Pest-removal services provided by birds on small organic farms in northern California

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ABSTRACT

Many studies have established that birds may provide a pest removal service on farms, although few studies have taken place in temperate row crop agriculture. Wildlife-friendly agricultural practices such as organic farming and the use of hedgerows can in turn provide needed habitat for birds in developed landscapes. In this study, we examined how pest removal provided by birds varies within and between "wildlife-friendly" organic row-crop farms in northern California, USA. We used point counts to assess bird diversity on 29 small organic farms and simulated lepidopteran pest outbreaks on each farm using sentinel pest experiments. We measured how the probability of pest removal varied with local habitat characteristics within the farm, and with bird diversity parameters between farms. We also used exclosure experiments to determine whether birds provide a significant pest removal service in organic row-crop agriculture. In the sentinel pest experiments, birds depredated between 0 and 80% of caterpillar presentation stations within 7 h, with a mean of 24% depredation per farm; the probability of pest removal was higher in areas close to uncultivated shrubby field margins ("hedgerows"). There was only weak evidence that the probability of pest removal was higher on farms with higher avian insectivore richness, and no evidence that pest removal varied with species diversity or abundance. Exclosure experiments on kale crops showed no significant effects of bird exclosure treatment on arthropod abundance or crop yield. However, natural caterpillar densities were relatively low during the exclosure experiment (approximately one caterpillar/m^2). These results suggest that birds may be more helpful in responding to pest outbreaks than in controlling pests at non-irruptive densities on organic row crop farms in this study system. The prevention of pest outbreaks is an essential ecosystem service on any farm, and the rapid response of birds to pest outbreak conditions is an indicator of resiliency in the agroecosystem. Therefore, the retention of uncultivated shrubby field margins in this system may benefit both birds and farmers.

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1. Introduction

Agriculture currently uses over 40% of the land area worldwide (McLaughlin, 2011). Global food demand is expected to double by 2050 in response to both a rising human population and a shift in dietary preferences and habits, prompting greater pressure to convert additional land to agricultural use and increase yields on lands already in production (Balmford et al., 2012; Green et al., 2005; McLaughlin, 2011; Tilman et al., 2011). Agricultural land conversion is one of the greatest threats to birds, as well as to numerous other taxa (Chamberlain et al., 2000; Donald et al., 2001; Sotherton, 1998). Therefore, many scientists argue that that wildlife-friendly farming, which encourages biodiversity within the farm (and often makes use of diversity on the landscape level), is key to conserving global biodiversity even if some crop yield is sacrificed (Fischer et al., 2008; Perfecto et al., 2009). Others argue that by increasing crop yield (often by increasing farming intensity), land may be spared for nature (Phalan et al., 2011; Trewavas, 2002). Researchers have noted that resolving this debate hinges on understanding the relationship between yield and biodiversity, the likelihood of land being spared, and external consequences of practices raising yield, such as agrochemical run-off (Grau et al., 2013; Green et al., 2005; Phalan et al., 2011). However, en
couraging wildlife that deliver ecosystem services and enhance production may enable high yield and wildlife-friendly farming strategies to be pursued simultaneously (Railsback and Johnson, 2014).

Organic farmers vary in their approach to pest control, and simply being organic does not necessarily directly lead to higher

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levels of biological pest control on the farm (Letourneau and Bothwell, 2008). One approach organic farmers may take to increase both their yield and the biodiversity within the farm is to encourage pest-eating songbirds on and around farms. Many studies have established that birds provide a valuable pest removal service on farms, both by regulating existing pest populations and by potentially stopping pest outbreaks from occurring (i.e., Greenberg et al., 2000; Jedlicka et al., 2011; Johnson et al., 2010; Perfecto et al., 2004; Van Bael et al., 2007). However, relatively few of these studies have taken place in temperate row-crop agriculture (see Triplett et al., 2012 for some examples), and many have taken place in agricultural systems that produce luxury goods such as coffee, wine, and chocolate. In this study, we examined the potential for pest control by birds in temperate row-crop vegetable farms.

We examined three predictions of the general hypothesis that birds provide pest control services in our study system. First, we used a sentinel pest experiment to simulate an insect irruption and tested the prediction that pest removal rate is positively correlated with insectivorous songbird species richness, abundance, and/or diversity. This prediction derives from the biodiversity-ecosystem function (BDEF) hypothesis and more recent work suggesting pest control by birds in agricultural systems is associated with species richness (VanBael et al., 2008), functional richness (Philpott et al., 2009), or predator abundance (e.g., Jedlicka et al., 2011). Second, because bird diversity and abundance on farms are often associated with hedgerows and/or woody field edges (Batary et al., 2010), we tested the prediction that sentinel pests placed closer to uncultivated habitat would have higher rates of pest removal, and that pest removal would vary with the type of uncultivated habitat surrounding the farm. Third, we used bird-proof exclosures to test the prediction that excluded crops would host higher insect pest abundances and suffer higher levels of insect damage than control plants, due to the release of insect pests from top–down bird interactions. This prediction follows from previous work showing that songbirds can significantly reduce herbivorous insects, and thereby decrease crop damage and increase productivity of a primary producer in agricultural systems through a top–down trophic cascade (e.g., Baumgartner et al., 1999; Johnson et al., 2010; Kirk et al., 1996; Terborgh et al., 2010; Van Bael et al., 2007).

2. Methods

2.1. Study system

This study took place on 29 organic farms in Humboldt County, California, USA. The farms were located along a coastal and elevational gradient, and therefore were situated across a variety of habitats. Farms ranged from approximately 1 to 47.5 km from the coast and from sea level to approximately 350 m in elevation. While not all of the farms were certified organic at the time of the study, they all strictly followed organic farming practices. Some farms occasionally received organic pest treatments such as *Bacillus thuringiensis* (Bt) spray, although only in response to the pest community and never as a regularly scheduled treatment. Each farm cultivated a variety of row crops providing similar low-structure habitat for birds; some farms grew additional crop types, such as orchard fruits, flowers, or wine grapes.

2.2. Bird point counts

Two experienced observers performed point counts on each farm once per month between May and August 2012. As all of the farms used in this study were relatively small (and often encompassed only one or two fields), we established a single point count site at each farm at a field edge (see Freemark and Rogers, 1995). We placed each point count site along the field edge closest to bird "source" habitat defined first as riparian habitat, second as forest, or third as mature hedgerow or tree line. When farms had multiple fields, we chose the field closest to bird "source" habitat as defined above. The majority of hedgerows were made up of blackberry bramble (*Rubus armeniacus*), and tree lines varied by farm and included coniferous and/or deciduous trees. All point count sites were pooled in analyses regardless of adjacent source habitat type.

Bird point counts followed the unlimited distance dependent double-observer method in order to calculate detection probability (Forcey et al., 2006; Nichols et al., 2000). The observers recorded each bird detected (either visually or aurally) as either less than or greater than 50 m from the point count site. In order to assess habitat use, we recorded whether each bird detected was in row crop, cultivated, hedgerow, natural habitat, unknown habitat, or a flyover. Cultivated habitat was defined as non-row crop cultivated land, such as orchards, vineyards, or pasture/fodder, while natural habitat was defined as any uncultivated areas including riparian and forested areas bordering the farms. If an individual bird used multiple habitat categories, we prioritized recording first whether they were in row crop or second in cultivated habitats. The observers completed the point counts for all farms within the span of six days per month, and within 3 h of dawn. All point counts were conducted on days without strong winds or rain.

We used program DOBSERV (Hines, 2000) to estimate avian abundances for each farm based on detection probabilities calculated from the double-observer point count method. We used species' proportional abundances to calculate a Shannon–Wiener diversity index for each farm for use as a predictor variable (Gotelli and Ellison, 2013). We also used these abundances to create a predictor variable describing the summed abundance of each bird species confirmed to be sentinel pest predators by motion activated camera footage ("key predator abundance").

2.3. Sentinel pest experiment

The speed and magnitude of avian response to an ecosystem change may be measured using "sentinel pest" experiments, which not only make pests more abundant, but also more available to predators. We used sentinel pest experiments to simulate the start of an lepidopteran pest outbreak to determine rate of insect removal by birds for each farm (*sensu* Perfecto et al., 2004). We performed all sentinel pest experiments within nine days at the end of June 2012, ensuring that they would all be completed within the peak bird breeding season.

We used kale (*Brassica oleracea,* Acephala Group) as a focal crop for both sentinel pest experiments and exclosure experiments as it is a widely grown row crop in our study area and may host many species of lepidopteran pests (e.g., *Pieris rapae, Trichoplusia ni, Plutella xylostella*, etc.). Kale is a specialty food crop: in 2012 kale represented only 0.1% of the total area of vegetables harvested in CA ("USDA: National Agricultural Statistics Service," 2012). However, in 2001, kale production in California brought in $9.8 million, and cultivation of kale is rapidly increasing, with a 56.6% increase in acres of kale harvested in the United States between 2007 and 2012 (USDA: National Agricultural Statistics Service, 2012).

Each pest presentation station consisted of two third or fourth instar cabbage looper (*T. ni*) caterpillars attached to the dorsal surface of a Lacinato kale (*B. oleracea*) leaf placed in a water pick (a plastic water vial used in the floral industry). The caterpillars were affixed to the leaf using a dot of cyanoacrylate adhesive at the posterior end of the abdomen, allowing the caterpillars a degree of natural movement. We placed 20 pest presentation stations on

each farm before dawn in a 4×5 grid of 5 m spacing among the row crops for a total presentation area of 15×20 m. We placed each grid as close to the point count site as possible while ensuring that all points within the grid were among row crops. Since small organic farms usually produce multiple crops, the grid of presentation stations necessarily spanned rows of several crop types (e.g, kale, onion, lettuce, etc.,) on most of the farms. Therefore, we included the surrounding crop type as a variable in the analysis of sentinel pest removal (see below). We also placed a motion-activated camera (Primos model Truth Cam 35 or Wild-game Innovations model Realtree Pro Series cameras) in front of four haphazardly chosen presentation stations at each farm. We returned approximately 7 h later (mean = 7 h 4 min, SD = 0.012 h) to remove the presentation stations, and to record the number of caterpillars that had been removed.

We measured several local-scale habitat characteristics at each caterpillar presentation station. These characteristics included whether crops surrounding the presentation station within a 1 m diameter circle were brassica crops (a binomial variable), the distance to uncultivated habitat in each of the cardinal directions (m), and a specification of the dominant uncultivated habitat category in each cardinal direction (grass, shrub, tree, or human construction such as buildings or roads).

2.4. Exclosure experiment

We conducted the exclosure experiments in September 2012 on the seven farms in the study system that were at that time growing Lacinato kale. The exclosure experiments took place later in the season than the sentinel pest experiments due to logistical constraints, but occurred during the same growing season within comparable growing and pest community conditions. We placed a single exclosure over five Lacinato kale plants at each of the seven farms, and selected five control plants approximately 1 m away from the exclosure. The exclosures were approximately $2 \times 0.75 \times 0.75$ m, and they were oriented with either a 2×0.75 m or a 0.75×0.75 m base depending on how densely the kale was planted on each farm. We constructed the exclosures from 25 mm square (35 mm diagonal) transparent mesh (Nylon Net Co., Memphis TN, USA) wrapped around CPVC pipe (post chlorinated polyvinyl chloride). This mesh was small enough to keep out all birds, while minimizing alteration of sunlight and precipitation.

At the time of exclosure placement, as well as at the time of removal 5 weeks later, we recorded the total number of leaves on each control and exclosure plant, as well as the number of "salable" leaves per plant. A leaf was defined as "salable" if it did not have major insect damage. We also recorded the number of lepidopterans and spiders on each plant.

2.5. Statistical analyses

2.5.1. Sentinel pests

We used generalized linear mixed models (GLMM) with binomial error structure to model the effects of avian diversity parameters and local-habitat characteristics on sentinel pest depredation. We described depredation as a binomial variable where success was defined as a caterpillar presentation station with at least one caterpillar removed. We modeled farm as a random effect, and all local-habitat characteristics (level-one predictors) and avian diversity parameters (level-two predictors) as fixed effects.

Level-one predictor variables comprised the local-habitat characteristics as described above, and included surrounding crop type (brassica or not), distance to uncultivated habitat averaged from all cardinal directions, minimum distance to uncultivated

habitat, and nearest uncultivated habitat category. We transformed (ln) the average distance to uncultivated habitat variable to normalize it.

The avian diversity parameters at the field-scale (level-two predictor variables) included avian abundance, Shannon–Wiener diversity (H'), species richness, and key predator abundance. In all avian diversity parameters, we only included "relevant species:" that is, only species that were detected at least once in either cultivated, row crop, or hedgerow habitat, that would be likely to consume caterpillars. We assigned species to the caterpillar-consumer guild using Ehrlich et al. (1988): we included all insectivorous or omnivorous species that forage by either foliage or ground gleaning. We further confirmed the foraging guild of many species using the birds of North America online database (Poole, 2012). We used birds detected within a 50 m radius for abundance estimates because we were interested in the abundance of individuals on or close to the farm at the time of the point count. We used unlimited distance detections for species richness estimates in order to account for all species in the area that might eventually move onto the farm.

We compared a priori model sets in two steps. We began by testing a model set including only local-scale habitat predictors, and used Akaike's Information Criterion for small samples (AIC$_c$) to select the best model from the set (Anderson, 2008). We then selected the best-supported local-scale habitat predictor variables to include in the final model set, alone and in combination with field-scale predictor variables. We compared the models again using AIC$_c$ and assessed model fit by computing both marginal and conditional R^2 (R^2GLMM$_m$ and R^2GLMM$_c$, Nakagawa and Schielzeth 2013).

2.5.2. Exclosures

We used GLMM with normal error structure to test the hypotheses that exclosure treatment affected the change in number of salable kale leaves, the change in total number of kale leaves, the change in number of lepidopteran pests present on the kale plants, and/or the change in number of spiders on the kale plants. We modeled farm as a random effect, and exclosure treatment as a fixed effect. We ranked null models and models including exclosure treatment as a predictor variable using AIC$_c$ to assess the importance of the exclosure treatment variable.

3. Results

3.1. Bird point counts

We detected a total of 105 bird species on all farms across all point counts, including seven California species of special concern. Of the 105 species, 60 species were detected at least once in cultivated, row crop, or hedgerow habitat. Among those 60 species, we determined that 39 species were likely to consume caterpillars (i.e., leaf or ground gleaning insectivores or omnivores, Table A.1). The detection probability estimated from the double-observer point count method was 0.996 for all species. Therefore, we used the raw abundances in both bird abundance and species diversity variables.

3.2. Sentinel pest experiment

We observed that predatory wasps and other insects were unable to remove the glued portion of sentinel prey, and instead removed pieces of the caterpillars in a few rare instances. Video footage showed that lizards were also unable to remove sentinel prey. Therefore if an entire caterpillar was removed from the pest presentation station, we considered it a bird depredation. Birds depredated 0–80% of caterpillar presentation stations on each

farm, with a mean of 24% depredated stations. Ten motion-activated video samples showed American robins (*Turdus migratorius*), four showed western scrub-jays (*Aphelocoma californica*), and one showed a European Starling (*Sturnus vulgaris*) eating sentinel pest caterpillars. The key predator abundance variable was calculated as the summed abundance of these three species on each farm. We found relatively high variation between farms in the avian diversity parameters used as predictor variables of sentinel pest removal, although all farms had relatively high bird richness and diversity biodiversity (Table 1).

Within the model set for predicting caterpillar depredation at the local habitat scale (level 1), the model with the strongest support (ΔAICc = 0, model weight = 0.38) included the minimum distance to uncultivated habitat, the type of that habitat, and whether or not the caterpillar presentation station was placed among brassica crops (Table 2). The null model had very little support (2% of the weight). Among the estimates from the top model, the only parameters with 95% confidence intervals that did not overlap zero were the non-brassica crop type category and closest uncultivated habitat category of shrub. Although several other models held some weight, we included all three local-scale predictor variables from the top model in the final model set.

Model selection indicated that local-scale variables were more important than field-scale variables in explaining variation in caterpillar removal. The most parsimonious model from among the final model set (ΔAICc = 0, model weight = 0.28) included only the local-scale habitat predictor variables (whether the surrounding crop was brassica, the minimum distance to uncultivated habitat, and the habitat category, Table 3). The top five models (cumulative model weight = 0.72) each included local-scale predictor variables in combination with a single field-scale predictor variable. Models that only included field-scale predictor variables all fell below the null model, and were poor predictors of depredation. Model weight was spread fairly evenly among the models that included the local-scale habitat predictor variables combined with field-scale predictor variables. The R^2GLMM_m and R^2GLMM_c for the full model were 0.09 and 0.36, respectively.

We averaged all of the models in the final model set. The only variables with confidence intervals that did not overlap zero when the coefficients were model averaged were again non-brassica crop type ($\beta = -0.759$, SE = 0.366) and closest uncultivated habitat category of shrub ($\beta = 1.493$, SE = 0.620, Table 4). Sentinel pest presentation stations placed closer to uncultivated shrub habitat had a higher probability of depredation (Fig. 1), as did those placed among brassica crops.

3.3. Exclosure experiment

We found approximately one caterpillar/m^2 on exclosure and control plants before exclosure placement. AICc rankings indicated that exclosure treatment was not an important predictor of the change in number of salable leaves, change in total number of leaves, or change in number of lepidopterans or spiders (Table 5). Furthermore, the confidence intervals for all response variables overlapped zero.

Table 1
Avian diversity parameters as estimated with double-observer point counts on 29 organic farms.

Parameter	Minimum	Mean	Maximum
Species richness	11	19	26
Species diversity[a]	0.82	1.99	3.91
Avian abundance	12	32	96
Key predator abundance[b]	0	9	75

[a] Shannon–Wiener diversity index.
[b] Abundance of American robins, European starlings, and western scrub-jays.

4. Discussion

4.1. Sentinel pest experiment

The results of the sentinel pest experiment suggest that the local-habitat characteristics of surrounding crop type, proximity to uncultivated habitat, and closest uncultivated habitat type were the most important determinants of the probability of pest removal service provision by birds. However, although the distance to uncultivated habitat variable was included in all models ranked above the null, that variable's 95% confidence intervals overlapped zero and thus we cannot conclude a significant distance effect. In contrast, Puckett et al. (2009) found increased bird foraging within 20 m of field edges. In our study, 64% of the pest presentation stations were within 20 m of a field edge. Future study on larger farms that include more presentation stations at greater distances from the field edge might further clarify the strength of the distance effect.

Although variability between and within farms was relatively high, the probability of depredation was highest in crops close to shrubs as compared to other uncultivated habitat types (Fig. 1). Preferential use of hedgerows by birds in agricultural landscapes has been fairly well established (e.g., Jobin et al., 2001; Batary et al., 2010; Cornulier et al., 2011). This data further suggests that insectivorous birds using shrubby field margins also forage in row crops and eat insect pests. While most studies have recommended the use of hedgerows and other natural field margins for bird conservation purposes, (Hinsley and Bellamy, 2000; Perkins et al., 2003; Vickery et al., 2002, 2009), results of this study suggest that farmers may also benefit by creating or maintaining these sources of bird habitat. Because not all natural field margins provide equally usable habitat for birds, it would be important when making recommendations to farmers to encourage the establishment of the most beneficial types of hedgerows or shrubby field margins (see Hinsley and Bellamy 2000 for recommendations).

Only 15% of the pest presentation stations were placed among brassica crops, but we found that the probability of depredation was higher for those stations. This may be due to avian foraging patterns, as birds may have a more appropriate search image for brassica pest caterpillars on brassica crops. This could lead to a higher rate of caterpillar detection among brassica crops.

The results of this study provide only weak evidence that species richness affects the probability of pest removal (i.e., species richness was included in the second best model, but the 95% confidence intervals overlapped zero). There has been much study and debate regarding the relationship between biodiversity and ecosystem functions (such as pest suppression) in various habitats and settings. One hypothesis suggests an asymptotic additive relationship; specifically, increased biodiversity is correlated with increased pest mortality, but only up to a point when functional redundancy within a suite of predators is reached (Chapin et al., 2000; Letourneau et al., 2009). It is of note that all farms used in this study had fairly large and diverse avian assemblages (Table 1). Therefore, an asymptotic relationship would be difficult to detect given the study system. Future inquiry including farms with smaller, less diverse avian assemblages (perhaps conventionally-managed farms) might further elucidate this possible effect of bird species richness on pest control. Currently there exists very little literature comparing bird diversity and pest control on organic vs. conventional farms.

We found no significant effect of predator abundance (either net bird abundance, or key predator abundance) on the probability of pest removal. This may have been driven by the fact that on some farms, individual birds may have been depredating multiple pest presentation stations, while on other farms multiple birds may have depredated the stations. Indeed, we have one video sample

Table 2
Support for preliminary set of generalized linear mixed models predicting probability of caterpillar depredation in a sentinel pest experiment.

Model	K	AICc	ΔAICc	w_i	Cumulative w_i	LL
Brassica[a] + minimum distance[b] + closest habitat type[c]	7	566.81	0	0.38	0.38	−276.31
Brassica + closest habitat type	6	568.04	1.22	0.20	0.58	−277.95
Minimum distance + closest habitat type	6	568.90	2.08	0.13	0.71	−278.38
Closest habitat type	5	569.45	2.64	0.10	0.81	−279.67
Brassica + minimum distance	4	570.08	3.27	0.07	0.89	−281.01
Minimum distance	3	571.57	4.75	0.03	0.92	−282.76
Brassica	3	572.16	5.35	0.03	0.95	−283.06
Minimum distance × closest habitat type	9	572.69	5.87	0.02	0.97	−277.19
Null	2	572.93	6.11	0.02	0.98	−284.45
Brassica + log (average distance[d])	4	574.15	7.34	0.01	0.99	−283.04
Log (average distance)	3	574.87	8.06	0.01	1	−284.42

Only local-scale habitat (level 1) variables are included in this model set. Models are ranked based on Akaike's information criterion (AICc), ΔAICc, and Akaike weights (w_i). Akaike's information criterion is based on 2 × log likelihood (LL) and the number of parameters (K) in the model. Cumulative model weights (cumulative w_i) are also reported.
[a] Binomial variable describing surrounding crop type (brassica or not).
[b] Minimum distance to uncultivated habitat (m).
[c] Closest uncultivated habitat category (grass, tree, shrub, or human construction).
[d] Mean distance to uncultivated habitat.

Table 3
Support for final set of generalized linear mixed models predicting probability of caterpillar depredation in a sentinel pest experiment.

Model	K	AICc	ΔAICc	w_i	Cumulative w_i	LL
(B + M + H)[a]	7	566.81	0	0.28	0.28	−276.31
(B + M + H) + richness[b]	8	568.40	1.59	0.13	0.40	−276.07
(B + M + H) + predators[c]	8	568.61	1.80	0.11	0.52	−276.18
(B + M + H) + diversity[d]	8	568.78	1.96	0.10	0.62	−276.26
(B + M + H) + abundance[e]	8	568.87	2.06	0.10	0.72	−276.31
(B + M + H) + richness + predators	9	569.67	2.86	0.07	0.79	-275.68
(B + M + H) + richness + abundance	9	570.36	3.55	0.05	0.83	−276.02
(B + M + H) + richness + diversity	9	570.44	3.62	0.05	0.88	−276.06
(B + M + H) + diversity + predators	9	570.64	3.82	0.04	0.92	−276.16
(B + M + H) + diversity + abundance	9	570.83	4.02	0.04	0.96	−276.26
Null	2	572.93	6.11	0.01	0.97	−284.45
(B + M + H) + richness + abundance + AMRO + diversity	11	573.61	6.79	0.01	0.98	−275.57
Richness	3	574.36	7.55	0.01	0.99	−284.16
AMRO	3	574.81	7.99	0.01	0.99	−284.38
Abundance	3	574.9	8.09	0	1	−284.43
Diversity	3	574.91	8.1	0	1	−284.43

Both local-scale habitat and field-scale (level 1 and level 2) variables are included in this model set. Models are ranked based on Akaike's information criterion (AICc), ΔAICc, and Akaike weights (w_i). Akaike's information criterion is based on 2 × log likelihood (LL) and the number of parameters (K) in the model. Cumulative model weights (cumulative w_i) are also reported.
[a] (B + M + H) are local-scale habitat (level 1 predictors): surrounding crop type (brassica or not, B), minimum distance to uncultivated habitat (meters, M), and closest uncultivated habitat type (grass, tree, shrub, or human construction, H).
[b] Species richness.
[c] Abundance of American robins, western scrub-jays, and European starlings.
[d] Shannon–Wiener diversity index.
[e] total bird abundance.

Table 4
Model averaged parameter estimates (β), unconditional standard errors, and lower and upper 95% confidence intervals from final set of generalized linear mixed models predicting probability of caterpillar depredation in a sentinel pest experiment.

Effect	β	SE	95% LCI	95% UCI
Local-habitat scale (level 1)				
Intercept—brassica crop, habitat type = building/man-made	−1.669	1.378	−4.370	1.032
Non-brassica crop[a]	−0.759	0.366	−1.477	−0.041
Habitat type—grass	0.553	0.591	−0.606	1.712
Habitat type—shrub[a]	1.493	0.620	0.278	2.709
Habitat type—tree	0.516	0.690	−0.837	1.868
Minimum distance to uncultivated habitat	−0.021	0.012	−0.045	0.003
Field scale (level 2)				
Species richness	0.068	0.088	−0.105	0.240
Key predator abundance	−0.014	0.022	−0.057	0.030
Species diversity (Shannon–Wiener)	0.119	0.524	−0.907	1.146
Avian abundance	-0.001	0.016	−0.033	0.031

[a] 95% CI does not overlap zero.
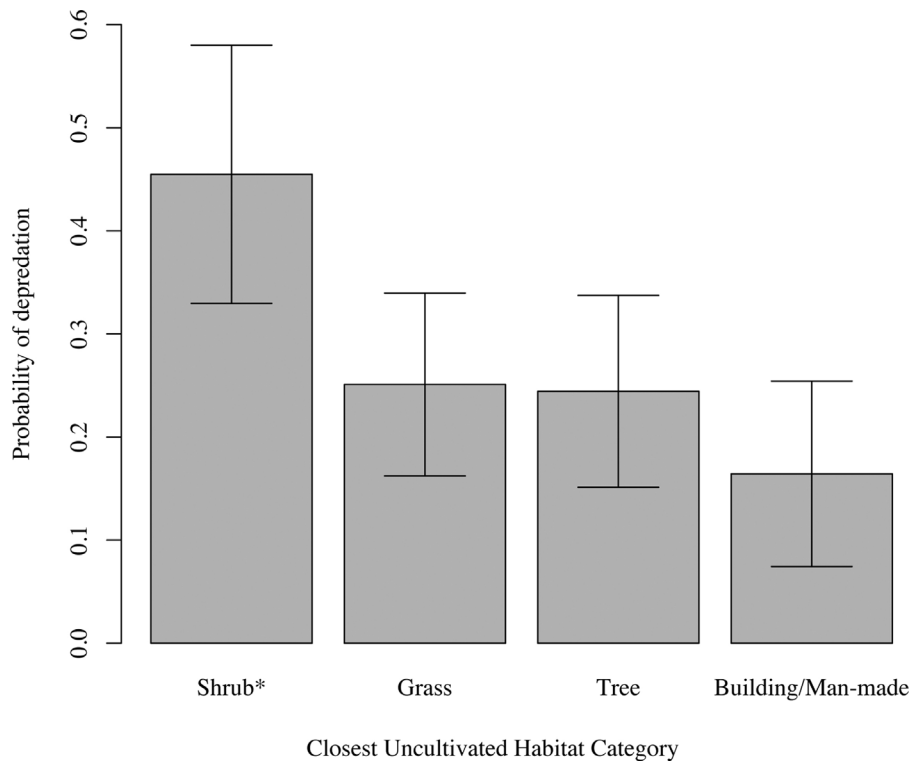
Fig. 1. Model averaged predictions ± SE of probability of caterpillar depredation as a function of closest uncultivated habitat category. *95% CI's of estimate do not overlap zero.

Table 5
Estimates of effect of bird exclosure over kale on four response variables. Standard error, 95% confidence intervals, and full model ΔAICc scores are reported.

| Response variable	Exclosure effect	SE	95% LCI	95% UCI	ΔAICcfrom null[a]
Change in number of salable leaves	3.471	3.543	−3.473	10.415	1.30
Change in total number of leaves	6.114	5.038	−3.760	15.988	0.80
Change in number of lepidopterans	−1.057	0.839	−2.702	0.588	0.68
Change in number of spiders	3.471	3.543	−3.473	10.415	1.30

[a] Model sets for each response variable included two models each: a null model and a model including exclosure treatment as the predictor variable.

that shows a western scrub-jay that had obviously collected caterpillars from multiple stations. Individual bird behavior as well as competition may have influenced whether individual birds depredated multiple stations, and thus influenced the abundance effect on the probability of pest removal.

4.2. Exclosure experiment

Results of the exclosure experiment suggest that birds did not significantly affect insect pest populations on Lacinato kale. The farms used in this study had a high degree of variation not only in
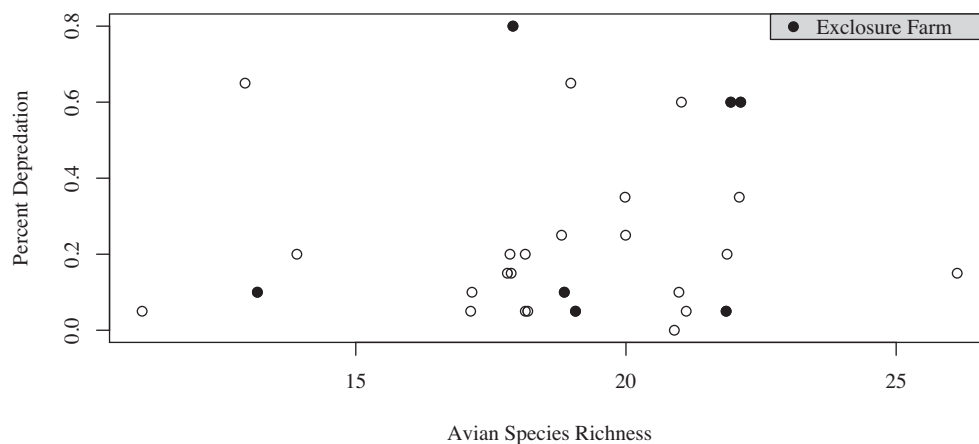
Fig. 2. Percent depredation (sentinel pest experiment) and avian species richness by farm. Filled in points represent farms used in the exclosure experiment, and data have been jittered to show overlapping points.

avian species richness, but also in the rate of insect pest removal during the sentinel pest experiment (Fig. 2). The farms used in the exclosure experiment represented a wide range of this variation. Therefore, the ability to detect a significant effect of bird predation with exclosures may have been affected by small sample size (i.e., number of farms), combined with wide variation between farms in habitat characteristics influencing bird predation.

Alternatively, top–down trophic effects on kale may have been weak or nonexistent in this study. Ecologists have long been interested in what affects the presence and strength of top–down trophic cascades. Research suggests that these cascades are positively associated with the productivity of the system, the levels of predator niche complementarity, and with less intraguild predation and/or interference (Terborgh et al., 2010). Agricultural systems are generally highly productive, and the relatively high avian diversity detected by the point counts suggests a high level of predator niche complementarity in our study system. Therefore, the lack of a significant top–down effect of birds on kale crop yield may be due to the high levels of intraguild predation inherent in a system with generalist insectivorous birds (see Martin et al., 2013). Most of the species of birds found in our study system will eat both insect pests and the arthropod predators of insect pests (Poole, 2012). When an insect pest is at low densities, such as during the exclosure experiment, the diet of insectivorous birds should include a variety of arthropods including those that prey on caterpillars. However, when insect pests are at outbreak levels, many birds show a dietary response to concentrate on the pest, yielding a more narrowed diet (Hogstad, 2005; Rotenberry et al., 1995). In these cases, intraguild predation may lessen as a result of a highly available alternative food source. Fluctuating levels of intraguild predation may therefore result in weak top–down effects when pests are at non-irruptive densities, and stronger top–down effects when pests increase to higher densities (pest outbreaks).

Most of the previous research on bird responses to pest outbreaks has occurred in forest systems (i.e., Crawford and Jennings, 1989; Hogstad, 2005). Crawford and Jennings (1989) found that forest birds more effectively controlled spruce budworm (*Choristoneura fumiferana*) pest populations when larvae densities were low and less effectively when larvae densities were very high. In contrast, our results showed no top–down effect of birds during low pest densities (exclosure experiment), and a stronger effect of birds during heightened pest availability (sentinel pest experiment). However, low pest density in the forest ecosystem was approximately 10 times higher than the average caterpillar density measured on kale plants in our study. At extremely low pest densities, such as those in our study system during the exclosure experiment, it is possible that caterpillar pests were not profitable prey for birds. However, when caterpillars were made more available in the sentinel pest experiment, birds showed a stronger response (similar to the response seen in forest ecosystems at "low" pest densities).

The control of pest outbreaks can be difficult to detect with exclosure experiments because they are sensitive to the arthropod assemblage that exists while the experiment is being conducted. The findings of an exclosure experiment might differ between pest outbreak years and low background pest density years. The sentinel pest experiment, which simulated a pest outbreak, certainly indicated that birds may provide a service during an outbreak (up to 80% of the caterpillars were depredated within approximately 7 h). Future study should examine between-year differences in exclosure treatment effects in order to determine whether significant exclosure treatment effects are more likely to occur during pest outbreak years due to dietary responses by birds.

5. Conclusions

We found no strong support for our hypothesis that bird diversity and/or abundance on the farm is correlated with the probability of pest removal. However, we did find support for our prediction that increased pest removal is associated with areas of potentially elevated bird diversity and/or abundance surrounding the farm (i.e., hedgerows). The presence of hedgerows and shrubby field margins may be beneficial at the landscape scale as well as at the farm scale, as they contribute to the heterogeneity of the landscape. Many studies have shown that heterogeneity within agricultural landscapes can affect landscape-wide bird biodiversity, and thus the capacity of the farm for "land-sharing," (e.g., Batary et al., 2010; Quinn et al., 2012).

While we found no support for our hypothesis that the exclusion of birds leads to increased pest density and decreased yield due to interruption of a top–down trophic cascade, we did find a rapid response to our simulated pest outbreak. The presence of self-regulated and robust regulating ecosystem services, such as pest outbreak control, is an important indicator of ecological resiliency in agroecosystems (Cabell and Oelofse, 2012). As future climate change increases the probability of pest outbreaks and invasion by foreign pests (Porter et al., 1991), it will become increasingly important to improve farmland resiliency. The results of this study suggest that on small organic row crop farms, the most significant service provided by birds may be to increase resiliency by responding to pest density increases rather than to reduce pest numbers in non-irruptive years. Pest outbreaks can be devastating to small organic farmers whose use of pesticide is restricted. Therefore, increasing the probability of pest removal by songbirds through the enhancement of bird habitat such as shrubby field margins (increasing the "wildlife-friendliness" of the farm) could be beneficial both to farmers and to birds. These shrubby field margins may enable land-sparing as well, by guarding against drastically decreased yield during pest outbreaks and thus reducing the need for development of more land when pest densities increase.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.agee.2015.04.023.

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