*Ecological Applications*, 30(5), 2020, e02115


# Shifts in species interactions and farming contexts mediate net effects of birds in agroecosystems

E. M. Olimpi,[1,8] K. Garcia,[2] D. J. Gonthier,[2] K. T. De Master,[3] A. Echeverri,[4] C. Kremen,[3,4,5] A. R. Sciligo,[3,9] W. E. Snyder,[6,10] E. E. Wilson-Rankin,[7] and D. S. Karp[1]

[1]*Department of Wildlife, Fish, and Conservation Biology, University of California, 1088 Academic Surge, 455 Crocker Lane, Davis, California 95616 USA*
[2]*Department of Entomology, University of Kentucky, Lexington, Kentucky 40546 USA*
[3]*Environmental Science, Policy, and Management, University of California, Mulford Hall, 130 Hilgard Way, Berkeley, California 94720 USA*
[4]*Institute for Resources, Environment and Sustainability, University of British Columbia, Vancouver Campus, AERL Building, 429-2202 Main Mall, Vancouver, British Columbia V6T 1Z4 Canada*
[5]*Biodiversity Research Centre, Department of Zoology, University of British Columbia, 2212 Main Mall, Vancouver, British Columbia V6T 1Z4 Canada*
[6]*Department of Entomology, Washington State University, PO Box 646382, Pullman, Washington 99164 USA*
[7]*Department of Entomology, University of California, 165 Entomology Bldg., Citrus Drive, Riverside, California 92521 USA*

*Citation:* Olimpi, E. M., K. Garcia, D. J. Gonthier, K. T. De Master, A. Echeverri, C. Kremen, A. R. Sciligo, W. E. Snyder, E. E. Wilson-Rankin, and D. S. Karp. 2020. Shifts in species interactions and farming contexts mediate net effects of birds in agroecosystems. Ecological Applications 30(5):e02115. 10.1002/eap.2115

*Abstract.* Some birds are viewed as pests and vectors of foodborne pathogens in farmlands, yet birds also benefit growers by consuming pests. While many growers seek to prevent birds from accessing their farms, few studies have attempted to quantify the net effects of bird services and disservices, let alone how net effects shift across farm management strategies. We quantified the net effect of birds on crop production across 20 California strawberry (*Fragaria* × *ananassa*) farms that varied in local management practices and landscape context. We surveyed farms for berry damage and bird droppings (as potential sources of pathogens) and implemented a large-scale exclusion experiment to quantify the impact of birds on production. We found that birds had only a slightly negative overall impact on strawberry production, reducing economic value by 3.6%. Direct bird damage and intraguild predation contributed equally to this net effect, underscoring the importance of indirect trophic interactions that may be less apparent to growers. In simple landscapes (e.g., low proportions of surrounding seminatural habitat), birds provided pest control in the interiors of farm fields, and costs from bird damage to crops peaked at field edges. In complex landscapes (e.g., high proportions of seminatural habitat), birds were more likely to disrupt pest control by feeding as intraguild predators. Nonetheless, seminatural habitat dampened bird services and disservices, and our models predicted that removing habitat around farm fields would increase costs from bird damage to crops by up to 76%. Fecal contamination of crops was extremely rare (0.01%). However, both fecal contamination and bird damage did increase on farms with higher densities of fencing and wires, where birds often perch. Our results demonstrate that maintaining seminatural habitat around farms may enhance bird diversity and mitigate bird damage without increasing food safety risks. We also show that the net effects of birds depend on farming context and vary in complex ways in relation to locations within a farm, local farm attributes, and the surrounding landscape. This context-specific variation must be considered in order to optimize the management of wild birds in agroecosystems.

*Key words:* *agroecology; bird; California agriculture; diversified farming; ecosystem services; foodborne pathogens; pest control; strawberry.*

Manuscript received 6 August 2019; revised 7 January 2020; accepted 29 January 2020. Corresponding Editor: John M. Marzluff.
[8]Present address: The Organic Center The Hall of the States, 444 N. Capitol St. NW, Suite 445A Washington D.C.20001 USA
[9]Present address: Department of Entomology University of Georgia Athens Georgia 30602 USA
[10]E-mail: eolimpi@gmail.com

## Introduction

Promoting biodiversity in agriculture is associated with both costs and benefits to humans. The net effect of the services and disservices associated with on-farm biodiversity often depends upon farming practices and the characteristics of surrounding seminatural habitats (Zhang et al. 2007). Diversified farming systems, production systems that integrate crop and noncrop components on farms and in surrounding landscapes, can help balance conservation and livelihood goals (Kremen and Miles 2012, Kremen et al. 2012). Indeed, multiple studies have shown that, by planting polycultures and restoring vegetation in grass strips, hedgerows, or adjacent forest patches, growers can sustain biodiversity on their farms and enhance valuable ecosystem services such as pest control, pollination, and soil fertility (Jedlicka et al. 2011, Klein et al. 2012, Karp et al. 2013, Blaauw and Isaacs 2014, Bender et al. 2016, Schulte et al. 2017, Kremen and Merenlender 2018). Yet diversified production systems may also promote species that threaten farmer livelihoods by consuming crops or beneficial organisms (Seward et al. 2004, Gebhardt et al. 2011, Martin et al. 2013), spreading pathogens (Lejeune et al. 2007, Jay-Russell 2013), damaging farm infrastructure (Dolbeer et al. 1994, Steele et al. 1996), and harming livestock (Woodroffe et al. 2005).

Birds in particular are often very abundant on farms (Sekercioglu et al. 2016) and are known to both benefit and threaten crop yields. For centuries, farmers and scientists alike have observed birds feeding on crops and reducing crop yields (Whelan et al. 2015). More recently, there has been growing recognition that birds can increase yields by consuming insect pests (Mols and Visser 2002, Karp et al. 2013, Maas et al. 2013, Classen et al. 2014, Kross et al. 2016, Peisley et al. 2016, Heath and Long 2019). Despite these dual roles, the net effects of bird-mediated services and disservices on agricultural systems are rarely quantified due to the difficulties of measuring direct and indirect effects and considering tritrophic interactions between birds, arthropods, and crops (Whelan et al. 2015, Pejchar et al. 2018; but see Hooks et al. 2003, Martin et al. 2013, 2015). In fact, bird impacts may be even more complicated as recent studies suggest that birds may also feed upon arthropod predators of crop pests (i.e., intraguild predation) and defecate on crops, potentially contaminating them with foodborne pathogens (Carlson et al. 2011, Martin et al. 2013).

As a high-value crop with strict quality controls, strawberries (*Fragaria* × *ananassa*) are vulnerable to the costs and benefits associated with wild birds (CDFA

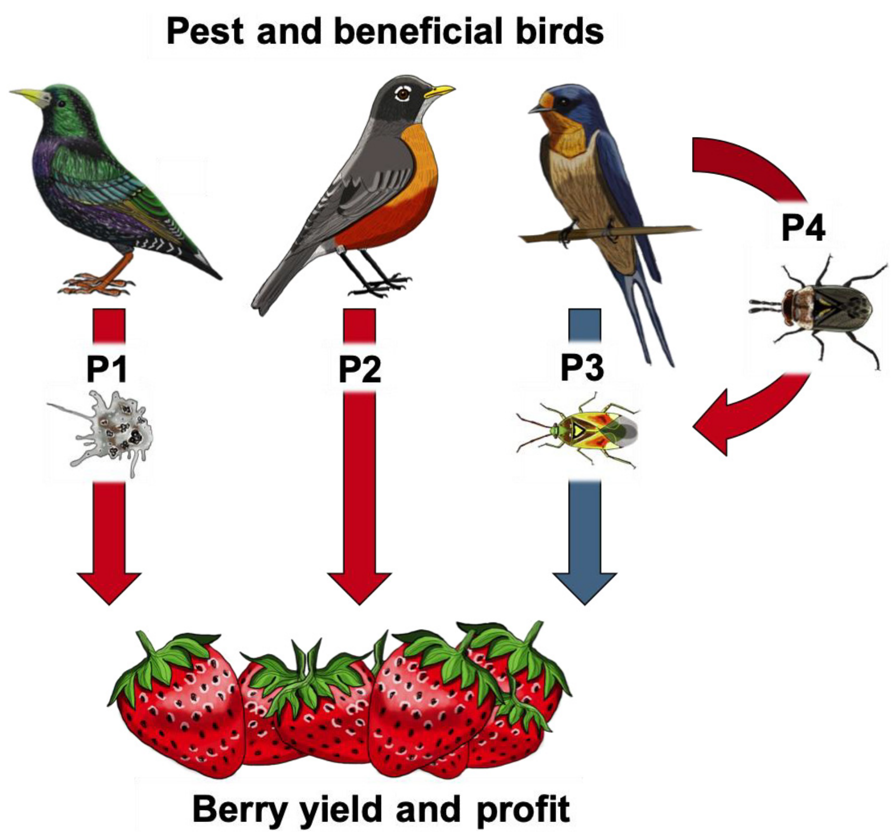


Fig. 1. Four pathways by which bird communities affect strawberry yield and profit. (P1) Pathway 1 refers to the negative impact of fecal contamination from birds like European Starlings (*Sturnus vulgaris*). (P2) Pathway 2 refers to the negative impact of strawberry damage via seed removal and frugivory by birds such as the American Robin (*Turdus migratorius*). (P3) Pathway 3 refers to the positive impact of pest control, such as suppression of lygus bugs (*Lygus hesperus*), mediated by birds such as Barn Swallows (*Hirundo rustica*). (P4) Pathway 4 refers to the negative impact of intraguild predation, such as the consumption of arthropod natural enemies like big-eyed bugs (*Geocoris* spp.). The net effect of birds on strawberry systems is the sum of these four pathways.

2018). The net effect of birds on strawberry yield and profit can be parsed into at least four pathways (Fig. 1). First, strawberries are highly susceptible to damage from insect pests (Swezey et al. 2007). Birds may increase strawberry yields by limiting insect pest infestations (e.g., *Lygus hesperus*) and preventing crop damage (Mäntylä et al. 2011, Gonthier et al. 2019). Second, however, birds may consume other beneficial organisms like pollinators or arthropod natural enemies, indirectly reducing yields (Martin et al. 2013). Third, birds may reduce strawberry yields directly via frugivory (Tracey et al. 2007). For example, annual crop damage from European Starlings (*Sturnus vulgaris*) alone has been estimated at a staggering US$800 million in the United States (Pimentel et al. 2005). Finally, because of increasing concern about birds transmitting foodborne diseases such as *Salmonella enterica* and enterohemorrhagic *Escherichia coli*, birds foraging near strawberries may contribute to yield loss through fecal contamination and mandatory removal of potentially contaminated crops (Carlson et al. 2011, 2014, California Leafy Green Products Handler Marketing Agreement (LGMA), 2019). As outbreaks of foodborne illnesses trigger sweeping reforms to farming practices (FDA 2015, California Leafy Green Products Handler Marketing Agreement (LGMA), 2019), buyers often require growers to refrain from harvesting produce within a given distance of fecal contamination and to take action to deter or eliminate birds on their farms (Stuart 2009, Lowell et al. 2010, California Leafy Green Products Handler Marketing Agreement (LGMA), 2019).

Here, we seek to elucidate how local and landscape diversification influence the net effects of birds on strawberry farms in the Central Coast region of California. We investigate how local farming practices and the amount of surrounding seminatural habitat (forest, shrub, grasslands, pasture, wetlands, and water features) in the landscape influence each of the four pathways by which bird communities affect crop yields and profits. To measure bird net effects, we manipulated bird access to strawberries in an exclosure experiment and quantified arthropod communities, berry damage, and bird fecal contamination on farms that ranged from locally homogenized (growing only strawberries) to diversified (growing multiple crops), across a gradient of simple, e.g., low proportions of surrounding seminatural habitat) to complex (e.g., high proportions of surrounding seminatural habitat) landscapes.

Based on conversations with growers, we predicted that the overall impact of birds on yields would be negative and that the primary pathway by which birds impact yields would be through direct consumption. We hypothesized that bird net effects would shift in response to position within the farm and landscape, such that bird-mediated pest control would be bolstered at field edges in complex landscapes, where insectivorous birds may be more abundant, and reduced at field centers in simple landscapes. We also predicted that local diversification, fences, and wires would increase bird abundance and activity, eliciting more crop damage and fecal contamination. Finally, we predicted that pest bird deterrent practices would reduce bird disservices.

## Methods

### *Study system*

We selected 20 focal organic strawberry farms for study in the Central Coast of California, an economically important agricultural region that produces 43% of strawberries in the United States (USDA NASS 2019). Both large, industrial monocultures and smaller, diversified farms exist in this region, as well as seminatural habitats, such as chaparral, woodlands, grasslands, and wetlands interspersed between farms (Appendix S1: Figure S1). We selected farms across a gradient of local and landscape diversification using surveys of grower practices and aerial imagery from the National Agricultural Imagery Project 2016 (*available online*).[11] We chose sites that maximized variation of local and landscape factors within a region to avoid spatial autocorrelation of farm sites.

### *Local practices and diversification*

To characterize local farm management practices, we defined a farm as contiguous land managed by a single grower or operation. We quantified a variety of local farm diversification metrics within one to six circles (50 m radius) arrayed throughout the farm. We aimed to characterize practices within the farm, and more sampling was needed to thoroughly characterize the larger farms. Within each sampling circle, we documented the percent cover of seminatural habitat (noncrop vegetation such as trees, shrubs, grasses, weeds, and floral strips; standing water), percent cover of weeds within crop fields (1, 0–5%; 2, 5–50%; 3, >50%), crop diversity (Simpson's index), the number of vegetative strata (ground cover and row crops, shrubs, trees), and the length of wildlife fencing and electrical wires (Appendix S2: Table S1). For farms with multiple sampling circles, we selected circle locations so that at least one-half of the circles included strawberries, and if farms bordered natural habitat, one-third of the circles included natural habitat and were centered at least 30 m into a crop field. We averaged values across subsampling circles on farms with more than one circle. Then, we calculated a local farm diversification index by scaling (subtracting the mean and dividing by the standard deviation) and averaging the percent cover of seminatural habitat, percent cover of weeds, vegetative strata, and crop diversity (Appendix S2: Table S1). We also documented the total number of pest bird deterrent practices that we observed on each farm, including (1) noise

[11] https://nrcs.app.box.com/v/naip/folder/18144379349

deterrents such as sound canons, whistlers, and raptor recordings; (2) visual deterrents such as sparkler streamers, scarecrows, owl and dead crow decoys, and kites resembling raptors; (3) habitat removal; (4) raptor perches; and (5) bird seed as an alternative food source (Appendix S2: Table S1).

### *Landscape diversification and crop diversity*

We manually digitized maps from National Agricultural Imagery Project imagery and classified seminatural habitat (forest, shrub, grasslands, pasture, wetlands, and water features) within a 1 km radius of all sampling points (exclosure and transect locations) using ArcMap 10.3.1 (ESRI, Redlands, California, USA). Previous research indicated that 1 km was an appropriate radius to analyze landscape effects on ecological communities (Gonthier et al. 2014). First, we calculated the proportion of seminatural habitat surrounding each sampling point within concentric buffer rings (every 50 m from 50 to 1,000 m). Then, we applied a Gaussian decay function to buffer rings to weigh seminatural habitat closer to sites more than areas further away based on the formula

$$W = \exp(-I^2/(2 \times d^2))$$

where $W$ is the weight assigned to each buffer ring, $I$ is the inner edge distance of the ring, and $d$ is the decay rate parameter (in this case, 250, 750, or 1,250; Karp et al. 2016). We calculated the proportion of seminatural habitat within 1 km without decay, and within 1 km with the three decay functions that placed greater emphasis on land cover closer to sites (Appendix S2: Table S1). We refer to simple and complex landscapes as opposite ends of the seminatural landscape gradient represented by our study sites, from simple landscapes with little seminatural habitat, to complex landscapes with more natural habitat.

To calculate crop diversity surrounding farms, we drew a polygon connecting all sampling points on a farm, and then created a 500-m buffer around the polygon. We then manually digitized maps from in-field surveys, assigning crop types within crop fields and orchards. From these maps, we calculated crop diversity using Simpson's index for each farm (Appendix S2: Table S1).

### *Exclosure experiment*

We excluded birds from strawberry plants with meshnet cages and compared berry damage and insect communities between exclosure (no birds) and control (bird accessible) plots. We constructed exclosure cages from PVC pipe frames (1.5 m long × 0.6 m wide × 0.4 m high) designed to fit over strawberry rows and envelop 8–24 (mean = 12) plants. We covered cages with monofilament gill netting (1.5 in stretched square mesh; Memphis Net & Twine, Memphis, Tennessee, USA) and secured cages to rows using metal garden staples to exclude birds and allow insects to pass through. Cages also excluded large rodents and bats, but likely allowed access to small rodents and lizards. We constructed control plots that were the same dimensions as exclosure plots by loosely wrapping caution tape around bamboo stakes to delineate the plot perimeter. We needed to use caution tape to ensure that farmworkers did not harvest berries in control plots. The risk of crops being harvested during our study may be higher than other systems; strawberries are harvested every 2–3 d during the peak season, and workers move quickly through the fields. We were careful not to stretch the caution tape too tightly, so it moved less than typical streamers used as bird deterrents, yet was not stable enough for birds to perch. We also added caution tape to the exclosure treatment plots to account for any effects that the caution tape could have on bird activity. In the field, we observed birds moving freely through control treatment plots and around caution tape. Importantly, any decline in bird activity due to caution tape would mute the effects of the exclosure experiment, making our results conservative.

We erected three paired exclosure and control plots on 15 farms for one month each during the spring (April–May, when strawberry yields were low) and summer (June–July, during peak strawberry production). Within each farm, we spaced paired plots at least 1 m apart (mean ± SE of distance between paired plots: 2.32 ± 0.42 m) and placed plots at the farm edge with the most seminatural habitat, as far from a farm edge as possible, and halfway in between. Paired plots included the same berry variety (Albion, Big Sur, Camarosa, Chandler, Maverick, Monterey, or Sweet Anne). Each week, we harvested berries from treatment plots and scored all ripe berries for damage. We defined bird damage as berries with angular wounds to strawberry flesh, berries with evidence of seed removal by seed-eating birds, or berries directly contaminated by bird feces (only 2 of ~10,000 berries).

We defined invertebrate damage as lygus bug (also known as Western tarnished plant bug, *L. hesperus*) damage (berry puckering or the characteristic "cat face" malformation; Zalom et al. 2011); leaf-rolling caterpillar (*Tortricidae* spp.) damage (tunneling with the presence of webbing; Zalom 2010); slug or snail damage (hollowed out wounds with mucous present); and other invertebrate damage (presence of small wounds and tunnels potentially attributed to early instar caterpillar damage, cucumber beetle damage, or thrips damage; Gonthier et al. 2019). *L. hesperus* feeds on developing strawberry seeds, causing the berry flesh around those seeds not to develop, in the same way that berry flesh fails to develop around seeds that have not been pollinated. Both *L. hesperus* damage and poor pollination can produce "cat face" malformations (Zalom et al. 2011); therefore, we included cat-faced berries as part of invertebrate damage, as the exact cause of berry damage could not be determined. We further categorized berries with economic damage, or damage attributed to vertebrates and invertebrates that would prevent berries from being sold (any vertebrate damage, bird fecal contamination, berries with >25% malformation due to *L. hesperus* or under-pollination, and other damage attributed to slugs, snails, or leaf-rolling caterpillars). We also calculated economic damage attributed to invertebrates only. We pooled all berry harvests within a plot for each season. We defined economic damage through conversations with growers while showing them berries that we had already scored for damage.

### *Exclosures: Invertebrate sampling*

We used a shredder vacuum (Stihl BG56; Stihl, Virginia Beach, Virginia, USA) retrofitted with a collection bag to sample invertebrates in exclosure and control plots and quantify abundances of pest and predatory invertebrates. At the beginning and end of each round of the exclosure experiment, we vacuum-sampled invertebrates from eight plants within each plot, using 1-s suction blasts (Zalom et al. 1993), and pooled samples by plot across each season. We sorted most invertebrates to order, but identified important pests and natural enemies of strawberries to family, genus, or species when possible. Natural enemies included big-eyed bugs (*Geocoris* spp.), minute pirate bugs (*Orius* spp.), damsel bugs (*Nabis* spp.), green lacewings (Neuroptera: Chrysopidae), brown lacewings (Neuroptera: Hemerobiidae), lacewing larvae (Order: Neuroptera), lady beetles (Coleoptera: Coccinellidae), hover flies (Diptera: Syrphidae), wasps (Order: Hymenoptera), and spiders (Order: Araneae). Pests included *Lygus Hesperus* and other *Lygus* spp., aphids (Hemiptera: Aphidae), spotted cucumber beetle (*Diabrotica undecimpunctata*), whiteflies (Hemiptera: Aleyrodidae), spotted-wing drosophila (*Drosophila suzukii*), and slugs and snails (Class: Gastropoda).

### *Exclosures: Net effects of birds on berry damage and invertebrate communities*

To compare the relative amount of bird vs. invertebrate damage to strawberries, we first calculated the proportion of bird and insect damage in each exclosure and control plot. Then, to assess the net effects of birds on strawberry damage, we calculated the change in the proportion of berries with damage attributed to invertebrates and vertebrates in exclosure relative to control plots. For the net effect of birds on invertebrate communities, we calculated the change in the proportion of invertebrate natural enemies or pests (from the beginning to the end of the experiment) in exclosure relative to control plots. For more information on how net effects of birds were calculated, see Appendix S3.

### *Berry damage and fecal transect surveys*

We surveyed bird damage, invertebrate damage, and bird fecal contamination along three parallel, 20-m transects in strawberry rows on each farm. We used transect surveys as a complement to our exclosure study, both to validate findings from the exclosures in ambient conditions and to expand our bird damage surveys across the farms. We also used transect surveys to quantify fecal contamination and bird flick damage (defined as small bits of scattered berries that indicates previous bird feeding). We used the flick damage measure because farmworkers frequently cull berries with bird damage. Even when bird-damaged berries are harvested, bird flick damage remains on the plastic mulch, providing a longer-term picture of where birds have been eating berries. We employed separate analyses for vertebrate berry damage and flick damage.

We located transects at the farm edge with the most seminatural habitat, as far from a farm edge as a possible, and halfway in between. Within 20 1-$m^2$ plots, we centered adjacent quadrants along each transect and recorded the number of bird fecal droppings on strawberry fruits, strawberry plants, plastic mulch, and within furrows. We also noted the presence of bird flick damage. Next, we recorded the number of strawberry fruits and scored berry damage, as in the exclosure experiment, on 20 plants per transect, sampling every five plants. We scored both white (under-ripe) and red berries; however, we focused analyses on red berries only as they were much more prone to damage and closer to being harvested.

### *Statistical analyses*

To evaluate the effects of birds on strawberry damage and insect communities, we modeled net effects from the exclosure study, the proportion of damaged berries from the exclosure experiment and transect surveys, and the presence or absence of vertebrate berry damage and bird flick damage using linear mixed models (LMMs) and generalized linear mixed models (GLMMs; Zuur et al. 2009). We included random intercept effects of farm (to account for spatial autocorrelation) and strawberry variety for exclosure experiment models, and random intercept effects of sampling week and farm for transect survey models. We first attempted to model all responses with a Gaussian distribution. We used square root (the density of fecal contamination in crop fields and on strawberry plants) and fourth root transformations (vertebrate berry damage from transect surveys) to increase normality of response variables from transect surveys. Vertebrate berry damage in the exclosure study and bird flick damage from transect surveys were infrequent; thus, we created binary responses (presence/absence of vertebrate berry damage or bird flick damage) and used binomial distributions. We included fixed effects for season (exclosure models only), local diversification, fencing and wire density, number of bird deterrent practices, distance from a noncrop edge, crop diversity (500 m), and seminatural habitat; none of these variables were collinear. We included interactions between season and local diversification (exclosure models only), season and seminatural habitat (exclosure models only), local diversification and seminatural habitat, distance from a noncrop edge and seminatural habitat, as well as crop diversity and seminatural habitat. For each response variable, we used $R^2$ values from linear models to choose the most predictive decay rate (spatial scale), and in most cases (7 out of 11 response variables), the proportion of seminatural habitat within 1 km (no decay) was the most predictive.

We used binomial models with a fixed effect of treatment to test whether berry damage types differed between exclosure treatments. We used paired $t$ test or Wilcoxon signed-rank tests to test for exclosure treatment effects on arthropod communities due to high variability in invertebrate data. To test the significance of fixed effects, we performed backward model selection, comparing nested models with likelihood ratio tests (Zuur et al. 2009). We stopped removing terms when likelihood ratio tests were <0.05 for all retained fixed effects.

### *Economic analysis*

To assess the impact of economic berry damage and fecal contamination, we received approval from the University of British Columbia's Behavioral Research Ethics Board (#H18-01018) to conduct surveys with growers and farm managers ($n$ = 20) to determine the average price for a flat of berries across the growing season, the packing method used for berry flats (e.g., pint baskets [1 dry pint = 550.60 $cm^3$], 1-pound clamshells, 2-pound clamshells [1 pound = 453.59 g]), and the use and size of no-harvest buffer zones (not harvesting produce within a given distance) around bird fecal contamination in crop fields. National and industry regulations regarding the implementation of no-harvest buffers are not standardized, so a survey was necessary to determine common regional practices and associated economic costs (Bihn et al. 2014, California Leafy Green Products Handler Marketing Agreement (LGMA), 2019). Ultimately, however, surveys revealed that growers experienced minimal loss due to no-harvest buffers around bird fecal contamination, and we chose not to include potential economic loss associated with no-harvest buffers. We did, however, include the loss of berries that were directly contaminated.

We estimated the net economic impact of birds on strawberry production ($N$, US\$/$m^2$ crop field/yr) for growers in our region by pairing the model for economic berry damage from the exclosure experiment with data from grower surveys and field measurements of the mass of berries in a strawberry flat. We used the formula

$$N = P_D \times \frac{\text{US\$}}{\text{mass berries}} \times \frac{\text{mass berries}}{\text{m}^2\,\text{crop field/yr}}$$

where $P_D$ is the change in the proportion of berries with economic damage in exclosure relative to control plots. This variable varied as a function of distance from a noncrop edge and the proportion of surrounding seminatural habitat (see *Results*). First, we calculated the average berry price (US$/mass berries) using the average price that growers reported for a flat of berries across the growing season, the packing method used for berry flats, and the average mass of berries in a flat based on the packing method (Appendix S2: Table S1). Strawberry flats vary in mass and are packed in three common ways that affect mass: 12-pint baskets; eight small (1-pound) clamshells; four large (2-pound) clamshells. We weighed two berry flats harvested from different rows at each of five farms to calculate the average mass of berries in a flat for each packing method.

Then, we calculated the average berry yield (mass/$m^2$ crop field/year) using the average mass of berries harvested from exclosure plots (exclosure treatment only) per week; the area of exclosure plots ($0.6 \times 1.5$ m = 0.9 $m^2$); the percent of crop fields dedicated to strawberry production (75% with typical 48-inch bed spacing [1 inch = 2.54 cm]: 36 inches for a strawberry bed and 12 inches for the furrow); and the length of the strawberry growing season in our study region (32 weeks from mid-March to mid-November; California Strawberry Commission 2018).

## Results

### *Exclosure treatment effects*

The proportion of berries with overall economic damage (mean ± SE; control 13.0% ± 1.4%; exclosure 9.4% ± 1.0%; $P < 0.01$), economic invertebrate damage (control 11.1% ± 1.3%; exclosure 8.9% ± 1.0%; $P = 0.03$), and economic vertebrate damage (control 1.9% ± 0.7%; exclosure 0.6% ± 0.3%; $P < 0.001$) were greater in control than exclosure plots. The proportion of berries with invertebrate damage (control 33.0% ± 1.9%; exclosure 32.0% ± 1.7%; $P = 0.33$) did not differ between treatments (Appendix S1: Figure S2; Appendix S4: Table S1). There were no significant differences between exclosure and control plots in the abundance of arthropod natural enemies (control 0.98 ± 0.57; exclosure 0.28 ± 0.56; $P = 0.28$) and pests (control −0.42 ± 0.76; exclosure 0.07 ± 0.61; $P = 0.80$), or the proportion of natural enemies (control 0.03 ± 0.03; exclosure 0.04 ± 0.03; $P = 0.68$) and pests (control 0.02 ± 0.03; exclosure −0.01 ± 0.03; $P = 0.77$).

### *Relative importance of bird service and disservice pathways*

We scored a total of 18,650 berries (10,770 from the exclosure study and 7,880 from transect surveys) and found relatively little vertebrate damage compared with invertebrate damage to berries. Direct bird damage and intraguild predation (e.g., greater economic invertebrate damage in control treatments) contributed equally to the net effects of birds on economic berry damage

(Appendix S1: Figure S2), although the relative importance of these pathways shifted in response to location within farms and surrounding landscape context. Vertebrates damaged a relatively small portion of berries (exclosure control plots 1.9% ± 0.7%; transect surveys 2.5% ± 0.83%). Birds were most likely responsible for most of this damage. We confirmed that at least 58% and 67% of vertebrate berry damage in exclosure plots and transect surveys, respectively, was caused by birds, and observed birds damaging berries much more often than other vertebrates (e.g., squirrels, rabbits). In contrast, invertebrates damaged nearly a third of berries, and approximately half of these berries were deformed due to under-pollination and/or *L. hesperus* damage (control 48.3% ± 2.8%; exclosure 44.4% ± 2.5%). Additionally, bird fecal contamination directly on

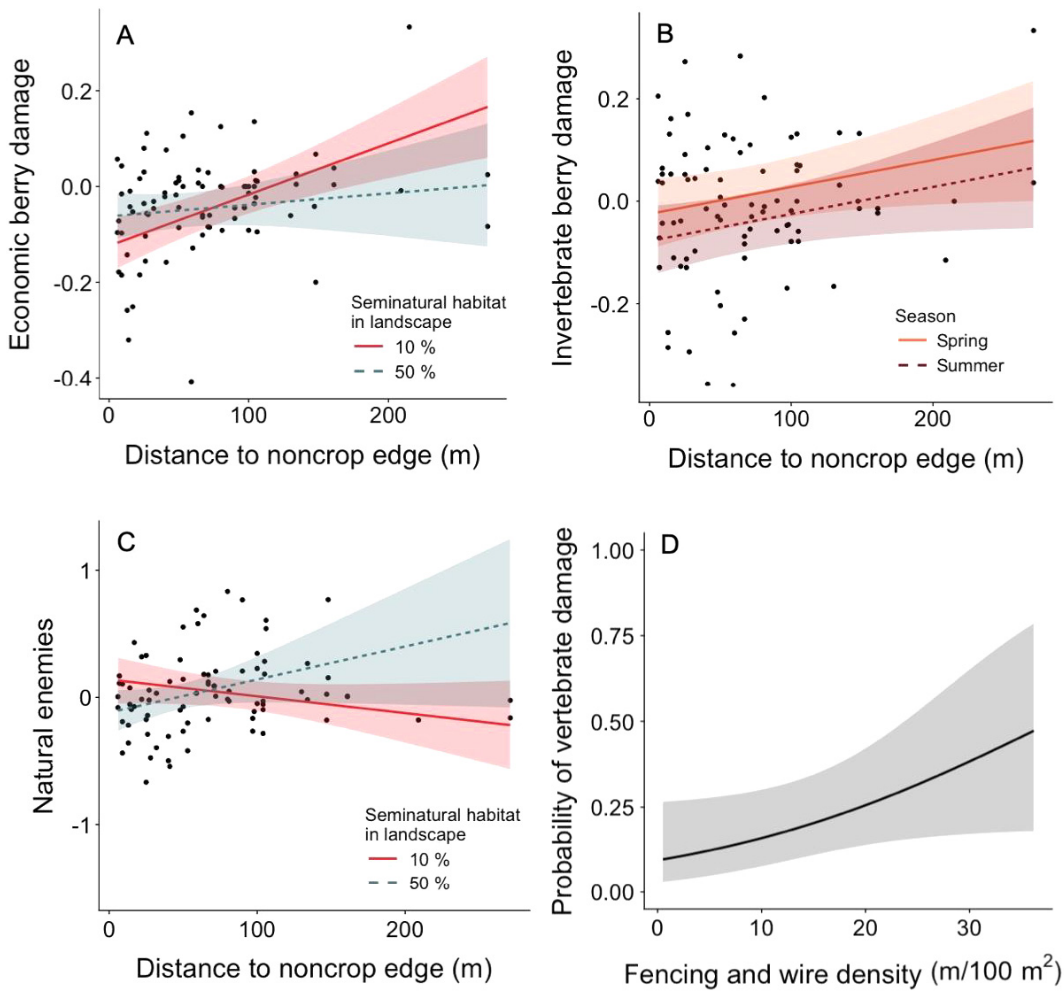


FIG. 2. Relationship between (A) net effect of birds on economic berry damage (difference between paired exclosure and control plots in the proportion of berries with severe damage that would prevent sale) and distance from a noncrop edge for farms in landscapes with different proportions of seminatural habitat; (B) net effect of birds on invertebrate berry damage (difference between paired exclosure and control plots in the proportion of berries with invertebrate damage) and distance from a noncrop edge for spring (April–May) and summer (June–July). The net effect of birds on berry damage is positive when birds provide net benefits, and negative when birds are associated with net costs. (C) Relationship between net effect of birds on the proportion of natural enemies (difference between paired exclosure and control plots in the proportion of natural enemies) and distance from a noncrop edge for farms in landscapes with different proportions of seminatural habitat. The net effect of birds on the proportion of natural enemies is positive when birds decrease the proportion of natural enemies in invertebrate communities, and negative when birds increase the proportion of natural enemies in invertebrate communities. (D) The relationship between probability of any vertebrate berry damage in control plots and fencing and wire density on farms. Points represent paired exclosure plots, lines indicate coefficient estimates from linear mixed models (LMM) and general linear mixed models (GLMM) parameters, and shaded regions represent standard errors of coefficient estimates. These graphs show that farms in more simple landscapes experience more extreme positive and negative net effects of birds compared with simple landscapes, birds are more likely to disrupt pest control services near noncrop edges and provide pest control services far from edges and birds are most likely to consume arthropod natural enemies (potentially disrupting pest control services) in more complex landscapes. Vertebrate damage (primarily caused by birds) increased on farms with a higher density of fencing and wires.

berries was extremely rare (0.01%, two berries in the exclosure experiment on one farm and no berries from transect surveys).

### *Influence of location on bird net effects*

The overall slight negative effect of birds on strawberries masked significant impacts that shifted as a function of location within a farm and landscape context. First, we found that the net effect of birds on economic berry damage was more negative near noncrop edges and more positive further from edges (Fig. 2a; Appendix S4: Table S3). The proportion of berries with vertebrate damage was negatively correlated with distance to a noncrop edge, providing partial evidence that birds also cause more direct berry damage near noncrop edges but this trend was not significant (Appendix S1: Fig. S3; Appendix S4: Table S3). However, birds were associated with significantly increased invertebrate damage to berries near noncrop edges, especially during the summer compared with spring. Within field centers, birds decreased invertebrate berry damage and provided pest control (Fig. 2b; Appendix S4: Table S3).

These analyses suggest that landscape may interact with these on-farm factors. The influence of distance from a noncrop edge was dampened in complex landscapes with more seminatural habitat (Fig. 3a, c; Appendix S4: Table S3), and amplified in simple landscapes, where birds were associated with more extreme net economic costs near edges and benefits farther away from edges (Fig. 3b, d). As an example to illustrate this idea, switching the landscape context of the two farms depicted in Fig. 3 (one surrounded by natural habitat and the other by crop fields) illustrates the protective effective of seminatural habitat in reducing the cost of bird disservices to strawberries. If the farm in the complex landscape were in the simple landscape (Fig. 3a, d), the reduction in seminatural habitat would increase the cost of birds by 76%. If the farm in the simple landscape were in a complex landscape (Fig. 3b, c), the increase in seminatural habitat would decrease the cost of birds by 23% (Appendix S4: Table S4).

In simple landscapes, excluding birds caused an increase in the proportion of natural enemies near crop edges (indicative of higher intraguild predation in control plots) and a decrease in the proportion of natural enemies far from crop edges (indicative of higher pest consumption in control plots). These trends reversed in complex landscapes (Fig. 2c; Appendix S4: Table S3). No predictors explained differences in the proportion of arthropod pests between exclosure treatments (Appendix S4: Table S3).

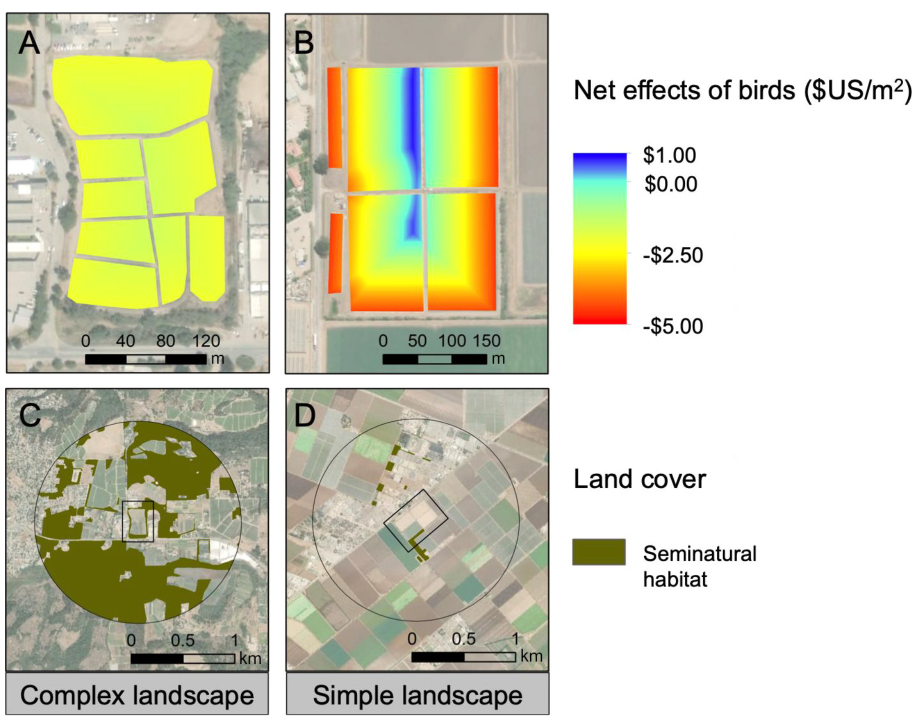


FIG. 3. Maps showing the net economic effects of birds on strawberry production across two farms in simple and complex landscapes that differ in the amount of surrounding seminatural habitat (within 1 km radius). Net economic effects are expressed as $US/m$^2$ of strawberry crop field across the strawberry growing season for (A) a farm with 49% seminatural habitat in the surrounding landscape and (B) a farm with 1% seminatural habitat in the surrounding landscape. Panels C and D show differences in the amount of surrounding seminatural habitat for farms in panels A and B, respectively, and black boxes outline farm locations. Farm maps demonstrate how the amount of seminatural habitat surrounding farms dampens the more extreme net economic effects of birds.

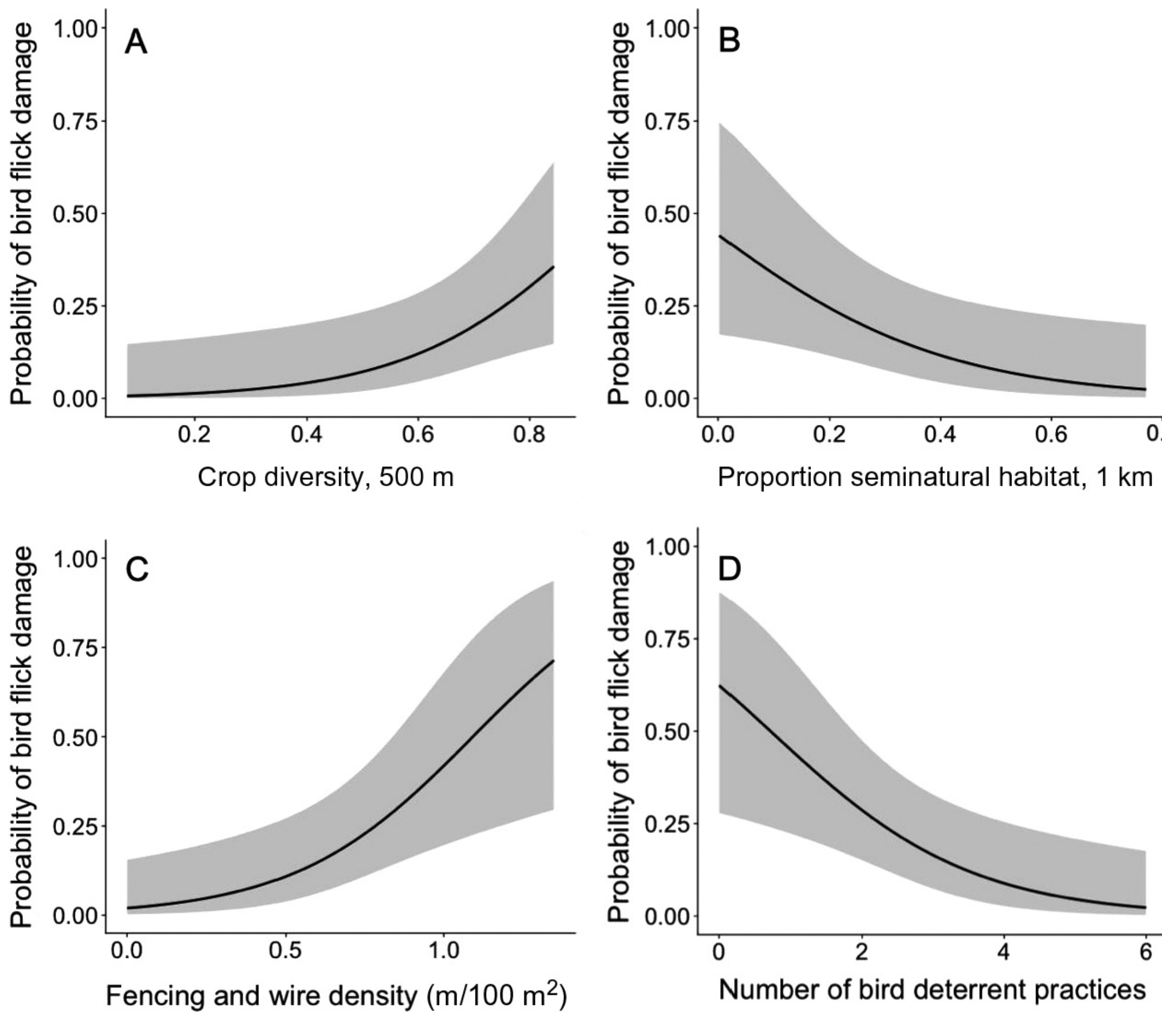


Fig. 4. Relationship between the probability of bird flick damage and (A) fencing and wire density on farms, (B) crop diversity (500 m radius) surrounding farms, (C) the total number of bird deterrent practices used on the farm, and (D) the proportion of seminatural habitat in the landscape. Lines indicate coefficient estimates from GLMM parameters, and shaded regions represent standard errors of coefficient estimates. Bird flick damage increased on farms that were surrounded by more crop diversity and had a higher density of fencing and wires, and decreased on farms that were surrounded by more seminatural habitat and used more bird deterrent practices.

The probability of bird flick damage also increased on farms that were surrounded by more crop diversity (500 m radius; Fig. 4a) and decreased on farms that were surrounded by a higher proportion of seminatural habitat (Fig. 4b).

### *Influence of local management practices and diversification on bird net effects*

Our findings from both the exclosure experiment and transect surveys indicate that fencing and wires on farms increased both direct bird berry damage and fecal contamination. We found vertebrate damage to berries (primarily caused by birds) and bird flick damage at half of our farm sites. Farms with more fencing and wires were more likely to experience these types of damage (Figs. 2d, 4c; Appendix S4: Table S3), as well as higher rates of fecal contamination (Fig. 5a, b). We found no evidence that local diversification influenced the net effects of birds on strawberries; however, farms that used more bird deterrent practices were less likely to experience bird flick damage (Fig. 4d).

## Discussion

Ecologists increasingly recognize the many benefits that nature provides to society. To realize the full potential of working landscapes to support biodiversity conservation and provide sustainable resources for humanity, we must consider both the benefits and costs associated with biodiversity (Zhang et al. 2007, Kremen and Merenlender 2018). Our research highlights the

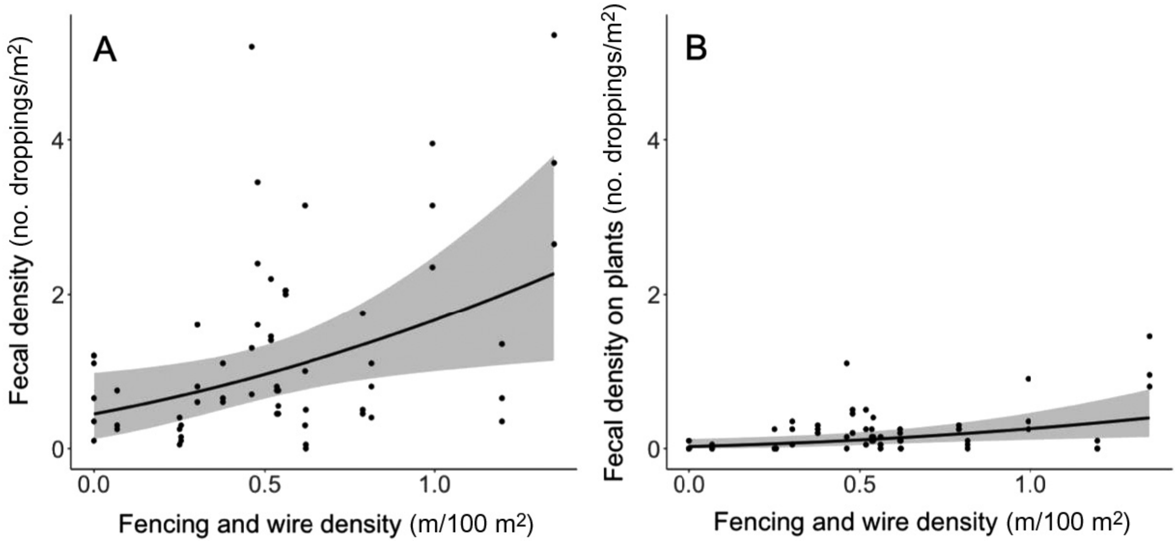


Fig. 5. Relationship between fecal density and fencing and wire density on farms for (A) fecal contamination in crop fields and (B) fecal contamination on strawberry plants. Points represent a single transect survey, lines indicate coefficient estimates from LMM parameters, and shaded regions represent standard errors of coefficient estimates. Fecal density, both in crop fields and on strawberry plants only, increased on farms with a higher density of fencing and wires.

potential for mismatch between management actions and goals when the net effects associated with biodiversity are not fully recognized, which can result in negative outcomes for wildlife conservation and agricultural production.

### *Net effects of birds*

Our research demonstrates that birds have a slightly negative effect on strawberry production, but this overall trend masks complex shifts in bird services and disservices across farming contexts. Although prior research often documents the highly visible damage that pest birds can inflict on crops (Peisley et al. 2015), our research shows that direct bird damage is responsible for relatively little berry damage compared with invertebrate damage. We found vertebrates (primarily birds) damaged only 1.9% of berries in the control exclosure plots and 2.5% of berries in transect surveys. These rates of bird damage to berries are similar to those documented in the literature in California strawberry systems (2–3%; Gebhardt et al. 2011, Gonthier et al. 2019), but pale in comparison with the damage inflicted by invertebrates (~32–33% of berries). However, while berries damaged by birds have no market value, berries with minor invertebrate damage can be sold. In contrast, a previous, smaller study in the same region found that direct and indirect interactions cancelled each other out, such that low levels of damage caused by birds were essentially balanced by bird control of invertebrate strawberry pests (Gonthier et al. 2019). It is possible that both studies provide an accurate assessment of bird services and disservices in years with different relative bird and invertebrate damage levels.

Although direct crop damage is always more apparent to growers than indirect trophic interactions (e.g., pest control and intraguild predation), our study demonstrates that less apparent indirect effects are at least equally important as direct effects. Indeed, both direct and indirect interactions contributed roughly equally to the slightly negative overall effect of birds on economic berry damage. This net negative effect was likely tempered by bird-mediated pest control, making indirect trophic interactions an even more critical aspects of birds' impacts in agroecosystems. The relative importance of direct vs. indirect effects also appeared to depend on farming context. For example, apart from field edges in simple landscapes, effects of pest control and intraguild predation outweighed direct strawberry consumption in dictating effects on crop yields.

### *Influence of location within a farm and landscape context*

We showed that the net effects of birds strongly depend on interactions between position within a farm field and the amount of seminatural habitat in the surrounding landscape. Specifically, the net effects of birds changed as a function of the distance from a noncrop edge, with more extreme costs and benefits on farms with less seminatural habitat in the landscape (Fig. 4). At field edges, birds harmed berries via both direct damage and intraguild predation, especially in more simple landscapes and during peak summer strawberry production. Away from edges, birds inflicted less berry damage, and were also more likely to provide (or not interfere with) pest control, especially in more simple landscapes. This may be because (1) birds that forage aerially over crop fields (e.g., swallows) specialize on arthropod pests;

(2) arthropod natural enemies may be more prevalent at field edges compared with field interiors (Macfadyen and Muller 2013); and (3) more simple landscapes may have a higher relative abundance of insectivorous birds that prefer to forage aerially compared with birds that prefer to perch and hunt.

In more complex landscapes, birds also acted as intraguild predators away from edges, whereas in more simple landscapes, birds had less of an effect on natural enemies, and only acted as intraguild predators near edges. These trends may occur because (1) natural enemies are more abundant on farms in complex landscapes (Chaplin-Kramer et al. 2011); (2) densities of some natural enemies are higher near noncrop edges than field interiors (Duelli and Obrist 2003, Tscharntke et al. 2005); and (3) birds may prefer to consume larger natural enemies, such as spiders and lady beetles, over smaller pests, such as aphids and spotted-wing *Drosophila*, because larger prey items are more energetically profitable (Krebs et al. 1977). At field edges, insectivorous birds that prefer to perch and hunt (i.e., snatching prey from the ground, gleaning prey from plants, hawking prey from the air) may have an advantage in spotting larger prey items compared with birds that prefer to forage aerially over crop fields, resulting in greater intraguild predation at edges. In simple landscapes with limited seminatural habitat, the few trees and hedgerows that border fields may concentrate perching bird foraging activity, which may explain why intraguild predation is more common near edges in simpler landscapes. In more complex landscapes, birds may be selectively feeding on arthropod natural enemies throughout farm fields, or communities may be composed of different species that prefer natural enemy prey. Intraguild predation may also have a stronger cascading effect during the summer, when strawberry production peaks and arthropods are more abundant, compared with the spring.

Regarding direct bird damage to berries (probability of bird flick damage), we found birds caused less damage on farms surrounded by more seminatural habitat, but more damage in landscapes with higher crop diversity (within a 500 m radius surrounding farms). While it is possible that birds relocated berries to eat them, resulting in flick damage in different areas of the field, we never observed this behavior. Additionally, crop diversity (500 m) was calculated at the farm level, and there was minimal variation in seminatural habitat (1 km) between transects on the same farm. If birds did relocate berries, these landscape-level predictors would still be significant.

Greater crop diversity surrounding farms could result in more direct berry damage if strawberry-eating birds prefer strawberries to the other crop types available nearby and thus concentrate in strawberry fields. In more simple landscapes, strawberry-eating birds may spend more time foraging on farms, compared with seminatural habitat, or these landscapes may support a higher proportion of strawberry-eating birds, both resulting in more direct bird berry damage. Castañeda (2018) found, for example, that Barn Owls (*Tyto alba*) spent more time foraging in agricultural habitats when there was less seminatural habitat in the surrounding landscape, and the same may be true of strawberry-eating birds. Our models predicted that removing seminatural habitat around farms would increase the cost of bird disservices by 76%, suggesting that maintaining noncrop habitat can provide significant benefits to growers.

### *Influence of local farm practices and characteristics*

While we found no evidence that local diversification practices affected the net effects of birds, farms with more fencing and wires, where birds are often perch, had more direct berry damage (higher probability of berries with vertebrate damage and bird flick damage) and fecal contamination. By increasing the availability of perches, fencing and wires may encourage birds that are central-place foragers to increase foraging pressure on nearby strawberries, and defecate more often nearby. We also found that bird berry damage (probability of bird flick damage) was less likely on farms that implemented a suite of bird deterrent practices, suggesting that when used in tandem, these practices can disrupt foraging by strawberry-eating birds. These findings are encouraging given that an earlier study found bird management practices to be ineffective (Gonthier et al. 2019) and that growers often express skepticism about the efficacy of auditory and visual scare devices, as well as other bird management practices (Anderson et al. 2013). Growers were often ambiguous when asked how frequently different bird deterrent practices were used, and we lacked resolution in our data to test each bird deterrent practice individually. Very few studies address the efficacy of specific bird management practices (Rivadeneira et al. 2018), and investigating how specific practices influence the net effects of birds would require a more focused study. Still, direct bird damage was not a major problem on most farms; thus, growers should consider the costs of implementation compared with direct bird damage when deciding whether or not to utilize bird deterrent practices.

### *Fecal contamination and food safety*

Growers in the study area have been pressured to remove habitat near crop fields in response to food safety concerns that equate birds and other wildlife with increased food safety risks (Stuart 2009, Karp et al. 2015a). Habitat removal is often recommended to decrease bird fecal contamination and bird berry damage, yet our results suggest that more seminatural habitat in the landscape can actually buffer against these bird disservices. While artificial structures (fencing and wires) increased fecal contamination by birds, we found no evidence that seminatural habitat, in the surrounding landscape or at field edges, increased food safety risks.

Moreover, recent analyses suggest that birds in our study area rarely carry foodborne diseases (Navarro-Gonzalez et al. 2019).

Although growers reported that birds perched in trees at field edges would defecate in crop fields, we found no evidence that trees and hedgerows at field edges increased fecal contamination in crops, perhaps because trees and hedgerows were not overhanging crop fields at our study sites. Similarly, Sellers et al. (2018) found that hedgerows did not increase the risk of fecal contamination in crop fields by rodents in California walnut and tomato systems. These results align with recent studies in the region that failed to find increased pathogen prevalence on farms with more surrounding seminatural habitat and reported preliminary trends of pathogen increases on farms that removed habitat (Karp et al. 2015b). Our results demonstrates that maintaining seminatural habitat around farms may thus constitute a win-win by enhancing bird diversity and mitigating bird damage without increasing food safety risk.

Our findings have important implications for food safety management. First, fecal contamination to berries was rare (0.01%) in our study. Growers are deeply invested in providing safe and healthy food to consumers, and all growers expressed that berries with fecal contamination would be culled. Because strawberries are harvested and inspected by hand, farmworkers are able to identify and cull contaminated berries. If birds are perching on fences and wires and defecating while they are perching, then crop fields adjacent to fences or beneath wires are most likely to be affected. It is also important to note that many growers reported installing fences to prevent wildlife intrusion into farm fields in response to food safety concerns. While fencing may help to prevent fecal contamination from wildlife such as deer and pigs, we found that fencing was associated with increased bird fecal contamination. Areas near fencing and wires could be more closely monitored for fecal contamination, or growers could choose not to plant crops in these areas that are packaged without washing and likely to be consumed fresh. While careful management can reduce the risk of fecal contamination, some growers incur additional economic costs associated with implementing no-harvest buffer zones around fecal contamination in crop fields. Popular guidelines in the Central Coast recommend a minimum 1.5-m buffer distance around fecal contamination unless the risk can be adequately controlled (LGMA, 2019), but some growers are required by buyers to implement larger buffers. However, these guidelines are subjective and do not distinguish between different types and size of fecal matter, or crops with aerial vs. drip irrigation, which likely affect pathogen transfer (LGMA, 2019, Weller et al. 2019). Growers in our study region reported variable required buffer distances (0.6–6.1 m), and the potential economic costs of implementing large buffers would be steep.

## Conclusion

We found that the net effects of birds on strawberry production shift in complex but predictable ways that were driven by trophic interactions and farming context. Although the net effects of birds were slightly negative overall, our research demonstrates that seminatural habitat can help to mitigate bird disservices. When considered in concert with how growers manage risks related to fecal contamination, our findings can provide general management recommendations that optimize bird services and minimize bird disservices, and may be applicable across other cropping systems and regional contexts.

## Acknowledgments

D. Gonthier and D. Karp conceived the ideas and methodology; E. Olimpi, K. Garcia, and A. Echeverri collected the data; K. Garcia created original artwork for Figure 1; and E. Olimpi analyzed the data and wrote the manuscript. All authors edited the manuscript and gave approval for publication. We thank all of the growers who participated in our research by providing access to their farms and taking our survey. We thank V. Glynn, E. Barbieux, and C. Zamora for field and GIS mapping assistance, and K. O'Hearn for assistance with insect identification. This research was funded by a grant from USDA NIFA (#2017-67019-26293) to D. Karp, K. De Master, W. Snyder, E. Wilson-Rankin, and D. Gonthier, and USDA Hatch (KY008079) to D. Gonthier.

## Literature Cited

Anderson, A., et al. 2013. Bird damage to select fruit crops: the cost of damage and the benefits of control in five states. Crop Protection 52:103–109.

Bender, S. F., C. Wagg, and M. G. A. Van Der Heijden. 2016. An underground revolution: biodiversity and soil ecological engineering for agricultural sustainability. Trends in Ecology & Evolution 31:440–452.

Bihn, E. A., M. A. Schermann, A. L. Wszelaki, G. L. Wall, and S. K. Amundson. 2014. On-farm decision tree project: Wildlife and animal management (Version 3). National Good Agricultural Practices Program, Cornell University, Ithaca, NY, USA. https://gaps.cornell.edu/sites/gaps.cornell.edu/files/shared/documents/wildlife/Animal Management-COMPLETE-FINAL.pdf. Accessed 17 July, 2019.

Blaauw, B. R., and R. Isaacs. 2014. Flower plantings increase wild bee abundance and the pollination services provided to a pollination-dependent crop. Journal of Applied Ecology 51:890–898.

California Department of Food and Agriculture 2018. California agricultural statistics review 2017–2018. California Department of Food and Agriculture, Sacramento, California, USA.

California Leafy Green Products Handler Marketing Agreement (LGMA). 2019. Commodity specific food safety guidelines for the production and harvest of lettuce and leafy greens (Version 16). Retrieved from the California Leafy Green Products Handler Marketing Agreement website: https://lgma-assets.sfo2.digitaloceanspaces.com/downloads/190419-CA-LGMA-Metrics_Accessible_0605.pdf

California Strawberry Commission. 2018. The pink sheet, Week Ending December 15, 2018. https://www.calstrawberry.com/Portals/2/Reports/Industry Reports/Volume Pink Sheet/2018/

Pink Sheet 12.15.18.pdf?ver=2018-12-21-090502-900. Accessed 17 July, 2019.

Callaway, T. R., T. S. Edrington, and D. J. Nisbet. 2014. Isolation of Escherichia coli *O157:H7 and* Salmonella *from migratory brown-headed cowbirds (*Molothrus ater*), common grackles (*Quiscalus quiscula*), and cattle egrets (*Bubulcus ibis*). Foodborne Pathogens and Disease 11:791–794.*

Carlson, J. C., A. B. Franklin, D. R. Hyatt, S. E. Pettit, and G. M. Linz. 2011. The role of starlings in the spread of Salmonella *within concentrated animal feeding operations. Journal of Animal Ecology 48:479–486.*

Castañeda, X. A. 2018. Hunting habitat use and selection patterns of barn owl (Tyto alba*) the urban-agricultural setting of a prominent wine grape growing region of California. Humboldt State University, Arcata, California, USA.*

Chaplin-Kramer, R., M. E. O'Rourke, E. J. Blitzer, and C. Kremen. 2011. A meta-analysis of crop pest and natural enemy response to landscape complexity. Ecology Letters 14:922–932.

Classen, A., M. K. Peters, S. W. Ferger, M. Helbig-Bonitz, J. M. Schmack, G. Maassen, M. Schleuning, E. K. V. Kalko, K. Böhning-Gaese, and I. Steffan-Dewenter. 2014. Complementary ecosystem services provided by pest predators and pollinators increase quantity and quality of coffee yields. Proceedings of the Royal Society B 281:20133148.

Dolbeer, R. A., N. R. Holler, D. W. Hawthorne, R. A. Dolbeer, and N. R. Holler. 1994. Identification and assessment of wildlife damage: an overview. In S. Hygnstrom, R. Timmand G. Larson, editors. The handbook: prevention and control of wildlife damage (pp. A1-A18). Internet Center for Wildlife Damage Management, University of Lincoln - Nebraska, NE, USA.

Duelli, P., and M. K. Obrist. 2003. Regional biodiversity in an agricultural landscape: the contribution of seminatural habitat islands. Basic and Applied Ecology 138:129–138.

Food and Drug Administration (FDA). 2015. Standards for the growing, harvesting, packing, and holding of produce for human consumption, 80 FR 74353. https://www.federalregister.gov/documents/2015/11/27/2015-28159/standards-for-the-growing-harvesting-packing-and-holding-of-produce-for-human-consumption. Accessed 6 April, 2020.

Gebhardt, K., A. M. Anderson, K. N. Kirkpatrick, and S. A. Shwiff. 2011. A review and synthesis of bird and rodent damage estimates to select California crops. Crop Protection 30:1109–1116.

Gonthier, D. J., K. K. Ennis, S. Farinas, H.-Y. Hsieh, A. L. Iverson, P. Batáry, J. Rudolphi, T. Tscharntke, B. J. Cardinale, and I. Perfecto. 2014. Biodiversity conservation in agriculture requires a multi-scale approach. Proceedings of the Royal Society B 281:20141358–20141358.

Gonthier, D., A. Sciligo, D. Karp, A. Lu, K. Garcia, G. Juarez, T. Chiba, and C. Kremen. 2019. Bird services and disservices to strawberry farming in Californian agricultural landscapes. Journal of Applied Ecology 56:1948–1959.

Heath, S. K., and R. F. Long. 2019. Multiscale habitat mediates pest reduction by birds in an intensive agricultural region. Ecosphere 10:e02884.

Hooks, C. R. R., R. R. Pandey, and M. W. Johnson. 2003. Impact of avian and arthropod predation on lepidopteran caterpillar densities and plant productivity in an ephemeral agroecosystem. Ecological Entomology 28:522–532.

Jay-Russell, M. T. 2013. What is the risk from wild animals in food-borne pathogen contamination of plants? CAB Review 8:1–16.

Jedlicka, J. A., R. Greenberg, and D. K. Letourneau. 2011. Avian conservation practices strengthen ecosystem services in California vineyards. PLoS ONE 6:e27347.

Karp, D. S., et al. 2013. Forest bolsters bird abundance, pest control and coffee yield. Ecology letters 16:1339–47.

Karp, D., P. Baur, E. Atwill, K. De Master, S. Gennet, A. Iles, J. Nelson, A. Sciligo, and C. Kremen. 2015*a*. The unintended ecological and social impacts of food safety regulations in California's Central Coast Region. BioScience 65:1173–1183.

Karp, D., S. Gennet, C. Kilonzo, M. Partyka, N. Chaumont, E. Atwill, and C. Kremen. 2015*b*. Comanaging fresh produce for nature conservation and food safety. Proceedings of the National Academy of Sciences USA 112:11126–11131.

Karp, D. S., R. Moses, S. Gennet, M. S. Jones, S. Joseph, L. K. M'Gonigle, L. C. Ponisio, W. E. Snyder, and C. Kremen. 2016. Agricultural practices for food safety threaten pest control services for fresh produce. Journal of Applied Ecology 53:1402–1412.

Klein, A., C. Brittain, S. D. Hendrix, R. Thorp, N. Williams, and C. Kremen. 2012. Wild pollination services to California almond rely on semi-natural habitat. Journal of Applied Ecology 49:723–732.

Krebs, B. Y. J. R., J. T. Erichsen, and M. I. Webber. 1977. Optimal prey slection in the great tit (Parsus major*). Animal Behavior 25:30–38.*

Kremen, C., and A. M. Merenlender. 2018. Landscapes that work for biodiversity and people. Science. 362:eaau6020.

Kremen, C., and A. Miles. 2012. Ecosystem services in biologically diversified versus conventional farming systems: benefits, externalities, and trade-offs. Ecology and Society 17:40.

Kremen, C., A. Iles, and C. Bacon. 2012. Diversified farming systems: an agroecological, systems-based alternative to modern industrial agriculture. Ecology and Society 17: 44. http://doi.org/10.5751/ES-05103-170444

Kross, S. M., T. R. Kelsey, C. J. McColl, and J. M. Townsend. 2016. Field-scale habitat complexity enhances avian conservation and avian-mediated pest-control services in an intensive agricultural crop. Agriculture, Ecosystems and Environment 225:140–149.

Lejeune, J., J. Homan, G. Linz, and D. L. Pearl. 2007. Role of the European Starling in the transmission of E. coli O157 on dairy farms. Pages 31–34 *In Proceedings of the 23rd Vertebrate Pest Conference.* University of California, Davis.

Lowell, K., J. J. Langholz, and D. Stuart. 2010. Safe and sustainable: co-managing for food safety and ecological health in California's Central Coast Region. The Nature Conservancy of California and the Georgetown University Produce Safety Project, San Francisco, CA and Washington, D.C., USA.

Maas, B., Y. Clough, and T. Tscharntke. 2013. Bats and birds increase crop yield in tropical agroforestry landscapes. Ecology Letters 16:1480–1487.

Macfadyen, S., and W. Muller. 2013. Edges in agricultural landscapes: Species interactions and movement of natural enemies. PLoS ONE 8:e59659.

Mäntylä, E., T. Klemola, and T. Laaksonen. 2011. Birds help plants: a meta-analysis of top-down trophic cascades caused by avian predators. Oecologia 165:143–151.

Martin, E. A., B. Reineking, B. Seo, and I. Steffan-dewenter. 2013. Natural enemy interactions constrain pest control in complex agricultural landscapes. Proceedings of the National Academy of Sciences USA 110:5534–5539.

Martin, E. A., B. Reineking, B. Seo, and I. Steffan-Dewenter. 2015. Pest control of aphids depends on landscape complexity and natural enemy interactions. PeerJ 3:e1095.

Mols, C. M. M., and M. E. Visser. 2002. Great tits can reduce caterpillar damage in apple orchards. Journal of Applied Ecology 39:888–899.

Navarro-Gonzalez, N., S. Wright, P. Aminabadi, A. Gwinn, T. Suslow, and M. Jay-Russell. 2019. Carriage and subtypes of foodborne pathogens identified in wild birds residing near agricultural lands in California: a repeated cross-sectional study. Applied and Environmental Microbiology 86:e01678-19.

Peisley, R. K., M. E. Saunders, and G. W. Luck. 2015. A systematic review of the benefits and costs of bird and insect activity in agroecosystems. Springer Science Reviews 3:113–125.

Peisley, R. K., M. E. Saunders, and G. W. Luck. 2016. Cost-benefit trade-offs of bird activity in apple orchards. PeerJ 4:1–20.

Pejchar, L., Y. Clough, J. Ekroos, K. A. Nicholas, O. L. A. Olsson, D. Ram, M. Tschumi, and H. G. Smith. 2018. Net effects of birds in agroecosystems. BioScience 68:1–9.

Pimentel, D., R. Zuniga, and D. Morrison. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. Ecological Economics 52:273–288.

Rivadeneira, P., S. Kross, N. Navarro-Gonzalez, and M. Jay-Russell. 2018. A review of bird deterrents used in agricutlure. Pages 218–223 In UC Agriculture & Natural Resources Proceedings of the Vertebrate Pest Conference. University of California, Davis.

Schulte, L. A., et al. 2017. Prairie strips improve biodiversity and the delivery of multiple ecosystem services from corn – soybean croplands. Proceedings of the National Academy of Sciences USA 114:11247–11252.

Sekercioglu, C., D. Wenny, and C. Whelan, editors. 2016. Why birds matter. University of Chicago Press, Chicago, Illinois, USA.

Sellers, L. A., R. F. Long, M. T. Jay-Russell, X. Li, E. R. Atwill, R. M. Engeman, and R. A. Baldwin. 2018. Impact of field-edge habitat on mammalian wildlife abundance, distribution, and vectored foodborne pathogens in adjacent crops. Crop Protection 108:1–11.

Seward, N. W., K. C. Vercauteren, G. W. Witmer, and R. M. Engeman. 2004. Feral swine impacts on agriculture and the environment. Sheep & Goat Research Journal 19:34–40.

Steele, D., R. Greenland, and B. Gregor. 1996. Subsurface drip irrigation systems for specialty crop production in North Dakota. Applied Engineering in Agriculture 12:671–679.

Stuart, D. 2009. Constrained choice and ethical dilemmas in land management: environmental quality and food safety in California agriculture. Journal of Agricultural and Environmental Ethics 22:53–71.

Swezey, S. L., D. J. Nieto, and J. A. Bryer. 2007. Control of western tarnished plant bug Lygus hesperus *Knight (Hemiptera: Miridae) in California organic strawberries using alfalfa trap crops and tractor-mounted vacuums. Environmental Entomology 36:1457–1465.*

Tracey, J., M. Bomford, Q. Hart, G. Saunders, and R. Sinclair 2007. Managing bird damage to fruit and other horticultural crops. Australian Governemnt, Bureau of Rural Sciences, Department of Agriculture, Fisheries, and Forestry, Canberra, Australian Capital Territory, Australia.

Tscharntke, T., T. A. Rand, F. J. J. A. Bianchi, S. Annales, Z. Fennici, S. Ecology, O. F. Herbivorous, T. Tschamtke, and T. A. Rand. 2005. The landscape context of trophic interactions: insect spillover across the crop-noncrop interface. Annales Zoologici Fennici 42:421–432.

USDA National Agricultural Statistics Service. 2019. Quick Stats Database. http://quickstats.nass.usda.gov

Weller, D. L., J. Kovac, D. J. Kent, S. Roof, J. I. Tokman, E. Mudrak, and M. Wiedmann. 2019. A conceptual framework for developing recommendations for no-harvest buffers around in-field feces. Journal of Food Protection 82:1052–1060.

Whelan, C. J., C. H. Sekercioğlu, and D. G. Wenny. 2015. Why birds matter: from economic ornithology to ecosystem services. Journal of Ornithology 156:S227–S238.

Woodroffe, R., S. Thirgood, and A. Rabinowitz, editors. 2005. People and wildlife: Conflict or coexistence? Cambridge University Press, Cambridge, UK.

Zalom, F. 2010. Identifying leafrollers including the light brown apple moth. California Strawberry Commission, Watsonville, CA, USA. https://www.calstrawberry.com/Portals/2/Reports/Research%20Reports/Production%20Guidelines/English/Identifying%20Leafrollers%20Including%20the%20Light%20Brown%20Apple%20Moth%20-%202010.pdf?ver=2018-01-12-155447-000 Accessed 17 July 2019:

Zalom, F. G., C. Pickel, D. B. Walsh, and N. C. Welch. 1993. Sampling for Lygus hesperus *(Hemiptera: Miridae) in strawberries. Journal of Economic Entomology* 86:1191–1195.

Zalom, F., J. Bi, and P. Thompson. 2011. Managing lygus bugs in strawberries. California Strawberry Commission, Watsonville, CA, USA. https://www.calstrawberry.com/Portals/2/Reports/Research%20Reports/Production%20Guidelines/English/Managing%20Lygus%20Bugs%20in%20Strawberries%20-%202011.pdf?ver=2018-01-12-155446-573. Accessed 17 July, 2019.

Zhang, W., T. H. Ricketts, C. Kremen, K. M. Carney, and S. M. Swinton. 2007. Ecosystem services and dis-services to agriculture. Ecological Economics 64:253–260.

Zuur, A. F., E. N. Ieno, N. Walker, A. A. Saveliev, and G. M. Smith. 2009. Mixed effects models and extensions in ecology with R. Springer, New York, NY.

## Supporting Information

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.2115/full

## Data Availability

Data are available from the Dryad Digital Repository: https://doi.org/10.25338/B8TK62