



Ungrazed seminatural habitats around farms benefit bird conservation without enhancing foodborne pathogen risks

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Abstract

Context Conservation in working landscapes is critical for halting biodiversity declines and ensuring farming system sustainability. However, concerns that wildlife may carry foodborne pathogens has created pressure on farmers to remove habitat and reduce biodiversity, undermining farmland conservation. Nonetheless, simplified farming landscapes may host bird communities that carry higher foodborne disease risks.

Objectives We analyzed the effects of local farming practices and surrounding landscapes on bird communities and food-safety risks across 30 California lettuce farms. Specifically, we sought to

determine how farmland diversification affects bird diversity, fecal contamination, and foodborne pathogen incidences, thereby identifying potential trade-offs between managing farms for bird conservation versus food safety.

Methods We surveyed birds at 227 point-count locations, quantified fecal contamination along 120 transects, and assayed 601 bird feces for pathogenic *E. coli*, *Campylobacter* spp., and *Salmonella* spp. We then used hierarchical models to quantify effects of farm management and landscape context on bird communities and food-safety risks.

Results Surrounding ungrazed seminatural areas were associated with higher bird diversity, more

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species of conservation concern, and fewer flocks that may increase risks from foodborne pathogens. In contrast, on-farm diversification practices and surrounding grazing lands offered weaker bird conservation benefits. Surrounding grazed lands were associated with more potentially pathogenic bird feces in crop fields.

Conclusions Our results suggest that habitat conservation around produce farms could support bird conservation without increasing foodborne pathogens, especially on farms further from grazing lands. Thus, interventions that diversify farming systems offer potential to simultaneously conserve biodiversity and provide safe food for human consumption.

Keywords Agroecology · Diversified farming system · Ecosystem services · Food safety · Human–wildlife conflict

Introduction

As biodiversity and its contributions to human well-being decline (Diaz et al. 2019), conservation scientists and practitioners are increasingly exploring strategies for conserving nature alongside people in ‘working landscapes’ of farms, rangelands, and forests (Kremen and Merenlender 2018; Arroyo-Rodríguez et al. 2020). Interventions that diversify farming systems (e.g., planting multiple crops and retaining non-crop vegetation at the farm and landscape scale) can bolster biodiversity and ecosystem services while maintaining high crop yields (Kremen and Miles 2012; Sirami et al. 2019; Tamburini et al. 2020; Beilouin et al. 2021). Yet conserving biodiversity in working landscapes is not without challenges. Working landscapes often host high biodiversity but also different species from those in protected areas (Frishkoff et al. 2014; Frishkoff and Karp 2019). In particular, range-restricted species of higher conservation concern are often disproportionately sensitive to habitat conversion and thus absent from working landscapes (Sykes et al. 2020), especially in the tropics (Newbold et al. 2020). In temperate areas, however, many species of conservation concern are associated with diversified farms but in decline due to the replacement of diverse agroecosystems with vast, conventionally-farmed monocultures (Donald et al. 2006; Kleijn et al. 2011; Gamero et al. 2017; Stanton et al. 2018).

Even when diversified farming practices increase biodiversity and/or ecosystem services, rates of adoption are often low (USDA NASS 2019; Wallander et al. 2021). For fresh produce growers in particular, one key barrier is the perceived or actual negative impact that wild organisms can have on crop production (Zhang et al. 2007; Carlisle et al. 2022). In particular, ever since a multi-state pathogenic *E. coli* outbreak was attributed to wild pigs near fresh produce fields in California (CDC 2006), growers have faced escalating pressure to prevent wildlife from entering their farms (Beretti and Stuart 2008; Gennet et al. 2013; Baur et al. 2016). Indeed, alongside many other sweeping transformations to U.S. agricultural production that were precipitated by the 2006 outbreak (FDA 2015; LGMA 2020; Devarajan et al. 2023), growers now regularly attempt to exclude wildlife by fencing their fields, clearing native vegetation, and replacing it with bare-ground buffers (Karp et al. 2015a; Baur et al. 2016; Olimpi et al. 2022; Weller et al. 2022). Despite evidence suggesting it does not improve food safety and, if anything, increases pathogen incidence, habitat removal continues to be widespread across U.S. fresh produce farms (Karp et al. 2015b; Baur et al. 2016; Olimpi et al. 2022; Weller et al. 2022; Adalja et al. 2023). Correspondingly, food-safety concerns are regularly cited as a major barrier to diversifying fresh produce farms (Carlisle et al. 2022).

Wild birds are of particular concern to farmers. First, birds can carry multiple pathogens that may cause disease in humans, including Shiga-toxin producing *E. coli*, *Salmonella* spp., and *Campylobacter* spp. (Navarro-Gonzalez et al. 2019; Smith et al. 2020b). Second, birds move long distances, including between cropland and livestock operations, where foodborne pathogens are often prevalent (Rivadeneira et al. 2016). Third, excluding birds is difficult: birds habituate to visual and auditory deterrents, and more effective methods are very costly (Anderson et al. 2013; Rivadeneira et al. 2018). Finally, birds are ubiquitous in produce fields, defecating in and around crops (Smith et al. 2019, 2020a; Olimpi et al. 2020). Flocking birds are of particular concern and explicitly flagged in regional food-safety guidance (LGMA 2020) because animal species that aggregate can produce high concentrations of fecal contamination.

Despite these concerns, the actual food-safety risks associated with wild birds in fresh produce fields remains unclear (Smith et al. 2020b). Only

one foodborne disease outbreak has been conclusively attributed to birds: *Campylobacter* from sandhill cranes (*Grus canadensis*) in Alaskan pea fields (Gardner et al. 2011). Additionally, foodborne diseases are rare in wild birds: one recent quantitative synthesis of > 11,000 pathogen tests across 94 species on produce farms reported prevalences of Shiga-toxin producing *E. coli* and *Salmonella* spp. of 0.22% and 0.46%, respectively (Smith et al. 2021). *Campylobacter* spp. prevalence was much higher (8%); however, recent work suggests *Campylobacter* strains in wild birds may be host-specific and thus unlikely to be a major source of foodborne illness in humans (Colles et al. 2009; Griekspoor et al. 2013; Smith et al. 2020b). Importantly, foodborne prevalences varied among species; for example, pathogens tended to be more common in species that associate with livestock (Smith et al. 2021).

Ultimately, engaging in conservation in working landscapes will require understanding how ecological communities change across farming contexts and what these changes might mean not only for conservation but also for food safety. For birds, diversified farming practices are known to bolster abundance and diversity (Gonthier et al. 2019; Smith et al. 2019), resulting in positive conservation outcomes. Our understanding of how farm management influences infectious disease risks, however, is more limited (Balmford 2021; Kremen and Geladi 2023). On the one hand, a more abundant bird community on diversified farms may be associated with increased fecal densities in crops and thus higher food-safety risks. On the other hand, if the higher-risk, livestock-associated species are rare on diversified farms, then diversified farming may not elicit higher food-safety risks. That is, changes in bird community composition between farm types may influence food-safety outcomes. Correspondingly, recent studies suggest that *Campylobacter* spp. prevalence in wild birds increases on farms surrounded by higher livestock densities and decreases on farms surrounded by more seminatural areas (Smith et al. 2020a; Olimpi et al. 2022).

Here, we used field surveys, molecular methods, and N-mixture models, to investigate the impact of farm management and surrounding landscapes on bird communities and associated food-safety risks in the California Central Coast. Specifically, we surveyed bird communities, fecal densities, and prevalences of

three foodborne pathogens (*E. coli*, *Salmonella* spp., and *Campylobacter* spp.) on 30 organic lettuce farms, distributed along gradients of local diversification as well as grazed and ungrazed seminatural areas surrounding farms. Farms with the lowest level of local diversification were monocultures with little non-crop vegetation, whereas farms with high local diversification grew a variety of crops as well as planted or maintained floral strips, hedgerows, and natural areas (*i.e.*, ground cover, shrubs, trees) that provide habitat for wildlife.

Our work was guided by three questions regarding biodiversity conservation and food-safety risks associated with wild bird communities. First, how do on-farm management (*i.e.*, local diversification practices) and landscape context (*i.e.*, amount of surrounding seminatural habitat) structure bird communities and their associated conservation value? We predicted that, given birds' high vagility, landscape composition would be the primary driver of community composition (Gonthier et al. 2014, 2019), with farms in more natural landscapes hosting the most diverse communities and species of highest conservation concern. Second, how do farm management and landscape context influence food-safety risks? We predicted birds would deposit more pathogenic feces on monoculture farms near grazed areas, where livestock-associated, flock-forming species, such as Brewer's blackbirds (*Euphagus cyanocephalus*), predominate. Finally, are there trade-offs between conserving birds and producing safe food on farms? We predicted that retaining natural vegetation within and surrounding farm fields benefits conservation and reduces food-safety risks, promoting bird species of higher conservation concern that are less likely to carry pathogens.

Methods

Study region

Our work focused on three counties in the California Central Coast (*i.e.*, Santa Cruz, San Benito, and Monterey Counties), one of the most productive and economically-important agricultural regions in the United States, especially for fresh produce (CDFA 2020). Across this region, we selected 30 organic farms as study sites, with farms defined as contiguous lands managed by a single grower or operation.

Though farmers often grew many crops (see Table S1 for farm summary statistics), all study sites included lettuce. None of the farms in this study were mixed crop and livestock operations and we are not aware of any concentrated animal feeding operations (CAFOs) near the study sites.

The Central Coast region experiences a temperate Mediterranean climate and exists as a landscape mosaic of large monoculture farms, small diversified farms, grazing lands, and other seminatural habitats (*e.g.*, grasslands, shrublands, forest, riparian habitat, and wetlands). To study the effects of on-farm management practices and landscape context, we selected farms that independently varied in local on-farm diversification, the proportion of surrounding grazed land (1 km radius), and the proportion of surrounding ungrazed semi-natural habitats (1 km radius), leveraging aerial imagery from the National Agricultural Imagery Project (NAIP, 30 m resolution). We limited our study to organic farms because organic farmers (1) are constrained in which agrochemicals can be applied and thus often rely on diversification practices such as crop rotations and preserving non-crop vegetation to maintain soil fertility and control pests, (2) are subject to intense scrutiny regarding food-safety requirements, and (3) represent a growing share of the lettuce market, with ~22% of California lettuce acreage currently in organic production, approximately half of which occurs in the Central Coast (CDFA 2020; Carlisle et al. 2022).

Bird point count surveys

We surveyed birds on each farm using 10 min, 50 m fixed-radius point count surveys. Farms were repeatedly surveyed three times over consecutive days from May–July in 2019 and 2020 to satisfy closure assumptions of N-mixture models (Royle 2004, Supplementary methods). Each year, we surveyed 20 farms ($N=30$ total), with some farms surveyed both years ($N=10$) and others ($N=20$) in only one year due to crop rotations. Point-count locations ($N=227$) were separated by at least 100 m (range: 100 m–1514 m, mean=459 m; Ralph et al. 1993), with the number of point counts per farm varying by farm size (point counts: range: 3–6, mean=5.7; point counts per 10 hectares: range: 0.1–11.4, mean=3.1). At least half of the count locations on each farm were centered in

lettuce; the other half were in other dominant crops (*e.g.*, strawberry, squash, broccoli). All surveys were conducted by the same skilled observer (T. Glaser), primarily between sunrise and 10:30 am and always in the absence of rain or heavy fog. All individuals seen or heard within the survey radius were identified to species and recorded, alongside key covariates that may influence bird detectability (*e.g.*, time of day, day of year, wind speed, temperature, presence of loud noises, etc.). We also noted the substrate (*e.g.*, crop field, tree, fence, etc.) associated with each bird observation.

Flocking birds and species traits

Flocking birds could increase food-safety risks by leaving concentrated deposits of fecal contamination on farms. We thus created a binary response variable to indicate whether flocks were observed during each survey. To reflect food-safety risks, we excluded observations of birds in trees (which were less likely to interact with the crops) and auditory detections when an individual's exact location was unknown (*e.g.*, crop field vs. tree). We also excluded swallows because they are usually observed flying above crop fields but seldom contact crops. Then, we defined flocks as a group of 7 or more individuals of the same species observed during a survey.

We also collected two species traits. First, we defined 'flocking species' as any species for which we observed flocking behavior (using the criteria listed above). Second, we collected conservation scores for each species from the 2016 State of North America's Birds report (North American Bird Conservation Initiative 2016), which incorporates information on population size, distribution, and other components of vulnerability. Because this report focused on native species only, we assigned the lowest conservation score possible to non-native species (*e.g.*, house sparrow (*Passer domesticus*) and European starling (*Sturnus vulgaris*)).

Local farm management practices and landscape context

We quantified the level of local (on-farm) diversification associated with each 50 m radius point-count location by building a composite index from measurements of crop diversity, non-crop vegetation cover,

and vegetation complexity (Supplemental methods). We also documented the total length of fencing in each point count radius. Next, we manually digitized seminatural habitats (forest, shrubland, grassland, pasture, and wetlands) from NAIP 2016 imagery within a 1 km radius of each sampling location using ArcMap 10.3.1 (ESRI, Redlands, CA, USA). To assess the effects of different types of seminatural habitat, we overlaid spatial grazeable land data from the Farmland Mapping and Monitoring Program (CDOC 2016) on top of our land-cover map. Grazeable land, or land where vegetation is suitable for grazing livestock in California, was dominated by grasslands and pastures. We thus further subdivided our maps into grazed seminatural habitat (areas of overlap between our seminatural habitat map and grazeable lands) versus ungrazed seminatural habitat (*i.e.*, forest, shrubland, grassland, and wetlands).

Bird fecal transects and pathogen testing

We surveyed bird fecal contamination along three parallel, 20 m transects in lettuce crops on each farm ($N=120$ transects across both years). Transects were located at the farm edge with the most seminatural habitat, as far from a farm edge as possible (up to 500 m from the edge), and halfway in between. We recorded the number of bird feces within 20, 1 m², adjacent quadrats centered along each transect. In 2019 only, we also collected 10 fecal samples from each transect, or extended sample collection beyond the transect as needed to obtain 10 samples. We placed samples in sterile cryotubes filled with 100% ethanol, immediately froze them in a liquid nitrogen dewar, and kept samples frozen until DNA extraction. We screened bird fecal samples for *E.coli* virulence genes, *Campylobacter* spp., and *Salmonella* spp. using multiplex polymerase chain reactions. Although Shiga-toxin producing *E. coli* that carries the *stx1* and/or *stx2* genes is responsible for causing disease in humans, other ‘virulence genes’ can contribute to pathogenesis. *E.coli* virulence genes carried by birds can be transferred between bacterial strains, and when combined with Shiga-toxins, can result in pathogenic *E.coli* strains that cause severe disease in humans (Paton and Paton 2002; Bryan et al. 2015; see Supplemental methods).

Statistical analyses

We used occupancy and N-mixture models that account for variation in detection probability to estimate species presence/absence and abundance, respectively, and to quantify changes in bird communities among sites (Royle 2004; Ficetola et al. 2018; Kéry 2018). Specifically, we created three types of N-mixture and occupancy models to (1) estimate the abundance/occupancy of each species at each point-count location, (2) understand how local and landscape diversification affects species- and community-level abundance/occupancy, and (3) measure how species traits interact with diversification variables to affect abundance/occupancy (Supplemental methods). We considered community-level parameters to be statistically significant when their 95% Bayesian credible interval did not overlap zero (BCI; the range between the 2.5 and 97.5th percentiles of the posterior distribution). In contrast, we considered species-level parameters to be statistically significant when their 90% BCI did not overlap zero, as species-level effects are estimated with lower sample sizes and thus less power (Frishkoff and Karp 2019). We also determined whether species varied in their responses to local diversification, landscape context, and/or their interactions by examining the variation (σ parameter) associated with each slope term (Supplemental methods). Responses were considered to vary significantly among species when the 90% highest posterior density interval of σ did not overlap 0 (Frishkoff and Karp 2019).

To quantify bird conservation metrics, we extracted the number of individuals (and occupancy state) for each species at each site across 3000 posterior iterations of the N-mixture and occupancy models. We then calculated the species richness, Shannon diversity, Simpson diversity, and total bird abundance for each point-count location and each posterior iteration. To quantify the ‘conservation value’ of each community, we extracted posteriors from the occupancy model and then calculated the average conservation score across all species estimated to occur at each site. Finally, we calculated the median and inverse interquartile range of each metric across all posteriors (see Supplemental methods for more information).

We measured pathogen risk in several ways. First, we quantified the number of feces detected within each 20 m transect (*i.e.*, fecal density). Next, we created binary responses to indicate whether each of the

assayed fecal samples tested positive for any pathogen. Finally, we quantified pathogen risk as the product of the total number of feces per 20 m transect and the fraction of feces testing positive for *Campylobacter* spp., *Salmonella* spp., or any *E.coli* virulence gene. We divided this number by 20 to ultimately arrive at an estimate of ‘potentially pathogenic fecal density’ or the number of potentially pathogenic feces per m².

We used generalized linear mixed models (GLMMs) to test the effects of local diversification and surrounding seminatural habitat on bird conservation and pathogen risk metrics. All models included fixed effects of local diversification, grazed and ungrazed seminatural habitat within 1 km, and two interactions between local diversification and grazed and ungrazed seminatural habitat. Fecal density and pathogen risk models also included distance from the fecal transect to the nearest non-crop edge as a fixed effect to account for spatial variation in bird activity. Pathogen prevalence, fecal density, and pathogen risk models included ‘day of year’ to account for seasonal effects that may impact pathogen exposure. Bird conservation models included the inverse of the inter-quartile range of richness, abundance, diversity, or conservation score across posteriors as model weights to allow estimates with less uncertainty to have more influence. All models included a random intercept of farm to account for spatial dependence of individuals captured on the same farm.

We used linear mixed models to analyze diversity, species richness, abundance, conservation score, fecal density, and pathogen risk. Some linear mixed models were built with estimates from N-mixture models (diversity, species richness, abundance) and occupancy models (conservation score). We used binomial GLMMs with a log link function for the probability of flocks occurring and pathogen prevalence. We transformed some variables (fourth-root: richness, abundance; log: fecal density + 1, pathogen risk + 0.1) to meet model assumptions, scaled covariates by subtracting by the mean and dividing by the standard deviation, and verified that models did not display multicollinearity (Pearson correlation coefficient < 0.6). We ran models with the glmmTMB package (Magnusson et al. 2016) and performed model selection with the MuMIn package (Bartoń 2020) in R. To do so, we first identified the best-supported models within 2 AIC of the top model and then used a model averaging approach of the best-supported models to assess variable

significance based on p-values within these top models (Burnham and Anderson 2002).

Finally, we visualized and analyzed community turnover between sites by first extracting the median abundance of each species at each site across all 3000 posteriors from N-mixture models and then calculating the community dissimilarity between each pair of sites (Bray–Curtis dissimilarity). We visualized differences in community composition between sites via Non-Metric Multidimensional Scaling and then used Permutational Multiple Analysis of Variance (PERMANOVA) with the ‘adonis’ function in the ‘vegan’ library (Oksanen et al. 2022), with farm as a blocking factor, to assess the influence of diversification on species turnover.

Results

We detected 8,088 individual birds representing 92 species. The most abundant species were cliff swallow (*Petrochelidon pyrrhonota*), house finch (*Haemorhous mexicanus*), barn swallow (*Hirundo rustica*), Brewer’s blackbird (*Euphagus cyanocephalus*), and European starling (*Sturnus vulgaris*), accounting for more than half of all observations. Three of these species were flock-forming (*H. mexicanus*, *E. cyanocephalus*, *S. vulgaris*). We also detected 2 IUCN red-listed species (tricolored blackbird [*Agelaius tricolor*], olive-sided flycatcher [*Contopus cooperi*]) and 5 species of conservation concern (North American Bird Conservation Initiative 2016).

How do farm management and landscape context structure bird communities?

Farms with higher local diversification hosted greater bird abundances ($p < 0.01$; Fig. 1D) but did not have greater diversity or species richness (Fig. 1A, S13; Table S7-10/12). Nonetheless, on average across communities, species abundances and occupancies were positively correlated with local diversification (Fig. S11/12). At the species level, 13/90 species had greater abundance and 16/91 species had higher occupancy with local diversification (Table S3/4; Fig. S1/6/11/12). PERMANOVA indicated a relatively small amount of community turnover along the local diversification gradient ($p < 0.01$; Fig. 2A, Table S13). These small community shifts did not

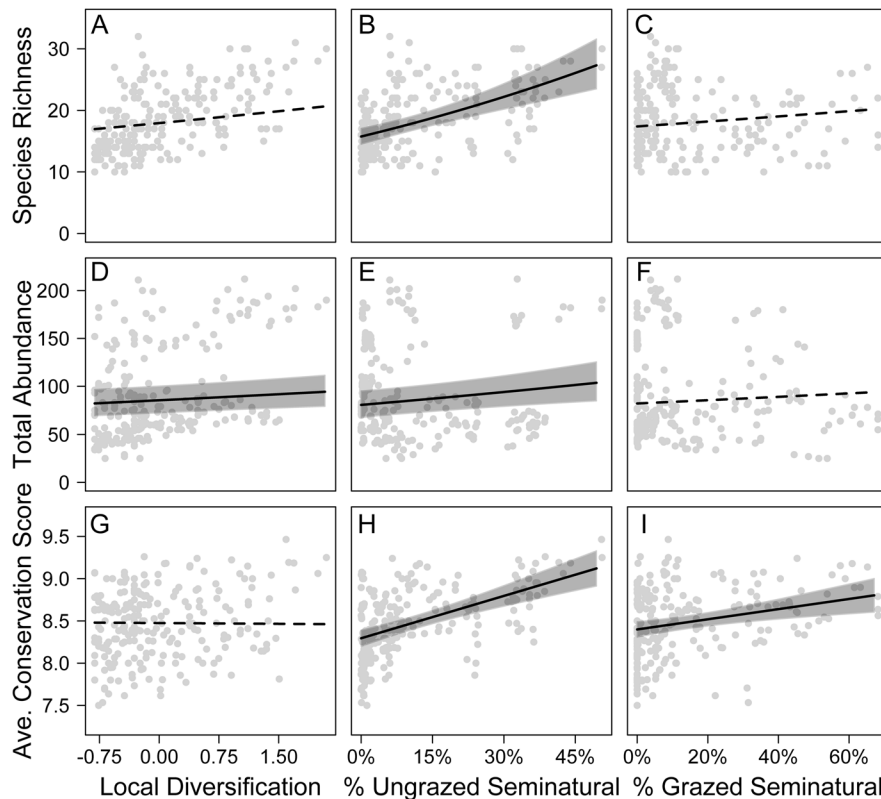


Fig. 1 Effects of local farm diversification and landscape context on bird biodiversity. Bird species richness was similar on diversified vs. simplified farms (A), was higher on farms surrounded by more ungrazed seminalural habitat (within a 1 km radius; B) and did not change with surrounding grazed seminalural habitat (C). Bird abundance was higher on more locally diverse farms (D) with more surrounding ungrazed seminalural habitat (E) but did not respond to grazed seminalural habitat (F). The conservation value of bird communities did not respond to local diversification (G), was much greater on farms

near ungrazed seminalural habitat (H), and slightly greater on farms near grazed seminalural habitat (I). Gray points correspond to point-count locations and represent median estimates across posteriors from N-mixture (richness, abundance) and occupancy (conservation score) models. The solid black lines and gray bands correspond to predictions and 95% confidence regions from the top mixed models. Dashed black lines indicate non-significant trends (and are graphed from global models including all predictors)

result in any changes to average conservation scores and species with higher conservation scores did not respond differently to local diversification than those with lower scores (Fig. 1G, Table S5/6/11/12).

Effects of surrounding ungrazed seminalural habitat were stronger than local diversification, with bird diversity ($p < 0.0001$), richness ($p < 0.0001$), and abundance ($p < 0.001$) all greater in areas with more surrounding habitat (Fig. 1B/E, S13; Table S7-10/12). On average across communities, species abundances and occupancies were greater in areas with more ungrazed seminalural habitat; at the species-level, 29 and 26 species had significantly higher abundance and occupancy, respectively (Table S3/4, Fig. S3/8/11/12). Nonetheless, there

was significant variation in how species responded, with 6 and 8 species exhibiting the reverse trend and having lower abundance and occupancy, respectively (Table S3/4, Fig. S3/8). Correspondingly, PERMANOVA indicated strong community turnover with ungrazed seminalural habitat ($p < 0.001$, Fig. 2B, S13). Species of higher conservation concern were particularly likely to have higher occupancy (but not abundance) at sites with more ungrazed seminalural habitat (Table S5/6). As a result, the average community-wide conservation score was higher at sites with more ungrazed seminalural habitat (Fig. 1H; Table S11/12).

Grazed seminalural habitat exhibited much weaker effects, with no significant effects on bird diversity,

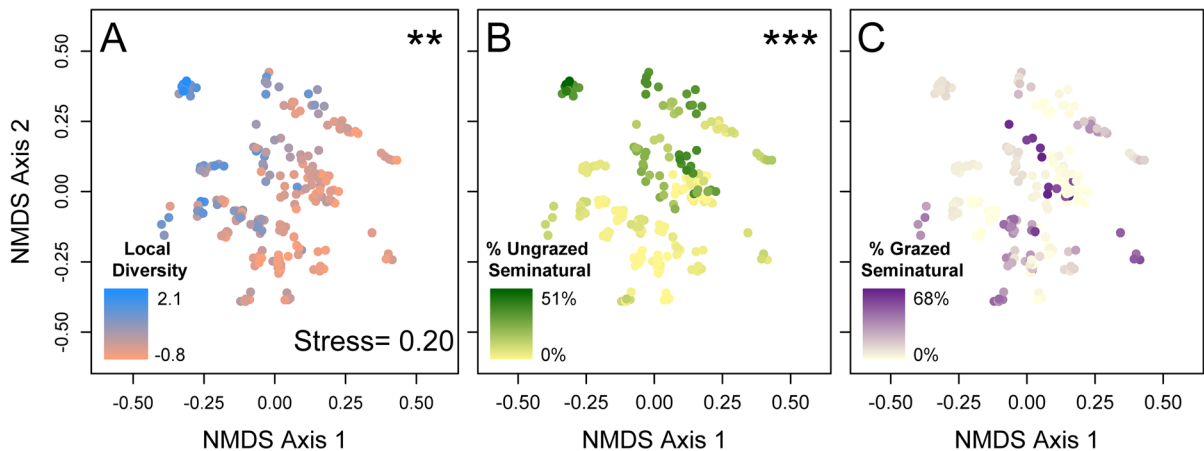


Fig. 2 Non-metric multidimensional scaling (NMDS) plots depicting effects of local farm diversification and landscape context on bird communities. The distance between points (point-count locations) represents distinctness in community composition, calculated as turnover in individuals (Bray–

Curtis). Axes represent ordination distances and plots show significant differences in bird composition along local diversification (A) and ungrazed seminatural habitat (B) gradients (Table S13) but not grazed seminatural habitat (C). ** indicates that $p < 0.01$, *** indicates that $p < 0.001$

richness, or abundance ($p > 0.05$; Fig. 1C/F, S13; Table S7-10/12). On average across the community, species had greater abundances and occupancies in areas with more grazed seminatural habitat, but this effect was much weaker than for ungrazed seminatural habitat (Table S3/4, Fig. S2/7/11/12). Moreover, at the species level, only 6 species had greater abundance, 6 had higher occupancy, and none had lower abundance on farms surrounded by more grazed areas (Table S3/4, Fig. S2/7). Species with greater abundance in grazed areas were all grassland, oak savannah or woodland, or chaparral habitat specialists. Likely because such species are often at-risk, species with higher conservation scores were more likely to be positively correlated with grazed habitat (Table S5/6/12). As a result, conservation scores were higher in areas with more grazed seminatural habitat, although this effect was much weaker than ungrazed habitat (Table S11/12). Though species varied in their abundance and occupancy responses to grazed seminatural habitat, PERMANOVA indicated that this variation was not enough for grazed habitat to elicit changes in community composition ($p = 0.99$, Fig. 2C; Table S13).

Finally, the effects of local diversification and surrounding seminatural habitat were largely independent. The top GLMM model sets for richness, diversity, abundance, and conservation scores did not include interactions between local diversification and

ungrazed or grazed seminatural habitat. However, occupancy models suggested that the positive effect of local diversification on bird species occurrence was stronger near grazed habitats and weaker in areas with more ungrazed seminatural habitat. N-mixture models suggested that the positive effect of local diversification on bird abundance was also weaker near ungrazed seminatural habitat.

How does diversification influence avian food-safety risks?

We detected *Campylobacter* spp. in 5.7% (34/601) and *E. coli* virulence genes in 8.2% (49/601) of samples. We did not detect *Salmonella* spp. or Shiga-toxin producing *E. coli* genes in any sample (Table S2). The average density of bird feces in crop fields was 0.2 feces/m² and the average density of potentially pathogenic feces (*i.e.*, feces that tested positive for *Campylobacter* spp. or any *E. coli* virulence gene) was 0.05 pathogenic feces/m² (Table S1).

Both local farm diversification and ungrazed seminatural habitat had no effect on pathogen prevalence, fecal density, or pathogen risk (Fig. 3A/B; Table S14-17/19). Species that flock were more likely to have lower abundance and occupancy on farms with higher local diversification and more surrounding ungrazed habitat. The likelihood of observing flocks in the field was negatively correlated with surrounding ungrazed

habitat but not with local diversification (Fig. 4, Table S18/19).

Unlike local farm diversification and surrounding ungrazed habitats, grazed seminatural habitat was associated with higher fecal density ($p=0.02$) and pathogen risk ($p=0.02$; Fig. 3C, Table S14/17/19). More grazed habitat was also associated with higher prevalence of *Campylobacter* spp. and *E.coli* virulence genes, but these trends were not significant. Finally, there were no significant effects of interactions between local diversification and grazed or ungrazed seminatural habitat on avian food-safety risks, including flocking birds.

Are there trade-offs between conserving birds and producing safe food on farms?

We found no strong evidence of trade-offs between managing to mitigate food-safety risks versus bird conservation (Fig. 5). At the farm level, pathogen risk was not associated with bird species richness, abundance, or conservation scores. Bird flocks were positively correlated with abundance and weakly negatively correlated with species richness and conservation scores, although these trends were not significant. However, conservation scores in grazed semi-natural habitats were somewhat higher than on

farms due to greater abundances of several grassland species of conservation concern.

Discussion

Our work suggests that on-farm diversification practices and habitat conservation in surrounding landscapes can benefit birds without necessarily increasing food-safety risks. Indeed, the only potential trade-off manifested on farms near grazed seminatural habitat, which slightly increased the average conservation score of bird communities but also incurred higher pathogen risks. Pathogen prevalence rates in bird feces were low, similar to other studies (Navarro-Gonzalez et al. 2019; Smith et al. 2020a; Olimpí et al. 2022). Thus, diversified farming practices offer potential to simultaneously conserve biodiversity and provide safe food for human consumption.

Bird communities and farmland diversification

Our results suggest that farmland birds benefit from diversification at the farm and landscape scales, with the strongest effects in response to surrounding ungrazed seminatural habitat. Compared to farms without surrounding ungrazed habitat, farms

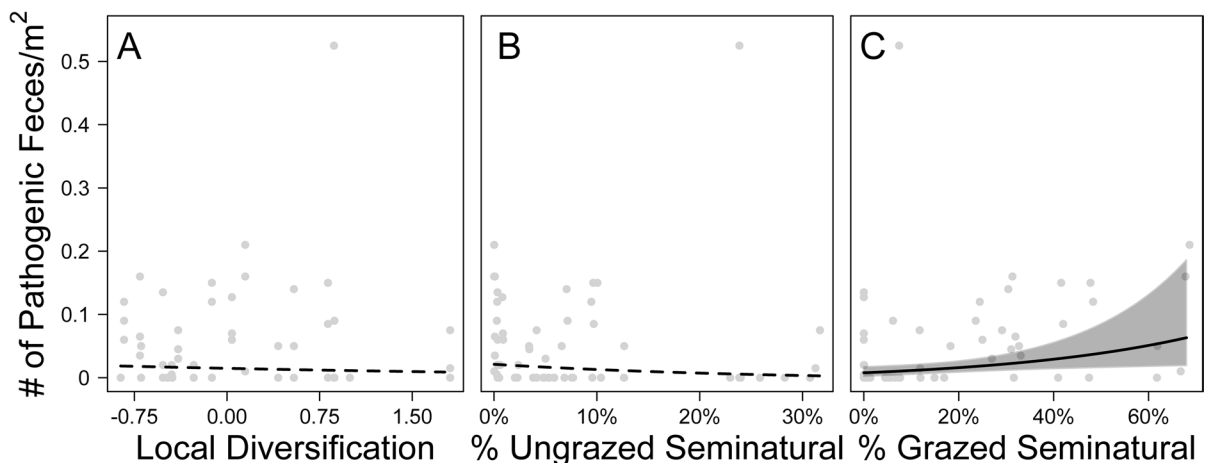


Fig. 3 Effects of local farm diversification and landscape context on the density of potentially pathogenic feces. The number of potentially pathogenic feces/m², defined as feces that tested positive for *Campylobacter* spp. or *E. coli* virulence genes, was greater on farms surrounded by higher amounts of grazed seminatural habitat (C). Local farm diversification (A) and ungrazed seminatural habitat (B) did not affect pathogen

risk. Gray points indicate numbers of pathogenic feces from each transect survey (3 per farm). The solid black line and gray band correspond to predictions and 95% confidence regions from the top mixed model. Dashed black lines indicate non-significant trends (and are graphed from global models including all predictors)

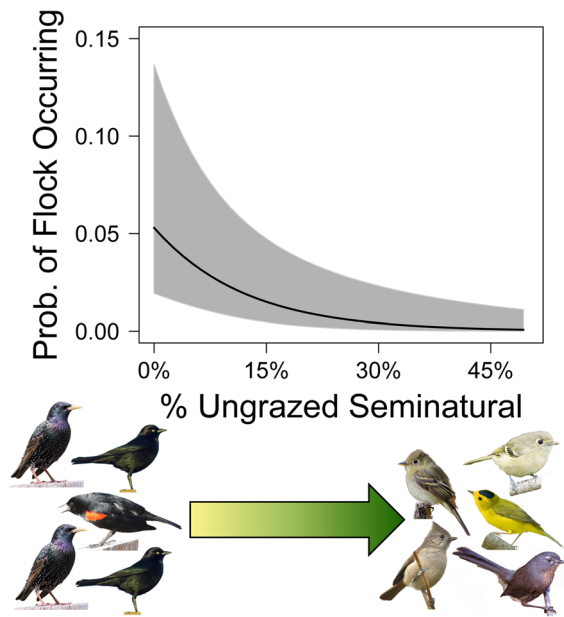


Fig. 4 Effect of ungrazed seminatural habitat surrounding farms (within a 1 km radius) on the probability of observing flocks of 7 birds or more in crop fields. Flocks were most likely to occur on farms surrounded by low amounts of ungrazed seminatural habitat. As community composition shifts in response to increasing ungrazed seminatural habitat (Fig. 2B), flocking species (depicted as European starling, Brewer's blackbird, and red-winged blackbird) are replaced by species of higher conservation value (Pacific-slope flycatcher, oak titmouse, Hutton's vireo, Wilson's warbler, and wren-tit icons; Table S4-7, Fig. S2/7). The solid black line and gray band correspond to predictions and 95% confidence regions from the top mixed model

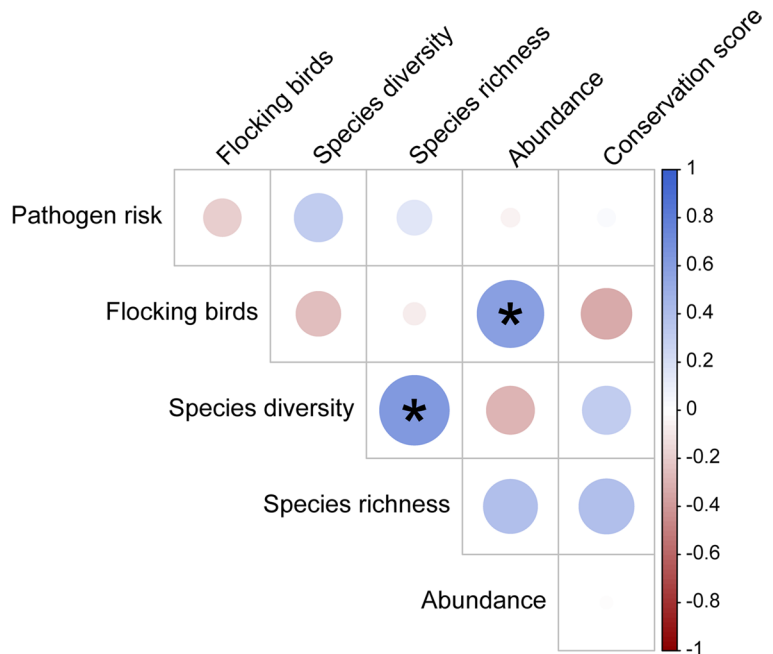
with 50% ungrazed habitat within 1 km had 73% higher species richness, 66% higher diversity, and 29% higher abundance. This result aligns with prior work in our study region (Olimpi et al. 2022; García et al. 2023) and elsewhere (Gonthier et al. 2014) that found birds to be most sensitive to habitat at landscape rather than local scales, perhaps because birds' high mobility buffers them against on-farm management changes (Gonthier et al. 2014). Still, not all species benefited, and, as such, bird communities in landscapes with ungrazed habitat were distinct from communities in simplified landscapes. Species of conservation concern were more consistently present and flocking species absent on farms near more ungrazed habitat. It is unsurprising that species of conservation concern benefit from surrounding ungrazed habitat, as agricultural intensification is

a major threat to North American birds (Stanton et al. 2018). In contrast, structurally complex vegetation in ungrazed habitats may deter the movement of flocking species that prefer more open habitats (Harris and Reed 2002), although we did not specifically measure structural complexity or heterogeneity. Indeed, species frequently observed flocking (e.g., Brewer's blackbird, *Euphagus cyanocephalus*; European starling, *Sturnus vulgaris*) often forage on or near the ground (Wilman et al. 2014) and are notably absent from heavily forested regions (Roberson 2002).

Compared to ungrazed habitats, grazed seminatural habitats were associated with weaker benefits for bird conservation and higher infectious disease risks. For example, only 6 species (none of conservation concern) had greater abundance and/or occupancy in areas with more grazed seminatural habitat, as opposed to ≥ 26 (3 of conservation concern) in areas with more ungrazed habitat. Bird abundance, diversity, and richness were not higher near grazed seminatural habitats, but the conservation value of bird communities was higher in these areas. The positive association between conservation value and grazed seminatural habitat was driven by grassland and oak woodland associated species (e.g., lark sparrow, *Chondestes grammacus* and western meadowlark, *Sturnella neglecta*; Ehrlich et al. 1988; Roberson 2002), a group of birds that is undergoing rapid declines (Rosenberg et al. 2019). The abundances of both lark sparrows and western meadowlarks were positively associated with grazed but not ungrazed seminatural habitat, suggesting that grazed areas are most important for those species associated with more open habitats. Still, overall, ungrazed habitat proved much more important for species of higher conservation value compared to grazed habitats: a 50% increase in grazed habitat was associated with a 3.6% increase in conservation scores, while the same increase in ungrazed habitat was associated with a 10.1% increase.

Locally, farms that implemented more diversified practices tended to have higher species abundances and occurrences. Planting multiple crops and/or native vegetation in the form of hedgerows, flower strips, or in small patches bolsters the abundance and diversity of plants and arthropods (Batáry et al. 2011; Gonthier et al. 2014; Tamburini et al. 2020). Correspondingly, species from a broad range of feeding guilds significantly benefited from local diversification, including granivores, insectivores, nectarivores, and

Fig. 5 Pairwise correlations between mean bird biodiversity (bird species richness, diversity, abundance, and conservation score) and food-safety risk (pathogen risk and probability of observing flocking birds) at each farm. We found limited evidence of trade-offs between managing food-safety risks and managing bird conservation. Larger circles and more intense colors correspond to stronger Pearson correlation coefficients; asterisks indicate significant relationships ($p < 0.05$)



generalists (Wilman et al. 2014), potentially reflecting the increased availability of both plant and arthropod resources on diversified farms. Similarly, the more complex vegetation structure present on diversified farms benefited species that feed on the ground (e.g., California quail, *Callipepla californica*), in shrubby vegetation (e.g., wrentit, *Chamaea fasciata*), and in trees (e.g., band-tailed pigeon, *Patagioenas fasciata*, (Wilman et al. 2014)). Local diversification may also provide predator protection, which is a major driver of ground-nesting bird declines in Europe (McMahon et al. 2020). In our case, however, we observed positive responses to local diversification across nesting guilds. As a result, the benefits of local diversification were broadly felt across the bird community and thus did not translate to significant shifts in community composition between simplified versus diversified farms and did not offer greater benefits for species of higher conservation concern. Interestingly, the relative impact of local diversification practices on bird abundance/occupancy was stronger in landscapes with less surrounding ungrazed seminatural habitat. This result is consistent with the intermediate landscape hypothesis, which states that biodiversity benefits are expected to be strongest in landscapes with some remaining natural habitat, but that local conservation measures may not meaningfully augment resources in complex landscapes (Tscharrntke et al. 2012).

Food safety and farmland diversification

We detected no *Salmonella*, no Shiga-toxin producing *E. coli*, and low prevalences of *E. coli* virulence genes and *Campylobacter* spp. in our sample of wild birds. The infectious disease risks associated with *Campylobacter* spp. and *E. coli* virulence genes are unclear. Mounting evidence suggests that *Campylobacter* strains may be host-specific, with strains detected in wild birds unlikely to be a major source of human infections (Colles et al. 2009; Griekspoor et al. 2013; Smith et al. 2020b). Furthermore, the presence of *E. coli* virulence genes does not represent a direct threat to food safety (without the presence of a Shiga-toxin producing gene, which was always absent). Still, *E. coli* are capable of horizontal transmission of virulence genes between strains; thus, the transfer of virulence genes from bacteria carried by birds to human pathogens could contribute to the emergence of virulent strains (Bryan et al. 2015).

Higher levels of local diversification and more surrounding ungrazed habitat were associated with greater bird abundance but not with higher pathogen risks. If anything, the density of potentially pathogenic feces was lower on farms surrounded by more ungrazed habitat (though not significantly so). This trend could be because species that form large flocks (thus easily contaminating crops with feces) were

less likely to benefit from diversification. Indeed, regional food-safety guidance directs growers to consider bird flocks as a food-safety risk factor (LGMA 2020). Another possibility is that birds on diversified farms or in complex landscapes preferentially forage within the non-crop vegetation, defecating on crops less often despite being present in higher numbers. Similarly, a recent study reported that, despite hosting higher mammalian abundance and diversity, hedgerows did not increase mammal intrusion into California orchards or tomato fields and thus did not increase food-safety risks (Sellers et al. 2018).

Managing birds and food safety near grazed lands

Grazed habitat was also associated with higher pathogen risk, as measured by the density of potentially pathogenic feces. For example, a 50% increase in surrounding grazing lands would mean that a single potentially pathogenic bird fecal sample in crop fields would be expected within 26m² as opposed to 128m². Our work extends previous studies that linked grazing lands and foodborne pathogen prevalence on produce farms (Benjamin et al. 2013; Karp et al. 2015b) by evaluating associations between farm management practices and two types of surrounding seminatural habitat. Associating with livestock seems to be a primary determinant of which bird species carry pathogens (Smith et al. 2021). Yet, importantly, our results suggest that the higher pathogen risk associated with grazed lands had more to do with higher fecal densities than increased pathogen prevalences. Because grazing lands were not associated with community turnover, more bird flocks, or greater abundance, we suggest that bird behavior could explain differences in fecal density. First, birds that utilize open habitats may be more inclined to move between seminatural areas and farms in landscapes with more grazing lands due to similarities in the low vegetation structure of crop fields and grasslands. A positive interaction between local diversification practices and grazed habitat on bird occurrence also suggests that diversified farms could encourage bird movement between farms and adjacent grazed lands. Second, bird fecal densities are often higher on fresh produce farms with high densities of fencing and wires, where birds often perch (Olimpi et al. 2020). In a post-hoc analysis, we found that farms surrounded by more grazing lands tended to have marginally higher densities of fencing,

likely to exclude livestock or other wildlife (Pearson correlation coefficient: $R = 0.13$, $p = 0.06$). Ultimately, studies that track bird movements between a variety of farm management types and adjacent grazed lands (e.g., Rivadeneira et al. 2016) are needed to resolve the level of infectious disease risk associated with diversifying farms near grazed lands.

Limitations

Our study is not without limitations. First, all bird surveys occurred in the morning to standardize effort across farms during periods of high bird activity. Nonetheless, different species may be active at different times, making it possible that we underestimated flocking behavior for some species and at some farms. Second, though rain was absent, differences in irrigation practices among farms could have influenced fecal density analyses if heavy irrigation washed feces away before they could be detected.

Finally, it is unclear whether the trends observed here would also be observed in other crops, regions, and/or production systems. Though our focal farms often also grew other crops, we focused on organic lettuce production because foodborne disease outbreaks have been linked to leafy greens, making them a focus of food-safety regulations (LGMA 2020). In addition, lettuce ranked as the most important agricultural commodity in Monterey and San Benito Counties (San Benito County Agricultural Commissioner 2020; County of Monterey Agricultural Commissioner 2021) and the seventh most important agricultural commodity in California in 2020 (total value, production, and acreage: ~US\$2.3 billion, ~3.3 million tons, and ~200,000 acres, respectively), with California leading the nation in its production (75.8% of U.S. receipts, (CDFA 2020). Encouragingly, many of the trends we report here paralleled observations in California strawberry fields (Olimpi et al. 2022; García et al. 2023).

Conclusions

Farmland birds are in decline (Stanton et al. 2018; Rosenberg et al. 2019). Our results suggest that maintaining non-crop vegetation on farms and, even more

importantly, in surrounding landscapes can result in large conservation gains, especially for species of conservation concern. Yet fear that birds, and other wildlife, represent significant food-safety risks has created pressure on growers to reduce biodiversity in their fields, resulting in widespread habitat clearing (Gennet et al. 2013; Karp et al. 2015b; Baur et al. 2016) and contributing to biodiversity declines.

Nonetheless, existing evidence suggests habitat conservation has neutral to positive effects on lowering pathogen risk (Karp et al. 2015b; Weller et al. 2022). Vegetated buffers around farm fields may filter pathogens out of runoff and reduce transmission to produce fields from adjacent grazed lands (Tate et al. 2006; Strawn et al. 2013; Glaize et al. 2021). Moreover, cleared non-crop vegetation may create species-poor communities that are dominated by species more likely to carry pathogens (Kilonzo et al. 2013; Smith et al. 2021), resulting in higher pathogen prevalences in homogenous, agricultural landscapes (Smith et al. 2020a, 2022; Olimpí et al. 2022).

Our work contributes to filling an important knowledge gap concerning how different farm management practices affect the risk of foodborne pathogens spread by wildlife. We demonstrated that farms without surrounding ungrazed seminatural habitat were associated with species-poor communities, dominated by flock-forming species of higher food-safety risk. Further, we found no evidence that heightened bird abundances on more diversified farms and in landscapes with surrounding ungrazed habitat were associated with higher fecal densities or pathogen prevalence. Grazed lands, however, were associated with higher pathogen risk. Together, our results suggest that halting habitat removal, conserving surrounding ungrazed seminatural areas, and diversifying produce farms far from grazing lands would likely result in large conservation gains without enhancing risks associated with foodborne pathogens.

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Author contributions DK, TB, CK, and EO designed the study; TG collected field data and prepared maps; WS led pathogen sample processing; AK led occupancy and N-mixture modeling, EO and DK performed other data analyses and wrote the first draft of the manuscript; and all co-authors provided critical feedback and approved the manuscript for publication.

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Data availability Data available from the Dryad Digital Repository: https://datadryad.org/stash/share/ctHMGc_ptHKdDMPjGNA-yaC5U1L1fhTxVAH3jh0-oIE (Olimpi et al. 2023).

Declarations

Competing interests The authors have no competing interests to disclose.

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