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Received: 5 April 2021 | Accepted: 15 December 2021

DOI: 10.1111/1365-2664.14124

Journal of Applied Ecology BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Semi-natural habitat surrounding farms promotes multifunctionality in avian ecosystem services

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Funding information
Department of Wildlife, Fish, and Conservation Biology at UC Davis; National Institute of Food and Agriculture, Grant/Award Number: 2017-67019-26293; U.S. Department of Agriculture Hatch, Grant/Award Number: CA-R-ENT-5091-H and KY008079; University of California, Davis; USDA

Handling Editor: Péter Batáry

Abstract

1. Farmland birds can suppress insect pests, but may also consume beneficial insects, damage crops and potentially carry foodborne pathogens. As bird communities shift in response to farming practices, so too do the benefits (services) and costs (disservices) from birds. Understanding how and why ecosystem services and disservices covary can inform management interventions that enhance synergies, avoid trade-offs and promote multifunctionality.
2. We investigated how farmland diversification practices influence the services and disservices provided by wild birds on 21 California strawberry farms. Specifically, we coupled 285 bird surveys, metabarcoding and other molecular analyses of ~1,000 faecal samples representing 55 bird species (mostly passerines) to determine which individuals consumed pests, natural enemies, and crops and carried foodborne pathogens. Then, we explored how farming practices shape ecosystem service bundles, or suites of consistently co-occurring services/disservices.
3. Avian services and disservices were shaped by interactions between local farming practices and landscape context. We found that the amount of semi-natural habitat surrounding each farm was the single most important driver of ecosystem services, with the best outcomes (highest multifunctionality) occurring on farms surrounded by semi-natural habitat.
4. Bundles were primarily influenced by landscape context. Increasing semi-natural habitat around farms was associated with more multifunctional bird communities that maximized services and minimized disservices. However, not all trade-offs were minimized in landscapes with more semi-natural habitat, suggesting that specific farming contexts can exacerbate or mitigate trade-offs as bird communities shift in response to diversification practices.
5. *Synthesis and applications*. Though growers are often pressured to remove non-crop habitat to reduce food-safety risks, our work suggests that conserving habitat can support bird conservation, mitigate food-safety risks and decrease

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crop damage from birds. More broadly, by considering the multiple roles that communities play in ecosystems, managers can simultaneously maximize services and minimize disservices to achieve multifunctionality.

KEYWORDS
agroecology, diversified farming system, ecosystem services, food safety, human–wildlife conflict, metabarcoding, multifunctionality, pest suppression

1 | INTRODUCTION

Working landscapes can simultaneously deliver multiple benefits to society, but management actions intended to promote benefits may inadvertently increase costs. For example, diversifying agricultural landscapes through planting multiple crops and retaining non-crop vegetation can increase biodiversity and ecosystem services (Karp et al., 2013; Letourneau et al., 2011). Yet, higher biodiversity on farms may also result in ecosystem disservices such as higher crop damage or foodborne disease transmission (Jay-Russell & Doyle, 2016; Martin et al., 2013). Managing landscapes for multifunctionality (i.e. maximizing services while minimizing disservices) thus remains a major challenge (Mastrangelo et al., 2014).

Identifying interventions that promote multifunctionality in working landscapes requires understanding both how and why ecosystem services and disservices interact (Kremen & Merenlender, 2018; Saidi & Spray, 2018). Ideally, such interventions would promote synergies and avoid trade-offs among ecosystem services. For example, conserving semi-natural habitat around California farms may promote synergies by increasing pest control while lowering bird damage to strawberries (Gonthier et al., 2019; Karp et al., 2016). In contrast, trade-offs may be associated with installing raptor nest boxes that enhance vertebrate pest control but may also attract birds that damage crops (Lindell et al., 2018). In practice, quantifying trade-offs and synergies often entails modelling changes in multiple services across broad scales and then grouping them into 'bundles' of consistently co-occurring services and disservices (Mouchet et al., 2014; Raudsepp-Hearne et al., 2010). However, the factors that drive ecosystem service bundles remain unclear (Spake et al., 2017). While many studies explore factors that enhance particular ecosystem services (Howe et al., 2014), very few attempt to elucidate mechanisms that underlie ecosystem service interactions (Mouchet et al., 2014).

Ecosystem services interactions are often thought to occur when different services respond to the same driver or when changes in one service trigger changes in another. An alternative and largely unexplored possibility is that trade-offs and synergies manifest within and across species. Sensale et al. (2006), for example, found that foodborne pathogen prevalence varied across bird species with different feeding habits. Thus, as bird communities shift across farms, it is possible that the species present on some farms may be more likely to consume pests than they are to host pathogens, whereas the opposite may be true on other farms. Changes in community composition (across species) and variation in response to environmental conditions (within species) could both influence ecosystem service interactions. Understanding how ecological drivers structure communities and influence ecosystem services may thus help to identify management interventions that shift suites of ecosystem services and forecast how bundles are likely to evolve under management and land-use change scenarios (Mouchet et al., 2014; Raudsepp-Hearne et al., 2010).

Birds represent a useful model taxon for exploring ecosystem service interactions as they are abundant, diverse and provide multiple services and disservices in agroecosystems (Pejchar et al., 2018; Sekercioglu et al., 2016). First, birds may increase crop yields by consuming arthropod pests and preventing crop damage (Gonthier et al., 2019; Karp et al., 2013). However, birds also consume arthropod natural enemies, which can release pests from top-down control and reduce crop yields (Grass et al., 2017). Furthermore, birds can act as pests themselves, reducing crop yields by consuming or damaging crops (Gebhardt et al., 2011). Finally, concerns about spillover of foodborne pathogens (e.g. enterohaemorrhagic *Escherichia coli*) from birds to humans may force growers to destroy crops that have been contaminated with bird faeces (California Leafy Green Products Handler Marketing Agreement, 2019; Smith, Snyder, & Owen, 2020). Few studies simultaneously assess the multiple ways that birds benefit and harm crop production (Pejchar et al., 2018; but see Gonthier et al., 2019; Olimpi et al., 2020), making it difficult to understand which farming contexts and management interventions promote multifunctional bird communities. Nonetheless, recent advances in molecular approaches may provide high-resolution data on bird diets and pathogen prevalence, thereby offering novel insights into the role of birds in agriculture (Garcia et al., 2020).

Here, we evaluate how local farming practices and the amount of semi-natural habitat surrounding strawberry farms influence multiple ecosystem services and disservices associated with wild birds in the California Central Coast, where many growers are experiencing pressure to remove habitat around farm fields in an effort to limit bird activity and reduce faecal contamination on farms (Olimpi et al., 2019). We focus on three central questions: (a) What farm management and landscape factors drive spatial variation in bird-mediated ecosystem services and disservices among farms? (b) How do ecosystem services interact? That is, are pairs of ecosystem services provided by bird communities positively or negatively correlated over space, causing trade-offs and synergies? (c) Can specific farming practices or landscape contexts minimize trade-offs within ecosystem-service bundles via shifts in bird diets, pathogen prevalence and community composition? To answer these questions, we collected 1,327 faeces from wild birds and used molecular methods to determine which individuals consumed pests, crops and natural enemies as well as which hosted foodborne pathogens.

2 | MATERIALS AND METHODS

2.1 | Study region

The California Central Coast is an economically important agricultural region that produces 43% of strawberries in the United States (USDA National Agricultural Statistics Service, 2019). The region experiences a temperate, Mediterranean climate. Farms sites were concentrated in the Pajaro and Salinas River Valleys of Santa Cruz and Monterey Counties, CA. Large, monoculture farms; small, diversified farms; and semi-natural vegetation (grasslands, shrublands, forest, wetlands) create a mosaic landscape across the region. We selected 21 organic strawberry farms using aerial imagery from the National Agricultural Imagery Project 2016 (NAIP, 1 m resolution) to maximize variation in local and landscape diversification indices (see Appendix S1 for more information on the study region and Tables S1 and S2 for farm summary statistics and sampling years by farm). Farms were defined as contiguous lands managed by a single grower or operation. Thus, farms could either represent a single parcel of land being farmed by a single grower or multiple adjacent parcels (being farmed by a single grower or operation).

2.2 | Bird data

We surveyed birds on each focal farm using 10 min, 50 m fixed-radius point count surveys, repeated three times over consecutive days from April to June of 2018–2019 (see Appendix S1 for more information on point count surveys). Point count data were used to (a) account for bird community composition when predicting the probability of birds providing ecosystems services/disservices at each farm and (b) calculate the mean relative abundance, richness and diversity at each farm by averaging data across the three visits to the point counts.

On each focal farm, we captured birds with mistnets and collected fresh faecal samples to characterize bird diets and assay foodborne pathogens. All research was approved by the IACUC of the University of California, Davis (protocol numbers 19354 and 21094). Farms were sampled over three consecutive days during a single year from May to July 2017–2019. We placed mistnets within and at the edge of crop fields, often adjacent to semi-natural habitat, to maximize capture rates (see Appendix S1 for more information on mistnet sampling). Bird faecal samples were placed in sterile cryotubes filled with 100% ethanol, placed in a −80°C liquid nitrogen dewar and kept frozen until DNA extraction.

2.3 | Local farm management practices and surrounding landscape context

We characterized local farm management practices, semi-natural habitat surrounding farms and crop diversity surrounding farms. First, we quantified local (on-farm) diversification by building a composite index from measurements of crop diversity, non-crop vegetation cover and vegetation complexity within each 50 m radius point count and then averaging across all point counts on each farm. High local diversification index values indicate less homogeneous farms that incorporated more crop types and non-crop vegetation. We also documented the density of fences and wires (i.e. where birds often perch) and the number of distinct bird deterrent practices, such as sound cannons and sparkler streamers, that we observed on each farm (see Appendix S1 for more information on local farm management practices).

Second, we manually digitized semi-natural habitat (forest, shrubland, grassland, pasture and wetlands) from aerial imagery within a 1 km radius of all sampling locations using ArcMap 10.3.1 (ESRI). A 1 km radius is an appropriate scale for examining effects of landscape composition on bird communities. We extracted surrounding land cover values using the R package 'TERRA' (Hijmans, 2021) and then used a Gaussian function to develop semi-natural habitat metrics that give greater influence to areas closer to the sampling sites (see Appendix S1 for more information).

Finally, as another measure of landscape context, we calculated the crop diversity surrounding each farm. We drew a minimum convex polygon connecting all sampling locations on each farm and then buffered the polygons by 500 m. We visually surveyed crops in the field, manually digitized maps of all observed crops, and calculated the crop diversity (Simpson's index) within the 500 m buffer. We used this same 500 m buffer to calculate the proportion of strawberry and caneberry crop areas.

2.4 | Bird diet profiles and pathogen prevalence

We used DNA metabarcoding, a high-throughput sequencing-based approach commonly used in diet analyses, to characterize bird diets from faecal samples (Alberdi et al., 2019; Jedlicka et al., 2013). We extracted DNA from faecal samples and amplified DNA using the arthropod-specific primer ZBJ (Zeale et al., 2011). We selected ZBJ as the best available primer at the time of analyses due to its broad amplification of taxonomic groups of interest (Zeale et al., 2011), while minimizing amplification of bird DNA. To determine whether birds consumed pests and/or natural enemies, we used the University of California Integrated Pest Management website (ipm.ucanr.edu) to define species and groups that have a significant impact on California agriculture. To supplement our diet sequencing data, we used a multiplex of berry-specific PCR primers to screen samples for the presence of strawberry and caneberry (e.g. blackberry, raspberry, etc.) DNA. Finally, we screened samples for *Campylobacter* spp. (*C. jejuni*, *C. coli*, *C. fetus* subsp. *fetus* and the 23S rRNA gene from *Campylobacter* species), *E. coli* virulence genes (*stx1*, *stx2*, *eaeA*, *hlyA* and *saa*) and *Salmonella* spp., as in Smith et al. (2020; see Appendix S1 for laboratory processing and diet categorization protocols). We corroborated our faecal proxies of ecosystem services by correlating the presence of strawberries, pests, and natural enemies in bird faeces with more direct measures of bird-mediated ecosystem services (see Appendix S1).

2.5 | Statistical analyses

We used generalized linear mixed models (GLMMs) to investigate the effects of local management and landscape context on each ecosystem service or disservice. GLMMs included a binomial distribution and a logit link function to predict the probability that individuals would provide services and disservices. We created binary response variables for each faecal sample to indicate whether the sample tested positive for strawberry; caneberry; one or more of the pests; one or more of the beneficial insects defined by UC IPM; one or more *Campylobacter* spp.; and one or more *E. coli* virulence genes. We also used these binary responses to build a multifunctionality index for each sample; specifically, the number of services that a bird provided plus the number of disservices it did not provide, divided by the total number of services and disservices considered.

All models included fixed effects of the local farm diversification index, crop diversity within 500 m, semi-natural habitat within 1 km, an interaction between the local diversification index and semi-natural habitat, and an interaction between crop diversity and semi-natural habitat. All diet models included additional fixed effects for the number of different bird deterrent practices used and the density of fencing and wires on the farm. Strawberry and caneberry consumption models included additional fixed effects of strawberry and caneberry crop areas within 500 m, respectively, to account for variation in resource availability that could influence consumption.

We included random intercept effects for individuals, species and farms to account for samples from recaptured birds, baseline differences between species, and spatial dependence of individuals captured on the same farm. To achieve convergence for the pathogen models, we removed the random effect of individual, as well as samples collected from recaptured birds. We modelled species identity as a random effect because we had very few samples for some species and could not model species independently. However, we ran an additional model to quantify variation among species in multifunctionality values. To do so, we limited the dataset to species with ≥10 samples and included species identity as a fixed effect.

We scaled all continuous variables by subtracting the mean and dividing by the standard deviation and verified the absence of multicollinearity before running models. All analyses were performed in R (V4.0.0). We ran models with the GLMMTMB package (Magnusson et al., 2016) and performed model selection with the MuMIn package (Bartoń, 2016) on all candidate models. We first identified the best-supported models (i.e. those within 2 AICc of the top model; Burnham & Anderson, 2002) and then used a model averaging approach of the best-supported models to predict the probability that faecal samples tested positive for crops, pests, natural enemies or pathogens on each farm. We reported conditional variance estimates to assess variable significance.

Next, we used predictions from our models to investigate interactions between ecosystem services and disservices. First, we used point-count data to determine the number of birds of each species present on each farm. Then, we predicted the probability that each bird within each farm community would provide each service/disservice using the model-averaged coefficients described above. Next, we averaged the probabilities across all birds present on each farm to arrive at a single average probability of birds on each farm providing each service/disservice. We then calculated farm-level Pearson correlation coefficients between all pairs of ecosystem service/disservices.

Finally, we defined ecosystem service bundles, or farm clusters with similar probabilities of birds providing services, to identify contexts in which ecosystem-service trade-offs could be minimized. We used a hierarchical clustering algorithm to define the optimal number of ecosystem service bundles (Scrucca et al., 2016; Appendix S1, Figure S2). To visualize the clusters, we plotted the first two axes of a Principal Component Analysis conducted on the six ecosystem service probabilities associated with each farm. We used one-way analysis of variance (ANOVA) tests to quantify differences in ecosystem services, farm characteristics and bird communities between clusters. Then, we tested for significant differences between clusters with subsequent post-hoc Tukey's HSD tests.

3 | RESULTS

After filtering, we analysed metabarcoding data for 988 samples from 52 species. Most of these high-quality faecal samples were also screened for berry consumption ($N = 971$ samples), screened for pathogen prevalence or virulence genes ($N = 980$ samples), and used to estimate species-specific multifunctionality ($N = 930$ samples, 21 species; see Appendix S1, Table S4 for detection rates, Table S5 for pest and natural enemy taxa represented in dietary profiles).

3.1 | Drivers of ecosystem services/disservices

Birds were more likely to consume strawberries on farms with less surrounding semi-natural habitat ($p = 0.05$; see Appendix S1, Tables S6–S13 for top model sets and Tables S14 and S15 for model-averaged results). The negative effect of semi-natural habitat on strawberry consumption was stronger on farms with more crop diversity within 500 m (interaction: $p = 0.03$; Figure 1a) but this effect weakened as crop diversity decreased. Birds were more likely to consume caneberries on farms with less surrounding semi-natural habitat; however, unlike strawberries, the negative effect of semi-natural habitat on caneberry consumption weakened as crop diversity surrounding farms increased (interaction: $p = 0.05$; Figure 1b).

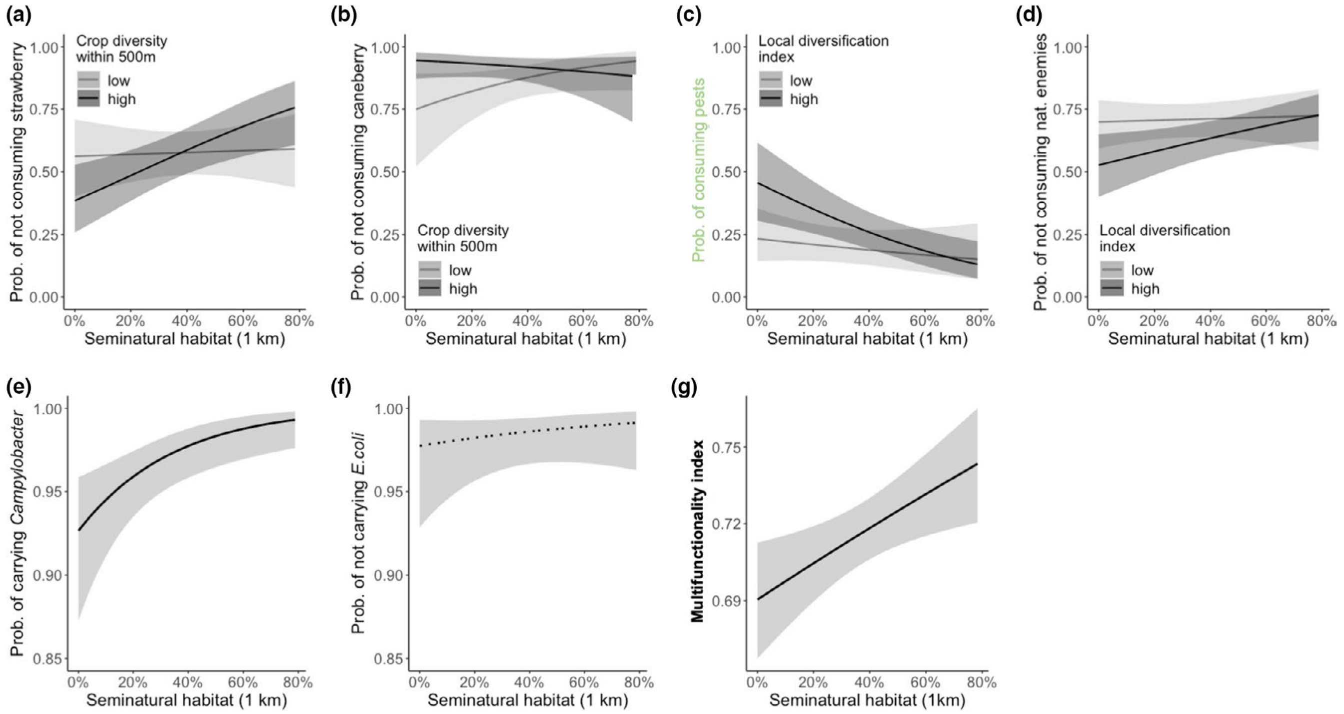

FIGURE 1 Influence of semi-natural habitat (within a 1 km radius surrounding farms) on the probability of birds providing ecosystem services (c, green text), not providing a disservice (a, b, d–f; black text), or on multifunctionality (g; bold text). Positive slopes indicate that semi-natural habitat was associated with more benefits and fewer costs. Higher multifunctionality index values indicate that birds are more likely to provide services and not disservices. The effect of semi-natural habitat was modified by an interaction with surrounding crop diversity (a, b) and the local diversification index (c, d), shown using two levels of continuous variables. Solid lines show coefficient estimates from the top-ranked generalized linear mixed models, dotted lines show relationships when the top model was null, and shaded areas represent standard errors of coefficient estimates

Birds were also less likely to consume strawberries on farms that used more bird deterrent practices ($p = 0.01$) and were marginally significantly less likely to consume strawberries on farms that had less fencing and wires ($p = 0.06$).

Birds were more likely to consume pests and natural enemies on diversified farms (pest: $p = 0.02$; natural enemy: $p = 0.02$) and farms surrounded by less semi-natural habitat (pest: $p = 0.01$; natural enemy: $p = 0.08$), although the effect of semi-natural habitat on natural enemy consumption was marginally significant. Importantly, the negative effect of semi-natural habitat on pest and natural enemy consumption was weak (i.e. near 0) when the local diversification index was low but was marginally strengthened as the local diversification index increased (interaction: pest: $p = 0.07$; natural enemy: $p = 0.06$; Figure 1c,d). Pest and natural enemy consumption were more likely on farms that used fewer bird deterrent practices (pest: $p = 0.09$; natural enemy: $p = 0.28$), although these trends were not significant.

We found an overall *Campylobacter* spp. prevalence of 3.6%, detected *E. coli* virulence genes in 2.4% of samples, and did not detect *Salmonella* spp. in any sample (Appendix S1, Table S4). We detected the Shiga-toxin producing *E. coli* gene stx2 in a single Song Sparrow (*Melospiza melodia*; 0.1%), the virulence gene *saa* in 2.3% of samples, and did not detect *stx1*, *eaeA* or *hlyA* in any sample. *Campylobacter* spp. prevalence decreased on farms surrounded by more semi-natural habitat ($p = 0.002$; Figure 1e). Neither farm characteristics nor surrounding semi-natural habitat were predictive of *E. coli* virulence gene prevalence (Figure 1f).

Finally, the multifunctionality index increased on farms surrounded by more semi-natural habitat ($p = 0.04$; Figure 1g) and marginally significantly increased on farms that used more types of bird deterrent practices ($p = 0.08$). Bird species ranked similarly in multifunctionality, although some species ranked higher than others; for example, Barn Swallows *Hirundo rustica* provided more services and American Goldfinches *Spinus tristis* imposed more disservices (Figure 2).

3.2 | Interactions among ecosystem services and disservices

We found that 8 of 15 pairs of ecosystem services/disservices were significantly correlated (Figure 3). First, we detected strong trade-offs in bird communities between pest control and multiple services. Farms that enjoyed high pest consumption rates from bird communities were also more likely to experience predation of natural enemies, direct crop damage (strawberry consumption) and greater food-safety risks (higher pathogen prevalence). However, we also detected synergies for multiple disservices. For example, farms with bird assemblages that were likely to consume strawberries were more likely to support birds that tested positive for *Campylobacter*

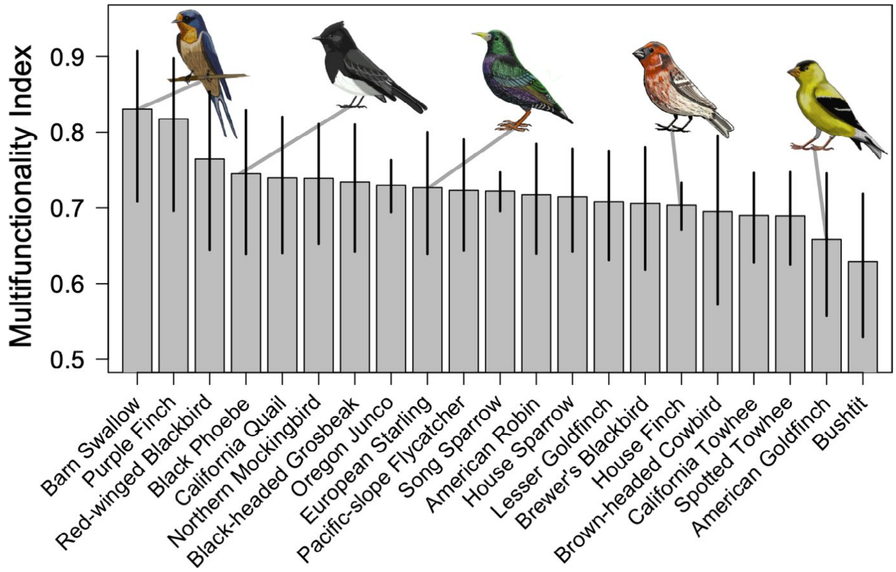

FIGURE 2 Multifunctionality index scores for species most commonly captured in mistnet sampling. Higher values indicate that birds species are more likely to provide services and less likely to provide disservices. Bars indicate multifunctionality estimates from the top-ranked generalized linear mixed model and whiskers represent standard errors of coefficient estimates

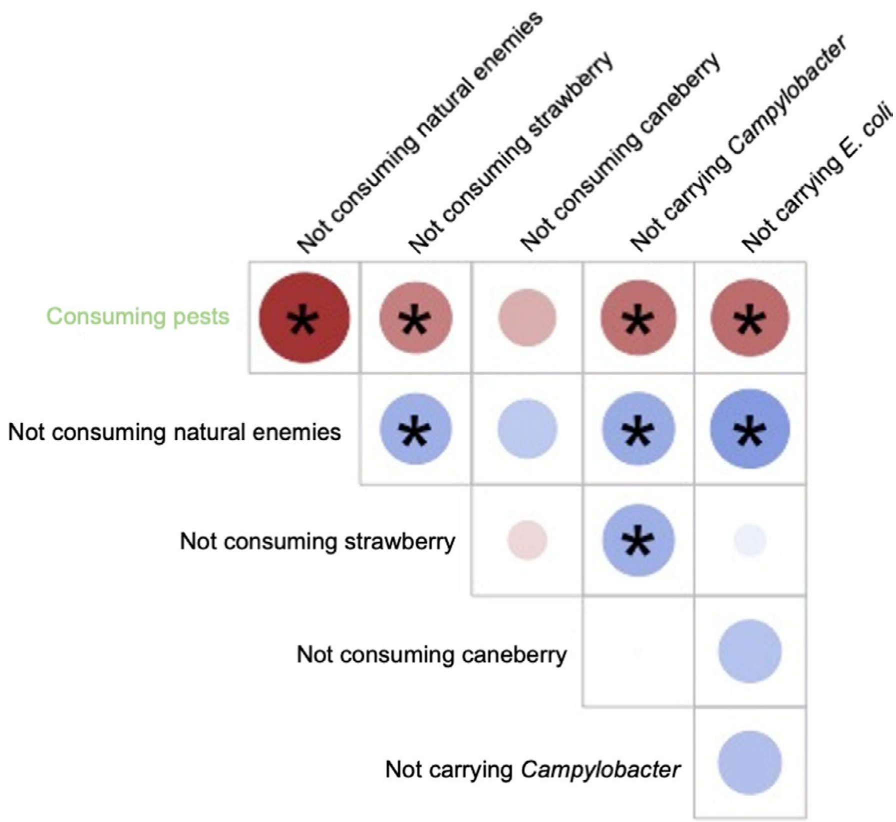

FIGURE 3 Pairwise comparisons of the probability that birds within the assemblage present on each farm would provide a service (green text) or not provide a disservice (black text). Trade-offs are shown in red, and synergies are shown in blue. Larger circles and more intense colours correspond to stronger correlation coefficients; asterisks indicate significance ($p \le 0.05$)

spp. Bird assemblages were also more likely to consume invertebrate natural enemies, damage strawberries and carry pathogens on the same farms.

3.3 | Farm cluster types and ecosystem service bundles

Cluster analyses based on service and disservice probabilities suggested that farms grouped into three coherent categories (Appendix S1, Figure S2) which we termed: Simple Landscape (N = 12 farms), Complex Landscape (N = 10 farms) and Very Complex Landscape (N = 2 farms; see Figures 4 and 5 and Appendix S1, Table S16–S18 for cluster mean effects, ANOVA and post-hoc tests, respectively). Farm clusters differed in the amount of surrounding semi-natural habitat and were named according to these differences. Bird assemblages on farms in the Simple Landscape cluster were more likely to consume pests, natural enemies and strawberries, carry foodborne pathogens, and have lower multifunctionality compared to birds in the Complex Landscape cluster.

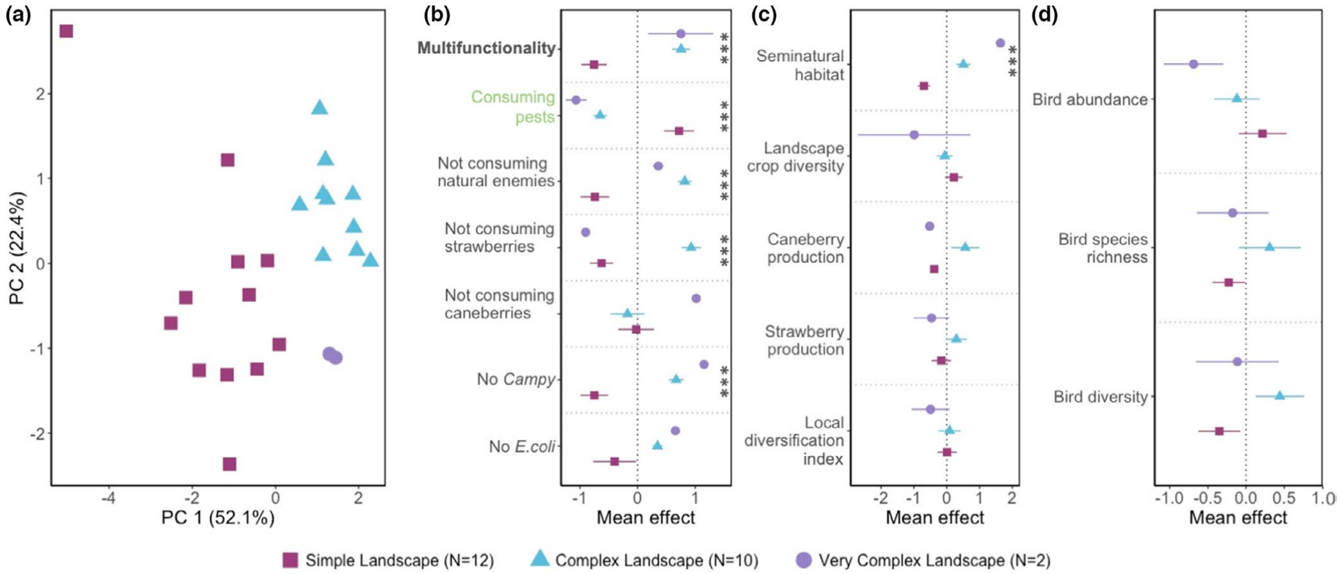

FIGURE 4 Hierarchical clustering identified three farm clusters with unique ecosystem service bundles, based on the probability that birds within the assemblage present on each farm would provide a service or not provide a disservice. (a) shows the first two principal components of a cluster analysis and points depict individual farms. (b) shows mean multifunctionality (bold text) and probabilities of birds providing services (green text) or not providing disservices (black text) for each cluster. Farm clusters can be described by contrasts in local farm management practices and landscape context (c) and bird communities (d). Mean effects and standard errors were scaled by subtracting the mean and dividing by the standard deviation; asterisks indicate significant ANOVA tests

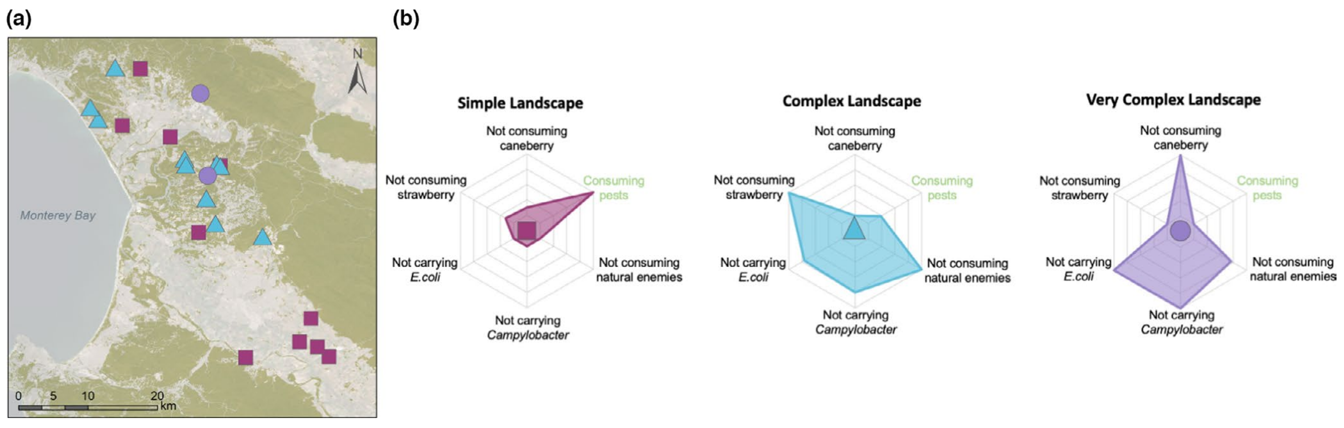

FIGURE 5 (a) Spatial distribution of ecosystem service bundles on farms across the study region. The olive green map overlay shows semi-natural habitat (forest, shrubland, herbaceous, pasture, wetlands) derived from values in the National Land Cover Database 2016. (b) Radar plots illustrate variation in multifunctionality (i.e. maximizing ecosystem services and minimizing ecosystem disservices) between farm clusters. The polygon vertices plotted on each axis represent the cluster mean probability that birds provided a service (green text) or did not provide a disservice (black text) such that higher values and larger shaded areas indicate higher multifunctionality

We found no significant differences in bird community metrics between clusters.

4 | DISCUSSION

Our research revealed that bird-mediated ecosystem services and disservices on California strawberry farms are shaped by interactions between local farming practices and landscape context. We evaluated services primarily provided by passerines and found that the amount of semi-natural habitat surrounding each farm was the single most important driver of ecosystem services, disservices and their interactions, with the best outcomes (highest multifunctionality) occurring on farms surrounded by more semi-natural habitat. Critically, we also found bird-mediated ecosystem services and disservices can be grouped into spatially co-occurring 'bundles', as bird communities respond to farmland diversification. Although the presence of taxa and pathogens in faeces is not a direct measure of bird-mediated ecosystem services and disservices, correlations between bird diets and more direct service measures (Appendix S1) suggest that our faecal proxies reflect the impact of birds on farms.

4.1 | Drivers of individual ecosystem services and disservices

We found that birds were less likely to consume strawberries and caneberries on farms with more surrounding semi-natural habitat. These trends align with our previous finding that berry damage from birds declines in more complex landscapes (Olimpi et al., 2020). Landscape effects on crop consumption may be driven by birds' dietary preferences. That is, surrounding semi-natural habitats may provide birds with higher quality food resources (e.g. seeds, fruits, insects) than strawberries and caneberries. Birds rarely fed on caneberries, except on farms surrounded by low levels of crop diversity and semi-natural habitat, which may suggest that caneberries are not a preferred food resource. In contrast, strawberry consumption peaked on farms surrounded by more crop diversity and less semi-natural habitat, which may suggest that birds prefer strawberries over other crops but not over more natural food resources.

Arthropod consumption was also influenced by an interaction between local farming practices and semi-natural habitat surrounding farms. Birds were more likely to consume both pests and natural enemies on diversified farms surrounded by less semi-natural habitat. One possible explanation for this trend might be that arthropods are more abundant on diversified than homogeneous farms (Gonthier et al., 2014). In intensive agricultural landscapes, economically important pests, and the subset of natural enemies that rely upon them as a key food resources, may comprise more of the arthropod community than in complex landscapes that support more diverse arthropod assemblages (Chaplin-Kramer et al., 2011; Gonthier et al., 2014). This could result in pests and natural enemies being more commonly encountered and consumed by birds. If patterns of pest consumption simply reflect lower pest densities in landscapes with more semi-natural habitat, then birds consuming relatively more natural enemies than pests in complex landscapes may not translate to lower yields.

Finally, we found very low overall rates of pathogen prevalence in birds. Just 3% of birds carried *Campylobacter* spp., 2.4% carried potential *E. coli* virulence genes, a single individual carried Shiga-toxin-producing *E. coli* (which can cause severe disease in humans), and we did not detect *Salmonella* spp. Although birds that carry *E. coli* virulence genes may not represent a direct threat to food safety, virulence genes could potentially contribute to the emergence of virulent strains and may represent increased food-safety risks (see Appendix S1 for further explanation). Surrounding semi-natural habitat was the strongest negative predictor of food-safety risks from birds. In line with Smith, Edworthy, et al. (2020), we found that individual birds were less likely to carry *Campylobacter* spp. in landscapes with more semi-natural habitat. Agricultural intensification could increase pathogen prevalence by amplifying interspecific and intraspecific transmission (Gibb et al., 2020). For example, intensive agricultural landscapes could support bird communities that are less diverse and favour more competent reservoir hosts (Burkett-Cadena & Vittor, 2018; Gonthier et al., 2019), increasing transmission and pathogen prevalence (Burkett-Cadena & Vittor, 2018; Kilonzo et al., 2013). Correspondingly, bird communities associated with farm clusters with more semi-natural habitat were marginally more diverse and were less likely to carry *Campylobacter* spp. than communities on farms with less semi-natural habitat (Figure 4b–d). Regardless of mechanism, this work suggests that efforts to improve food safety by removing wildlife habitat around farms may be misguided (Olimpi et al., 2019).

4.2 | Linking ecological drivers, species, communities and ecosystem service bundles

More generally, our work demonstrates how relationships between ecosystem services and disservices can arise when biotic communities provide a complex array of services and disservices. By acknowledging that communities play multiple roles in ecosystems, managers can better achieve multifunctionality by (a) identifying key drivers that shape ecological communities and (b) asking which drivers promote communities that provide more benefits and fewer harms. In contrast, when management efforts are focused on a particular service in isolation from other services, important trade-offs may be easily overlooked.

Landscape context was the core driver of multiple services and disservices in our study system. Specifically, we saw a decrease in multiple disservices (i.e. crop damage, pathogen prevalence, natural enemy consumption) and one service (i.e. pest consumption) and an increase in multifunctionality with increasing semi-natural habitat. While some of these effects may reflect differences in resource availability (e.g. higher relative abundance of pests in intensive agricultural landscapes), our prior work in this system showed that conserving semi-natural habitat mitigated bird-mediated disservices and resulted in more positive net effects (services and disservices) of birds on strawberry yields (Olimpi et al., 2020). Shifts in bird communities may also explain the positive influence of semi-natural habitat on avian services. In a previous study on many of the same farms, we found that the relative abundance of insectivorous birds increased and strawberry-eating birds decreased with increasing semi-natural habitat (Gonthier et al., 2019). Gonthier et al. (2019) also found that bird species richness and abundance increased with increasing semi-natural habitat, suggesting that habitat conservation can support bird conservation and promote bird multifunctionality.

When we evaluated farm clusters associated with ecosystem services bundles, we found that semi-natural habitat promotes multifunctional bird communities that provide ecosystem services and are not associated with significant costs. For example, bird communities associated with the Complex Landscape cluster were less likely to damage strawberries, consume natural enemies, and host pathogens than birds associated with the Simple Landscape cluster.

Managing for bundles allows important trade-offs and synergies to be identified. In certain contexts, synergies may be enhanced, and trade-offs may be minimized or avoided. For example, we identified the strongest trade-off between pest and natural enemy consumption. This trade-off was minimized in the Simple Landscape cluster where pest and natural enemy consumption were similarly high but was strengthened in the Complex and Very Complex Landscape clusters where birds were almost twice as likely to consume natural enemies compared to pests. This example suggests that some trade-offs may be mitigated or exacerbated in certain farming contexts, highlighting the importance of managing for ecosystem service bundles.

Finally, understanding which species are associated with more benefits and fewer costs opens the door towards implementing targeted management interventions that promote multifunctional species. For example, we found that Barn Swallows ranked highest in multifunctionality. Allowing Barn Swallows to continue to nest on buildings within and adjacent to farms (a common occurrence in our study system) could thus result in positive outcomes for farmers. More generally, installing nest boxes could promote pest-eating, insectivorous species that carry lower food-safety risks and infrequently damage crops (Jedlicka et al., 2011; Smith et al., 2021). Importantly, nest boxes can be designed with entrance holes tailored to specific birds; for example, smaller entrance holes sized for swallows and bluebirds may prevent larger birds associated with more disservices (e.g. European Starling) from entering (Baumgartner et al., 2019). Indeed, our multifunctionality analyses also identified more problematic species (e.g. American Goldfinches) that growers might consider discouraging from visiting their farms via bird deterrents (Rivadeneira et al., 2018).

4.3 | Study limitations

We acknowledge that our metabarcoding analyses have several limitations. All primer sets will have their biases as DNA from different species will amplify at different rates such that some species may be over-represented in the final dataset (Clarke et al., 2014). Using multiple primer sets may increase the completeness of dietary assessments but can be expensive. It remains unclear if metabarcoding and pathogen assays with PCR can provide an estimate of the relative proportion of each diet item. Quantifying the relative importance of diet items could improve estimates of bird-mediated ecosystem services and elucidate whether birds are more likely to provide or disrupt pest control. Metabarcoding may also detect secondary consumption (e.g. berries consumed by an insect that was subsequently consumed by a bird). If secondary consumption contributed significantly to strawberry detection from our metabarcoding analyses, then we would expect that strawberry and pest consumption would be highly correlated. However, this is not what we observed. Moreover, bird damage to berries was positively correlated with berry consumption via diet analyses. Thus, while we cannot rule out some degree of secondary consumption, it is unlikely to be the main driver of patterns observed in this study. Future research could quantify the contribution of secondary consumption in bird diets and assess the degree to which gut retention time of the prey and primer selection influence diet analysis (Clarke et al., 2014; Wallinger et al., 2013).

5 | CONCLUSIONS

Our work illustrates that bird communities play multiple key roles in ecosystems, simultaneously providing ecosystem services and disservices. We also showed that specific farming contexts can exacerbate or mitigate trade-offs in ecosystem services and disservices provided by birds in agroecosystems. By assessing trade-offs and synergies associated with specific farming contexts and species, management interventions can be identified that better achieve multifunctionality. Our framework for coupling ecological drivers and community structure to assess spatial variation in ecosystem service bundles provides a promising path forward for managing multifunctional landscapes.

ACKNOWLEDGEMENTS

We thank all the growers who participated in our research by providing access to their farms and the many undergraduate students and laboratory personnel that made this research possible. This research was funded by a grant from USDA NIFA (#2017-67019-26293) to D.S.K., W.E.S., E.E.W.-R. and D.J.G.; a USDA Hatch (KY008079) grant to D.J.G.; a USDA Hatch (CA-R-ENT-5091-H) grant to E.E.W.-R.; and support from the Department of Wildlife, Fish, and Conservation Biology at University of California, Davis to E.M.O.

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

AUTHORS' CONTRIBUTIONS

D.J.G. and D.S.K. conceived the ideas and methodology for data collection; E.M.O. and K.G. collected the data; E.E.W.-R. led the sample processing for diet data; W.E.S. led the sample processing for pathogen detection; E.M.O. and D.S.K. planned the data analyses; E.M.O. analysed the data and wrote 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/10.25338/B8H93C (Olimpi et al., 2022).

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REFERENCES

Alberdi, A., Aizpurua, O., Bohmann, K., Gopalakrishnan, S., Lynggaard, C., Nielsen, M., & Gilbert, M. T. P. (2019). Promises and pitfalls of using high-throughput sequencing for diet analysis. *Molecular Ecology Resources*, *19*, 327–348. https://doi.org/10.1111/1755-0998.12960

Bartoń, K. (2016). *MuMIn: Multi-model inference*. R package version 1.15.6.

Baumgartner, J., Kross, S., Heath, S., & Connor, S. (2019). *Supporting beneficial birds and managing pest birds*. Wild Farm Alliance.

Burkett-Cadena, N. D., & Vittor, A. Y. (2018). Deforestation and vector-borne disease: Forest conversion favors important mosquito vectors of human pathogens. *Basic and Applied Ecology*, *26*, 101–110. https://doi.org/10.1016/j.baae.2017.09.012

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multi-model inference: A practical information-theoretic approach* (2nd ed.). Spring-Verlag.

California Leafy Green Products Handler Marketing Agreement. (2019). *Commodity specific food safety guidelines for the production and harvest of lettuce and leafy greens*.

Chaplin-Kramer, R., O'Rourke, M. E., Blitzer, E. J., & Kremen, C. (2011). A meta-analysis of crop pest and natural enemy response to landscape complexity. *Ecology Letters*, *14*, 922–932. https://doi.org/10.1111/j.1461-0248.2011.01642.x

Clarke, L. J., Soubrier, J., Weyrich, L. S., & Cooper, A. (2014). Environmental metabarcodes for insects: In silico PCR reveals potential for taxonomic bias. *Molecular Ecology Resources*, *14*, 1160–1170. https://doi.org/10.1111/1755-0998.12265

Garcia, K., Olimpi, E., Karp, D., & Gonthier, D. (2020). The good, the bad, and the risky: Can birds be incorporated as biological control agents into integrated pest management programs? *Journal of Integrated Pest Management*, *11*, pmaa009. https://doi.org/10.1093/jipm/pmaa009

Gebhardt, K., Anderson, A. M., Kirkpatrick, K. N., & Shwiff, S. A. (2011). A review and synthesis of bird and rodent damage estimates to select California crops. *Crop Protection*, *30*, 1109–1116. https://doi.org/10.1016/j.cropro.2011.05.015

Gibb, R., Redding, D. W., Chin, K. Q., Donnelly, C. A., Blackburn, T. M., Newbold, T., & Jones, K. E. (2020). Zoonotic host diversity increases in human-dominated ecosystems. *Nature*, *584*, 398–402. https://doi.org/10.1038/s41586-020-2562-8

Gonthier, D., Sciligo, A., Karp, D., Lu, A., Garcia, K., Juarez, G., Chiba, T., & Kremen, C. (2019). Bird services and disservices to strawberry farming in Californian agricultural landscapes. *Journal of Applied Ecology*, *56*, 1948–1959. https://doi.org/10.1111/1365-2664.13422

Gonthier, D. J., Ennis, K. K., Farinas, S., Hsieh, H.-. Y., Iverson, A. L., Batary, P., Rudolphi, J., Tscharntke, T., Cardinale, B. J., & Perfecto, I. (2014). Biodiversity conservation in agriculture requires a multi-scale approach. *Proceedings of the Royal Society B: Biological Sciences*, *281*, 20141358. https://doi.org/10.1098/rspb.2014.1358

Grass, I., Lehmann, K., Thies, C., & Tscharntke, T. (2017). Insectivorous birds disrupt biological control of cereal aphids. *Ecology*, *98*, 1583–1590. https://doi.org/10.1002/ecy.1814

Hijmans, R. J. (2021). *terra: Spatial data analysis*. R package version 1.4-11. Retrieved from https://CRAN.R-project.org/package=terra

Howe, C., Suich, H., Vira, B., & Mace, G. M. (2014). Creating win-wins from trade-offs? Ecosystem services for human well-being: A meta-analysis of ecosystem service trade-offs and synergies in the real world. *Global Environmental Change*, *28*, 263–275. https://doi.org/10.1016/j.gloenvcha.2014.07.005

Jay-Russell, M., & Doyle, M. P. (2016). *Food safety risks from wildlife: Challenges in agriculture, conservation, and public health*. Springer International Publishing Switzerland.

Jedlicka, J. A., Greenberg, R., & Letourneau, D. K. (2011). Avian conservation practices strengthen ecosystem services in California vineyards. *PLoS ONE*, *6*, e27347. https://doi.org/10.1371/journal.pone.0027347

Jedlicka, J. A., Sharma, A. M., & Almeida, R. P. P. (2013). Molecular tools reveal diets of insectivorous birds from predator fecal matter. *Conservation Genetics Resources*, *5*, 879–885. https://doi.org/10.1007/s12686-013-9900-1

Karp, D. S., Mendenhall, C. D., Sandi, R. F., Chaumont, N., Ehrlich, P. R., Daily, G. C., Sandí, R. F., Chaumont, N., Ehrlich, P. R., Hadly, E. A., & Daily, G. C. (2013). Forest bolsters bird abundance, pest control and coffee yield. *Ecology Letters*, *16*, 1339–1347. https://doi.org/10.1111/ele.12173

Karp, D. S., Moses, R., Gennet, S., Jones, M. S., Joseph, S., M'Gonigle, L. K., Ponisio, L. C., Snyder, W. E., & Kremen, C. (2016). Agricultural practices for food safety threaten pest control services for fresh produce. *Journal of Applied Ecology*, *53*, 1402–1412. https://doi.org/10.1111/1365-2664.12707

Kilonzo, C., Li, X., Vivas, E. J., Jay-Russell, M. T., Fernandez, K. L., & Atwill, E. R. (2013). Fecal shedding of zoonotic food-borne pathogens by wild rodents in a major agricultural region of the Central California Coast. *Applied and Environmental Microbiology*, *79*, 6337–6344. https://doi.org/10.1128/AEM.01503-13

Kremen, C., & Merenlender, A. M. (2018). Landscapes that work for biodiversity and people. *Science*, *362*, eaau6020. https://doi.org/10.1126/science.aau6020

Letourneau, D. K., Armbrecht, I., Rivera, B. S., Lerma, J. M., Carmona, E. J., Daza, M. C., Escobar, S., Galindo, V., Gutiérrez, C., López, S. D., Mejía, J. L., Rangel, A. M. A., Rangel, J. H., Rivera, L., Saavedra, C. A., Torres, A. M., & Trujillo, A. R. (2011). Does plant diversity benefit agroecosystems? A synthetic review. *Ecological Applications*, *21*, 9–21. https://doi.org/10.1890/09-2026.1

Lindell, C., Eaton, R. A., Howard, P. H., Roels, S. M., & Shave, M. E. (2018). Enhancing agricultural landscapes to increase crop pest reduction by vertebrates. *Agriculture, Ecosystems and Environment*, *257*, 1–11. https://doi.org/10.1016/j.agee.2018.01.028

Magnusson, A., Skaug, H., Nielsen, A., Berg, C., Kristensen, K., Maechler, M., & Brooks, M. (2016). *glmmTMB: Generalized linear mixed models using template model builder*.

Martin, E. A., Reineking, B., Seo, B., & Steffan-dewenter, I. (2013). Natural enemy interactions constrain pest control in complex agricultural landscapes. *Proceedings of the National Academy of Sciences of the United States of America*, *110*, 5534–5539. https://doi.org/10.1073/pnas.1215725110

Mastrangelo, M. E., Weyland, F., Villarino, S. H., Barral, M. P., Nahuelhual, L., & Laterra, P. (2014). Concepts and methods for landscape multifunctionality and a unifying framework based on ecosystem services. *Landscape Ecology*, *29*, 345–358. https://doi.org/10.1007/s10980-013-9959-9

Mouchet, M. A., Lamarque, P., Martín-López, B., Crouzat, E., Gos, P., Byczek, C., & Lavorel, S. (2014). An interdisciplinary methodological guide for quantifying associations between ecosystem services. *Global Environmental Change*, *28*, 298–308. https://doi.org/10.1016/j.gloenvcha.2014.07.012

Olimpi, E. M., Baur, P., Echeverri, A., Gonthier, D., Karp, D. S., Kremen, C., Sciligo, A., & De Master, K. T. (2019). Evolving food safety pressures in California's Central Coast region. *Frontiers in Sustainable Food Systems*, *3*, 1–24. https://doi.org/10.3389/fsufs.2019.00102

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

Olimpi, E. M., Garcia, K., Gonthier, D. J., Kremen, C., Snyder, W. E., Wilson-Rankin, E. E., & Karp, D. S. (2022). Data from: Semi-natural habitat surrounding farms promotes multifunctionality in avian ecosystem services. *Dryad Digital Repository*. https://doi.org/10.25338/B8H93C

Pejchar, L., Clough, Y., Ekroos, J., Nicholas, K. A., Olsson, O. L. A., Ram, D., Tschumi, M., & Smith, H. G. (2018). Net effects of birds in agroecosystems. *Bioscience*, *68*, 1–9. https://doi.org/10.1093/biosci/biy104

Raudsepp-Hearne, C., Peterson, G. D., & Bennett, E. M. (2010). Ecosystem service bundles for analyzing tradeoffs in diverse landscapes. *Proceedings of the National Academy of Sciences of the United States of America*, *107*, 5242–5247. https://doi.org/10.1073/pnas.0907284107

Rivadeneira, P., Kross, S., Navarro-Gonzalez, N., & Jay-Russell, M. (2018). A review of bird deterrents used in agrictulre. In *UC Agriculture & Natural Resources Proceedings of the Vertebrate Pest Conference* (pp. 218–223). University of California, Davis. https://doi.org/10.5070/V42811040

Saidi, N., & Spray, C. (2018). Ecosystem services bundles: Challenges and opportunities for implementation and further research. *Environmental Research Letters*, *13*, 113001. https://doi.org/10.1088/1748-9326/aae5e0

Scrucca, L., Fop, M., Murphy, T. B., & Raftery, A. E. (2016). mclust 5: Clustering, classification and density estimation using Gaussian finite mixture models. *The R Journal*, *8*, 289–317.

Sekercioglu, C., Wenny, D., & Whelan, C. (2016). *Why birds matter*. University of Chicago Press.

Sensale, M., Cuomo, A., Dipineto, L., Santaniello, A., Calabria, M., Menna, L. F., & Fioretti, A. (2006). Survey of *Campylobacter jejuni* and *Campylobacter coli* in different taxa and ecological guilds of migratory birds. *Italian Journal of Animal Science*, *5*, 291–294. https://doi.org/10.4081/ijas.2006.291

Smith, O. M., Edworthy, A., Taylor, J. M., Jones, M. S., Tormanen, A., Kennedy, C. M., Fu, Z., Latimer, C. E., Cornell, K. A., Michelotti, L. A., Sato, C., Northfield, T., Snyder, W. E., & Owen, J. P. (2020). Agricultural intensification heightens food safety risks posed by wild birds. *Journal of Applied Ecology*, *57*, 2246–2257. https://doi.org/10.1111/1365-2664.13723

Smith, O. M., Olimpi, E. M., Cornell, K. A., Frishkoff, L., Jay-Russell, M., Navarro-Gonzalez, N., Northfield, T. D., Bowles, T., Edworthy, A., Eilers, J., Fu, Z., Garcia, K., Gonthier, D. J., Jones, M. S., Kennedy, C. M., & Karp, D. S. (2021). A trait-based framework for predicting foodborne pathogen risk from wild birds. *Ecological Applications*, e2523. https://doi.org/10.1002/eap.2523

Smith, O. M., Snyder, W. E., & Owen, J. P. (2020). Are we overestimating risk of enteric pathogen spillover from wild birds to humans? *Biological Reviews*, *95*, 652–679. https://doi.org/10.1111/brv.12581

Spake, R., Lasseur, R., Crouzat, E., Bullock, J. M., Lavorel, S., Parks, K. E., Schaafsma, M., Bennett, E. M., Maes, J., Mulligan, M., Mouchet, M., Peterson, G. D., Schulp, C. J. E., Thuiller, W., Turner, M. G., Verburg, P. H., & Eigenbrod, F. (2017). Unpacking ecosystem service bundles: Towards predictive mapping of synergies and trade-offs between ecosystem services. *Global Environmental Change*, *47*, 37–50. https://doi.org/10.1016/j.gloenvcha.2017.08.004

USDA National Agricultural Statistics Service. (2019). Quick Stats Database [WWW Document]. Retrieved from http://quickstats.nass.usda.gov

Wallinger, C., Staudacher, K., Schallhart, N., Peter, E., Dresch, P., Juen, A., & Traugott, M. (2013). The effect of plant identity and the level of plant decay on molecular gut content analysis in a herbivorous soil insect. *Molecular Ecology Resources*, *13*, 75–83. https://doi.org/10.1111/1755-0998.12032

Zeale, M. R. K., Butlin, R. K., Barker, G. L. A., Lees, D. C., & Jones, G. (2011). Taxon-specific PCR for DNA barcoding arthropod prey in bat faeces. *Molecular Ecology Resources*, *11*, 236–244. https://doi.org/10.1111/j.1755-0998.2010.02920.x

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How to cite this article: Olimpi, E. M., Garcia, K., Gonthier, D. J., Kremen, C., Snyder, W. E., Wilson-Rankin, E. E. & Karp, D. S. (2022). Semi-natural habitat surrounding farms promotes multifunctionality in avian ecosystem services. *Journal of Applied Ecology*, *59*, *898–908*. https://doi.org/10.1111/1365-2664.14124