

RESEARCH ARTICLE

Bird services and disservices to strawberry farming in Californian agricultural landscapes

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Abstract

1. Bird conservation in agricultural settings can be controversial. While some bird species damage some crops, others suppress insect pests. Few studies have simultaneously compared bird services and disservices to assess their net impact.
2. Using an exclusion experiment in six California strawberry farms, we show that bird suppression of berry damage by insect pests (about 3.8% of berries) is similar in magnitude to the damage birds inflict on strawberries (about 3.2% of berries).
3. Across 27 farms, we found that bird species richness and the relative abundance of insectivorous birds increased, while the relative abundance of strawberry-eating birds and bird damage decreased on farms with more semi-natural land cover in the surrounding landscapes (1000 m radius).
4. Relative to homogeneous farms, those that implemented diversification practices, such as hedgerows, flower strips or increased crop diversity, had greater bird species richness, total relative abundance, insectivore abundance and strawberry-eating bird abundance.
5. *Synthesis and applications.* Conserving semi-natural land cover in the surrounding landscape benefits bird species richness locally and aids farmers through reduced abundance of strawberry-eating birds and bird damage. These results highlight the need to consider both the services and disservices of birds when making management decisions.

KEYWORDS

agriculture, agroecology, bird, diversified farming systems, ecosystem services, human-wildlife conflict, pest suppression, strawberry

1 | INTRODUCTION

As agriculture now occupies nearly half of Earth's land surface, developing strategies to conserve biodiversity in agricultural landscapes has become a major research focus (Tschardtke, Klein,

Kruess, Steffan-Dewenter, & Thies, 2005). Globally, agriculture is intensifying rapidly, displacing many species, such as grassland birds, which are in decline across North America (Brennan & Kuvlesky, 2005). Yet "diversified farming systems" that integrate crop and non-crop vegetation in and around farms are increasingly recognized for

retaining high concentrations of biodiversity (Batáry, Báldi, Kleijn, & Tschardt, 2011; Heath, Soykan, Velas, Kelsey, & Kross, 2017; Kremen, Iles, & Bacon, 2012). Moreover, there is mounting evidence that many of the species that benefit from agro-ecological practices can provide valuable ecosystem services to farmers, such as natural pest control and pollination (Garibaldi et al., 2017; Kremen & Miles, 2012).

Still, promoting native biodiversity in agricultural landscapes may come with costs, as not all wild species are beneficial to agricultural yields or other management objectives (Peisley, Saunders, & Luck, 2015). For example, some bird species damage stone fruits, berries, grains, nuts and vegetables by consuming produce or defecating on crops (Anderson et al., 2013; Clark, 1976; Peisley et al., 2015), while others help to control crop pests (Mols & Visser, 2002). A recent comprehensive review on birds in agriculture shows that 71.4% of the 70 studies examined focused only on the costs associated with birds as crop pests (Peisley et al., 2015). Thus, promoting bird species in agricultural systems may not always benefit farmers. Indeed, some farmers use visual or auditory deterrents or even shoot or trap birds (Anderson et al., 2013; Clark, 1976).

At the same time, some bird species provide ecosystem services including dispersal of seeds, pollination of flowers, scavenging carrion, cycling nutrients, consuming weed seeds and acting as effective pest control agents of agricultural pests (Whelan, Şekercioğlu, & Wenny, 2015), leading to increased yields in such crops as apples, oil palm, coffee, cacao and grapes (Jedlicka, Greenberg, & Letourneau, 2011; Koh, 2008; Maas et al., 2015; Mols & Visser, 2002; Peisley et al., 2015; Railsback & Johnson, 2014; Van Bael et al., 2008). For example, Jedlicka et al. (2011) added nest boxes that attract insectivorous birds to vineyards in California that increased the rate of removal of sentinel pests that were placed in the field. However, few studies have simultaneously measured the services and disservices of birds in agriculture (Peisley et al., 2015). Even fewer studies have examined how farming practices influence the net effects of birds on crops (Pejchar et al., 2018).

Diversified farming practices could increase insectivorous bird abundance that can provide pest control and enhance yields or instead bolster pest bird abundance, resulting in yield loss. Previous research shows that diversified farming practices (Perfecto et al., 2004) and natural land cover (Karp et al., 2013) increase the abundance of insectivorous birds and lead to greater suppression of insect pests by birds in some systems. However, to our knowledge, few studies have simultaneously assessed the impact of diversified farming practices and surrounding landscape complexity as well as the trade-off between services and disservices due to changes in bird communities.

In this study, we compared the services and disservices of birds in strawberries in California's Central Coast. We evaluated the importance of both farm management and landscape level features in influencing overall bird abundance and functional groups that are considered beneficial (insectivores) and harmful (frugivorous) to farmers. We predicted that some bird species would damage strawberry fruits, while others would provide quantifiable benefits

to farmers by reducing insect pests. We hypothesized that local diversification features and semi-natural land cover would increase overall bird diversity and pest control services provided by birds. Yet we also hypothesized that strawberry-eating bird abundance would increase on farms with more diversification features, increasing disservices as well.

2 | MATERIALS AND METHODS

2.1 | Study system and site selection

Our study was conducted in the California Central Coast, one of the most economically important agricultural regions in the United States, driven by its lettuce and berry production (Gennet et al., 2013). Although large-scale industrial farms dominate the region, natural land cover patches, including shrub-chaparral, woodlands, grasslands, wetlands and riparian and floodplain corridors, exist within the farmland mosaic. Our research focused on several sub-regions within the Central Coast, including: the Salinas valley (farms = 8, point counts = 31), the Watsonville area including the Pajaro valley (farms = 8, point counts = 26), Prunedale (farms = 8, point counts = 30) and the north coast (farms = 3, point counts = 12), which included farms north or parallel to Santa Cruz (Figure 1). Farms and landscapes, as well as bird communities, exhibited some differences across these four sub-regions (see Table S1 in Supporting Information). Within these sub-regions, we selected organic strawberry farms with practices that ranged from diverse to homogenous (monoculture), using on-farm vegetation surveys and surveys of grower practices (Table 1). These farms also varied across a gradient of semi-natural land cover, which we identified using aerial photos from the National Aerial Imagery Program (NAIP; <http://datag>

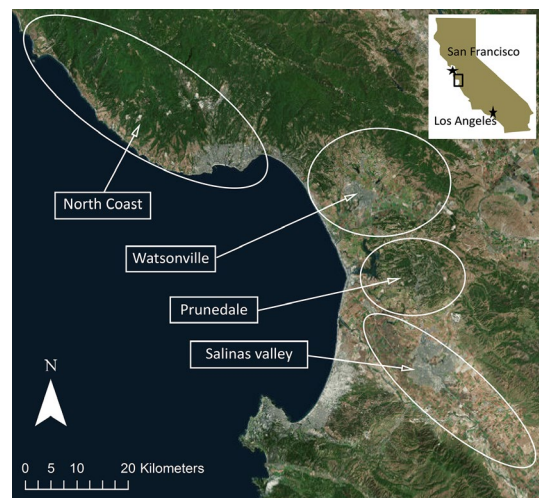


FIGURE 1 Study sub-regions where 27 diversified and homogenous farms were located: North coast, Watsonville, Prunedale and Salinas valley. Given the socio-economic objectives of studies associated with funding for this research, the exact location of farms is left obscure to protect the identity of growers. Farms stretch across three California counties: San Mateo, Santa Cruz and Monterey

TABLE 1 Basic statistics of diversification practices, bird deterrents and semi-natural land cover in the landscape for diversified and specialized farms

	Farm type	
	Diversified	Homogenized
Diversification practices		
Floral strips ^a	63% (10/16)	10% (1/11)
Flowering hedgerow ^a	57% (9/16)	19% (2/11)
Perennial non-flowering windblock ^a	25% (4/16)	10% (1/11)
Annual non-flowering windblock ^a	13% (2/16)	37% (4/11)
Livestock ^a	44% (7/16)	0% (0/11)
Water sources ^a	69% (11/16)	64% (7/11)
Crop diversity ^b	1.73 (0.66–2.66)	0.15 (0–1.09)
Number of div. practices ^b	3.34 (1.25–6)	1.42 (0–3)
Bird deterrents		
Sound cannons/bird whistlers ^a	7% (1/16)	10% (1/11)
Other sound deterrents ^a	19% (3/16)	46% (5/11)
Bird sparklers ^a	13% (2/16)	46% (5/11)
Scarecrows ^a	13% (2/16)	28% (3/11)
Bird seed attractants ^a	7% (1/16)	19% (2/11)
Bird traps ^a	7% (1/16)	19% (2/11)
Number of bird control practices ^b	0.56 (0–4)	1.64 (0–4)
Semi-natural land cover in the landscape (1000 m)		
250 decay function ^b	30% (0%–78%)	16% (0%–71%)
500 decay function ^b	32% (0%–73%)	17% (0%–72%)
750 decay function ^b	33% (0%–75%)	17% (0%–71%)

^aPercent (number of sites with practices/total number of sites).

^bMean (minimum value – maximum value).

ateway.nrcs.usda.gov/) (Table 1). Across the 27 farms selected, there was no correlation ($r = 0.14$, $p = 0.16$) between farm level diversification and landscape diversification factors.

2.2 | Diversification practices and classification

We documented the use of the following diversification practices that were expected to affect bird activity on each farm: (a) presence or absence of flowering perennial hedgerows- planted with species that have attractive flowers; (b) presence or absence of annual flower strips- planted within field rows; (c) presence or absence of non-flowering perennial windblocks- trees or shrubs planted on field borders in order to block wind; (d) presence or absence of non-flowering annual windblocks- planted within field blocks to block dust from agricultural roads; (e) the presence or absence of livestock; and (f) the presence or absence of water sources. Additionally, we used handheld GPS devices (Garmin GPSMAP 64st; accuracy ~3.1 m) and ArcGIS 10.1 (ESRI, 2011) to map and digitize the production area of

all farms, document the relative cover of all crop species; and (g) estimate crop diversity (Shannon's Diversity index). From these seven diversification practices, we used a hierarchical cluster analysis to categorize diversification practices (pvclust function, pvclust package, program R version 3.2.0). The pvclust function computes p -values for all clusters at all levels of the hierarchy with the Ward's D clustering method and a Euclidean distance metric. Using Calinski's Criterion, we determined that two clusters were optimal. We therefore categorized farms into locally homogenous and locally diversified farms based on this optimal clustering.

2.3 | Bird deterrent practices

Farms varied in the number and type of bird deterrent practices along the local and landscape diversification gradients. We quantified the use of bird deterrent practices, including: noise deterrents such as sound cannons, bird whistlers and recordings of hawks; visual deterrents such as bird sparklers and scarecrows; alternative food sources such as applying birdseed adjacent to fields; and bird traps. Vertebrate pest management plans often recommend the combination of more than one practice to control bird pests (Anderson et al., 2013; Clark, 1976); therefore, we also computed the number of bird deterrent practices used per farm (Table 1).

2.4 | Semi-natural land cover in the landscape

To describe landscape diversification, we hand-digitized semi-natural land cover, urban features and croplands within 1000 m of each farm from NAIP imagery (2014; ESRI, 2011). Semi-natural land cover was defined to include forests and riparian woodlands, exotic tree woodlots, chaparral and scrublands. We focused analysis on semi-natural land cover because it was negatively correlated with agricultural land cover and due to its importance for bird conservation. Previous research suggests that bird richness and abundance respond to variation in land cover at 1000 m distance (Gonthier et al., 2014), therefore we elected to digitize 1000 m buffers around each farm. Within the 1000 m distance around sampling locations, we weighted semi-natural land cover closer to farms more heavily than areas further away by creating an index of the surrounding semi-natural land cover, as in Karp et al. (2016). This logic follows the assumption that semi-natural land cover nearer to farms would have a greater impact on the services and disservices of birds, but that distant patches of semi-natural land cover would have lesser, but relevant impact. First, we quantified the amount (m^2) of semi-natural land cover in 20 concentric rings, with inner radii distributed uniformly every 50 m between 50 and 1000 m. Then, we used a Gaussian function to assign weights to each ring, with farther rings given lower weightings W , based on the formula $W = \exp(-l^2/(2 \times d^2))$, where l is the inner edge distance of the ring and d is a decay rate parameter that specifies how quickly the weightings decrease with increasing distance. Thus, larger values of d indicate the increased influence of more distant land cover. Although we found the most predictive decay rate to be $d = 750$, all models (i.e. with decay rates of 250, 500 and 750) were

indistinguishable based on Akaike Information Criteria (AIC) values (see Table S2).

2.5 | Exclosure experiment

We compared control plots (bird-accessible plots) to bird-excluded plots to quantify the percent of berry damage caused by birds and invertebrate pests. We constructed bird exclusion plots from polyvinyl chloride (PVC) frames (0.6 m × 1.5 m × 0.4 m) that fit within a single row of strawberry raised beds. We covered polyvinyl chloride (PVC) frames with monofilament gill netting (1.5 in square mesh; www.memphisnet.net), which prevented bird access, but allowed arthropod pests to pass. This netting also excludes large rodents and bats, but small mice could potentially move through mesh netting to consume berries. These dimensions minimized interruption of farm activities and allowed for 12 strawberry plants to grow unobstructed. To avoid creating perching structures for potential insectivorous or strawberry-eating birds above control plots, we opted to construct open-framed control plots with caution tape that did not support the weight of birds above plots. Control plots were within 5 m of the exclusion plots. Three pairs of exclusion and control plots were placed in each of six out of the 27 farms ($n = 18$ pairs), with at least 50 m between pairs. Because we were unable to establish exclosures on all farms, we did not measure the experimental impact of local and landscape factors on bird suppression of pests.

Plots were established in May, the middle of the songbird breeding season and deployed for 12 weeks. Weekly, we harvested and scored all ripe berries for damage in all plots. Bird damage was defined as berries with angular wounds to strawberry flesh. Some seed-eating birds remove seeds from strawberries; therefore, we scored seed-damaged berries as those with more than five seeds removed per berry. We measured different categories of invertebrate pest damage which included: *Lygus hesperus* damage—berry puckering or the characteristic “cat eye” malformation; leaf-rolling caterpillar damage—tunnelling with the presence of webbing; slug damage—hollowed out wounds with mucous present; and other invertebrate damage—presence of small wounds and tunnels that are potentially early instar caterpillar damage, cucumber beetle damage or thrip damage such as berry bronzing (CSC & CMCC, 2003).

At the end of the 12-week sampling period, we used vacuum sampling during warm weather and in the absence of rain, heavy fog and strong winds; ideal conditions for collecting arthropods (Zalom, Pickel, Walsh, & Welch, 1993) to sample eight plants within each experimental plot to determine the impacts of exclusion on the arthropod community. Vacuum sampling was achieved by converting a leaf blower (Stihl BG55) to a leaf-sucking configuration and attaching a mesh collection bag on the nozzle. We focused a 1-s rapid suction effort on each of the central-most eight strawberry plants and pooled samples by plot. We then sorted all arthropods collected to order and subsequently identified all important species of pests and natural enemies that predate pests.

To determine how bird exclusion affected berry damage and insect abundance, we modelled proportion and count data using

GLMMs (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). Berry damage proportion data exhibited over-dispersion, therefore we aggregated data across the sampling weeks and across sampling stations within each farm. This aggregation eliminated the issues of over-dispersion. We modelled the proportion of berries damaged by birds or insect pests using binomial distributions with exclosure treatment as a fixed effect and farm as random effect. Thus, we did not assess the impact of time on the proportion of berry damage. We modelled the number of insect pests or natural enemies per plot using Poisson distributions with exclosure treatment as a fixed effect and treatment pair nested within farm as random effects.

2.6 | Bird surveys

To assess the relationship between farm level diversification and semi-natural land cover and bird community variables, we conducted four 10 min, 50 m radius point counts, spaced at least 100 m apart per farm, with at least one of those counts in strawberry (for farms with multiple crops). For small farms, we scaled down the number of counts accordingly. The observer entered the field and waited 5 min before beginning the count. We then documented all birds heard or observed within the 50 m radius. Birds farther than 50 m away or that flew overhead were noted, but not included in the count. Radii were arranged so that the count edges did not extend beyond farm boundaries, but did include farm features such as natural vegetation, hedgerows and developed areas. We conducted point counts from sunrise to 10.30 hr, always in the absence of rain, heavy fog and strong winds. Given that farms were relatively open, we assume that detectability did not substantially vary across sites.

To describe the bird community, we calculated bird species richness and total relative abundance within each point count. We also grouped bird species by their primary and secondary diets as reported in Ehrlich, Dobkin, and Wheye (1988). Insectivorous birds were defined as those species with primary diets of insects (see Table S3). We further defined strawberry-eating birds as any species that has been documented as a pest of berry crops in the literature (Anderson et al., 2013; Clark, 1976; CSC & CMCC, 2003) or that we observed consuming strawberries during the field sampling period (see Table S3). We acknowledge the limitations of these categories as diets may shift within species with age, seasonality and geography.

2.7 | Bird damage and insect pest measures

To determine the amount of bird damage on all 27 farms, we surveyed three sampling stations within a strawberry block. At each station, we surveyed a grid of strawberry plants approximately 10 m wide and four rows long. Along each row, we assessed five strawberry plants every 2 m for a total of 20 plants per station (60 per farm). For each plant surveyed, we searched for signs of bird damage marks on the plastic row covers because birds often flick and scrape strawberry flesh onto the plastic covering, which remains long after the damage event.

At each sampling station, we used vacuum suction to sample 100 plants and assess the arthropod community (Zalom et al. 1993). Within each row, we sampled 10 strawberry plants separated by 5 m, skipping a row between samples. We focused a 1-s rapid suction effort on each plant and pooled samples by station. We then sorted all arthropods collected to order and then identified important pests and natural enemies to species.

2.8 | Beta-diversity measurements

To determine the relationship of local (on-farm scale) diversification and the amount of semi-natural land cover on the beta-diversity of birds, we first restricted the data to include only point counts with at least five bird observations to allow beta-diversity indices to be calculated. We computed multiple beta-diversity indices: two presence-absence indices (Sorenson and Simpson) and two abundance-based indices, (Bray–Curtis and Bray Bal). The different metrics reflect different components of beta-diversity (Anderson et al., 2011). For each index, we calculated the multivariate distance from each site to the centroid of all diversified farm sites and for all homogenized farm sites. To compare the differences between beta-diversity, we compared the mean centroid distance within diversified and homogenized farms with linear mixed models for each of the four beta-diversity indices. Farm was included as a random factor, nested within the random factor sub-region and significance was assessed through comparing models with and without the local diversification predictor via likelihood ratio tests evaluated against a chi-square distribution as in Karp et al. (2018). This analysis was repeated for all four indices for the amount of semi-natural land cover surrounding farms by binning all farms into two categories, "high" semi-natural land cover (>50% of landscape) and "low" semi-natural land cover (<50% of landscape).

2.9 | Community analysis

To understand how on-farm diversification features, bird deterrent practices and semi-natural land cover influenced bird and arthropod community variables, we modelled count data using GLMMs. We included the fixed effects of bird deterrents, local diversification, semi-natural land cover and their interaction. We also included time of day and day of year as covariates. In all models, we included farm nested within sub-region as random effects. Farm was included to account for the different number of point counts per farm and sub-region was included to account for differences in microclimate and topography among sub-regions (see Table S1).

For all dependent variables defined by count data, we compared the fit of Poisson and negative binomial models with AIC and dispersion to determine the fit of each distribution. We also assessed a normal distribution and log-transformed normal distribution when models did not fit Poisson or negative binomial distributions. We used a Shapiro–Wilk Normality Test to assess the fit of a normal distribution to the data. GLMMs were performed with the function "glmer" in the R-package lme4 (Program R 3.3.3). We tested for

collinearity between dependent variables using variance inflation factors (VIF).

Given the large number of explanatory variables included in community models, we conducted model selection of all possible combinations of explanatory variables using a multi-model inference approach using the function dredge in the R-package MuMIn (program R 3.3.3). We determined the best-ranked model set as all models with delta AIC less than two. Further, for all explanatory variables included in the best-ranked model set, we compared the relative variable importance (RVI) as the sum of the Akaike weights across all the models in the best-ranked set (Burnham & Anderson, 2004). To summarize best-ranked model sets, we performed conditional model averaging within the best-ranked model set.

3 | RESULTS

3.1 | Bird enclosure experiment (service vs. disservice)

Across the 12-week experiment, birds damaged $3.2 \pm 0.7\%$ of berries in control plots, compared to only $0.8 \pm 0.2\%$ in bird enclosure plots; a statistically significant difference (Figure 2a; $est = -1.29 \pm 0.2$, $p < 0.0001$). The majority of the bird damage came in the form of flesh damage, with only 9% of damaged berries receiving seed removal damage.

In contrast, insect pests damaged $23.6 \pm 1.6\%$ of berries in control plots and $27.4 \pm 1.7\%$ of berries in bird enclosure plots (Figure 2a; $est = 0.1 \pm 0.04$, $p = 0.0332$). Most insect damage (88%) was from *L. hesperus*. *Lygus hesperus* damaged $21.2 \pm 0.2\%$ of berries in control plots and $23.8 \pm 0.2\%$ of berries in enclosure plots ($est = 0.05 \pm 0.05$, $p = 0.273$). All other insects damaged $2.5 \pm 0.1\%$ of berries in control plots and $3.6 \pm 0.1\%$ of berries in exclusion plots ($est = 0.39 \pm 0.11$, $p = 0.0005$).

The total abundance of pest insects (Figure 2b; $est = 0.18 \pm 0.05$, $p = 0.0253$) and abundance of *L. hesperus* ($est = 0.6 \pm 0.3$, $p = 0.00641$) was lower in control relative to bird enclosure plots. Arthropod natural enemies did not differ between exclusion treatments (Figure 2b; $est = -0.05 \pm 0.25$, $p = 0.83$), nor did any specific natural enemy; big-eyed bugs (*Geocoris* spp.; $est = 0.3 \pm 0.3$, $p = 0.37$) and pirate bugs (*Orius* spp.; $est = -0.05 \pm 0.3$, $p = 0.86$).

3.2 | Local and landscape relationships with bird community variables

Across the 99 point counts on 27 farms, we detected 1,341 bird individuals (see Table S2). The most abundant species were the House Finch ($n = 281$), Dark-eyed Junco ($n = 89$) and Bushtit ($n = 62$). Insectivorous bird species represented 15% of all bird detections. The most abundant insectivores were the Barn Swallow ($n = 52$), Black Phoebe ($n = 36$) and Cliff Swallow ($n = 32$). Strawberry-eating bird detections represented 38% of all detections ($n = 514$), with the House Finch ($n = 281$), American Goldfinch ($n = 47$) and Brewer's Blackbird ($n = 47$) being the most abundant species.

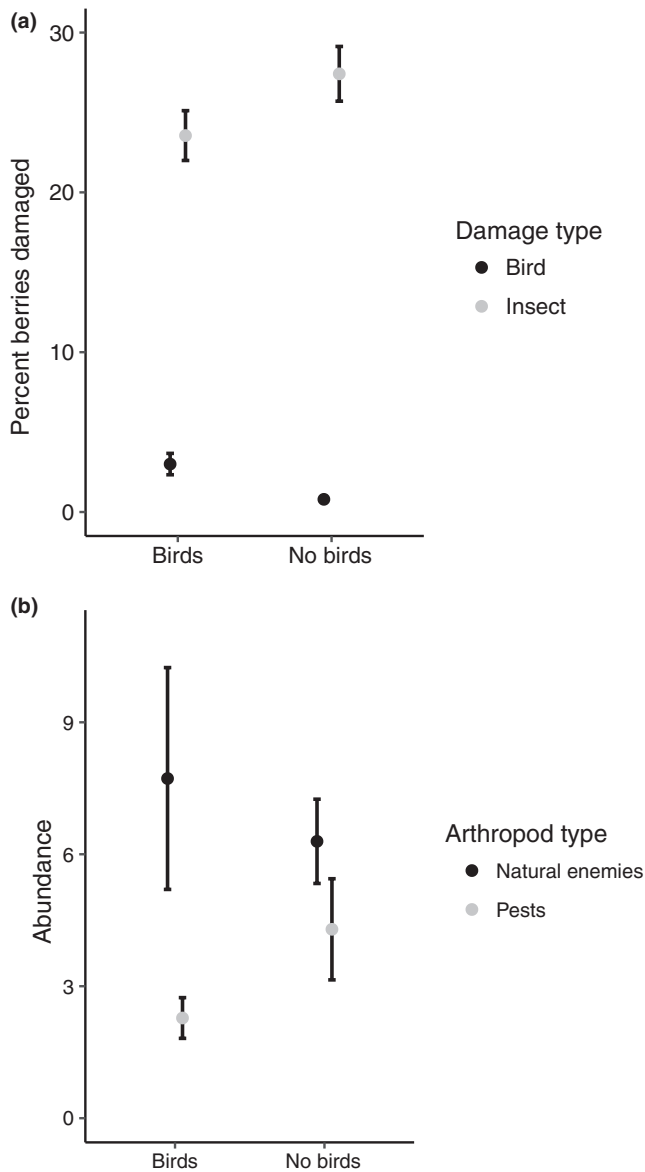


FIGURE 2 Results of bird exclusion experiment across six farms with 18 pairs of bird exclusion and control (open access) plots for berry damage (a) and arthropod abundance (b) ($M \pm SE$)

There was no difference between bird beta-diversity in diversified and homogenized farms or in low versus high amounts of surrounding semi-natural land cover when distances to group centroids were measured with the Sorensen ($X^2_{local} = 0.34$, $p = 0.5607$; $X^2_{landscape} = 0.8$, $p = 0.3734$), Simpson ($X^2_{local} = 0.6$, $p = 0.4347$; $X^2_{landscape} = 1.5$, $p = 0.2281$), Bray-Curtis ($X^2_{local} = 0.3$, $p = 0.5972$; $X^2_{landscape} = 0.9$, $p = 0.3519$) or Bray Bal ($X^2_{local} = 0.4$, $p = 0.5466$; $X^2_{landscape} = 2.3$, $p = 0.1296$) indices.

Bird species richness per point count increased with both farm diversification and the amount of semi-natural land cover (Table 2; Figure 3a,b). Total relative abundance increased with farm diversification and with the amount of semi-natural land cover (Table 2; Figure 3b; see Table S4).

TABLE 2 Conditional model averaging across best-ranked model sets ($AIC_c < 2$) for bird community dependent variables

	Est \pm SEM	RVI	N in best model set
Species richness (Poisson)			
Local diversification	0.78 \pm 0.19	1	6/6
Semi-natural land cover	0.21 \pm 0.08	1	6/6
Local diversif x semi-natural	—	0	0/6
No. bird deterrent practices	—	0	0/6
Time of day	0.05 \pm 0.06	0.2	2/6
Day of year	-0.14 \pm 0.09	0.48	3/6
Farm size	-0.1 \pm 0.09	0.3	2/6
Total relative abundance (neg. binomial)			
Local diversification	0.65 \pm 0.21	1	10/10
Semi-natural land cover	0.23 \pm 0.12	0.75	7/10
Local diversif x semi-natural	0.25 \pm 0.23	0.22	2/10
No. bird deterrent practices	0.07 \pm 0.11	0.07	1/10
Time of day	0.1 \pm 0.09	0.36	4/10
Day of year	0.08 \pm 0.11	0.07	1/10
Farm size	-0.14 \pm 0.09	0.54	5/10
Insectivorous bird abundance (neg. binomial)			
Local diversification	0.57 \pm 0.31	0.7	8/12
Semi-natural land cover	0.26 \pm 0.17	0.43	5/12
Local diversif x semi-natural	—	0	0/12
No. bird deterrent practices	-0.18 \pm 0.15	0.26	4/12
Time of day	—	0	0/12
Day of year	-0.14 \pm 0.15	0.07	1/12
Farm size	-0.17 \pm 0.14	0.24	3/12
Strawberry-eating bird abundance (log trans. normal)			
Local diversification	0.48 \pm 0.25	0.83	15/18
Semi-natural land cover	-0.17 \pm 0.15	0.6	11/18
Local diversif x semi-natural	0.35 \pm 0.26	0.22	4/18
No. bird deterrent practices	0.18 \pm 0.13	0.4	7/18
Time of day	0.13 \pm 0.11	0.23	5/18
Day of year	—	0	0/18
Farm size	-0.14 \pm 0.12	0.23	5/18

Note: AIC, Akaike Information Criteria; N in best model set, the number of models within the best model set for which a given explanatory variable is present; RVI, Relative variable importance which is equal to the sum of the Akaike weights.

Insectivorous and strawberry-eating bird abundance increased with diversification (Table 2; Figure 3c,d; see Table S5). However, these two groups had different responses to semi-natural land cover and the number of bird deterrents. The abundance of insectivorous birds increased with the amount of semi-natural land cover, but decreased with the number of bird deterrents (Table 2; Figure 3c).

In contrast, strawberry-eating bird abundance decreased with the amount of semi-natural land cover and increased with the number of bird deterrents (Table 2; Figure 3d).

The number of bird damage marks increased with local diversification and the number of bird deterrents, but decreased with the amount of semi-natural land cover (Table 2; Figure 4a,b; see Table S6). In a separate analysis, strawberry-eating bird abundance was positively related to the number of bird damage marks (est = 0.18 ± 0.07, $p = 0.0128$).

Farm diversification, the amount of semi-natural land cover and the number of bird deterrents were not common predictors in the best-ranked model sets for the total relative abundance of insect pests and *L. hesperus* (Table 3, Figure 4c). However, arthropod natural enemies increased with the amount of semi-natural land cover (Table 3, Figure 4d). In separate analyses, the abundance of insect pests (est = 0.003 ± 0.05, $p = 0.95$) and *L. hesperus* pests (est = -0.06 ± 0.05, $p = 0.18$) had no relationship with the abundance of insectivorous birds.

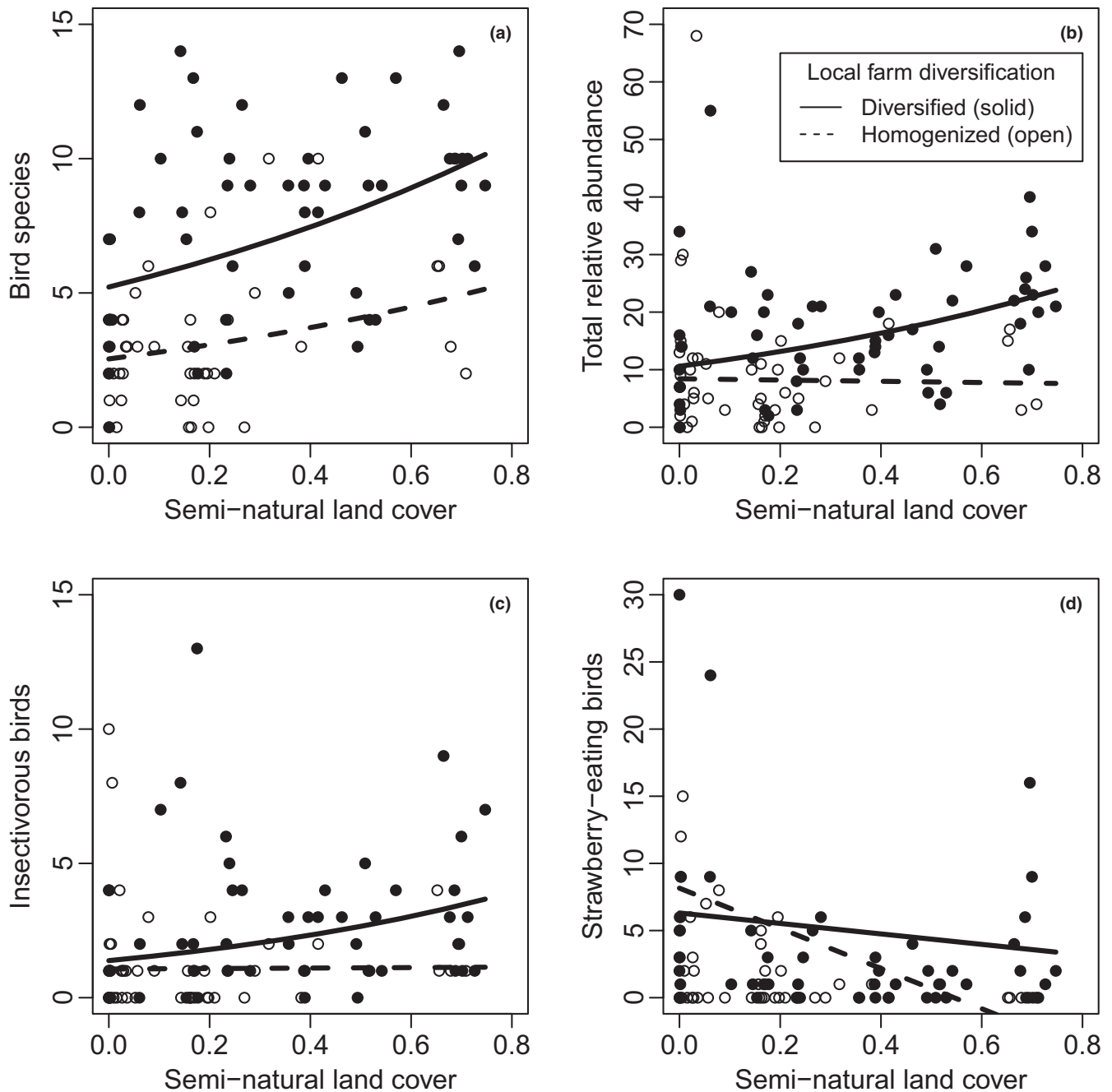


FIGURE 3 Influence of local diversification practices (i.e. hedgerows, flower strips or increased crop diversity) and the amount of semi-natural land cover on bird richness (a), total relative abundance of birds (b), the relative abundance of insectivorous birds (c), and the relative abundance of strawberry-eating birds (d). Filled symbols represent diversified farms and open symbols represent homogenous farms. The solid lines indicate the mean slopes estimated from generalized linear mixed model parameters

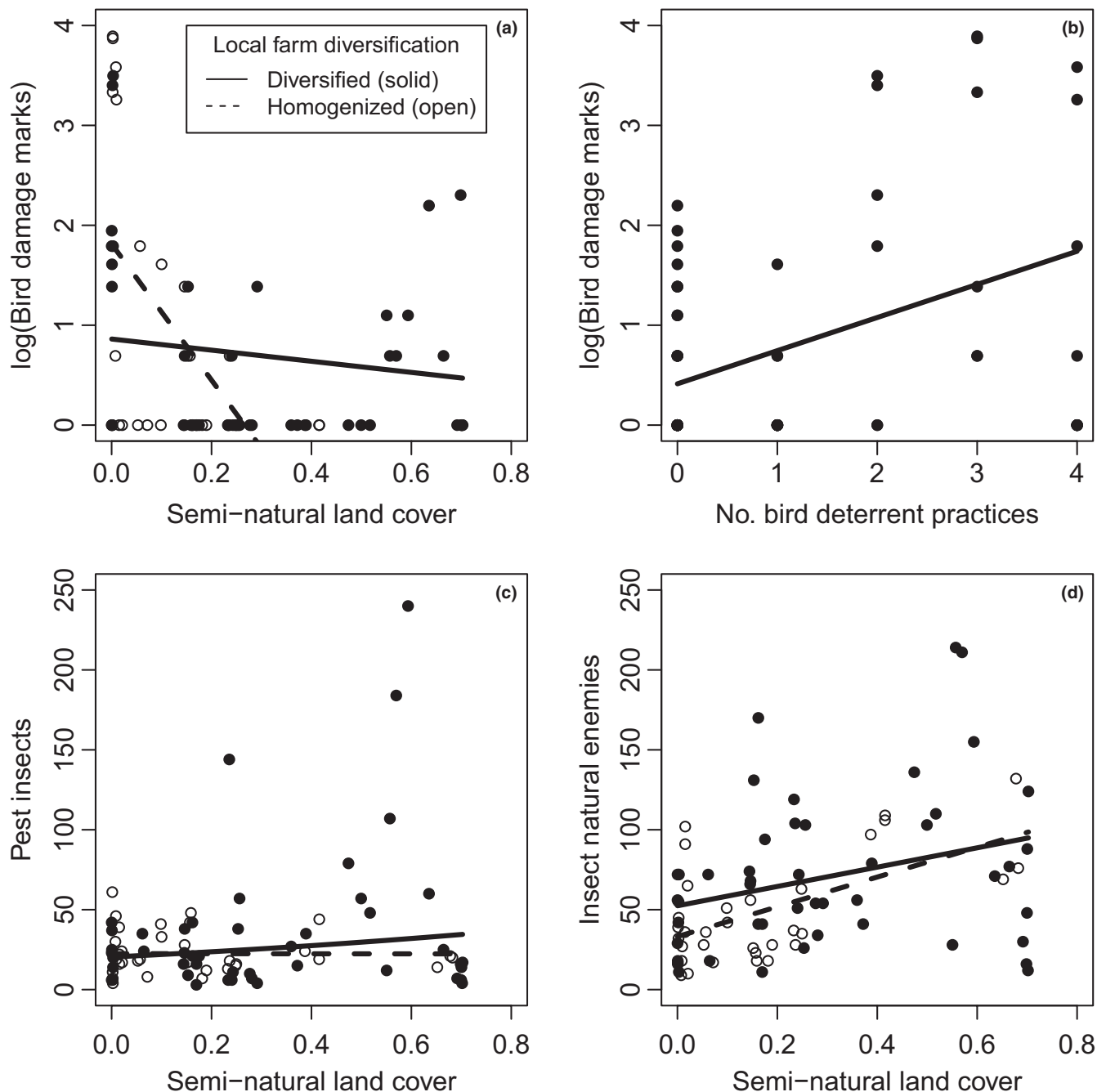


FIGURE 4 Influence of local diversification practices and the amount of semi-natural land cover on the amount of bird damage marks (a). The relationship between bird deterrent practices and bird damage marks (b). Influence of local diversification practices and the amount of semi-natural land cover on total relative abundance of insect pests (c) and insect natural enemies (d). For Figure 4a,c, and d, filled symbols represent diversified farms and open symbols represent homogenous farms. The solid lines indicate the mean slopes estimated from generalized linear mixed model parameters

4 | DISCUSSION

4.1 | Bird services versus disservices

In our study, we observed a mean of 3.2% of berries damaged by birds in control plots (Figure 2a). This level of damage is comparable to other studies in California strawberries. For instance, Gebhardt, Anderson, Kirkpatrick, and Shwiff (2011) estimated that birds and

rodents damage berries on about 30% of total farm acreage and in those areas, they damage about 2.6% of yield. We also observed 0.8% damage to berries within exclusion plots, which we assume may be due to birds potentially pecking through netting, small mice or human error in scoring.

While some bird species damaged some berries, we also show that birds reduced the number of berries damaged by insect pests by 3.8%. This result suggests that bird services roughly equate to bird

TABLE 3 Conditional model averaging across best-ranked model sets ($AIC_c < 2$) for bird damage and insect pest and natural enemy dependent variables

	Est \pm SEM	RVI	N in best model set
Bird damage marks (log trans. normal)			
Local diversification	0.63 \pm 0.44	0.44	2/4
Semi-natural land cover	-0.78 \pm 0.60	0.48	2/4
Local diversif x semi-natural	1.11 \pm 0.52	0.28	1/4
No. bird deterrent practices	0.46 \pm 0.18	1	4/4
Insect pests (neg. binomial)			
Local diversification	–	0	0/3
Semi-natural land cover	0.13 \pm 0.13	0.26	1/3
Local diversif x semi-natural	–	0	0/3
No. bird deterrent practices	-0.12 \pm 0.13	0.24	1/3
<i>Lygus hesperus</i> abundance (neg. binomial)			
Local diversification	-0.32 \pm 0.24	0.34	1/3
Semi-natural land cover	-0.09 \pm 0.12	0.19	1/3
Local diversif x semi-natural	–	0	0/3
No. bird deterrent practices	–	0	0/3
Natural enemy abundance (normal)			
Local diversification	12.3 \pm 15.09	0.22	1/3
Semi-natural land cover	17.21 \pm 7.37	1	3/3
Local diversif x semi-natural	–	0	0/3
No. bird deterrent practices	-7.56 \pm 7.68	0.26	1/3

Note: AIC, Akaike Information Criteria; N in best model set, the number of models within the best model set for which a given explanatory variable is present; RVI, Relative variable importance which is equal to the sum of the Akaike weights.

disservices, thus rendering birds net neutral for producers. It should be pointed out that while all bird damage results in lost berries because they must be culled, not all insect damage results in direct losses. *L. hesperus* caused the majority of insect damage, which produces malformation in berries. However, depending on the extent of the malformation and to which market the berries will be sold, many of these berries may still be marketable. Therefore, estimation of berry loss caused by insects was beyond the scope of this study. For this study, we conclude that birds do deliver services in addition to disservices and future studies should focus on detailed estimates of economic benefits and costs associated with insect versus bird damage for different markets.

4.2 | Effects of landscape and local diversification

Our study indicates that the presence of natural and semi-natural land cover is negatively related to strawberry-eating birds. This may be for three reasons: the habitat generalization of strawberry-eating birds, attraction to food in farmland-dominated landscapes and increased predation pressure from birds of prey near semi-natural land cover. European Starlings, House Finches and other strawberry-eating species are habitat generalists that are well adapted to the human-dominated landscape and frequently nest within human-made structures. These species may find more nesting and preferred foraging sites and have higher fecundity in farmlands (Lindell et al., 2016). If strawberry-eating birds depend on strawberries and other fruit crops for the majority of their diet, then they will likely be drawn into landscapes with dense concentrations of strawberry (or other fruit) resources. Strawberries are harvested in this region from February to November, with off-cycle strawberries extending the harvest season even further, making strawberries and other fruits available for most of the year. Semi-natural land cover may promote birds of prey that reduce the abundance of strawberry-eating birds. This hypothesis is supported by work in New Zealand vineyards where the introduction of falcons reduced pest bird abundance and damage (Kross, Tylanakis, & Nelson, 2012). These three hypothetical phenomena are not mutually exclusive and could act in concert to reduce the attractiveness of farms with high amounts of semi-natural land cover to strawberry-eating bird species.

Strawberry-eating birds and bird damage marks were higher on diversified farms compared to homogenized farms. This may be because diversified farms have greater vegetative complexity, including the presence of vegetative features that provide cover and perching locations that likely benefits all birds, including strawberry-eating birds. While monocultures of strawberries may provide a surplus of food resources for strawberry-eating birds, they may require some adjacent vegetative complexity to facilitate foraging in strawberry fields.

In contrast, insectivorous bird abundance increased with farm diversification and with semi-natural land cover. These birds may exert effective pest control without costs because they do not eat strawberries. In other systems, diversification features (Perfecto et al., 2004) and natural land cover (Karp et al., 2013) increased the pest suppression services provided by birds. However, we found no relationship between pest insect abundance and the amount of semi-natural land cover or the abundance of insectivorous birds. There may be several reasons for this lack of pattern. First, insectivorous birds may only infrequently forage in strawberry fields, weakening their impact on pest insects. Foraging in other parts of farms or in surrounding habitats may be more rewarding for insectivorous species. Second, it could be that only a few insectivorous species eat pest insects. Third, it is possible or even likely that abundant birds considered pests, are simultaneously eating insect pests. For example, European Starlings and American Robins are considered important pests of strawberry, but they are also known consumers of insects and likely to contribute to the suppression of insect pests (Garfinkel & Johnson, 2015).

While our study highlights the importance of farm diversification and semi-natural land cover for supporting many bird community variables, we failed to observe any relationships with beta-diversity, using four different metrics. The lack of a relationship may result from sites within diversified or homogenized farms being too self-similar, resulting in low turnover of species across sites. Additionally, it is hypothesized that dispersal limitation drives many patterns in beta-diversity. This hypothesis may help explain why the beta-diversity of some communities responds to agriculture management intensity and others do not (Clough et al., 2007). Birds are highly mobile and many species are capable of long-distance dispersal (Tittler, Villard, & Fahrig, 2009). In our study region, the heterogeneity in farm diversification or semi-natural land cover may not have been strong enough to drive differences in the beta-diversity in highly mobile bird communities.

4.3 | Bird management to reduce disservices

In Californian agriculture, farmers have implemented practices to reduce bird damage (Anderson et al., 2013; Clark, 1976). However, many of the practices deployed are thought by farmers to be inadequate. Indeed, we found that bird deterrents were positively related to strawberry-eating birds and berry damage marks. This positive relationship likely reflects that farmers with more bird problems implement more bird deterrents than farmers without bird problems. Our results highlight the need to revise recommendations for controlling birds.

One recommendation for farmers with bird problems is to remove or eliminate habitat in and around farms (Clark, 1976; CSC & CMCC, 2003). In 2006 an outbreak of food borne pathogens resulted in recommendations for farmers to eliminate wildlife habitat to reduce the risk of produce contamination of foodborne diseases (Karp et al., 2015). Between 2005 and 2009 research suggests that these recommendations resulted in the loss of 13.3% of the remaining riparian habitat in the Salinas Valley (Gennet et al., 2013). However, our findings suggest that large amounts of semi-natural land cover reduce rather than increase bird damage to berries. Additionally, previous research studying the contamination of produce by food-borne pathogens revealed no relationship between the amount of semi-natural land cover and produce contamination (Karp et al., 2015). Instead, in fields where high amounts of semi-natural land cover had been previously removed, contamination of produce actually increased (Karp et al., 2015) and was also correlated with the reduction of the biological control provided by arthropods (Karp et al., 2016). Together, our study and these previous studies suggest that semi-natural land cover is beneficial because it promotes services and reduces disservices. Given that no scientific publication, to the best of our knowledge, has demonstrated that semi-natural land cover increases bird damage and food-borne pathogens, recommendations to remove habitat should be reconsidered.

4.4 | Considerations for future work

This research identifies several urgently needed investigations to inform agricultural policies related to bird and semi-natural land cover

management: (a) While we compared the damage caused by birds to the damage prevented by birds, we did not measure the costs associated with faecal contamination. Until this cost is assessed, regulators in California are unlikely to change guidelines to limit bird habitat. (b) To guide bird management practices, it is important to document which bird species are threats to food safety and which birds are pest control agents. (c) It will be important to understand the mechanism behind the reductions of strawberry-eating bird damage on farms with greater amounts of semi-natural land cover.

5 | CONCLUSIONS

Given this study's finding that birds suppress insect pests at levels comparable to the amount of damage that birds inflict, farmers may not need to consider birds as enemies to strawberry production. Conserving semi-natural land cover benefits bird conservation, which may also benefit farmers through reduced abundance of strawberry-eating birds and bird damage. These results highlight the need to consider both the services and disservices of birds when making management decisions.

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AUTHORS' CONTRIBUTIONS

D.J.G., A.R.S., D.S.K. and C.K. conceived the ideas and designed methodology; all authors collected the data; D.J.G. analysed the data; D.J.G. and A.R.S. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.41bh21r> (Gonthier et al., 2019).

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SUPPORTING INFORMATION

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