0.00</b>	<b>-36.92</b>	<b>5</b>	<b>0.59</b>
	Complex/Simple + PC1	<b>162.10</b>	<b>1.80</b>	<b>-76.10</b>	<b>5</b>	<b>0.21</b>	97.66	13.82	-42.83	6	0.00
	Complex/Simple + distance to riparian + PC1	164.10	3.80	-76.10	6	0.08	101.33	17.49	-43.66	7	0.00
	Complex/Simple + distance to riparian + PC1 + PC2	165.10	4.80	-75.60	7	0.05	102.15	18.31	-43.08	8	0.00
	Complex/Simple + distance to riparian x PC1 + PC2	166.50	6.20	-75.20	8	0.02	112.42	28.58	-47.21	9	0.00
	(Complex/Simple + distance to riparian + PC1) <sup>2</sup> + PC2	168.30	8.00	-74.20	10	0.01	124.14	40.30	-51.07	11	0.00
	(Complex/Simple + distance to riparian + PC1 + PC2) <sup>2</sup>	173.60	13.30	-73.80	14	0.00	137.73	53.89	-54.86	14	0.00
Field-Edge	Null model	243.10	59.80	-118.50	3	0.00	94.73	18.39	-43.36	4	0.00
	Complex/Simple	188.00	4.70	-90.00	4	0.04	<b>76.34</b>	<b>0.00</b>	<b>-33.17</b>	<b>5</b>	<b>0.74</b>
	Complex/Simple + PC1	<b>183.30</b>	<b>0.00</b>	<b>-86.70</b>	<b>5</b>	<b>0.37</b>	78.42	2.08	-33.21	6	0.26
	Complex/Simple + distance to riparian + PC1	<b>183.40</b>	<b>0.10</b>	<b>-85.70</b>	<b>6</b>	<b>0.35</b>	94.44	18.10	-40.22	7	0.00
	Complex/Simple + distance to riparian + PC1 + PC2	<b>185.00</b>	<b>1.70</b>	<b>-85.50</b>	<b>7</b>	<b>0.16</b>	95.59	19.25	-39.80	8	0.00
	Complex/Simple + distance to riparian x PC1 + PC2	186.90	3.60	-85.46	8	0.06	112.42	36.08	-47.21	9	0.00
	(Complex/Simple + distance to riparian + PC1) <sup>2</sup> + PC2	189.10	5.80	-84.52	10	0.02	125.86	49.52	-51.93	11	0.00
	(Complex/Simple + distance to riparian + PC1 + PC2) <sup>2</sup>	194.4	11.10	-84.22	13	0.00	140.38	64.04	-56.19	14	0.00

\* GLMM stands for generalized linear mixed effects model, LMM stands for linear mixed effects model. Complex/Simple refers to whether the field had some form of edge habitat (at least 2 trees >1.5 m tall to be considered complex). PC1 and PC2 represent Principle Components Analysis axes for the complexity of field-edge habitat. Variables in parentheses followed by <sup>2</sup> have up to 2-way interactions included amongst them, variables separated by an ‘x’ include an interaction term.

the interior of our exclosures via rodent burrows. We only observed one frog inside of an exclosure on a single site visit. Over the two years the experiment was conducted, we observed birds (all savannah sparrows, *P. sandwichensis*) inside of exclosures on five site visits (<3% of visits), and on all occasions the birds were able to

fly out through a hole or wide gap in the wire as we approached. After our experiments were finished in 2014, a gopher snake (*Pituophis catenifer*) became entangled and died in the nylon netting at the base of one exclosure which was set to the side of a field before being removed from the site. This prompted us to



**Fig. 3.** Avian species richness at field edges in winter as a function of the first principle components axis (PC1) describing field-scale complexity: mean edge height, width, and number of canopy layers of habitat at the field edge. The line shows the predicted relationship based on the results of a generalized linear mixed effects model, and points show the avian species richness for each field in the study, with fields classified as having a 'Edge Habitat' shown with triangles, and fields classified as having a 'Simple Edge' shown with circles. PC1 had a negative loading on all three habitat variables, therefore sites with more negative PC1 loadings had greater field-scale habitat complexity (height =  $-0.58$ , width =  $-0.56$ , number of layers =  $-0.59$ ).

switch to using only chicken wire along the sides of the enclosures after which no other snakes became entangled.

#### 4. Discussion

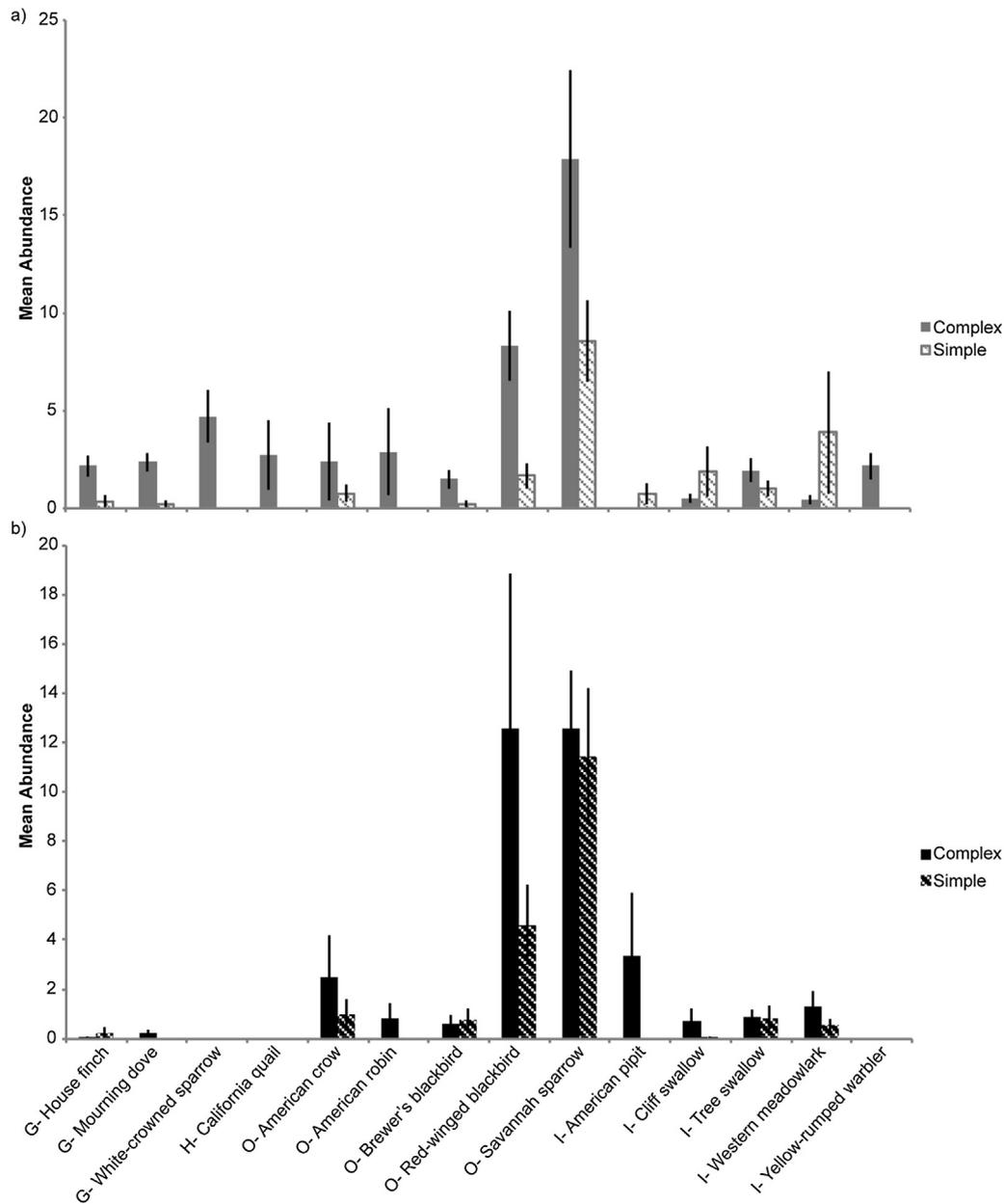
Here we have documented that birds provide pest control services in an intensively-cultivated forage crop in a temperate ecoregion. Our exclusion experiment results suggest that birds play a significant role in the control of weevils in alfalfa fields and that increasing avian abundance in fields can lead to lower weevil densities. Furthermore, our results show that the complexity of field edge habitat increases overall diversity and abundance of birds and we suggest that targeted management actions designed to increase and protect bird and other wildlife diversity in agricultural systems can also increase this ecosystem service. These results are also unique because they provide guidelines to farmers and land managers wishing to simultaneously increase the level of ecosystem services on their land and benefit biodiversity. By planting taller, wider and more varied edge habitat, growers can increase the biodiversity value of their fields and simultaneously benefit from ecosystem services provided by these birds.

In our best supported model, avian abundance acts to reduce the baseline number of weevils in alfalfa fields (Fig. 2). Interestingly, while avian abundance was negatively associated with weevil densities near the edge of the fields, we found the opposite effect at sampling points 55m into the fields. The reason for this difference cannot be explained by our study design. However, one potential reason may be that sites with high weevil densities attract more birds since weevils are the main arthropod in winter alfalfa fields. Another potential explanation is that, since our bird sampling methods did not quantify the location within the field where birds were observed, some sites with high bird abundance may only have had birds near the field edge, since many birds prefer to forage close to refuge habitat (Somers and Morris, 2002).

Future studies examining the effects of bird foraging on pest-control should incorporate a distance-from-habitat measure and explicitly quantify where birds are observed foraging within fields.

Common and abundant species provide the bulk of ecosystem services (Gaston, 2010), although both diversity and abundance of wildlife have been demonstrated to be important for the delivery of ecosystem services (e.g. Letourneau et al., 2009; Van Bael et al., 2008). Our results suggest that bird abundance, rather than bird diversity, is a primary factor driving bird-mediated pest control services in this system. It is notable that only two species, savannah sparrow and red-winged blackbird, were very abundant in our study fields, indicating that relatively few species may be responsible for the pest control service we observed. Both of these species prefer open grassland habitats and are known to consume large numbers of insects, including weevils, in natural and agricultural settings (Dolbeer, 1990; Judd, 1901). However, when we analyzed our results including only these two most abundant species, there was no longer a significant relationship between bird abundance and weevil densities. This suggests that the impact of abundance is at least in part being mediated through other less-abundant species. Furthermore, most of the other species recorded in our estimates of bird abundance are at least partially insectivorous and are likely to contribute to overall predation rates on weevils. From a biodiversity conservation perspective, our findings show that providing some edge habitat not only increases the abundance of common birds in fields, which was linked to decreased weevil abundances, but it also resulted in a nearly threefold increase in avian diversity along the field edge.

Because virtually all of the natural wetlands and grasslands have been removed from the Central Valley (Frayer et al., 1989; Katibah, 1984), alfalfa fields are likely to play an important role in the annual habitat requirements of the savannah sparrow and other open-country, insect-eating birds we observed in our fields during this study, including Western meadowlark (*Sturnella neglecta*), American pipit (*Anthus rubescens*) and red-winged



**Fig. 4.** The mean ( $\pm$ SE) number of individual birds counted for the most common birds within a) field edge habitat; and b) field interiors for sites with Edge Habitat and for sites with Simple Edges. Birds are sorted according to their non-breeding diet as described in De Graaf et al. (1985), except for Savannah sparrow which is based on Judd (1901), with birds preceded by G—representing granivores, H—representing herbivores, O—representing omnivores, and I—representing insectivores.

blackbirds. Our results indicate that the presence of even small, linear strips of non-crop vegetation, including at least 2 small trees, along field edges can harbor over-wintering birds in California, an important and often overlooked avian community of conservation concern (Dyballa et al., 2015). The fact that we observed 74 different species across all of our sites indicates that alfalfa field edges can harbor significant avian diversity, even in an intensive agricultural landscape. Unsurprisingly, sites with the highest avian diversity also had the most habitat complexity, and were often the sites located immediately next to riparian habitats.

We did not find an effect of landscape-scale habitat variables on the abundance or diversity of birds utilizing alfalfa fields or their edges, which is surprising given the importance of landscape-scale habitat in predicting bird use of agricultural fields in other systems (e.g. Karp et al., 2013) and the important role of this habitat for

overwintering birds in the Central Valley (Dyballa et al., 2015). This may be a function of the low overall habitat complexity across the intensive agricultural landscape in which our alfalfa fields were embedded. Importantly, despite the lack of a landscape-scale effect, local habitat complexity is still able to attract a large number of species (over 13 on average at sites with field edge habitat, and up to 31 different species at the site with maximum diversity). The effects of edges on avian diversity, and therefore avian pest control services, may be more pronounced in homogenous landscapes, such as our study sites, whereas the importance of edge habitat may be diminished in relatively heterogeneous agricultural landscapes (e.g. Howard and Johnson, 2014).

The results of this study offer only a small indication of the role that birds play in intensive agricultural systems. Our study sites were embedded within a highly modified and intensive agriculture

matrix consisting of a number of different crops grown over different seasons. The effects of providing habitat for a diverse assemblage of bird species likely extends beyond the alfalfa fields we studied and into neighboring and subsequent crops. For example, species such as woodpeckers, flickers and nuthatches were observed along fields with edge habitat and these species have recently been shown to consume overwintering codling moth in walnut orchards in our study region (S. Heath, personal communication). Many of the species that utilized the field edge habitat are resident in California year-round and are insectivorous during the breeding season, the time of year that most California row-crops are grown and attacked by other insect pests. Conversely, birds such as red-winged blackbirds and house finches (*Haemorrhous mexicanus*) are identified as major pests in crops such as grapes and rice (Gebhardt et al., 2011), so providing habitat for them in winter may contribute to damage later in the year. Importantly, many of the assumptions about the potential for birds to provide pest-control services or to cause damage to crops during other seasons are based on grower opinions and surveys, and have rarely been quantified through formal field experiments. Future studies to describe these complex interactions between habitat restoration and the spectrum of avian ecosystem services to crop damage are essential to untangling these complex relationships.

The adoption of farm management practices, such as increasing habitat complexity along field margins, is a commonly proposed conservation practice to increase biodiversity within intensively cultivated landscapes. However, adoption of these practices by farmers is low, generally due to costs implementation and lack of educational programs. Our results suggest that simple actions, such as planting small trees along field margins can not only enhance biodiversity, they can simultaneously lead to significant pest-control benefits that are a direct benefit to farmers. Hedgerows have also been shown to benefit growers in our study area by increasing pollinators (e.g. M'Gonigle et al., 2015; Sardiñas and Kremen, 2015) and other beneficial insects (Morandin et al., 2014). Farm edge habitats can also benefit growers by serving as windbreaks that reduce erosion, improve water quality, and increase water-efficiency (Schoeneberger et al., 2012). Our results provide empirical support for the development of hedgerows and other simple habitat enhancements in intensively managed agricultural landscapes that will directly benefit both wildlife and sustainable farming.

#### 4.1. Conclusions

Here, we have demonstrated the first example of birds providing valuable pest control services for an intensively grown and broadly planted forage crop in temperate ecoregions and have shown that not only do birds reduce the abundance of pest insects by over 33%, but that the density of weevils near the edges of fields decreases with increasing avian abundance, which in turn is driven by the presence of complex edge habitat. By planting a small number of trees along field edges, farmers are able to simultaneously increase the biodiversity value of their fields and benefit from increased pest-control services from birds. As alfalfa cultivation is expanded into new areas such as parts of Asia, the impacts to bird diversity can be reduced and growers can benefit from either retaining or planting field-edge habitat to take advantage of these potential ecosystem services.

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