



Semi-natural habitats on organic strawberry farms and in surrounding landscapes promote bird biodiversity and pest control potential

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ABSTRACT

Agricultural intensification and expansion have degraded biodiversity in agroecosystems, jeopardizing the ecosystem services provided by wildlife. Birds can act as particularly important purveyors of ecosystem services to farmers by consuming arthropod pests. Some bird species, however, may sometimes act as pests themselves by consuming crops. Further, on-farm management practices (e.g., crop diversity, vegetative structure) and the complexity of the surrounding landscape can shift the balance of bird-mediated ecosystem services and disservices through changes in bird community composition. Here, we explored how organic strawberry farms in California could be managed to bolster bird biodiversity and shift community composition from strawberry-consuming to pest-eating species. Using multi-species N-mixture models we found that semi-natural habitat at the landscape (1000 m) and farm (50 m) scales were positively associated with mean abundance of all birds, with varying effects on different species. In particular, we found that the mean local abundance of species that consume *Lygus* spp. (a major pest), but not strawberry-consuming species, increased with semi-natural habitat at the farm scale. Nest density in developed areas within farms also increased with greater semi-natural habitat in the landscape, while nest density in semi-natural habitat within farms decreased with increasing semi-natural habitat in the landscape. Further, nest density of *Lygus* spp. eating birds increased with increasing local semi-natural habitat. These results suggest that increasing semi-natural habitat at the landscape and local scales can bolster bird abundance across farms, while pest control can be promoted locally by conserving or restoring semi-natural vegetation at the farm scale.

1. Introduction

Agricultural intensification and expansion have inadvertently contributed to the degradation of biodiversity and the ecosystem services it provides to farmlands, threatening the resiliency of agroecosystems worldwide (Bommarco et al., 2013). Rapid growth in global crop production, increased use of agrochemicals, and conversion of natural ecosystems to agricultural lands have aided in reducing food shortages, but at great environmental costs that threaten ecosystem functions (Tilman et al., 2001). Thus, a key challenge looking forward is finding sustainable methods of food production that simultaneously

conserve biodiversity and promote ecosystem services.

The insidious consequences of agricultural intensification and expansion are severe and wide-ranging across various taxa, with agriculture posing a great threat to bird biodiversity (Donald et al., 2001; Green et al., 2005; Stanton et al., 2018). Indeed, populations of birds associated with agricultural habitat have rapidly declined in North America from 1966 to 2013 (Stanton et al., 2018). This loss of birds may lead to subsequent declines in the ecosystem services that birds provide in agricultural habitats. While some bird species can act as pests or pose risks to agricultural commodities (e.g., by consuming or damaging crops, by acting as intraguild predators in which birds consume

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arthropods that benefit crop protection such as generalist predators like spiders, or by posing food safety hazards), other bird species provide benefits (e.g., via biological control of insect pests; Garcia et al., 2020). Anderson et al. (2013) estimated that damage by birds to five fruit crops across five U.S. states totaled nearly \$2 M USD per year. Yet a recent global-scale meta-analysis found that wild birds in agroecosystems generally reduced crop damage, reduced pest abundance, and increased yield (Díaz-Sieffer et al., 2021). Thus, due to the mixed effects of bird activity in farms, bird conservation within agricultural landscapes is viewed favorably by some stakeholders but negatively by others across different farming contexts. This underscores the importance of disentangling the local and landscape features that promote beneficial bird species while minimizing risks and costs to farm production.

In contrast to agricultural intensification practices, ecological-based practices, such as the incorporation of on-farm diversification features such as insectary strips, hedgerows, or polyculture at the farm scale, and structurally-complex habitat within agricultural landscapes surrounding farms can make farmlands more permeable and hospitable to wildlife (Kremen and Miles, 2012; Kremen, 2020). For example, at the landscape scale, higher proportions of semi-natural habitat in the landscape surrounding strawberry (*Fragaria x ananassa*) farms in Central Coast California increased bird abundance and richness (Gonthier et al., 2019). In another region of California, orchard fields with borders comprised of woody vegetation harbored greater bird diversity and abundance than those with less complex (bare or weedy) margins (Heath et al., 2017). In addition to making agricultural landscapes more appealing to wildlife, the adoption and implementation of ecological-based practices at landscape and local scales can assist in harnessing ecosystem services by birds to meet food production goals. At the landscape scale, for example, greater forest cover was correlated with increased bird consumption of an economically damaging insect pest in Costa Rican coffee (*Coffea arabica*; Karp et al., 2013). The presence of non-crop vegetation at the local (farm) scale can also promote birds and their ecosystem services in agricultural systems. Kross et al. (2016), for example, found that the presence of a complex field edge, defined as woody and shrubby vegetation taller than 1.5 m, both increased bird abundance in an intensive agricultural field and reduced insect pest populations.

A great body of literature, largely bird exclusion experiments, demonstrates that bird communities can be beneficial, harmful, or net neutral to agroecosystems (Mäntylä et al., 2011; Karp et al., 2013; Peisley et al., 2016; Gonthier et al., 2019; Olimpi et al., 2020). However, bird exclusion studies often fail to identify which bird species are responsible for services or disservices. While some studies have relied on observational methods to identify bird species that consume crops and to estimate consumption rates (e.g., Hannay et al., 2019), these methods are better suited for conspicuous bird activity such as crop consumption (i.e., disservices). Whereas it may be more difficult to apply observational methods to identify birds that are consuming pest insects, given the small size and high mobility of insects. Direct observational methods have been deemed ineffective methods for identifying avian predators of key insect pests in agroecological systems such as apples (*Cydia pomonella*; see Mangan et al., 2017 discussion) and coffee, where the small size of a key pest (coffee berry borer beetle *Hypothenemus hampei*; ~2 mm) makes it unlikely to witness consumption events of this pest (Karp et al., 2014). Indeed, it is difficult to observe precisely what a bird consumes in the field, particularly as many species are aerial generalist predators. Therefore, without knowing which bird species deliver services or disservices it is difficult to manage agroecological features that may increase beneficial species and reduce harmful species. Within the last decade, however, the emergence of novel DNA-based methods such as high-throughput sequencing (HTS) has made it possible to create comprehensive diet profiles from DNA extracted from fecal samples (Alberdi et al., 2019). High-throughput sequencing has been a useful tool in describing the diets of bird communities in agroecosystems such as in Australian macadamia (*Macadamia integrifolia*) orchards (Crisol-Martinez et al., 2016) and in soybean (*Glycine max*) fields in Illinois,

US (Garfinkel et al., 2022). Here we utilize DNA metabarcoding to help elucidate the diet of birds found in a network of strawberry farms to assess their roles as biological control agents and potential crop pests.

We studied how local and landscape scale diversification affected bird community diversity, abundance, nest density, and their diets in the California Central Coast, an agriculturally rich area spanning six counties that produces a diversity of crops including high-value strawberries. In Monterey County, approximately 10,444 acres valued at \$923 M USD were devoted to growing strawberries in 2020, making it the highest valued crop for the county in that year (Monterey County Agricultural Commissioner, 2020). Monterey and Santa Cruz Counties combined produce nearly 40% of the total strawberries grown in California which, as a state, grows over 90% of the nation's strawberries (USDA NASS 2020). Strawberry farms in this area range in size and local diversification practices from large (e.g., 100.3 ha) intensive monocultures to small (e.g., 1.3 ha), diversified farms (Gonthier et al., 2019; Olimpi et al., 2020). Farms in this region also vary in the proportion of surrounding semi-natural habitat (shrubland, grassland, forest, and wetland). This range in local and landscape diversification results in bird species richness and abundance varying substantially among different farm operations (e.g., Gonthier et al., 2019). However, very little is known about how variation in local and landscape diversification impacts nesting density of birds in this area.

While some bird species consume strawberries in the region, some birds consume insect pests of strawberries. Like many other soft-bodied fruits, strawberries are highly susceptible to insect pest damage. The *Lygus* spp. complex (Hemiptera:Miridae), consisting primarily of *Lygus hesperus* Knight, are considered to be the greatest insect pests to strawberries in this area (Strand, 2008). *Lygus* spp. are hemipterans with haustellate (i.e., piercing-sucking) mouth parts that can cause cosmetic malformation to strawberries by feeding on flowers or immature fruit, usually rendering fresh mature fruit unmarketable (Handley and Pollard, 1993). Previous enclosure experiments in the region suggest 3.2% of berries are damaged by birds, while bird pest control saves 3.8% of berries from damage to insect pests (including *Lygus* spp.; Gonthier et al., 2019). However, the identities of these birds have only been approximated by observations but see Olimpi et al. (2022), where we used molecular diet analysis methods to estimate consumption rates of strawberries, caneberries, California-wide agricultural pests, and natural enemies in addition to screening for pathogen prevalence to investigate local and landscape-level drivers of community-wide avian-mediated multifunctionality (i.e., maximizing ecosystem services while minimizing disservices). In Olimpi et al. (2022) we found that semi-natural habitat at the landscape scale (1 km) was the main driver of multifunctionality across these agroecosystems. This study builds on Olimpi et al. (2022) by focusing on strawberry and *Lygus* spp. consumption (whereas Olimpi et al., 2022 looked at all CA crop pests and caneberry consumption in addition to strawberry consumption) to create functional groups based on these functional traits (described in Methods below), which may be the most relevant to strawberry growers in the area, and assess how the abundances of these groups change in relation to farm and landscape-level features to better inform actionable knowledge of how these groups can be better managed. Further, this study is the first in the area (to our knowledge) to investigate how nest density in agroecosystems varies across different farming contexts.

There is growing evidence that increasing bird nest density in agroecosystems by installing nest boxes for beneficial birds may increase the abundance and enhance pest control activity by insectivorous birds. Olmos-Moya et al. (2022), for example, found 43% greater consumption of sentinel prey in Chilean vineyard plots where nest boxes were deployed relative to control plots. Similarly, García et al. (2021) found greater predation pressure of apple pests evidenced by increased proportion of sentinel prey models damaged by birds, reduction in biomass of apple tree-dwelling arthropods, and a reduced probability of apple pest occurrence in Asturian cider-apple orchards with artificial nest boxes. These results are not surprising given the greater food demands

associated with birds during breeding season, when adult birds seek protein-rich insect prey to feed their nestlings (Nyffeler et al., 2018). While there is a growing interest in the installation of artificial nests for pest control, there is scant attention on naturally occurring nest density within agroecosystems as well as the local and landscape factors that may influence nest density in farming systems.

In this study, we sought to understand how local (farm level) diversification and landscape complexity influence bird biodiversity conservation, and the abundance and nest density of *Lygus*- and strawberry-eating birds. First, we used molecular diet analyses to characterize avian diets and identify *Lygus*-eating birds and strawberry-eating birds, building on previous research (Gonthier et al., 2019) that was done in the same area in previous years (2015–16) but where molecular analyses methods were not used and bird species categorization as insectivorous or frugivorous was assigned based on literature trait data or observations, respectively. We analyzed two years of point count data to determine the influence of local and landscape factors on abundance and richness of these different bird groups. Finally, we explored how nest density within farm boundaries changed across local and landscape gradients, and whether birds within our network were more likely to nest in developed (e.g., buildings, artificial materials) or natural (e.g., trees, shrubs) habitat features within farms.

2. Methods

2.1. Study system

Our study took place across 20 organic strawberry farms in the California Central Coast during 2017–2019. Some of these participating farms were part of previous research in 2015–16 (Gonthier et al., 2019) but new farms were also recruited for this project. To ensure that farms in our study fell along orthogonal local and landscape diversification gradients, we selected farms based on two measures: (1) survey responses from growers were used to gauge adoption of local diversification practices, and (2) aerial imagery from the National Agricultural Imagery Project (NAIP) by the USDA Farm Service Agency was used to examine landscape heterogeneity surrounding each farm (Olimpi et al., 2020; NAIP). Farms had a mean minimum distance between farms of 2.8 km (range: 0.5–7.2 km).

2.2. Bird surveys

To quantify bird abundance, we conducted 10-minute, 50 m fixed-radius point count surveys at each farm from April–June in 2018 and 2019. Surveys were conducted over three consecutive days by the same observer to meet closure assumptions of N-mixture models (i.e., that metapopulation dynamics including immigration, emigration, extinction, and colonization would be negligible between survey visits) (Kéry and Schaub, 2011). Surveys were conducted between sunrise and 13:30 (average time 8:30) in the absence of rain or heavy fog. While all point counts were separated by at least 100 m (Ralph et al., 1995; Olimpi et al., 2022), the number of point count locations per farm varied by farm size. The smallest farm accommodated one point count location and the largest hosted six locations (point counts: range 1–6, mean=4.5; point counts per 10 ha: range 0.6–12.8, mean=5.5; Olimpi et al., 2022). For farms growing multiple crops, half of the point count locations were placed in strawberries and half in other crops. All birds heard and seen within the survey radius were recorded and included in analyses. Birds outside of the survey radius and flyovers were recorded but excluded from analyses.

2.3. Local diversification and landscape composition

First, to quantify local (farm-level) diversification, we recorded the proportion of semi-natural habitat (e.g., trees, hedgerows, weeds, floral strips, etc.), the number and proportion of crops (used to calculate crop

diversity via Simpson's index), the number of strata present (i.e., ground, understory, canopy), and the length of fencing and wires within each 50 m radius bird survey location (see below). Further, because we noticed that the proportion of weeds growing within the field boundaries varied greatly by farm, we scored the relative cover of weeds within crop fields per point count radius, adopting a scale in which 1 = 0–5% cover, 2 = 5–50% cover, and 3 > 50% cover. We also recorded the number of unique bird deterrent practices observed at each farm.

Second, to describe diversification at a landscape scale, we manually delineated all land cover types within 1000 m of the bird survey locations on each farm in ArcMap using the most recently available aerial imagery from NAIP for these regions. As detailed in Olimpi et al. (2020), we then calculated the proportion of semi-natural habitat classes (e.g., grassland, chaparral, forest) within 1000 m.

Finally, to quantify crop diversity at a landscape-level, we manually mapped, via ground-truthing, the surrounding crops within 500 m of the bird survey locations on each farm. For this analysis, we used a 500 m scale rather than a 1 km scale (as above) due to restrictions in accessing adjacent private lands. These maps were then used to calculate landscape-level crop diversity and to calculate the landscape-level proportion of strawberry (within 500 m).

2.4. Nest site availability

To quantify nest density, we also intensively searched for and documented all nests within farm boundaries in 2019. Nest searching took place between April and June 2019 across 19 farms, during the breeding season when nesting activity is most apparent (Martin and Geupel, 1993). Because farms differed in size as well as in the amounts of managed non-crop vegetative habitat and developed areas within farm boundaries, the amount of area searched and the amount of time spent searching were standardized. Managed non-crop vegetative habitat included only managed vegetation such as hedgerows, wind breaks, shrubs, grass strips, etc. within the farm boundaries, but we did not include adjacent forests outside of farm boundaries, as the extent of management in these forests was generally unknown and because it was too difficult to accurately observe nests in these unmanaged areas. Developed areas included artificial structures such as buildings and sheds and structures specific to agriculture such as hoop houses. A minimum area of 0.5 ha and a maximum area of 2 ha at each farm were searched, with one hour of active searching per each 0.5 ha. When a bird was encountered and suspected to be nesting, it was continuously observed for 15–20 mins until the nest was found or no conclusive signs of nesting activity were displayed. This time period was deemed appropriate considering most female passerines return to nests within 6–10 min (Martin and Geupel, 1993). Time spent observing a particular bird suspected to be nesting did not count towards the total active searching time.

When a nest was discovered, a GPS point near the nest was taken and then the habitat type (semi-natural habitat versus developed areas), the substrate that the nest was laid on, the height of the nest, and the bird species were all recorded. Nest status (building, incubating, nestlings, etc.) and other relevant nesting activities (parents carrying nesting material, guarding nest, etc.) were also noted. Farms were searched for nests three times, but individual nests were only counted once unless they were suspected to be housing a second brood. To estimate nest density per species per habitat (developed vs. seminatural) at each farm, the number of nests of each species in each type of habitat (developed vs. seminatural) were divided by the total area of that habitat type searched at each farm.

2.5. Mistnets to capture birds and collect fecal samples

In order to classify birds within this study as consumers of *Lygus* spp., strawberries, or both, we used molecular data extracted from fecal samples of birds caught via mistnets under protocol numbers 19354 and

21094 approved by the IACUC of the University of California at Davis. The methods used are described in [Olimpi et al. \(2022\)](#). Briefly, mistnets were deployed on 3 farms in 2017, 20 farms in 2018, and in 1 additional farm in 2019. For each farm visit, mistnets were mostly deployed over three consecutive days within a single year between May-July of each year, with the exception of three farms that were sampled on three consecutive days during two different years. A total of 10 mistnets were deployed at each farm for each visit, with some placed near field borders and some within strawberry fields. Mistnets were often placed near semi-natural vegetation to maximize captures whereas surveys were often centered in crop fields. Mistnet and point count surveys were not co-occurring. Mistnets were deployed for 5 h per day, beginning at sunrise ([Ralph et al., 1995](#)) and checked every 20–30 min. Captured birds were extracted from nets, placed in breathable sterilized cotton bags, and transported to a nearby banding station. Birds were identified to species and banded with aluminum bird bands of the appropriate size. Fecal samples were collected from the sterilized cotton bags and placed in cryotubes containing ethanol and stored in – 80 C until processing. To avoid mixing fecal samples from different birds, sterilized cotton bags were only used once until they were sterilized in the wash with bleach. During mistnet capture, the presence of strawberry remnants on a bird's beak ('berry bill' hereafter) was also recorded.

2.6. Classification of *Lygus* and strawberry eating birds from fecal samples

Methods for DNA extraction and amplification from bird fecal samples, library preparation, bioinformatics, and targeted PCR to screen for strawberry are detailed in [Olimpi et al. \(2022\)](#); see [Supplementary Materials](#) for detailed methods). Following DNA extraction and bioinformatics, we removed any amplicon sequence variants (ASV) that could not be classified to a genus level or did not have at least 1000 reads total. Any diet items (ASVs) that represented $\leq 1\%$ of the total diet items from each sample were also removed, as were any ASVs with 10 reads or fewer. From this dataset, it was possible to determine how many of the fecal samples collected from birds had *Lygus* spp. in their diet. To determine which birds consumed strawberry, we used a strawberry-specific PCR primer to screen extracted fecal samples for the presence of strawberry DNA (details in [Supplementary Materials](#)). Because *Lygus* spp. are the most deleterious insect pests to strawberries in the region, we restricted classification of birds as *Lygus* or strawberry eaters to bird species from which we had collected at least 5 fecal samples ([Garfinkel et al., 2022](#)). A threshold of at least 5 fecal samples per species allowed us to eliminate samples of species for which we only had a few, often one, fecal samples from and where calculating proportions of *Lygus* or strawberry detections per species could not be assessed from these data. This resulted in $N = 388$ samples from 21 species to determine *Lygus* spp. eaters and $N = 380$ samples from 20 species to determine strawberry eaters as it was a subset of samples that were screened for strawberry presence with targeted PCR approaches. We focused on *Lygus* spp. given their important pest status in the study region (see introduction) and their small size (adults ~ 6 mm; [Strand, 2008](#)), which makes it difficult to identify which bird species are consuming these pests through field observations. Given that each fecal sample represented a snapshot of a single meal consumed by that bird, we took a frequency of occurrence approach of diet items of interest to determine which bird species included *Lygus* and strawberries in their diets at greater frequencies. A bird was considered to be a *Lygus* consumer if it had a 15% frequency of occurrence (FOO; i.e., proportion of samples with *Lygus* detected divided by total samples of that species analyzed) of diet items including *Lygus* spp. While there are currently no existing guidelines specifying what frequency of occurrence of a specific insect pest in a bird species' diet indicates significant pest suppression by a bird species, it is generally believed that predators with greater FOO of insect pests may be particularly relevant for pest regulation ([Mata et al., 2021](#)). Bird species were classified as strawberry consumers if at least

15% of the species' samples tested positive for strawberries (under PCR) and 15% of the individual birds were found to have berry bill during capture. This conservative approach to identify strawberry consumers aims to account for secondary consumption of strawberries (i.e., if a bird consumed an insect that had recently fed on a strawberry) as berry bill represents evidence of direct strawberry consumption and demonstrates a probable history of consuming berries, given that it would be unlikely for a single strawberry consumption event to result in the accumulation of fruit residue on the bill.

2.7. Data Analyses

2.7.1. N-mixture model for point count data

We used hierarchical multi-species multi-season N-mixture models to quantify the effects of landscape and local site covariates on bird species abundance, while simultaneously accounting for detection ([Royle, 2004](#)). Further, multi-species models allow for insights at both the individual and group level, where we can observe how covariates affect specific bird species but also observe community-level trends ([Kéry and Royle, 2020](#)).

Here, we let $\lambda_{i,j,t}$ denote the mean local abundance of species I at site j in year t . We assume that the true abundance $N_{i,j,t}$, which is a latent variable (i.e., unobservable due to detection error), is drawn from a negative binomial distribution with success probability $\lambda_{i,j,t}$ and a dispersion parameter denoted by r ([Kéry and Schaub, 2011](#)). We let $p_{i,j,k}$ denote the probability that species I was detected at site j during survey k . We assume that our observed count data $C_{i,j,k,t}$ of species I at site j during survey k in year t is described by a binomial distribution with sample size $N_{i,j,t}$ and detection probability $p_{i,j,k}$. In summary, the structure of our hierarchical N-mixture model to estimate local species (1) abundance and (2) detection is described as follows:

$$N_{i,j,t} \sim \text{Negative Binomial}(\lambda_{i,j,t}, r) \quad (1)$$

where r is the dispersion parameter.

$$C_{i,j,k,t} \sim \text{Binomial}(N_{i,j,t}, p_{i,j,k}) \quad (2)$$

Given that this model fundamentally consists of two linked generalized linear models (GLMs), it is appropriate to introduce the effects of site-specific covariates and survey-specific covariates through log and logit-link functions on abundance and detection, respectively ([Kéry and Schaub, 2011](#)).

As such, we assume the following log-transformed model to describe expected abundance:

$$\log(\lambda_{i,j,t}) = \beta_0 + \beta_{\text{species}[i]} + \beta_{\text{farm}[j]} + \beta_1 * \text{Semi_1km}_{j,t} + \beta_2 * \text{Cropdiv}_{j,t} + \beta_3 * \text{Cropdiv_50m}_{j,t} + \beta_4 * \text{Weeds}_{j,t} + \beta_5 * \text{Strata}_{j,t} + \beta_6 * \text{Semilocal}_{j,t} + \beta_{\text{year}} * t \quad (3)$$

In this model, β_0 is an intercept that denotes mean abundance, $\beta_{\text{species}[i]}$ is a species-specific random effect, and $\beta_{\text{farm}[j]}$ is a farm-specific random effect. Semi_1km denotes the proportion of semi-natural habitat at the landscape (1 km) scale, $\text{Cropdiv}_{j,t}$ denotes crop diversity within 500 m, $\text{Cropdiv_50m}_{j,t}$ denotes crop diversity within the 50 m point-count radius, $\text{Weeds}_{j,t}$ denotes the level of weediness within each 50 m point count radius, $\text{Strata}_{j,t}$ denotes the different number of strata within the 50 m point count radius, and $\text{Semilocal}_{j,t}$ denotes the amount of semi-natural habitat within the 50 m point count radius. Finally, we include $\beta_{\text{year}} * t$, a fixed-effect of year that allows abundances to vary between our two survey years ($t = 0$ for 2018 and $t = 1$ for 2019). Other predictors that we included in the model but subsequently removed included the number of bird deterrent practices at each farm, the length of fences and wires within each 50 m point count radius, and the proportion of strawberry within 500 m. These predictors, which were non-significant (i.e., the Bayesian credible intervals (BCI) included zero at both the community and species levels), were removed from the model after several runs to avoid over-parameterization.

For detection, we adopted the following logit-transformed model to introduce fixed-effects that might influence detection probabilities:

$$\text{logit}(p_{i,j,k}) = \alpha_0 + \alpha_1 * \text{Wind}_{j,k} + \alpha_2 * \text{Timeday}_{j,k} + \alpha_3 * \text{Noise}_{j,k} + \alpha_4 * \text{People}_{j,k} + \alpha_5 * \text{Day}_{j,k} \quad (4)$$

Here, α_0 is an intercept, $\text{Wind}_{j,k}$ denotes the average wind meter measurement during point count, $\text{Timeday}_{j,k}$ denotes time of day that the point count commenced, $\text{Noise}_{j,k}$ denotes the level of noisiness during the point count (on a scale of 1–4 with 1 being the quietest and 4 being the loudest), $\text{People}_{j,k}$ denotes the number of people within the 50 m radius during the point count event, and $\text{Day}_{j,k}$ denotes the day of year (Julian date). The detection portion of the model originally included a random effect of species ($\alpha_{\text{species}[i]}$) and farm ($\alpha_{\text{farm}[j]}$) but these were omitted to facilitate model convergence after initial runs.

We ran our model under three scenarios: (1) all detected species (i.e., full-species model), (2) the subset of birds classified as *Lygus* eaters, (3) the subset of birds classified as strawberry eaters. We used 95% Bayesian credible intervals (95% BCI) to identify “significant” trends for communities and 90% Bayesian credible intervals (90% BCI) for species-specific responses. Specifically, we inferred local and landscape effects to be “significantly” different from zero at the community level when the 95% BCI for the mean did not include zero. For species-specific responses to local and landscape variables, we used a less strict 90% credible interval (Frishkoff and Karp, 2019).

We estimated avian species richness by using posterior samples from the community presence/absence matrix which we can derive from the posterior samples for the latent abundance matrix using the ‘step’ function from JAGS (Kéry and Royle, 2020).

We ran our models in a Bayesian framework using JAGS version 4.3.0 (Plummer, 2017) and R (version 4.0.0) via the R package rjags (Plummer et al., 2019) for direct interface across platforms, and runjags (Denwood, 2016) which employs Markov chain Monte Carlo (MCMC) methods for Bayesian estimation of posterior distribution of parameters. Full species models consisting of 3 chains were run for 200,000 iterations, thinning every 200 iterations and with a burn-in of 20,000 iterations. *Lygus* and strawberry eating guild models consisting of 3 chains were run for 200,000 iterations, thinning every 200 iterations, with the first 20,000 iterations discarded as burn-in. Model convergence was assessed through visual inspection of chain trace plots and by ensuring that the Gelman-Rubin statistic was less than 1.1 for all parameter estimates (Rhat < 1.1; Gelman-Rubin, 1992). Uninformative priors were used throughout. Specifically, we assumed means of random effects and fixed-effects were drawn from a normal distribution $\sim N(0, 0.01)$, standard deviations for random-effects were drawn from a uniform distribution $\sim U(0, 10)$, and the dispersion parameter for the negative binomial was drawn from a uniform distribution $\sim U(0, 50)$.

2.7.2. Linear-mixed effects models for nest data

We used linear mixed effects models (LMMs) to examine the effects of local diversification and landscape composition on nest density. Models included fixed effects of local crop diversity, the level of weediness, number of strata, local proportion of semi-natural habitat (50 m), proportion of semi-natural habitat in the landscape, crop diversity within 500 m, proportion strawberry production within 500 m, and density of fencing and wires. These local and landscape diversification metrics were calculated by averaging measurements that were taken at 2019 point count locations for a farm-wide estimate. We also included the number of bird deterrent practices at each farm as a fixed effect. Farm was included as a random effect. We ran the models on all of the nests, and then ran models on nests of *Lygus* spp. eaters and strawberry eaters. We applied log transformations to predictor variables to meet assumptions of normality, which was then assessed with Shapiro-Wilk normality test. Models were fitted using “lmer” function in the package lme4 (Bates et al., 2014) in R version 4.1.0.

3. Results

3.1. Avian communities in strawberry farms

We detected 86 bird species within our study system across 2018 and 2019. 15 bird species were classified as *Lygus* spp. eaters, 8 species were classified as strawberry eaters, which includes 5 species that were classified as both *Lygus* spp. eaters and strawberry eaters (Fig. 1). Birds that overlapped in diet guild classification were included in both *Lygus* spp. and strawberry eaters analyses. The three species most commonly observed were house finches (*Haemorhous mexicanus*) with 983 counts (13.7% of total observations), followed by Brewer’s blackbird (*Euphagus cyanocephalus*) with 659 counts (9.2% of total observations), and barn swallows (*Hirundo rustica*) with 381 counts (5.3% of total observations). Detection was lower when there was greater wind ($\alpha = -0.054$, 95% BCI = (-0.092, -0.017)) but was not influenced by time of day, noise, amount of people within survey area, or Julian date (Fig. 2A).

3.1.1. Community-wide abundance trend

At the community level, mean local abundance (i.e., mean abundance at each site) was positively related to the proportion of semi-natural habitat in the surrounding landscape (1 km) and locally (50 m) with $\beta = 0.369$ (95% BCI = (0.103, 0.653)) and $\beta = 0.179$ (95% BCI = (0.071, 0.283)), respectively (Fig. 2B; Fig. 3A-B). Species richness estimates were positively correlated with the amount of local and landscape scale semi-natural habitat (Fig. 3C-D). At the species level, the abundances of 14 species were positively related to semi-natural habitat at the local scale (50 m) (Fig. 4 A). At the species level, the abundances of 35 species were positively related to semi-natural habitat at the landscape scale (1 km) (Fig. 4B), while the abundances of 12 species were negatively related to semi-natural habitat at the landscape scale.

3.1.2. Abundance of *Lygus* spp. and strawberry eaters

Semi-natural habitat at the local scale had a positive effect on local abundance of birds classified as *Lygus* spp. eaters ($\beta = 0.177$, 95% BCI = (0.026, 0.331)), with significant species-level effects on California quail (*Callipepla californica*), spotted towhee (*Pipilo maculatus*), black-headed grosbeak (*Pheucticus melanocephalus*), black phoebe (*Sayornis nigricans*), and Pacific-slope flycatcher (*Empidonax difficilis*) (Fig. 5A-B). Although semi-natural habitat at the landscape scale (1 km) was not significant at the group level for *Lygus* spp. eaters, seven species responded positively and three negatively (European starling, northern mockingbird, and barn swallow; Fig. 5A).

We did not find that any site-specific covariates related to mean local abundance of strawberry eaters.

3.2. Nest Density

We found nests of 16 species across 12 farms that were searched for nests in 2019, with 25 nests found in developed areas and 27 nests found in semi-natural habitat within farm boundaries. Species that built nests in developed areas within farms were barn swallow, black phoebe, cliff swallow (*Petrochelidon pyrrhonota*), European starling, and house sparrow. Species that built nests in semi-natural habitat within the farm were black-headed grosbeak, bushtit (*Psaltriparus minimus*), common yellowthroat (*Geothlypis trichas*), Eurasian collared dove, lesser goldfinch (*Spinus psaltria*), northern mockingbird, Pacific-slope flycatcher, and song sparrow. Species that built nests in both types of habitats were American robin (*Turdus migratorius*), Brewer’s blackbird, and house finch. We found nests for 5 of 8 strawberry-eating species and 8 of 15 *Lygus*-eating species.

Overall, we found that there was a significant interaction between the type of nesting habitat within the farm and the proportion of semi-natural habitat in the landscape (Table 1). After sub-setting the data to only nest density in developed areas, we found no relationship between nest density and within farm boundaries and semi-natural habitat

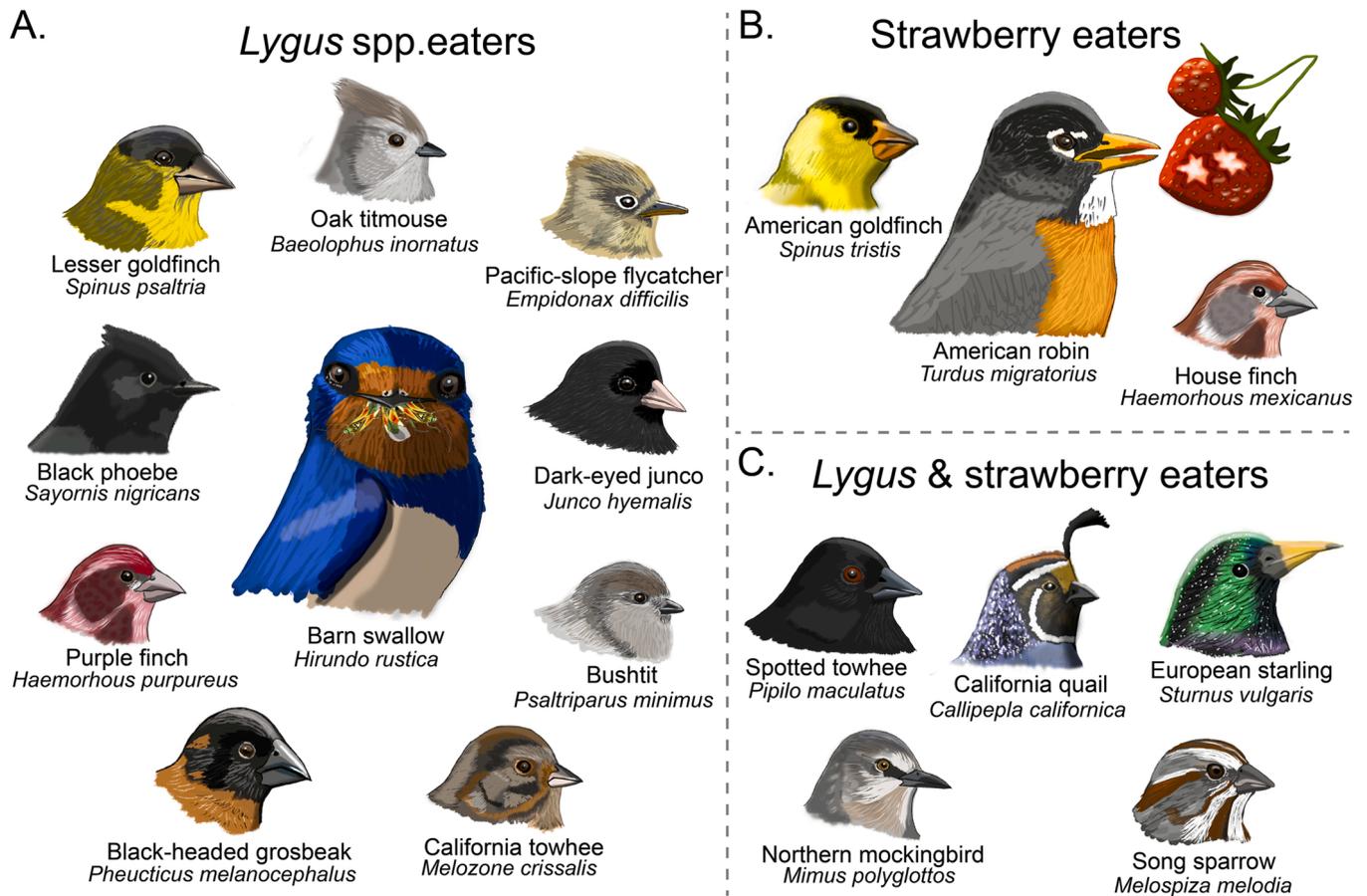


Fig. 1. *Lygus* spp. eaters and strawberry eaters, Birds that were classified as (A) *Lygus* spp. eaters, (B) strawberry eaters, or (C) both. Common North American and scientific names are written below birds' heads. Illustrations by K. Garcia.

in the landscape ($F=0.550$, $p = 0.499$). After sub-setting the data to only nest density in managed non-crop vegetative habitat within farm boundaries, we found a decrease in density with increasing semi-natural habitat in the landscape ($F=8.405$, $p = 0.0145$; Fig. 6A). For strawberry eating birds, we found the same significant interaction between the type of nesting habitat and the proportion of semi-natural habitat in the landscape (Fig. 6B; Table 1). After sub-setting this data to only nest density in developed areas we found no relationship between nest density and semi-natural habitat in the landscape ($F=6.969$, $p = 0.058$) but when sub-setting to nest density in managed non-crop vegetation we found a decrease in nest density with increasing semi-natural habitat in the landscape ($F=7.470$, $p = 0.019$). When restricting to *Lygus* spp. eating birds, we found that nest density was greater in farms with greater proportions of local semi-natural habitat (Fig. 6C; Table 1).

4. Discussion

In this study, we identified which birds consumed *Lygus* spp. and determined which birds consumed strawberry crops through the use of molecular diet analysis and the adoption of a 15% threshold of frequency of occurrence for these diet items. The pairing of molecular methods with ecological approaches is essential to identify which beneficial birds may be delivering pest control services to farmlands. While a plethora of enclosure experiments have documented community-wide impacts of birds on pests and yield (Mäntylä et al., 2011), enclosure experiments often fail to identify which species actually deliver the pest control services. The use of molecular diet tools aid in the identification of communities of beneficial and harmful birds, so that management practices can target the attraction of beneficial species and deter of harmful species. A growing number of studies are using

molecular diet analysis to identify birds that consume insect pests (e.g., Crisol-Martinez et al., 2016, Karp et al., 2013, Mangan et al., 2018). The use of molecular methods to determine which bird species are consuming detrimental insect pests will complement observational methods that are currently used to identify bird pests of crops but that are not suitable for less conspicuous bird activity such as arthropod predation. Linking these identifications to practices that conserve, restore, or augment the population of avian pest control agents on farms will provide growers with actionable knowledge for how to enhance the benefits of these species.

While molecular analysis approaches can aid in detecting the presence or absence of arthropod diet items, they have several limitations in determining the true pest control potential of bird species. First, birds rapidly pass diet items through the gastro-intestinal tract and the presence or absence of diet items in a single fecal sample is only a snapshot of what that bird consumed over time. Molecular diet analyses do not elucidate the frequency for which a bird species consumes a particular diet item. While this study used a frequency of occurrence approach of diet items to identify which birds consumed *Lygus* and strawberries, this method cannot be used to extrapolate crop damage levels or pest suppression levels. Future studies should seek to pair molecular diet analysis with visual observations of bird species consumption of insect pests, although few studies have been able to accurately identify insect prey taken by aerial predators in flight, but some have had success in identifying key predator bird species by pairing sentinel experiments with motion capture video cameras to capture foliage-gleaning of sentinel pests (see Garfinkel and Johnson, 2015).

This study found that 15 bird species that consume *Lygus* spp., a group of major insect pests of strawberries, are promoted by semi-natural habitat at the farm scale (50 m). Of the birds identified as

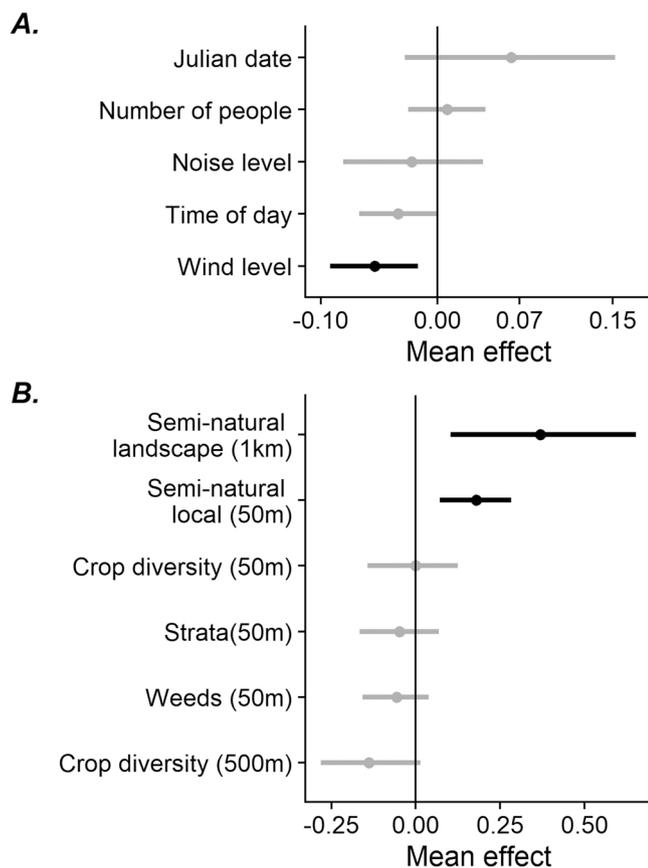


Fig. 2. Mean effects on detection and abundance. The mean effect (A) of visit-level predictors on detection of birds and the mean effect (B) of site-level variables on mean local abundance of birds. Dark lines indicate that 95% BCI did not include zero.

Lygus spp. eaters, oak titmouse belong to the family Paridae, Pacific-slope flycatcher and black phoebe belong to the family Tyrannidae, dark-eyed junco, song sparrow, spotted towhee, and California towhee belong to the family Passerellidae, bushtit belong to the family Aegithalidae, lesser goldfinch and house finch belong to the family Fringillidae, black-headed grosbeak belong to the family Cardinalidae, barn swallow belong to the family Hirundinidae, northern mockingbird belong to the family Mimidae, California quail belong to the family Odontophoridae, and European starling belong to the family Sturnidae. Of these species, California quail, California towhee, dark-eyed junco, purple finch, and lesser goldfinch are thought to primarily be granivorous, while barn swallow, black phoebe, Pacific-slope flycatcher, oak titmouse, bushtit, black-headed grosbeak, song sparrow, and European starling are thought to primarily consume insects, while spotted towhee and northern mockingbirds are described as omnivorous (Cornell Lab of Ornithology, 2019). There was no evidence that strawberry-eating bird communities were promoted by semi-natural habitat at local scales, suggesting that conserving semi-natural habitat on farms such as woody vegetation, grassland, and flower strips for *Lygus* spp. eating birds may come with minimal tradeoffs. Other local diversification features, like crop diversity, vegetative strata, or weediness did not increase *Lygus* spp. eating bird abundance. Past research has shown that proximity to semi-natural habitat can promote insect pest removal. Garfinkel and Johnson (2015), for example, found that pest control by birds increased with greater proximity to uncultivated shrubby field margins. A systematic review by Boesing et al. (2017) found that avian-mediated pest control was often greater in agricultural landscapes with greater semi-natural habitat cover and agricultural patches in closer proximity to native habitats. It is perhaps surprising that small scale semi-natural

habitat patches within farm (50 m) were more explanatory of *Lygus* spp. eating bird abundance than large scale semi-natural habitat in the surrounding landscape. In a synthesis of the literature, Gonthier et al. (2014) found vertebrate (including birds) richness increased with landscape complexity but did not respond to local (farm level) management changes across studies. It is hypothesized that the high mobility of birds allows them to experience the landscape at larger scales and utilize resources across larger areas, including habitats outside of crop fields (Tschamtko et al., 2005). This would suggest small-scale habitat features are of less importance to birds relative to the surrounding landscape context. However, our study suggests that *Lygus* spp.-eating bird species may utilize small patches of semi-natural habitat on farms for foraging and nesting sites. This finding may be key to managing pest control services provided by birds because small-scale farm level semi-natural habitat patches, unlike most landscape level habitat patches, are within the control of land and farm managers. Managers have the potential to modify on-farm habitat to increase the amount of semi-natural habitat. Identifying key individual local diversification practices that promote beneficial species is critical, as the farm scale is likely where incentivized farmers can enact the most changes at the individual scale. In this study region, semi-natural habitat patches on farm may promote increased foraging and nesting by birds that consume *Lygus* spp.

While individual farms can bolster their functionality through local efforts, it is believed that concerted efforts at the landscape scale by various stakeholders will be needed to support landscape level ecosystem services and biodiversity (Landis, 2017). While our study did not find a significant positive relationship between landscape level semi-natural habitat and *Lygus* spp. eater abundance, it should be noted that seven species had significantly positive relationships with semi-natural habitat at the landscape scale (Fig. 5A). The abundances of three *Lygus* spp. eating bird species (European starling, northern mockingbird, and barn swallow) were negatively correlated with semi-natural habitat, however northern mockingbird and European starlings are also strawberry eating birds and therefore are less desirable species to conserve. Barn swallows on the other hand, had the highest FOO of *Lygus* spp. However, barn swallows appear to prefer open habitat for foraging and may require different conservation strategies to promote their abundance on farm. While there were no relationships observed between the strawberry eating bird group and local and landscape metrics, it should be noted that in the full-species model (Fig. 4) American robins responded positively to semi-natural habitat at the landscape scale while house finches responded negatively to semi-natural habitat at the landscape scale. In some contexts where strawberry damage by birds may be high, managing for strawberry eating birds may be more important than managing for bird communities, highlighting the importance of considering species-specific responses when making management decisions.

Birds that consume both *Lygus* spp. and strawberries will be particularly challenging to manage for. An additional N-mixture analysis on the species that were classified as both *Lygus* and strawberry eaters (the species depicted in Fig. 1C), found no evidence that any site-specific covariates related to mean local abundance of this group. Of the birds that were classified as both *Lygus* and strawberry eaters, European starlings were detected $n = 377$ times (5.3% of total detections), song sparrows were detected $n = 362$ times (5.04% of total detections), spotted towhees were detected $n = 194$ times (2.7% of total detections), California quail were detected $n = 167$ times (2.3% of total detections), and northern mockingbirds were detected $n = 104$ times (1.5% of detections). Of these species, spotted towhee and California quail responded positively to local semi-natural habitat (50 m) while spotted towhee also responded positively to landscape level semi-natural habitat (1 km) (Fig. 5A). Further, northern mockingbird and European starlings had a negative relationship with semi-natural habitat at the landscape scale (Fig. 5A). Future studies should aim to determine whether species that consume *Lygus* spp. and strawberries contribute more to one

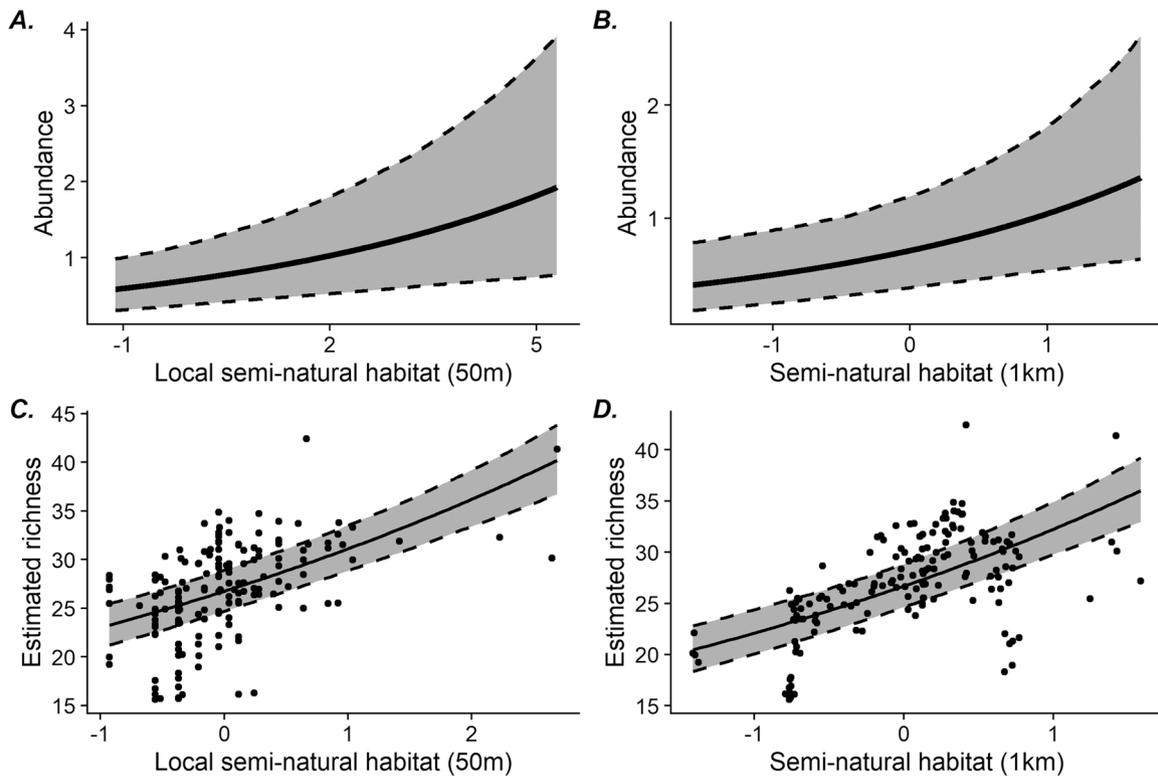


Fig. 3. Community-wide trends. Community-wide predicted abundance trends increasing in response to increasing semi-natural habitat at the (A) local (50 m) and (B) landscape scale (1 km). Estimated richness values derived from N-mixture model increasing in relation to (C) increasing proportion of local semi-natural habitat and (D) increasing proportion of landscape semi-natural habitat. Estimated richness values were fit to a generalized linear model with a Poisson distribution. The shaded areas denote a 95% BCI (values on x-axis are scaled).

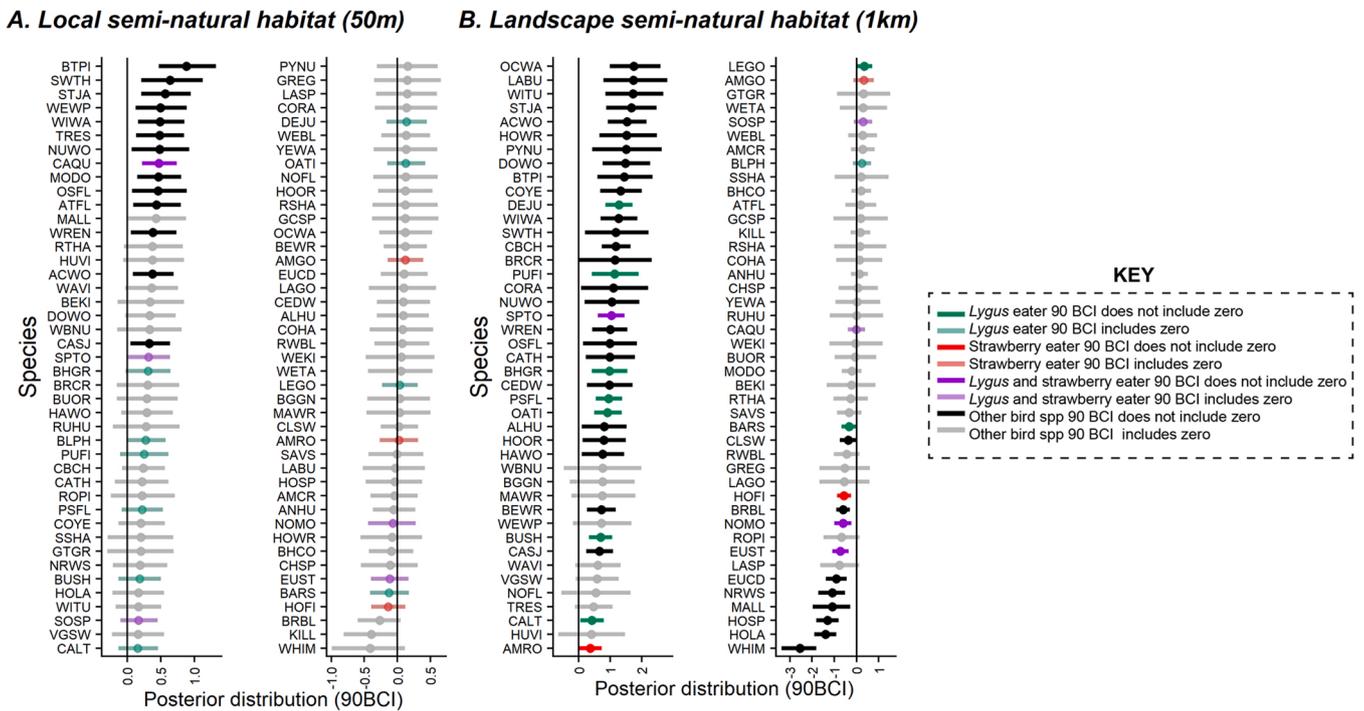


Fig. 4. Species-level responses to semi-natural habitat. (A) Species-specific responses to semi-natural habitat at the local scale (50 m) at 90% BCI. (B) Species-specific responses to semi-natural habitat at the landscape scale (1 km) at 90% BCI. Green lines represent *Lygus* spp. eaters, red lines represent strawberry eaters, and purple lines represent bird species that consumed both *Lygus* spp. and strawberries. Dark lines indicate that 90% BCI did not include zero while light bars indicate that 90% BCI included zero. See Supplementary Materials for table displaying which bird species correspond to four-letter codes.

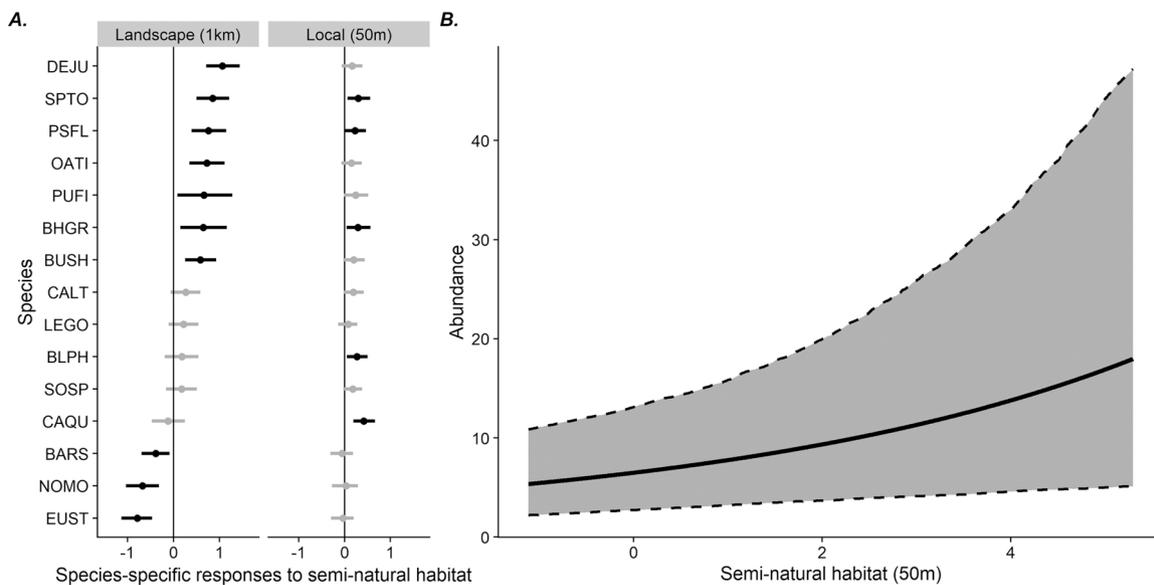


Fig. 5. N-mixture results for *Lygus* spp. eaters. (A) Depicts species-specific responses to semi-natural habitat at the landscape and local scale where dark lines indicate that 90% BCI did not include zero. (B) Depicts predicted abundance increasing as local semi-natural habitat increases (values on x-axis are scaled). See Supplementary Materials for table displaying which bird species correspond to four-letter codes.

Table 1
Effects of local and landscape variables on nest density of all bird species, strawberry eating bird species, and *Lygus* spp. eating birds.

Predictors	Coefficient estimate	±SE	p
All bird species			
(Intercept)	1.82	0.24	< 0.001
Habitat[nat]	-1.21	0.23	< 0.001
Local crop diversity	0.42	0.28	0.15
Weed	-0.03	0.3	0.934
Strata	-0.3	0.24	0.213
Local semi-natural (50 m)	0.48	0.25	0.074
Semi 1 km	0.05	0.34	0.895
Crop diversity (500 m)	0	0.27	0.993
Proportion strawberry (500 m)	-0.27	0.25	0.294
Habitat[nat]*Semi 1 km	-0.81	0.23	0.002
Strawberry eating bird species			
(Intercept)	1.03	0.26	0.001
Habitat[nat]	-0.59	0.3	0.062
Local crop diversity	0.25	0.29	0.396
Weed	0.12	0.31	0.702
Strata	-0.36	0.24	0.145
Local semi-natural (50 m)	0.27	0.27	0.314
Semi 1 km	0.05	0.36	0.892
Crop diversity (500 m)	0.25	0.28	0.386
Proportion strawberry (500 m)	-0.09	0.27	0.727
Habitat[nat]*Semi 1 km	-0.66	0.29	0.036
<i>Lygus</i> spp. eating bird species			
(Intercept)	1.04	0.21	< 0.001
Habitat[nat]	-0.74	0.28	0.016
Local crop diversity	0.24	0.2	0.233
Weed	-0.15	0.22	0.515
Strata	-0.2	0.16	0.231
Local semi-natural (50 m)	0.54	0.19	0.01
Semi 1 km	-0.16	0.26	0.539
Crop diversity (500 m)	-0.18	0.2	0.391
Proportion strawberry (500 m)	-0.27	0.19	0.175
Habitat[nat]*Semi 1 km	-0.26	0.27	0.344

functional group than the other, as this will better inform management actions by farmers. Determining *Lygus* and strawberry consumption rates of these species will be key when considering potential tradeoffs when making management decisions that may affect abundances of these particular species.

Of the bird species whose nests were found in both developed areas

and semi-natural habitat within the farms, it has been documented that American robin, black phoebe, cliff swallow, Eurasian collared dove, house finch, house sparrow, and Pacific-slope flycatcher nest both on artificial structures and natural features (Cornell Lab of Ornithology, 2019). Whereas black-headed grosbeak, Brewer’s blackbird, bushtit, common yellowthroat, lesser goldfinch, and song sparrow are known to typically nest in natural and semi-natural features such as shrubs, trees, and grasses (Cornell Lab of Ornithology, 2019). Barn swallow nesting typically occurs on artificial features including barns, sheds, and bridges (Cornell Lab of Ornithology, 2019). While nest density of *Lygus* spp. eating birds increased with farm level semi-natural habitat (50 m), patterns for the nest density of all birds and strawberry eating birds were more complex. For all birds and strawberry eating birds, we found that there was a significant interaction between the type of nesting habitat within the farm and the proportion of semi-natural habitat in the landscape (Fig. 6). Nest-density in semi-natural habitat within farm boundaries decreased with the proportion of semi-natural habitat in the landscape, while nest-density in developed areas within the farm increased with semi-natural habitat in the landscape. This may suggest that bird species that require nesting sites in natural or semi-natural habitat may be selecting higher quality or more abundant nest sites in the surrounding semi-natural habitat in the landscape rather than semi-natural habitat patches on farms. In farms that were surrounded with low amounts of semi-natural habitat in the landscape, these birds are more likely to find and nest within semi-natural habitat patches on farm because they are among the only valuable nesting sites. This pattern may be indicative of nest site limitation for birds requiring or preferring natural or semi-natural habitat for nesting. It is believed that the majority of species that nest in natural and semi-natural habitats occupy both low-quality and high-quality habitats across their ranges (Donovan and Thompson III, 2001). Further, birds who opt to nest in semi-natural habitat may benefit from protection from predators conferred by higher proportion of shrub cover and vegetation density (Foggia et al., 2018).

Overall, we found that semi-natural habitat at the landscape scale generally increased abundance of birds across many species, highlighting the value of semi-natural habitat for bird conservation in agricultural landscapes. Further, we found that semi-natural habitat at the local scale increased the abundance and nest density of birds eating *Lygus* spp., underscoring the importance of semi-natural habitat at the

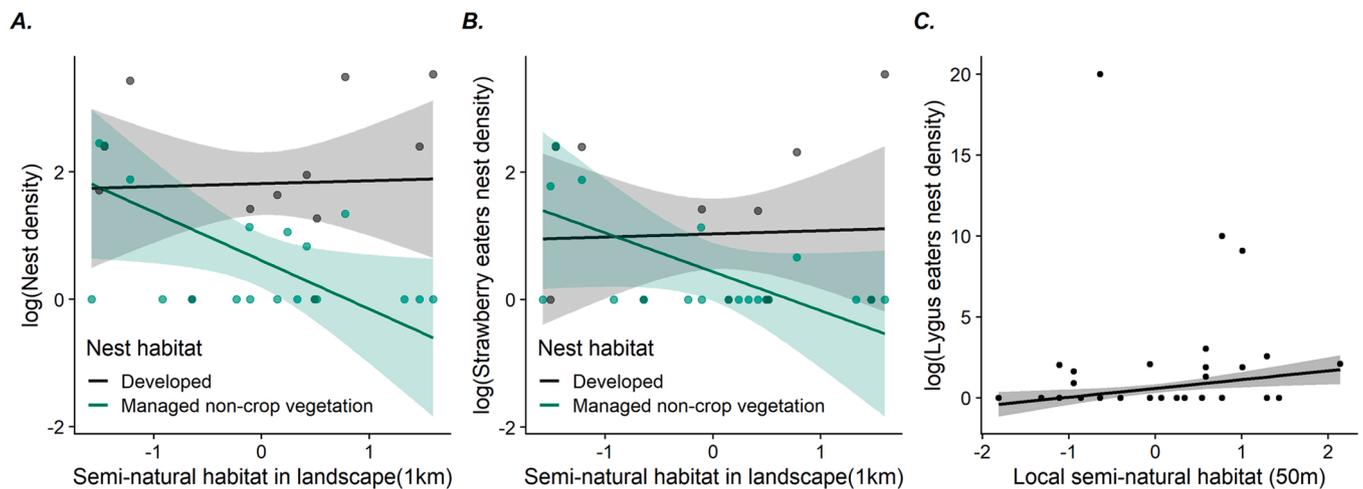


Fig. 6. Nest density. Influence of semi-natural habitat in the landscape on nest density for (A) all nests and nest density of (B) strawberry eaters. (C) The positive relationship between nest density of *Lygus* spp. eating birds and local semi-natural habitat (50 m). Points represent raw nest density values and bands indicate 95% confidence intervals.

farm scale to harness biocontrol services from beneficial bird species. Importantly, semi-natural habitat at the farm scale did not promote the abundance of strawberry-eating birds, indicating that bird-associated benefits of natural habitat may outweigh potential costs. This suggests that an appropriate management action to promote the presence of *Lygus* spp. eating birds, includes the conservation or introduction of semi-natural habitat at the farm scale.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.agee.2023.108353](https://doi.org/10.1016/j.agee.2023.108353).

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