

A bustle in the hedgerow: Woody field margins boost on farm avian diversity and abundance in an intensive agricultural landscape



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ABSTRACT

Considerable funding has been allocated to conservation management of non-crop habitat in agricultural landscapes, particularly field margin habitat such as hedgerows. Evaluation of the biodiversity benefits of non-crop habitat has lagged behind implementation, however, especially in the United States where this habitat has the potential to supply important resources for both common and rare species of birds. We examined the effects of woody field margin vegetation on winter and breeding season avian communities at 103 fields, row crops, and orchards in California's Central Valley, one of the most intensively-farmed landscapes on Earth. We found that margins with hedgerows, treelines or remnant riparian habitat harbored 2–3 times as many bird species, significantly greater species evenness, and 3–6 times higher maximum total abundances of birds than bare or weedy margins. The effect of margin type on richness was modulated by water year, whereas the effect of margin type on maximum total abundance was modulated by adjacent crop type. At the landscape scale, hedgerow and riparian margins that were further from woodland harbored greater species richness; a result that supports our recommendation for targeted development of hedgerows in simplified agricultural landscapes. These results demonstrate that non-crop woody habitats, both planted and remnant native patches, increase the biodiversity value of farms, providing support for policies to preserve remaining habitat and incentivize installation of woody hedgerows.

1. Introduction

With ~40% of the world's ice-free land surface devoted to agriculture (World Bank, 2015), expansion and intensification of farming threaten to further alter already-stressed ecosystems (Foley et al., 2005). Agricultural intensification has had broad-scale negative effects on biodiversity through habitat loss and certain management activities (Balmford et al., 2012; Geiger et al., 2010; Green et al., 2005). Furthermore, increasing agricultural intensification has been linked to degradation of the ecosystem services provided by biodiversity (Power, 2010) including pollination (Kremen et al., 2007) and biological pest control (Tscharntke et al., 2007). Finding a balance between producing the food, fuel, and fiber required by our growing human population and reversing biodiversity declines remains one of the greatest conservation and social challenges we face.

Avian populations, in particular, are projected to decline with the continued expansion and intensification of agriculture worldwide (Green et al., 2005; Scharlemann et al., 2004), as has been empirically documented throughout Europe (e.g., Donald et al., 2006; but see Reif et al., 2008). In North America, this trend in agriculture has been associated with declines of both rare and common species and is considered a continent-wide threat to land birds (Rosenberg et al., 2016). Nonetheless, there remains potential for supporting abundant populations of many bird species in agricultural landscapes by maintaining landscape heterogeneity (Benton et al., 2003; Peterjohn, 2003) and by providing resources for birds during all periods of their annual cycle, including during breeding (Rodenhous et al., 1992; Swolgaard et al., 2008), bi-annual migration (Estrada and Coates-Estrada, 2005) and over-wintering periods (Kross et al., 2016; Strum et al., 2013).

If quality resources in agricultural lands supplement those found in

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remnant natural habitats, or if agricultural lands offer better than available alternatives in severely modified landscapes, then sustainable management of them is necessary for biodiversity conservation (Koh and Gardner, 2010). Agri-environment schemes (AES), which are management schemes and policies designed to offset or reverse the negative effects of agricultural intensification on wildlife, have been implemented by governments, non-governmental organizations and industry groups around the world. These schemes encourage farmers to implement specific measures designed to protect and enhance the environment, including habitat management to accommodate wildlife. Birds, as a highly-visible and culturally-valued taxonomic group, have been the focus of many such schemes (Kleijn et al., 2006; Strum et al., 2013). Arguably the policy and management schemes with the largest scope and most thorough scientific assessment are found in the European Union, where nearly €20 billion was spent on AES between 2007 and 2013 (European Commission, 2017). In the United States (US), programs funded by the US Department of Agriculture's Natural Resources Conservation Service earmarked \$6.35 billion for nationwide voluntary on-farm conservation projects in 2016 through the Agriculture Act of 2014 (commonly known as the Farm Bill).

For birds in particular, an important conservation practice incorporated into AES has been the retention or re-planting of field margin vegetation (Quinn et al., 2014; Vickery et al., 2004). Managed linear strips of trees and/or shrubs, often called hedgerows, have been a key component of historic low-intensity farming landscapes (Baudry et al., 2000) and provide birds with resources for perching, nesting, refuge from predators, and foraging in an otherwise inhospitable agricultural environment (Baudry et al., 2000; Hinsley and Bellamy, 2000; Vickery et al., 2004). European studies demonstrate that woody hedgerows and other on-farm habitats can contribute significantly to bird diversity and abundance in the agricultural landscape and that hedgerow structure, composition, plant diversity, and proximity to water influence the numbers and species richness of birds in hedgerows (Hinsley and Bellamy, 2000).

Far less research has examined how woody field margin habitat—such as hedgerows, tree lines, or stream/ditch side riparian vegetation—impact bird communities in North America, with notable exceptions showing benefits to birds in Québec (Jobin et al., 2001), in Florida (Jones et al., 2005) and in shrublands adjacent to agricultural lands of North Carolina (Shake et al., 2012), but a negative impact on grassland birds in prairie regions (Quinn et al., 2012; Tack et al., 2017). Furthermore, it is understood that the efficacy of field margin habitats can vary depending on landscape context (Batáry et al., 2011). In spite of ongoing investments and their perceived benefits, few guidelines exist in the US for how field margin management practices can be implemented to target bird communities and increase avian diversity and abundance (Evans et al., 2014).

Here, we present the results of a large-scale study of the effects of woody field margins and landscape-scale habitat characteristics on over-wintering and breeding-season bird communities in California's Central Valley, one of the world's most intensively-farmed regions. Historically, the Central Valley was a matrix of seasonal wetland, riparian forest, grass- and forblands, and oak woodland and savannah but today over 95% of those habitats have been replaced by agriculture and urban areas (McCalla and Howitt, 2016). Currently, most field margins in the Central Valley are comprised of mowed weedy strips, or maintained as 'clean' margins devoid of vegetation. The diversity of historic habitats and the relatively recent transition to a farm-dominated landscape means that hundreds of species of birds, including habitat generalists and species that rely on woodland, riparian, grassland, and wetland habitats, utilize the Central Valley's agricultural lands either for breeding, overwintering, migrating, or as year-round habitat. Creating 'working lands' that support both agriculture and wildlife conservation is a goal of both farming and conservation stakeholders (Central Valley Joint Venture, 2006). In 2016, a total of \$88 million was reserved for the State of California's Environmental Quality

Incentives Program. Among other practices, this program supports the continued planting of native vegetation hedgerows, riparian canal plantings, and other farm margin habitats to increase biodiversity on farms and to regionally enhance habitat for wildlife, a practice that has been implemented in this region for over two decades (Bugg et al., 1998; Earnshaw, 2004; Long and Anderson, 2010). Despite the goal of providing habitat for birds, research on woody field margin habitats in California has focused on evaluating their benefits for pollinators and other agriculturally-beneficial insects (Morandin et al., 2014; Morandin and Kremen, 2013). Studies detailing the effects of hedgerows and other field margin habitats on birds in California have been preliminary (White et al., 2013), or have focused on single crop-types or seasons (Jedlicka et al., 2014; Kross et al., 2016). To inform and improve state and national policies and incentive programs, we evaluated the effects of different field margin habitat features on both breeding and winter season avian community structure in the context of several local and landscape scale habitat characteristics.

2. Methods

2.1. Study area

We sampled birds in the uncultivated margins around field, row, and orchard crops of Yolo and Solano counties of the Sacramento Valley, California, USA, where farmland occupies 71% and 77% of total county land area, respectively, and is bordered to the west by oak, conifer, and chaparral woodlands and grasslands of California's interior coast range and to the east by the Sacramento River (Fig. 1). In these counties, livestock forage, fruit and nut orchards, wheat, and processing tomatoes are the largest hectareage crop types (Solano County, 2013; Yolo County, 2014). The Sacramento Valley is ranked highest in agricultural production and lowest in agrobiodiversity compared to a set of seven other agrobiodiversity research regions around the globe

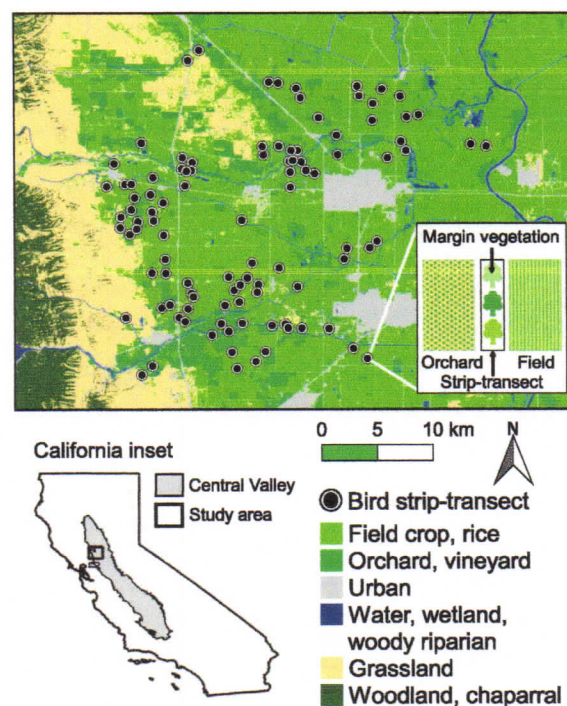


Fig. 1. Study area in Yolo and northern Solano Counties of the Sacramento Valley, with field-scale schematic of strip-transect placement, and California inset identifying the Central Valley and the study area.

Basemap modified from the 2012 Cropland Data Layer (Han et al., 2012).

(Jackson et al., 2012). Nonetheless, the valley is located within the biodiversity hotspot of the California Floristic Province (Myers et al., 2000), and has an increasingly active network of public and private partnerships incentivized to improve biodiversity and ecosystem services in uncultivated margins around working croplands (Brodt et al., 2009; Garbach and Long, 2017). The valley experiences hot, dry growing seasons and cool, wet winters typical of Mediterranean climates. During the two water years encompassing our study (Oct. 1, 2012–Sep. 30, 2013 and Oct. 1, 2013–Sep. 30, 2014), the valley experienced the 23rd driest and the driest years on record (1895–2016), respectively (NOAA, 2016).

2.2. Study design

Within the study area, we combined data from three distinct but coordinated research efforts designed to characterize bird communities in different types of margin habitats. The primary research project selected an equal number of replicates, at least 1 km apart, for each of two general margin type categories: *hedgerows* and *controls*. *Hedgerow* margins contained linear native vegetation patches planted specifically for farmland biodiversity improvements and were a mix of California native riparian (*Salix*, *Populus*), oak (*Quercus* spp.), and chaparral tree and shrub species such as blue elderberry (*Sambucus mexicana*), coffee berry (*Rhamnus californica*), coyote bush (*Baccharis pilularis*), and toyon (*Heteromeles arbutifolia*), and some also included forbs and grasses such as phacelia (*Phacelia californica*), goldenrod (*Euthamia occidentalis*), creeping wild rye (*Leymus triticoides*), and deergrass (*Muhlenbergia rigens*; Long and Anderson, 2010). Controls were margins without *hedgerows*. The two subsequent projects selected an equal number of replicates, at least 1 km apart, for each of two margin type categories: simple (bare ground or non-woody weedy vegetation), or complex (woody vegetation, not exclusively *hedgerows*). Once data from all three research efforts were combined we re-characterized all margins as four distinct types for analysis (Fig. A1): 1) *bare/weedy*, areas of bare ground or mowed grass and forb strips composed of invasive species such as *Brassica* and yellow star thistle (*Centaurea solstitialis*); 2) *treelines*, single planted rows of conspecific trees such as valley oak (*Q. lobata*), Monterey pine (*Pinus radiata*), *Eucalyptus* spp., or olive (*Olea*); 3) *riparian*, remnant or more recently colonized vegetation associated with perennial or intermittent streams and ditches, characterized by a mix of valley oak (*Q. lobata*), willow (*Salix* spp.), Fremont cottonwood (*P. fremontii*), California black walnut (*Juglans californica*), Himalayan blackberry (*Rubus americanus*), or blue elderberry; and 4) *hedgerows*, defined above. Adjacent crop types were *orchards* (walnut or almond orchards, a few vineyards) or *row crops* (primarily tomato and sunflower, and including alfalfa and wheat fields or prepped soil for future crops). Seven percent of adjacent farms were certified organic or organically managed in terms of pesticide use while 93% were conventionally managed.

2.3. Bird counts

To estimate indices of bird abundance, species richness, and species evenness during two winter (November–February) and two breeding (April–July) seasons, we performed fixed distance strip-transects (Bibby

et al., 2000) from November 2012 to July 2014 (Table 1). Transects ($n = 111$) were located along margins parallel to row crop or orchard edges, were 200–375 m long, 20 m wide, and spaced at least 1 km apart in most cases (Fig. 1). Because the transects that were < 1 km apart (after combining projects) did not meet our study design criteria for spatial independence, we assigned these transects the same *site* code and included *site* ($n = 103$) as a random effect in our statistical models. We sampled transects while walking at a rate of approximately 10 min per 100 m (e.g., we sampled 200 m and 375 m transects for 20 min and 37.5 min, respectively). Transects were sampled at least twice and up to six times per season depending on project, with visits usually spaced > 4 days apart. Field ornithologists experienced in identifying birds by sight, songs, and calls recorded all individuals and species detected within transects. We assumed that detectability was similar among observers and between transects of different margin types. All surveys were completed within 4 h after sunrise, and we did not sample during inclement weather or heavy farm activity.

2.4. Local and landscape scale characteristics

We characterized local scale vegetation physiognomy and landscape scale features at all 111 transects (Table 2). We measured within-transect margin vegetation height to the nearest 0.1 m at five evenly spaced locations. At the same five locations, we quantified vertical vegetation structure by tallying the number of pre-determined height categories in which plant canopies intersected an imaginary vertical plane perpendicular to the transect (height categories in Table 2). We recorded the crop types adjacent to the transect, and with geographical information systems (Google Earth, 2014; QGIS Development Team, 2014) measured the length (m) and width of the total vegetation patch within which the transect was embedded, and calculated patch area. We calculated landscape variables using the 2012 land use cropland data layer from the National Agricultural Statistics Service (Han et al., 2012), resampled to a 100 m × 100 m resolution in ArcMap 10.1 (ESRI, 2012). We calculated distances (m) from transects to nearest riparian habitat, nearest woodland habitat, and nearest urban area, and calculated the number of different land cover classes within a 500 m buffer around transects (see Table 2).

2.5. Statistical analysis

Before building predictive models of bird species richness, evenness, maximum total abundance, and maximum species abundance, we examined the relationships between all potential fixed effect predictor variables (Table 2, Tables B7 and B8). If any two continuous covariates had a Pearson's correlation coefficient ≥ 0.5 , one was excluded from the pool of predictors used in modeling, thereby minimizing collinearity.

Having identified a reduced set of predictor variables, we next examined the relationships between them and our four bird indices. Given the large number of potential predictors, replication of sampling over time and at the site level, uncertainty about the form of the relationships between predictors and response variables, and a desire to generate easily-interpretable results, predictive modeling was done in multiple stages, using three different methods: 1) boosted regression

Table 1

Number of bird strip-transects by calendar and water year, season, and margin type. Vertically summed totals are numbers of unique transects across years and seasons.

Calendar year	Water year	Season	Bare/weedy	Treeline	Riparian	Hedgerow	Total
2012–2013	2012–2013	Winter	13	3	3	21	40
2013	2012–2013	Breeding	13	3	3	21	40
2013–2014	2013–2014	Winter	17	2	5	16	40
2014	2013–2014	Breeding	33	12	10	17	72
Total			49	13	15	34	111

Table 2

Local and landscape variables measured and categorized for this study. Distance and land cover categories are from the 2012 Cropland Data Layer (CDL; Han et al., 2012).

Variable	Description	Categories/values
Water year	October 1–September 30, ecologically relevant annual period in Mediterranean climates capturing the majority of rainfall	2012–13, 2013–14
Season	Avian lifecycle season during which surveys were conducted	Winter (Nov–Feb), Breeding (April–July)
Origin	Origin of data for this study; 3 distinct but coordinated projects	Heath, Kross, Audubon California
Site	Geographic locations (> 1 km apart) where one or more strip-transects were situated	103 different geographical sites contained 111 transects; used as random effect
Margin type	Categorical description of row crop or orchard margin type within strip-transects	Bare/Weedy, Treeline, Hedgerow, Riparian
Transect length	Length of strip-transect surveyed	200–375 m
Vegetation height	Mean vegetation patch height within strip-transect	0–22 m
Vertical layers	Mean number of vertical canopy categories present in transect; categories: 0–20 cm, 21–50 cm, 51 cm–1 m, 1.1–5 m, 5.1–10 m, > 10 m	0–6 layers
Adjacent crop	Identity of adjacent crop types	Both orchards, ≥ 1 row crop (including fields)
Management	Pesticide use on adjacent crops	Conventional or organic
Patch area	Total area of vegetation patch in which the strip-transect is embedded. Derivative of Patch Width and Patch Length (GIS).	Patch width * patch length (0–5.83 km ²)
Land cover	Number of different CDL land cover classes within 500 m of site	4–26 classes
Urban	Distance to nearest CDL category urban	0–1602 m
Woodland	Distance to nearest CDL categories woody wetland, deciduous forest, evergreen forest, and mixed forest.	19–5419 m
Riparian	Distance to nearest CDL categories open water, herbaceous wetland, and woody wetland.	0–1939 m

trees (De'ath, 2007; Elith et al., 2008), 2) generalized additive mixed-effects modeling (Zuur et al., 2009), and 3) linear/generalized linear mixed-effects modeling (Zuur et al., 2009). These three stages were then followed by model selection and model averaging based on AICc to yield a final consensus model for each response variable. The first stage involved building a BRT model for each response variable that included all non-collinear predictors. We used BRTs in this stage of the analysis because of their ability to handle numerous predictor variables, to model non-linear relationships between predictor and response variables, and to automatically model interactions between predictor variables (De'ath, 2007; Elith et al., 2008). However, at present BRTs are not able to appropriately handle repeat sampling of sites, a design best analyzed with mixed-effects models (Zuur et al., 2009).

The second stage of our analysis involved running a generalized additive mixed-effects model for each response variable with site as a random effect and the BRT-reduced set of predictors as fixed effects, along with any interactions identified as important in the BRT analysis. A GAMM modeling framework allowed us to appropriately analyze the relationship between predictors and the response variable. The splines used in GAMMs provide information on the shape of the relationship between variables and the estimated degrees of freedom required to describe the relationship. However, splines are not very intuitive and do not provide a direct understanding of the relationships being modeled.

We, therefore, used the result of the GAMM models to build linear (richness and evenness) and generalized linear (maximum total abundance) mixed-effects models (GLMMs), incorporating any non-linearities and interactions identified as significant in the GAMM analysis. Linear mixed effects models relied on a Gaussian distribution as the data were normally distributed, whereas the GLMMs used a Poisson link function to account for over-dispersion of the count data. Linear mixed-effects models and GLMMs provide coefficients that directly link the response variable to the predictor variables, facilitating a general understanding of the system. These three methods were used for analysis of species richness, evenness, and maximum total abundance, but not maximum species abundance.

Modeling maximum abundance at the species level (maximum species abundance), rather than for all species combined (maximum total abundance) required that species, in addition to site, be treated as a random variable. Given the presence of two random variables, and the fact that one of them was replicated dozens of times for certain species, we elected to use mixed-effects models from the start for the analysis of maximum species abundance. As a first step, we modeled the individual relationship between each continuous predictor variable and species

abundance using GAMMs, with species and site as random effects. We used these results as a guide in building univariate GLMMs with a Poisson link function. Then, we used the results of the univariate GLMMs as a guide to build a multivariate GLMM with each of the coefficients that had a *p*-value < 0.10 in the univariate analysis.

Recognizing that often more than one competing model is a valid description of the relationships being investigated (Burnham and Anderson, 2002), we used the R package MuMin (Bartoń, 2014) to build a consensus model for each of the response variables via model selection and model-averaging.

See A1 of Appendix A for detailed information on response variable derivation and for further details on the analytical methods used in this study.

3. Results

We detected 113 bird species in margin strip-transects (Table B1). Correlations between predictor variables and results for the BRT and GAMM analyses are discussed in detail in section A2 of Appendix A, and Appendix B includes additional result tables not presented in the main text.

Rarefied species richness was significantly higher in margins with hedgerows, riparian vegetation, or treelines than in bare/weedy margins during both water years, with the exception of treelines in 2012–2013 (Fig. 2a, Table B2). During both water years, hedgerows and treelines had similar numbers of species; in 2012–2013 riparian margins had significantly more species than hedgerows, whereas in 2013–2014 they had significantly more species than treelines. Richness, by margin type, increased from the first water year to the second for all but the bare/weedy margins. An interaction between margin type and distance to woodland was evident in the fact that richness increased with increasing distance from woodlands for hedgerows and riparian margins (across most distances measured in this study), changed little for bare/weedy margins, and declined for treelines (Fig. 2b). Different aspects of model fit (BRT cross-validated correlation and deviance explained, GAMM and GLMM adjusted-R² values) indicate that the predictors of species richness model explained approximately 60 to 80% of the variability in the data (Table B6).

Rarefied species evenness (of the subset of sites with ≥ 20 individuals) was significantly higher in margins with hedgerows, riparian vegetation, or treelines than in bare/weedy margins (Fig. 3a, Table B3); there were no significant differences in evenness among the three woody margin types. Evenness was higher in the breeding season than

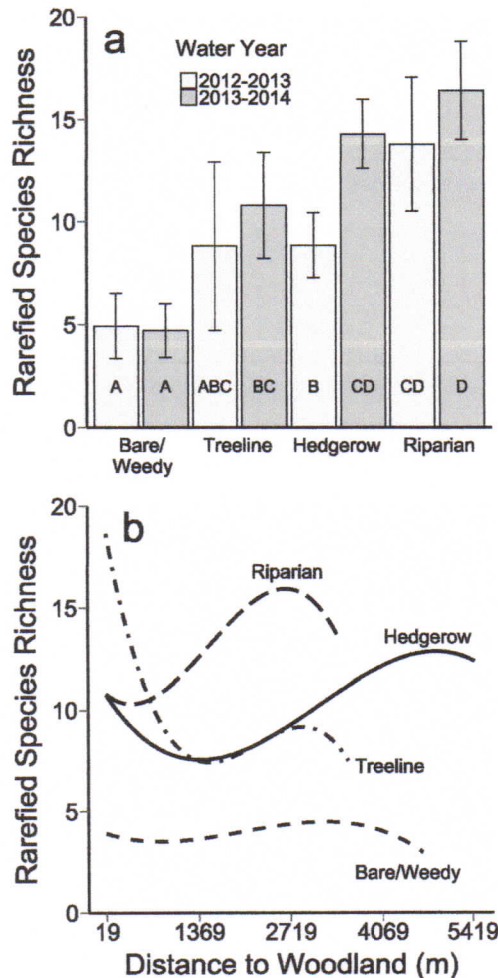


Fig. 2. Rarefied species richness model-averaged predictions: a) Richness by margin type and water year, with 95% confidence intervals. Combinations that differ significantly from each other (p -value < 0.05) are indicated by lettering inside the bars. b) Richness versus distance to woodland by margin type; 95% confidence intervals excluded here for clarity of presentation (but plotted in Fig. A2). Bar heights and lines represent the full-model average estimates for each variable, controlling for the effects of the other continuous covariates and with non-plotted categorical covariates set to their default values (for 2b, Water Year = 2012–2013). Changing the values of the categorical covariates would have the effect of shifting the estimates up or down, but would not change their position relative to one another.

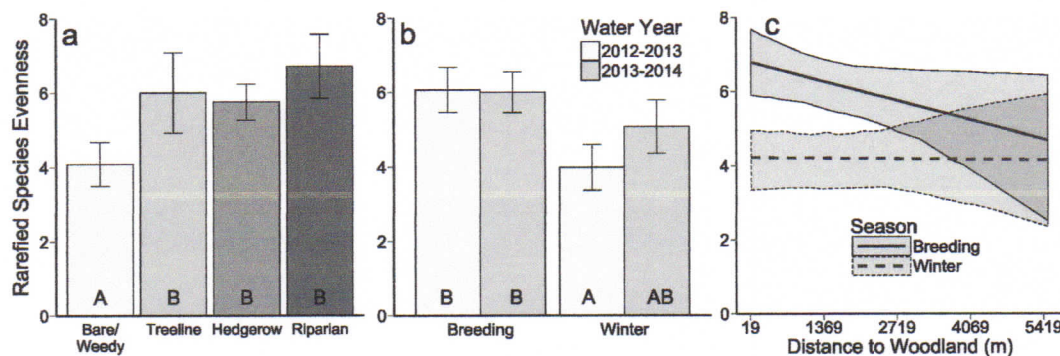


Fig. 3. Rarefied species evenness model-averaged predictions (for the subset of sites with ≥ 20 individuals): a) Evenness by margin type with 95% confidence intervals. The other categorical covariates are set to their default values (Water Year = 2012–2013, Season = Breeding). b) Evenness by season and water year with 95% confidence intervals. Default categorical covariate Margin Type = Hedgerow. c) Evenness versus distance to woodland by season; gray shading represents 95% confidence intervals. Other categorical covariate defaults same as in Panels a and b. Other details are as in Fig. 2.

in the winter, though the difference between seasons was only significant in the first water year of the study (Fig. 3b). Finally, evenness declined with increasing distance from woodland for both seasons (though the decline was non-significant in the final model); it was steeper during the breeding season (Fig. 3c). Approximately 28 to 35% of the variability in the data was explained by predictors of species evenness (depending on validation approach; Table B6).

Maximum total abundance was higher in treeline, hedgerow, and riparian margins than in bare/weedy margins, when both adjacent crop types were orchards (Fig. 4a, Table B4); however, there were no differences in total abundance among woody margin types. When at least one row crop was present, maximum total abundance was still higher in hedgerow and riparian margins than in bare/weedy margins, but the difference was not significant due to high variability; hedgerows had significantly greater total abundance than treelines when at least one row crop was present. Maximum total abundance was significantly higher in the winter than the breeding season, though the difference between seasons was greater in the first water year of the study (Fig. 4b). Finally, maximum total abundance increased with increasing distance from woodland (Fig. 4c). Predictors of maximum total abundance explained approximately 12 to 44% of the variability in the data (Table B6).

Predictor variables in the final maximum species abundance model accounted for very little variation in maximum species abundance (Fixed effects adjusted- $R^2 = 0.04$; Table B6); thus, although we describe the patterns revealed via GLMM, we recommend that they be interpreted in light of this fact. Maximum species abundance was highest in hedgerow margins, but also higher in riparian and treeline margins than in bare/weedy margins (Fig. A3a, Table B5). Maximum species abundance was higher in margins when both adjacent crop types were orchards (Fig. A3b), and higher in the winter than the breeding season, though the difference between seasons was greater in the first water year of the study (Fig. A3c). There was a positive linear association between maximum species abundance and both patch area (Fig. A3e) and the number of land cover classes (Fig. A3f). There was also a positive association between maximum species abundance and distance from woodland for distances 1–4 km; for shorter and longer distances the association leveled off or decreased (Fig. A3g). Finally, there was significant variation in species abundance among the projects providing data for this study (Fig. A3d).

4. Discussion

Crop margins with hedgerows, treelines, or remnant riparian vegetation harbored significantly more bird species, greater species evenness, and higher maximum total abundances of birds than bare or weedy margins. Although this qualitative result did not come as a

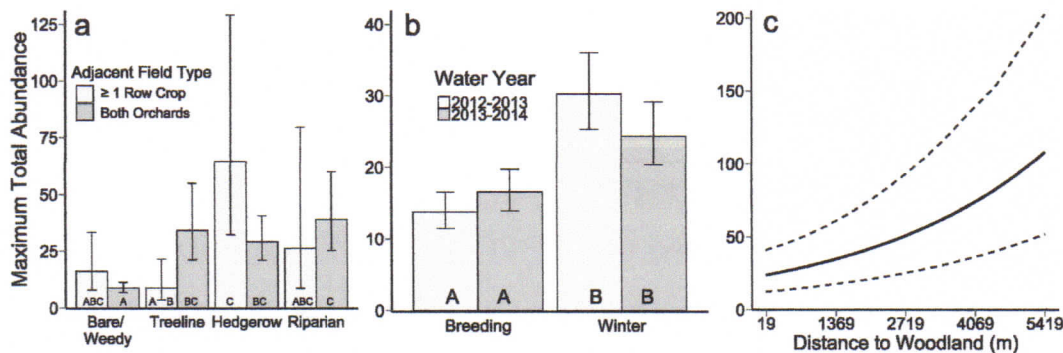


Fig. 4. Maximum total abundance model-averaged predictions: a) Maximum total abundance by margin type and adjacent crop type, with 95% confidence intervals. The other categorical covariates are set to their default values (Water Year = 2012–2013, Season = Breeding). b) Maximum total abundance by season and water year; other categorical covariates are set to their default values (Margin Type = Hedgerows, Adjacent Crop Type = Both Orchards). c) Maximum total abundance versus distance to woodland; dashed lines represent 95% confidence intervals. Other categorical covariate defaults same as in Panels 4a and b. Other details are as in Fig. 2.

surprise—for example, comparatively fewer birds utilized the scant resources found in margins with bare ground or mowed weeds (i.e., 5 species and < 15 maximum individuals on average)—the quantitative differences, even for the simplest woody margin habitat, treelines, were unexpected (i.e., 2–3 times as many species and 3–6 times as many maximum individuals as bare/weedy margins on average). Given the intensity of agricultural practices on these farmlands we did not expect that narrow, linear, woody plant margins would host the diversity of birds observed in this study. Importantly, these findings provide evidence for the benefit of common farmland diversification practices being promoted within these intensified croplands, providing sound scientific support for existing agri-environment schemes and policies.

In addition to the overall increase in diversity and abundance in woody margin types, we also found that species richness in hedgerows and riparian margins increased with increased distance from natural woodlands (for most distances measured in this study); likewise maximum total abundance increased with increased distance from woodlands, regardless of margin type. Tschamtké et al. (2012) proposed and Batáry et al. (2011, 2010) provided evidence for the hypothesis that agricultural land diversification practices have a stronger positive impact on biodiversity in simple agricultural landscapes (i.e. with 1–20% semi-natural habitat) versus those with cleared landscapes (< 1% semi-natural habitat) or complex landscapes (> 20% semi-natural habitat). Our results corroborate this hypothesis. The majority of the landscape in our study region is highly simplified with very little natural habitat. Woodlands in the study area are generally present in two forms: 1) restored and protected patches of deciduous riparian vegetation and oak woodlands embedded in the agricultural mosaic, and 2) extensive natural oak and evergreen woodlands on the undeveloped ridge slopes west of the valley (Fig. 1). The peak in species richness in hedgerows and riparian margins at approximately 5 km and 2.7 km from woodlands, respectively, likely reflects lower use of margin patches by birds when natural woodlands are nearby. This highlights the relative importance of installing patch habitats on farms in more simplified landscapes to support a greater number of species and individuals across the larger landscape and to complement conservation of natural areas in the broader region. It is also worth noting that our results suggest species richness in hedgerows initially declines with distance from woodlands and then increases as sites exceed 1 km from woodlands. This would make sense if many of the species using hedgerows preferentially use woodlands that are nearby, only remaining in hedgerow habitats when woodlands exceed regular dispersal distances. This distance effect may be useful in optimally siting hedgerows by prioritizing installation in simplified landscapes > 2 km from natural habitats. We did not detect the same effect of distance from woodland for treelines, however. One possible explanation for this is that treelines are relatively simple habitats (usually comprised of a single tree

species) and perhaps offer relatively little habitat value in the absence of nearby natural habitats.

Species evenness and maximum total abundance (but not richness) were strongly associated with season. Evenness was higher in the breeding season versus the winter, whereas the opposite was observed for total abundance. Significant differences in evenness and total abundance between seasons might partially reflect changes in bird behavior over the annual cycle. For example, our estimates of greater evenness during the breeding season matched predictions by Tramer (1969) who expected territoriality to be associated with greater evenness (but see Alatalo and Alatalo, 1980; Craig and Klaver, 2013). Spatiotemporal migration patterns likely explain our estimates of higher abundance during the winter; the most abundant species detected during surveys, Gambel's white-crowned sparrow (*Zonotrichia leucophrys gambelii*), is an austral migrant that only occupies the study region in winter before migrating northward for breeding.

The effects of water year on three of the four bird indices examined could reflect the influence of an extreme event within a multi-year drought; the second water year of our study was the driest year on record in the Sacramento Valley (NOAA, 2016). In each case, water year interacted with either margin type or season. The largest effect we found was for species richness, which was higher during the driest year on record in the Sacramento Valley for all margin types except for bare/weedy types. We hypothesize that more bird species concentrated in treeline, hedgerow, or riparian margins during extreme drought conditions when food resources throughout the drier landscape were likely less plentiful (e.g., in less frequently irrigated crops, more empty ditches, fewer tailings ponds). Indeed, there is evidence for reduced farmland arthropod abundance in agricultural crops during experimental drought conditions and increased abundance after an experimental increase in irrigation (Frampton et al., 2000). Furthermore, among all margin types, we estimated the highest number of bird species in riparian streamside margins during the second water year; riparian habitats are expected to serve as wildlife refugia during severe drought conditions predicted under climate change scenarios in this region because of the relatively higher productivity, cooler temperatures, and higher abundances of arthropods found in riparian zones versus upland habitat types (Seavy et al., 2009).

Generally, our results align with previous research on woody field margin habitats in Europe (e.g., Hinsley and Bellamy, 2000) and other regions of North America (Best et al., 1995; Deschênes et al., 2003; Jones et al., 2005), which also demonstrated positive effects of woody field margin habitat on avian diversity or abundance. We did not find strong relationships between the bird indices examined and characteristics of the field margin vegetation (i.e., vegetation height, number of vegetation layers), after accounting for the effects of margin type and landscape context (Tables B36 and B37; though these

variables were important if margin type was excluded from the analysis). Thus, our results suggest that detailed metrics of vegetation height and vertical structure matter less for bird diversity and abundance than the mere presence of woody vegetation (at least in this system). Grassland bird communities likely provide an important exception to the aforementioned patterns, as they have been found to respond negatively to woody vegetation edges of the North American prairie region and elsewhere (Best, 2000; Quinn et al., 2012; Tack et al., 2017). Though grassland species such as horned larks (*Eremophila alpestris*), western meadowlarks (*Sturnella neglecta*), and savannah sparrows (*Passerculus sandwichensis*) utilized bare/weedy and woody margins in this study (Table B1), we did not further investigate patterns by species or guild.

Our study was also not designed to assess the potential pitfalls for birds occupying margin habitats in this agricultural environment. When evaluating the conservation value of agricultural lands for birds, an important but understudied consideration is the fitness potential of the habitats in question and the population dynamics of the bird community, neither of which can be assessed by counts alone (Kleijn et al., 2011; Komar, 2006). In a majority of compared bird studies it was found by Bock and Jones, 2004 that bird density was positively correlated with survival or reproduction and thus bird counts may be sufficient proxies for evaluating and comparing bird habitats; the important exception was that negative relationships between bird density and reproductive success were more often found in anthropogenically-disturbed landscapes. There may be features of margin habitats that are unfavorable to avian survival or reproduction, which can lead to ecological traps (Battin, 2004). Patch and landscape characteristics associated with margin habitats (e.g., linearity, high edge to area ratio, landscape isolation, and variation in matrix permeability and risk) are predicted to be associated with higher rates of bird mortality, nest parasitism and predation, and susceptibility to harsh abiotic environments (Sisk and Battin, 2002). Additionally, exposure to agrochemicals can have direct and indirect negative effects on avian reproduction or survival (Gibbons et al., 2015), and has been associated with bird declines (Hallmann et al., 2014; Mineau and Whiteside, 2013). In theory, if farmland woody margins are ecological traps, they can influence population dynamics on a larger scale and lead to regional bird declines by becoming population sinks in which attractive habitat cues (e.g., concentrated food resources) may lure birds to lower quality habitats (e.g., those with greater predation risk during dispersal), and the reproductive rate of the regional population is unable to exceed its mortality rate (Pulliam and Danielson, 1991). These types of questions need attention in agricultural landscapes, but are far beyond the scope of the current study.

One additional caveat is that the study design did not allow us to control for differential detectability across species or habitat types. We doubt that interspecific variation in detectability influenced our results, however, since the focus was on aggregate measures of species diversity and abundance. Additionally, all of our observers were well trained in detecting small bird movements and identifying calls; we are confident that even non-visible birds in thicker vegetation were mostly accounted for. Finally, if there were differences in detectability among habitat types, we would expect detectability to be near perfect in bare/weedy margins but lower than actual abundance in more complex woody habitats; it would follow that if there were detectability issues, the differences in actual abundance between habitat types would likely have been even greater than our estimates.

Given that there are ca. 40,000 km of agricultural ditches and canals in the Central Valley (not to mention other types of margins), even if only a fraction were planted with hedgerows or other margin vegetation, it would likely provide many benefits for birds. Encouragingly, woody margin habitats may also benefit farmers: research has positively linked bird diversity and the presence of field margin vegetation with increased pest-control by birds (Garfinkel and Johnson, 2015; Kross et al., 2016), although it is important to note that some birds

cause significant crop damage for farmers (Gebhardt et al., 2011). Hedgerows, in particular, have been shown to also harbor pollinators (Morandin and Kremen, 2013) and predatory and parasitic insects which are then exported into nearby crops with demonstrated benefits to farmers in the form of pest reduction (Morandin et al., 2014). Collectively, these findings indicate that preserving riparian habitats and treelines or installing hedgerows along crop margins will increase the diversity and abundance of multiple beneficial animals, whose combined effects likely increase ecological services for farmers, which can in turn create support for on-farm conservation action (Garbach and Long, 2017; Kross et al., 2017). Further research into the benefits or costs of attracting birds to different crop types, however, will be essential to understanding the net outcome for farmers (Peisley et al., 2015; Saunders et al., 2016; Triplett et al., 2012).

5. Conclusion

Hedgerow, riparian, and even simple treeline crop margins increased bird species richness, evenness, and abundance, and hedgerow plantings were most effective at distances of 3.4–5.4 km from patches of woody habitat. These combined results increase our confidence in the benefits of woody field margin habitats to bird communities in other highly intensified non-prairie agricultural landscapes in North America and Mediterranean climates worldwide. While protecting and retaining natural habitat within the agricultural matrix is ideal, agricultural expansion and intensification worldwide has led to a loss of these features, especially in highly productive landscapes. Furthermore, our findings coupled with those of other studies in the Central Valley (Gardali et al., 2006; Latta et al., 2012), indicate that retention and restoration of riparian habitat—one of the predominant natural habitat types before conversion to agriculture—increases the abundance and diversity of songbirds during winter and breeding seasons. We therefore argue that in intensifying agricultural landscapes, land management decisions should strive to first preserve and/or restore whatever natural fragments remain, and that hedgerows should be established along margins in areas where natural habitats have already been replaced by farming. Our findings provide strong evidence that the funding allocated to protecting or establishing habitat for birds along field margins is successful at attracting a diverse assemblage of birds to farms.

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Appendix A and B. Supplementary materials.

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