Unraveling the Influence of Uncultivated Habitat on Avian Grape Damage in a Viticultural Landscape

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ABSTRACT: Uncultivated habitats within and near farms can strongly affect the ecosystem services and disservices delivered by birds in agriculture. In winegrape vineyards, previous work suggests insect-eating birds have the potential to remove pests, but grape-eating birds can cause crop losses by damaging or removing ripe grapes. We conducted avian point counts and grape damage surveys at 20 and 6 vineyards, respectively, in Napa Valley, California in late summer 2023 to investigate the hypothesis that uncultivated habitats increase the abundance of grape-damaging birds and grape damage. We detected 22 bird species considered to potentially damage grapes. The three most common species – dark-eyed juncos, European starlings, and house finches – accounted for 45% of all detections. The number of potential winegrape damagers was, on average, 46% lower in vineyard interiors than near edges (>75 m or <30 m from vineyard edge, respectively). Overall, we observed very little (<1%) grape damage from birds, though the timing of our surveys may have been early for this vintage marked by a cool wet spring. We found mixed support for the hypothesis that grape damage is positively associated with uncultivated habitats. As predicted, grape bunch damage was higher on sample plots with nearby grassland habitat (within 25 m). However, at a larger landscape scale, we found that grape bunch damage increased with more urban habitat and increased at further distances from uncultivated habitat. These results suggest that the proximity of wooded uncultivated habitats, such as forests, oak woodlands, and riparian habitats, did not lead to increased grape damage in this study. Given how little bird-caused grape damage was observed, we suspect the benefits of native habitat along edges and in the landscape for attracting insect-eating birds outweigh the costs of a few more grape-damaging birds, though this should be investigated formally.

KEY WORDS: birds, damage assessment, grape damage, *Haemorhous mexicanus*, *Junco hyemalis*, *Sturnus vulgaris*, uncultivated habitat, viticulture

Proceedings, 31st Vertebrate Pest Conference (R. M. Timm and D. M. Woods, Eds.)
Paper No. 35. Published December 21, 2024. 13 pp.

INTRODUCTION

Birds in agricultural habitats can help control pests but also act as pests themselves (Dolbeer et al. 1994, Gebhardt et al. 2011, Díaz-Siefer et al. 2022, Monteagudo et al. 2023). The types and magnitude of ecosystem services and disservices delivered by birds on farms varies with the functional traits of species present and their seasonality (Saunders et al. 2016, Garcia et al. 2020). While insect-eating birds can be beneficial by consuming pests that damage crops (Peisley et al. 2016), fruit and grain-eating birds can consume crops, and, in certain seasons, large flocks of these birds can inflict significant damage. For example, in the fall, flocking American crows (*Corvus brachyrhynchos*) and European starlings (*Sturnus vulgaris*) caused damage to honeycrisp apples in Washington exceeding $7,000 USD per ha (Anderson et al. 2013). Similarly, during Africa's wet seasons, large aggregations of red-billed queleas (*Quelea quelea*) reduced cereal crop harvests by up to 13%, imposing $4.7 billion USD in economic losses (De Mey et al. 2012). Moreover, some bird species switch from being primarily insectivorous in the breeding season to more omnivorous afterward, so some species can simultaneously provide ecosystem services and disservices from the farmer's perspective (De Graaf et al. 1985, Garcia et al. 2020). Thus, researchers should investigate the relative strength and scope of avian services and disservices to disentangle the various roles of birds in agroecosystems.

Recent work has revealed that habitat complexity in and around farms can strongly affect the costs and benefits of birds in agriculture. For example, in strawberry farms in central California, birds eat insect pests, such as lygus bugs (*Lygus* spp.), but they can also eat insect predators of those pests (i.e., intraguild predation), damage the fruit directly, and introduce fecal contamination (Garcia et al. 2020). The relative strength of these costs and benefits are shaped by interactions between local farming practices and landscape context (Olimpi et al. 2020). Specifically, Olimpi et al. (2020) found that the amount of uncultivated (semi-natural) habitat surrounding each farm was the single most important driver of avian ecosystem services, with the best outcomes (highest multifunctionality) occurring on farms surrounded by uncultivated habitat. On a local scale, uncultivated habitats along the edges of or within farms may affect bird services (or disservices) based on individual birds' behavioral responses. For example, birds may make short-distance forays from natural habitats into the adjacent farmland and remove pests or damage fruit (Railsback and Johnson 2014, Kross et al. 2016). At a larger landscape scale, abundant natural habitats nearby could boost local populations of insect-eating and/or fruit-eating birds, with concomitant costs and benefits to local farms (Boesing et al. 2018, Lindell et al. 2018, Garcia et al. 2023). Nearby uncultivated habitats could also draw birds away from agricultural fields, reducing their role – whether positive or negative – on the farms themselves (Tscharntke et al. 2016). Indeed, there are numerous potential mechanisms for how habitat complexity could affect the delivery of ecosystem services on farms (Tscharntke et al. 2016), which likely vary depending on crop types and the ecology of the local avifauna and pest species. This context-dependent nature of avian ecosystem services and disservices underscores the importance of field-based work to quantify bird abundances and their damage across a wide range of crop and landscape settings.

In winegrape vineyards, previous work suggests insect-eating birds have the potential to remove pests (Jedlicka et al. 2014, Paiola et al. 2020), but grape-eating birds can cause crop losses by damaging or removing ripe grapes (Somers and Morris 2002). Winegrape losses from birds have been reported to be as high as 50% or more in Australia (Bomford and Sinclair 2002, Tracey and Saunders 2003), up to 27% in New Zealand (Saxton 2006, Kross et al. 2011), and 25% in Ontario, Canada (Somers and Morris 2002). In California, estimates suggest that bird-caused damage is typically much less than these figures (i.e., <2%; DeHaven 1974). There is also some evidence that damage may be spatially heterogenous, peaking near vineyard edges in California (Kross et al. 2016) as suggested elsewhere (Somers and Morris 2002, Tracey and Saunders 2003), but this has not yet been studied extensively.

How edge habitat affects grapes likely depends on which bird species cause damage in California's vineyards. Though early work emphasized the importance of European starlings and house finches (*Haemorhous mexicanus*; DeHaven 1974), no studies have systematically surveyed for potentially damaging bird species within California vineyards, and the role of surrounding habitats on potential grape-damaging birds remains unresolved. Thus, "who damages California's grapes, how much, and why" remains understudied. These are important research gaps because California winegrapes are economically vital to the state and important nationally, contributing more than $170 billion to the U.S. economy annually (Dunham & Associates 2022).

In this study, we investigated how local habitat and landscape composition is associated with winegrape damage and the abundance of grape-damaging birds in Napa Valley, California. Our study had three objectives: 1) quantify the abundance of birds that could potentially damage winegrapes, 2) quantify bird-caused winegrape damage, and 3) investigate factors associated with the abundance of these birds and bird damage. Based on previous work conducted in other regions, we hypothesized that uncultivated habitats increase the abundance of grape-damaging birds and observed rates of winegrape damage. Specifically, we tested predictions that bird abundance and grape damage are positively associated with the amount of uncultivated land cover types at two scales, 25 m and 200 m, and negatively associated with the distance to uncultivated land cover.

METHODS

Study Area

We conducted this study across 20 vineyards in Napa Valley, California, located approximately 100 km north of San Francisco (Figure 1) and bordered by the Mayacamas Mountains on the west and the Vaca Range on the east. The region is characterized by a Mediterranean climate which, together with its unique geologic history, microclimates, and diverse soils, supports 16 viticultural appellations (Napa Valley Vintners 2020). The agricultural habitats in the northern region of the valley are bordered primarily by mixed oak and conifer forests, whereas the southern region of the valley is surrounded by grasslands and oak savannas (Napa County 2010, Napa Valley Vintners 2020), with narrow riparian woodlands throughout the valley along the Napa River and its tributaries. Approximately half of the vineyards that we studied had existing nest boxes for cavity-nesting songbirds, and half did not.

Bird Surveys

We used point counts to quantify bird abundance by recording all birds seen or heard during 16 minutes within a 50-m radius of the observer (Ralph et al. 1995). To maximize farm coverage while minimizing double-counting individuals, we distributed survey points within vineyards at least 150 m from each other. Half of the points were located at least 75 m from a vineyard edge (interior points) and half were located near vineyard edges (4 vines or two rows in, often with a dirt road along edge; usually 20-30 m from the habitat edge; Figure 1). Vineyards varied in size from 12.5 to 72 hectares, so the number of survey points per vineyard also varied from 2 to 12, for a total 149 point count sites (74 edge, 75 interior; mean per vineyard 3.7 and 3.75, respectively). We conducted point count surveys once at each point from 21 August to 13 September 2023 to coincide with anticipated fruit ripening based on previous years' timing. Surveys began at sunrise and continued for 5 hours. With the aid of binoculars, all birds seen and heard were recorded, and any species observed damaging winegrapes were noted. We also noted birds observed beyond the edge of the fixed radius or flying overhead (i.e., not using the habitat); however, these individuals were not included in analyses. Flying birds that were actively using the habitat (i.e., foraging swallows) were recorded as standard detections within the plot and used in analyses.

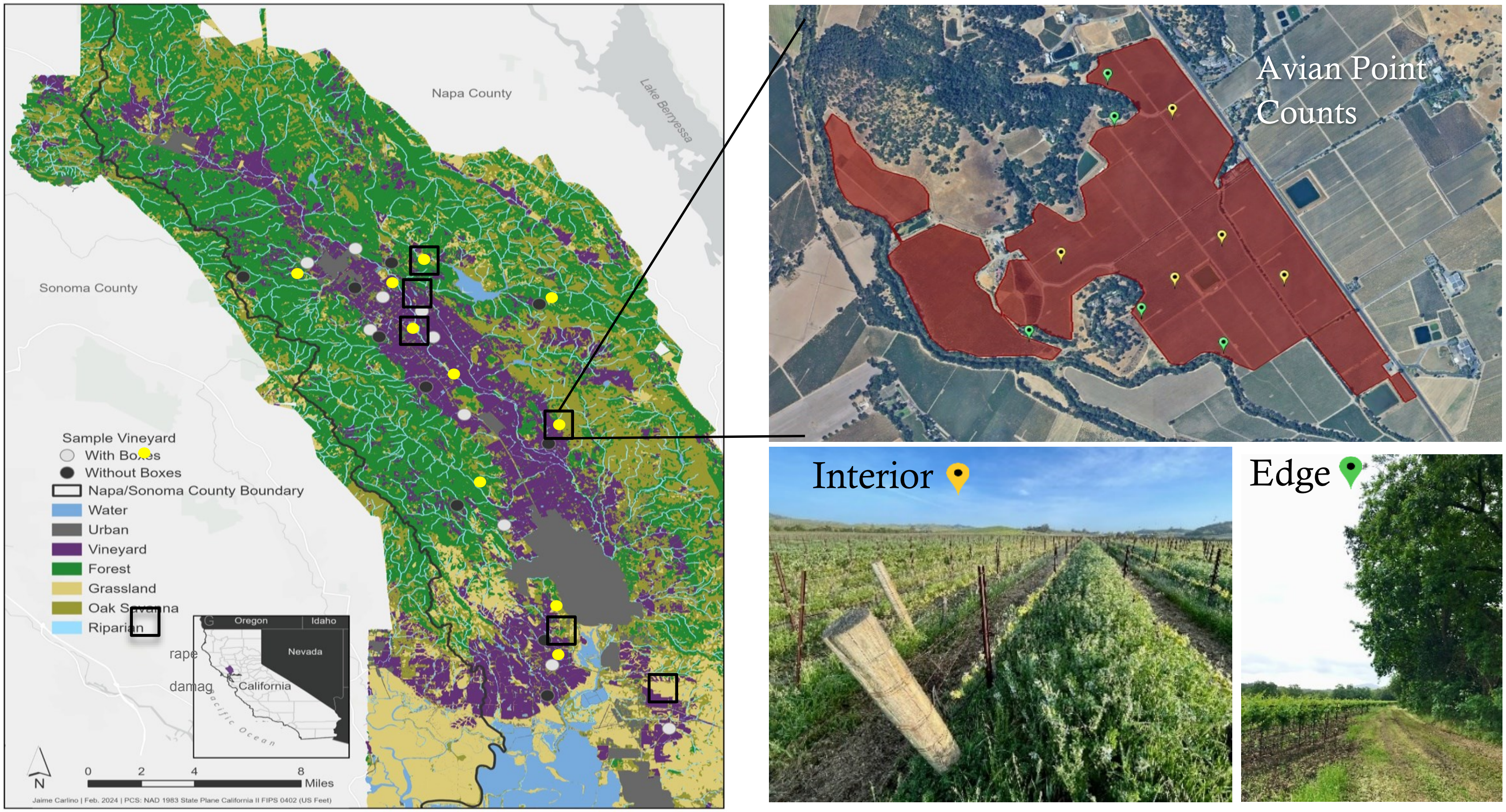

Figure 1. Napa Valley study area showing land cover types and 20 vineyards where avian point counts were conducted, and 6 vineyards where grape damage surveys were conducted. Insets depict the distribution of point count stations among vineyard edge and interior habitats.

We acknowledge that birds were imperfectly detected (i.e., detection probability <100%). However, given the structural similarity of our bird survey locations (all survey points were within vineyard rows), we assume detection probabilities varied minimally across sample points and vineyards such that bird detections could provide a meaningful index of spatial variation in relative bird abundance.

Our aim was to understand how land-use patterns may affect the abundance of birds that could damage winegrapes; thus, we filtered data to only those species classified as "potential winegrape damagers." These species were identified by three steps. First, species were considered if fruit was noted in either of the first two food preferences in the Birder's Handbook (Ehrlich et al. 1988). Second, we used the Elton Traits database (Wilman et al. 2014, Table 1) to confirm that fruit accounted for 10% or more of those species diets, excluding any species that had a score of zero for fruit as a part of their diet (this removed band-tailed pigeon (*Patagioenis fasciata*) and oak titmouse (*Baeolophus inornatus*); see Table 1 for all scientific names). Third, we added any species that were observed actively damaging winegrapes in Napa during our survey work (A. Turner, pers. observ.; this added dark-eyed junco and pileated woodpecker). We then summed the number of these birds detected at each point count station as our index of the abundance of potential winegrape damagers. We did not systematically examine each species individually, though we did run a few *a posterior* models on individual species to aid in interpretation of findings.

Grape Damage Surveys

Our project aimed to assess damage to both white and red grapes, as varietal color, timing, and aroma can have an impact on bird damage (DeHaven 1974). Based on conversations with vineyard managers, six of the 20 vineyards were selected for damage surveys, each of which contained both red and white varietals, had no wide-spread use of bird deterrents or netting, and had projected ripening dates in 2023 that coincided with our bird surveys. To obtain a sufficient number of white samples, which are less commonly cultivated in Napa Valley, we examined both Chardonnay and Sauvignon Blanc. For the red grape variety, we focused only on Cabernet Sauvignon, the most common varietal grown in the region.

On each vineyard, we mapped a grid of 25 × 25 m possible sampling plots on the vineyard blocks (discrete fields within a vineyard, usually defined by farm roads) containing one of the selected grape varieties (*sensu* Kross *et al.* 2011). Each grid cell was then classified as edge (sample plots with one or more edges directly adjacent to uncultivated habitat; woodland, shrubland, grassland, etc.) or interior (sample plots with all four edges adjacent to other vines). We randomly selected 510 of these grid cells as sampling plots, stratified by the acreages of winegrape varietal to achieve proportionally 20% sampling density by area. We then divided each variety's allocation equally between edge and interior sampling plots. To assess bird damage within each sample plot, we walked a random distance (0-20 m) towards the center of the plot from the edge to ensure samples were collected different distances from the vineyard edge.

Table 1. Birds identified as potentially damaging winegrapes in Napa Valley, California, and the source of the information used for this determination (e.g., E&W indicates birds shown to eat fruit in Ehrlich et al. 1988 and confirmed with Wilman et al. 2014; Obs. indicates the species was observed eating fruit in this study).

Common Name	Scientific Name	Total Detections	Source
Acorn Woodpecker	*Melanerpes formicivorus*	61	E&W
American Crow	*Corvus brachyrhynchos*	3	E&W
American Robin	*Turdus migratorius*	8	E&W, Obs.
California Scrub-jay	*Aphelocoma californica*	29	E&W
California Towhee	*Melozone crissalis*	58	E&W, Obs.
Chestnut-backed Chickadee	*Poecile rufescens*	8	E&W
Common Raven	*Corvus corax*	11	E&W
Dark-eyed Junco	*Junco hyemalis*	154	Obs.
European Starling	*Sturnus vulgaris*	233	E&W, Obs.
House Finch	*Haemorhous mexicanus*	508	E&W, Obs.
Hutton's Vireo	*Vireo huttoni*	1	E&W
Northern Mockingbird	*Mimus polyglottos*	12	E&W, Obs.
Orange-crowned Warbler	*Leiothlypis celata*	4	E&W
Pileated Woodpecker	*Dryocopus pileatus*	0	Obs.[A]
Say's Phoebe	*Sayornis saya*	1	E&W
Steller's Jay	*Cyanocitta stelleri*	2	E&W
Warbling Vireo	*Vireo gilvus*	2	E&W
Western Bluebird	*Sialia mexicana*	108	E&W, Obs.
Western Tanager	*Piranga ludoviciana*	85	E&W, Obs.
Wild Turkey	*Meleagris gallopavo*	12	E&W
Willow Flycatcher	*Empidonax traillii*	1	E&W

[A] This species was observed damaging grapes during field work but was never recorded within the 50 m radius of the point counts, so this observation is not included in the analyses of the abundance potentially damaging birds.

After arriving at a sampling location, we randomly selected one grape bunch from each of 20 vines, including 10 sequential vines on each side of the vineyard row to account for sun exposure. We selected grape bunches randomly by drawing two numbers, based on 10 cm intervals, to represent the horizontal and vertical position of the bunch (Tracey and Saunders 2010). Bunches were visually examined to quantify the percentages of plucked (the whole grape missing), pecked (a piece of grape missing), and undamaged grapes (Figure 2). All three observers (BM, AT & KA) underwent training on photos and field bunches to calibrate their estimates [as recommended by Saxton (2006)] .

Vine Structure and Grape Attributes

We collected data on grape varietal, height of the grape vine canopy (nearest 1 cm), trellis system (VSP [vertical shoot position], Angled VSP, High quadrilateral, or Lyre trellis), extent of cover crop (none, only between vine rows [partial], or between and under vine rows [full]), and the vine stem diameter (nearest cm) measured at 10 cm above the ground. We also calculated days before harvest from harvest dates provided later by the winegrowers.

Local and Landscape Land Cover

We documented the amount of uncultivated land cover within a 25 m and 200 m radius of the center of each sample plot, which reflects spatial scales relevant to foraging movements and occupancy distribution of birds, respectively. Local land cover (25 m radius) was assessed visually with the aid of a rangefinder in the field and estimated to the nearest 5%. Landscape land cover (200 m radius) was quantified using a four-meter resolution habitat GIS raster developed using remotely sensed data, including National Aerial Imagery Project and Light Detection and Ranging data and vector-based data on hydrography and agriculture (Corro 2021, Carlino 2024). In each case, we recognized 5 land cover types: grassland, riparian vegetation, woody upland habitat (forest, oak savannah, or shrubland), vineyard, and urban. We also pooled the first three categories into a "uncultivated habitat" for some analyses. For the local scale, we also distinguished a road cover type (usually dirt or grass farm road, occasionally paved) that was not distinguishable with our GIS layer. These categories accounted for more than 90% of all the area at the local and landscapes scales, so we did not include an "other" category. The distributions of local landcover values were extremely right skewed for the grape damage sample plots, so we collapsed these continuous scores into binary presence or absence scores for each land cover type within the 25 m radius. Lastly, distance to uncultivated habitat was measured in GIS for use in grape damage analyses.

Analyses

For bird abundance, our response variable was the pooled number of potential winegrape damagers detected at each point count station (n = 149). For grape damage, we quantified the mean % of grapes plucked or pecked (or combined as % damaged) per bunch at each sample plot (20 bunches per sample plot, n = 510 sample plots; though 4 were removed due to incomplete data), hereafter referred to as percent individual grapes plucked, pecked, or damaged. These values were very low (see results) and proved difficult to model. We thus also calculated the proportion of the 20 bunches at each sample plot that showed any sign of damage (0 or 1 per bunch, with the proportion ranging from 0-1 for each sample plot), hereafter referred to grape bunch damage, and used this value for modeling effects of habitat. We tested the correlation between percent individual grapes damaged and percent bunches damaged with a Pearson's r test. All analyses were performed in R (V 4.4.1) (R Core Team 2024).

To model effects of habitat variables on bird abundance and grape bunch damage, we grouped explanatory variables into three functional groups: vine structure/grape attributes, local landcover, and landscape landcover, as previously described. We used correlation matrices and variance inflation factors from the car package (vif; Fox and Weisberg 2019) to identify highly collinear variables (Pearson's $r > 0.7$ or vif > 5; James et al. 2017) resulting in the removal of the % vineyard within a 25 m and 200 m radius. Unsurprisingly, edge vs. interior was also collinear with distance to uncultivated habitat and several of the land cover compositions at both the 25 m and 200 m radii. Therefore, final candidate models (see below) contained either the binary edge vs. interior classification or the variables of % land cover types, but not both. We scaled all numerical explanatory variables to aid in model convergence and to enable more intuitive comparison of coefficients across variables. Nest boxes attract primarily insect-eating songbirds, and, indeed, the presence or absence of existing nest boxes (n=10 vineyards each) showed no association with the abundance of potential grape damaging birds (see Results). We thus omitted whether or not a vineyard had nest boxes from further analysis. Likewise, though sample size of vineyards was smaller for grape bunch damage (6 vineyards, 3 with and 3 without existing nest boxes), there was also no evidence that damage differed based on nest box presence (see Results), so it was omitted from further analysis.

Our emphasis was on investigating effects of habitat variables on birds and bird-caused grape damage, but vine structure and grape attributes may affect the spatial distribution of damage and could mask patterns from habitat if unaccounted for. We thus used a tiered approach to develop final candidate model sets. First, we used a fully parameterized model (all non-collinear predictor variables) to explore various error structures (gaussian, Poisson, negative binomial, etc.) and random factors (vineyard, vineyard blocks nested within vineyard) to arrive at a model structure that converged, fit well, and met assumptions of overdispersion and homoscedasticity, assessed with the DHARMa package (Hartig 2022). For bird abundance, we settled on a negative binomial error distribution with vineyard as a random (intercept) effect. For grape bunch damage, we found that a binomial error distribution with vineyard block nested within vineyard as random effects worked best. Next, we ran an initial 'saturated' model containing all additive combinations of the non-collinear vine structure and grape attributes, along with all non-collinear local or landscape effects. We then selected only those vine structure and grape attribute variables that had coefficients with 95% confidence intervals that did not overlap zero.

Figure 2. Images of two bunches of grapes depicting undamaged, pecked, and plucked grapes, Napa Valley California, 2023.

Akaike's information criterion corrected for small sample size (AICc) was used to rank models in each candidate set. Models within 2 ΔAICc were considered competitive with the top model (Burnham 2010). To assess model fit of top models, we report the conditional and marginal R^2 values calculated with the performance package in R (Lüdecke et al. 2019).

RESULTS

In total, we detected 1,973 individuals of 70 bird species, of which 1,301 detections of 22 bird species were considered potential winegrape damagers (Table 1). The three most detected species – dark-eyed juncos, European starlings, and house finches – accounted for 45% of all detections (69% of all detections of potential damagers). Preliminary modeling showed that only cover crop extent was significantly associated with the number of potential winegrape damagers (with more birds detected on points with partial cover crops than at points with full cover crop), so this variable was included in all models in the final candidate model set. There was no evidence that other vine structure or grape attribute variables affected bird abundance. Likewise, there was no evidence that the abundance of potential winegrape damagers detected per point count differed between vineyards with and without nest boxes (mean ± s.d.; 8.48 ± 8.68 and 8.95 ± 10.90, respectively).The top model for predicting the pooled relative abundance of all potential grape-damaging birds contained the single habitat variable of vineyard edge vs. interior, carrying 53% of the model weight (Table 2). This model fit the data well (marginal $R^2 = 0.14$, conditional $R^2 = 0.20$), and no other model in the candidate set was competitive (all ΔAICc > 2). The number of potential winegrape damagers was, on average, 46% lower at interior than at edge point count stations (Figure 3), and the 95% confidence interval for the coefficient for this predictor did not overlap zero (Table 4). When modeling the three most commonly detected species individually, the amount of uncultivated habitat at the local (25 m) and landscape (200 m) scale were included in the top models for European starlings and dark-eyed juncos, with starlings positively and juncos negatively associated with uncultivated habitat. The top model for house finches included a negative association with uncultivated habitat at the landscape scale.

Overall, we observed very little grape damage. The mean ± s.d. percent grapes plucked at a sample plot (average of 20 bunches per plot) was 0.22% ± 1.08%, ranging from 0 to 14.9%). The mean % pecked was 0.62% ± 1.05%, ranging from 0 to 9.9%. Finally, the mean total damaged (plucked + pecked) of individual grapes was 0.84% ± 1.67%, ranging from 0 to 18.8%. The mean percent of bunches exhibiting any degree of damage (out of 20 on a sample plot) was 16.8% ± 17.7%, ranging from 0 to 85%. There was a significant positive correlation between the mean percent of grapes damaged on a sample plot and the percent of bunches showing sign of damage on a sample plot ($t = 18.64$, df = 504, $P < 0.01$, $r = 0.64$). For subsequent analyses, we used the latter as our measure of grape damage.

Table 4. Top models for the abundance of potential winegrape damagers and observed grape bunch damage, showing the estimate and 95% confidence limits for each predictor variable. Variables whose confidence intervals do not overlap zero are considered statistically important and are bolded.

Predictor Variable	Estimate	Lower CL	Upper CL
Fixed effects for model of bird abundance			
Intercept	2.9229		
Interior (edge)	**-0.6144**	**-0.961**	**-0.268**
Full cover crop (partial)	**-0.7732**	**-1.359**	**-0.187**
No cover crop (partial)	-1.0962	-2.704	0.512
Fixed effects for model of grape bunch damage			
Intercept	-2.382		
Chardonnay (cabernet sauv)	**-0.854**	**-1.514**	**-0.194**
Sauvignon Blanc (cabernet sauv)	0.371	-0.170	0.913
Days to harvest	-0.124	-0.341	0.094
No cover crop (full)	**0.996**	**0.460**	**1.532**
Partial cover crop (full)	0.790	-0.313	1.893
Presence of grassland within 25m	**0.678**	**0.461**	**0.896**
Presence of woody upland within 25m	0.167	-0.024	0.359
Presence of riparian within 25m	-0.179	-0.431	0.073
Presence of road within 25m	-0.118	-0.291	0.056
Grassland within 200m	0.081	-0.050	0.212
Woody upland within 200m	-0.004	-0.143	0.135
Riparian within 200m	-0.094	-0.219	0.031
Urban within 200m	**0.156**	**0.065**	**0.247**
Distance to habitat	**0.126**	**0.029**	**0.223**

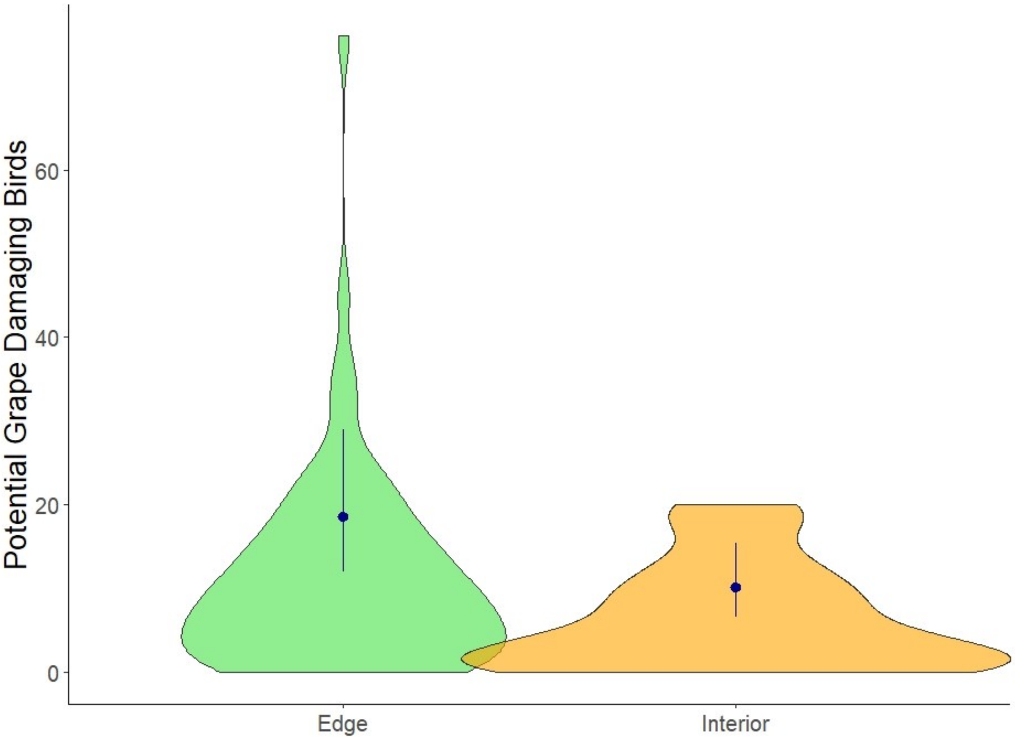

Figure 3. Violin plot (of raw data) and point estimates ± 95% CI (of top model in Table 2) of the relative abundance (number of birds detected per point count) of species potentially damaging grapes (see Table 1) at edge and interior point count stations in Napa Valley vineyards, Aug-Sept 2023.

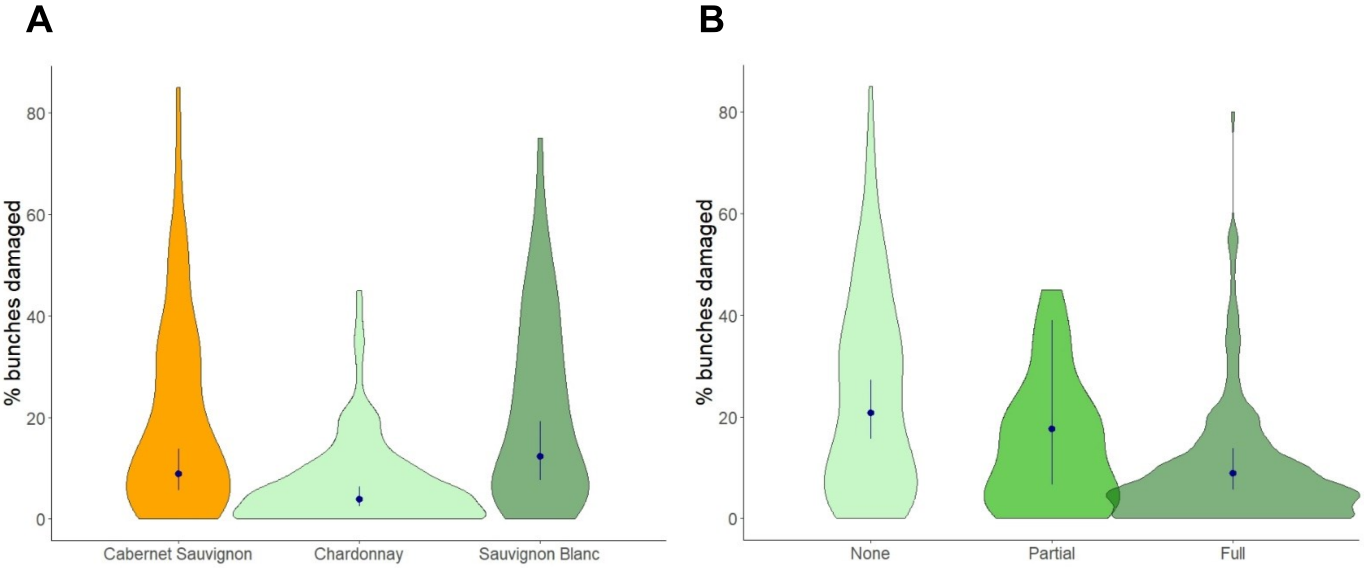

Figure 4. Violin plots (of raw data) and the predicted point estimates ± 95% CI (of top model in Table 3) of the % grape bunches with evidence of damage, disaggregated by (A) grape varietal and (B) the extent of cover crop in Napa Valley vineyards, Aug-Sept 2023.

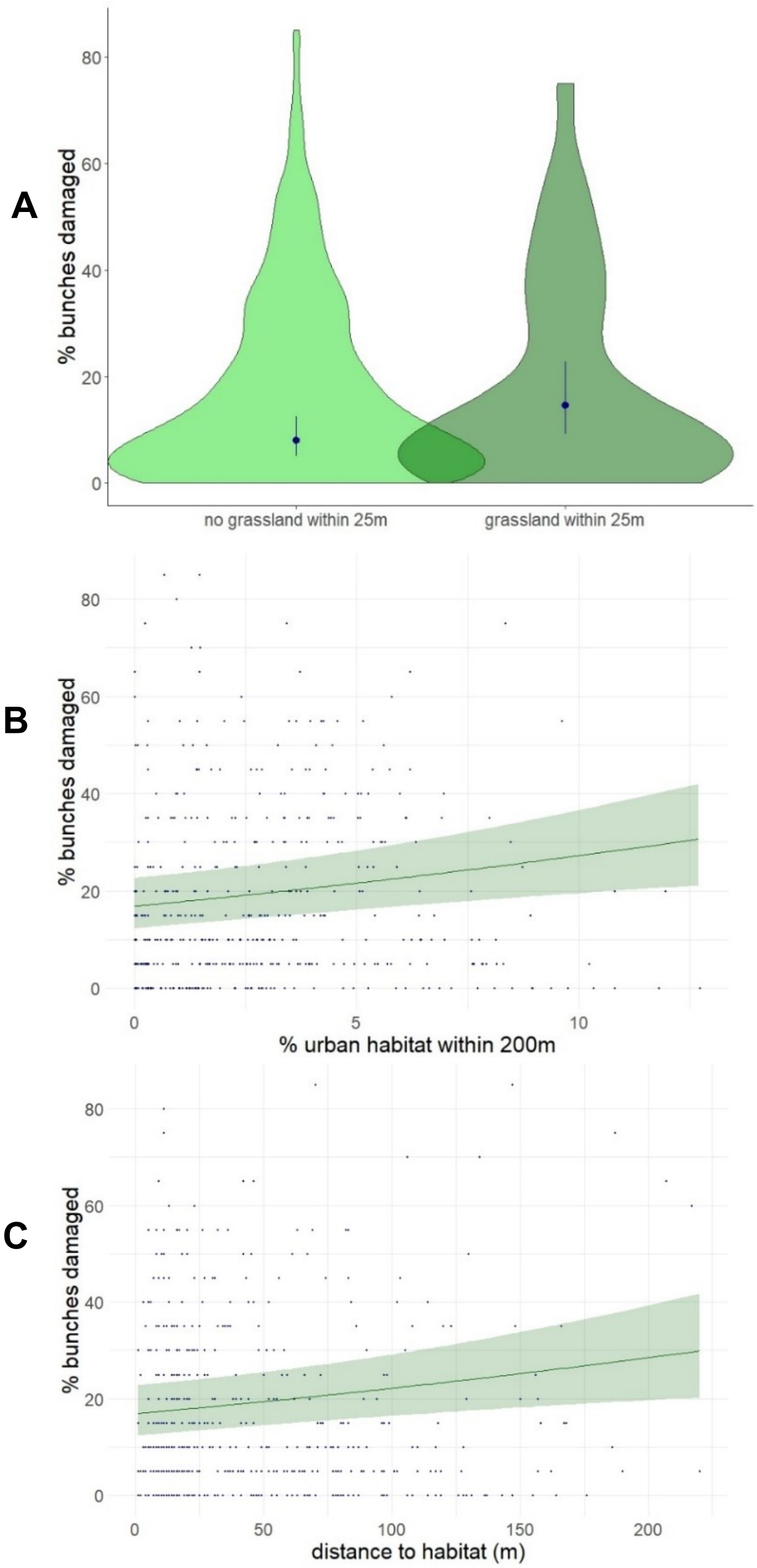

Figure 5. (A) Violin plots (of raw data) and point estimates ± 95% CI (of top model in Table 3) of the % grape bunches with evidence of damage on sample plots with and without grassland land cover within a 25 m radius. Raw data and predicted response curves ± 95% CI (of the top model in Table 3) for the association between % bunches damaged and (B) the amount of urban land cover within 200 m radius and (C) the distance to uncultivated habitat, Napa Valley vineyards, Aug-Sept 2023

Grape bunch damage was similar between edge and interior sample plots (mean ± s.d.: 16.3± 2.0% vs. 17.3% ± 2.4%, respectively). Initial modeling of vine structure and grape attributes variables revealed that grape bunch damage was significantly lower for Chardonnay than for Sauvignon Blanc or Cabernet Sauvignon varietals (Figure 4A). Damage was also higher on samples plots with no cover crop compared to those with partial (grown between vine rows) or full cover crop (grown between and under vine rows; Figure 4B). There was no significant relationship with trellis type, vine canopy cover, vine height, or vine trunk diameter. These variables were thus omitted for subsequent analysis. The mean number of days before harvest was 31 ± 12.7 days and ranged from 2 to 101. There was a non-significant negative relationship with days before harvest (Table 4), suggesting that, as expected, damage increased as fruit ripened, and the harvest date approached. We thus retained this variable for subsequent modeling. There was substantial variation among vineyards and no evidence that grape bunch damage differed between vineyards with and without nest boxes (9.4% ± 10.8% and 22.3% ± 19.7%, respectively).

The top model for predicting grape bunch damage included the presence/absence of local landcover types (within 25 m), the % of landcover types in the landscape (within 200 m), and the distance to nearest patch of uncultivated habitat (Table 3), carrying 89% of the model weight (Table 3). This model fit the data well (marginal $R^2 = 0.46$, conditional $R^2 = 0.90$), and no other model in the candidate set was competitive (Table 3). Based on predictors whose coefficients had confidence intervals that did not overlap zero (Table 4), grape bunch damage was higher on sample plots that contained local grassland within 25 m (Figure 5A). Damage was also positively associated with the amount of urban habitat at the landscape scale (200 m) and the distance to nearest uncultivated habitat (Table 3, Figure 5B/C).

DISCUSSION

In this study, we aimed to understand how bird communities, land cover at the local and landscape scale, and vine attributes may influence bird-caused winegrape damage. We found that overall grape damage caused by birds was very low (<1%) in our study system. Nonetheless, we did find several patterns in grape bunch damage. We found mixed support for the hypothesis that grape damage is positively associated with uncultivated habitats. As predicted, grape bunch damage was higher on sample plots with nearby grassland habitat (within 25 m, Figure 5A). However, at a larger landscape scale, we found that grape bunch damage increased with more urban habitat in the landscape (Figure 5B) and increased as distance to uncultivated increased (Figure 5C). These results suggest that the proximity of woody uncultivated habitats, such as forests, oak woodlands, and riparian habitats, did not lead to increased grape bunch damage whereas proximity to uncultivated grassland did. We also found that damage was lower in areas with full cover crop compared to partial and no cover crop. Perhaps there is a higher availability of alternative food sources, especially arthropods, where cover crops are full (Arlettaz et al. 2012, Duarte et al. 2014, Geldenhuys et al. 2021).

These results are encouraging from the perspective of biodiversity conservation, but are somewhat surprising because previous work has shown that bird-caused damage to grapes can be higher near habitat edges (Somers and Morris 2002, Kross et al. 2011) and because bird surveys in this project showed higher abundance of potentially damaging birds near vineyard edges (Figure 3). We found no evidence that bird-caused damage was higher very close to edges (within 25 m) than in the interior (mean % bunches damaged 16.3% vs. 17.3%), but we did find that grape bunch damage increased with distance to uncultivated habitat at a larger scale (Figure 5C). There are several possible explanations for these apparently conflicting results. First, our list of bird species of potentially damaging birds was crudely based on fruit presence in the diet and may not accurately reflect the abundance of the most problematic species. Previous work in California has highlighted the importance of house finches and European starlings as grape damagers (DeHaven 1974). We detected similar numbers of house finches at edge and interior point count stations (mean ± s.d. = 3.3 ± 3.9 vs. 3.5 ± 4.2, respectively), but we detected more starlings near edges than in vineyard interiors (2.5 ± 9.2 vs. 0.6 ± 2.3, respectively). It is thus possible that individual bird species could be affecting spatial patterns of grape damage, but these patterns are masked when all potentially damaging species are pooled. Moreover, when these species were modeled individually, they both showed a negative association with uncultivated habitat at the landscape scale (200 m), suggesting vineyards with uncultivated habitat in the landscape could reduce the abundance of these known winegrape damagers. Starlings and house finches can be associated with urban habitats (Seress and Liker 2015), and, in our study, grape bunch damage increased with more urban habitat in the landscape.

Second, some previous work suggests that flocking species of grape-damaging birds, such as non-breeding starlings and American robins (*Turdus migratorius*), may concentrate in vineyard interiors (Kross et al. 2011, 2020). Thus, the abundance of and damage from these species could counteract higher abundances of other winegrape damagers near edges, leading to little difference in damage with respect to edge. However, like with starlings, we detected more robins near vineyard edges than in interior point count stations, though their low numbers indicate they were not yet flocking when we conducted our surveys. Because flocking species often traverse large areas, the number of birds detected at sites is far more stochastic than for solitary species that remain near a certain habitat patch. The timing of our bird surveys may therefore have missed detecting flocks of birds at sites where they had previously foraged. Though we did record several large flocks of blackbirds (e.g., 123 in one point count station), many of the birds we detected in our surveys were not yet showing full sign of flocking behavior. Later surveys may have captured more flocks of birds aggregating in areas of ripening grapes.

A third possible explanation for no apparent edge effect on grape damage is that predatory birds could have altered the behavior of grape damaging birds, forcing them to avoid edges where they may be more exposed. Kross et al. (2011) found that New Zealand falcons (*Falco* *novaeseelandiae*) reduced the abundance of some bird pests that pluck grapes in the Malborough region, including European starlings, blackbirds (*Turdus merula*), and song thrushes (*Turdus philomelos*). The falcons did not reduce the abundance of grape-pecking silvereyes (*Zosterops lateralis*), yet pecking damage was reduced in the presence of falcons, suggesting the risk of predation could have limited crop damage by affecting the silvereyes' behavior. The idea that fear could be leveraged to affect the behavior of fruit-eating birds has a long history in crop protection (Enos et al. 2021) but has received less attention in the ecological and conservation literature (see Gaynor et al. 2021). We detected relatively few bird-eating raptors in our surveys (27), so we cannot fully evaluate this hypothesis, but the possibility that falcons could protect winegrapes in California is a popular idea that merits additional research (Robinson 2019).

Lastly, 2023 was marked by late winter rains (see below for more comments on this topic), and grapes were still ripening as we conducted our damage surveys. Perhaps the fruits were slightly riper and thus more likely or be damaged near vineyard interiors, where there is less shade than on edges. Lindel et al. (2018) also showed that the amount of bird damage is influenced by the general availability of foods in the landscape and differences in abiotic factors such as temperature or precipitation. The conditions favoring the slow grape harvest in 2023 could have favored other food supplies in the surrounding area, reducing overall bird damage to grapes and dampening an effect of local habitat. Additional work is needed to better understand the role of individual species of grape-damaging birds, and to examine patterns of ripening and bird distributions.

Local and landscape habitat heterogeneity can affect the provisioning of ecosystem services by mobile animals such as birds in agricultural systems (Kremen et al. 2007, Heath and Long 2019, Kross et al. 2020). For example, birds inhabiting uncultivated habitat and only occasionally making forays into vineyards could both damage grapes and help remove insects. Kross (2016) found this pattern in Yolo County California, where landscape heterogeneity is limited, but, using similar methods, Howard and Johnson (2014) did not see this effect in more heterogeneous landscapes in California's Sonoma and Mendocino counties (underscoring the potential for landscape context to mediate effects of local habitat (McCarty and Winkler 1999, Heath and Long 2019). In this study, we observed on multiple occasions western tanagers (*Piranga ludoviciana*) – a species closely associated with forests – moving into vineyard edges to feed on grapes (Turner, pers. observ.). We also observed pileated woodpeckers (*Dryocopus pileatus*) doing the same, though this species was never detected on our point counts (Table 1) and was thus not included in analysis. On the other hand, pest-eating birds also likely concentrate feeding along edges (Puckett et al. 2009, Garfinkel and Johnson 2015). Confirming that the mediating effect of habitat edges on the relative strength of ecosystem services and disserves in vineyards merits further investigation. In addition, the presence of native habitats in the general landscape can boost local populations of birds, including both those that could help remove insect pests and some that could damage grapes (Kross et al. 2020). In this study, given how little bird-caused grape damage was observed, we suspect the benefits of native habitat along edges and in the general landscape for attracting insect-eating birds may very well outweigh the costs of a few more grape-damaging birds, though this should be investigated formally.

While the presence of uncultivated habitats can attract birds to vineyards, vineyard managers can also deploy songbird nest boxes to attract cavity nesting bird species that consume large amounts of insects while provisioning their young. In California, the target species are typically western bluebirds and tree swallows (*Tachycineta bicolor*), in hopes that their presence may help reduce insect pests. Tree swallows are almost exclusively insectivorous and will not damage grapes (McCarty and Winkler 1999), but bluebirds have occasionally been observed foraging on winegrapes. Our data indicated that vineyards with nest boxes did not have more potential grape damaging birds than those without nest boxes. Given how rare grape damage was overall, we again expect that any benefits from these birds attracted to nest boxes may provide for pest removal will outweigh the negligible effect they may have on grape damage.

Several caveats related to our sampling design should be noted. First, late winter and spring were especially cold and wet in Napa in 2023, delaying grape and bird phenology relative to other years. Field logistics demanded we plan the timing of our bird and grape damage surveys well before knowing their ripeness. In hindsight, our grape damage surveys were likely earlier than optimal; on average, we surveyed about a month before harvest. All fruits sampled were in the process of veraison (when sugars begin to accumulate and start to attract bird pests during the process of ripening). Nonetheless, sampling grape damage at a later date, when fruits were riper and had been sitting out on the vine longer, could have resulted in higher rates of observed grape damage. Though we surveyed birds on 20 vineyards, we only sampled grape damage extensively on six vineyards due to logistic constraints and ripening on some vineyards that was too late for aligning with the availability of our housing and personnel. Thus, our design did not enable us to associate bird abundance and grape damage at the same sampling points. Therefore, the six vineyards sampled may not be representative of vineyards in the region that experienced higher levels of bird-caused grape damage, despite being spread well across Napa Valley (Figure 1). In the future, we recommend researchers balance fewer samples per vineyard with more vineyards sampled and consider focusing on vineyards with known problematic grape damage, which may require funds to compensate growers for losses if deviations from typical bird-deterrent management practices are needed for the study design.

The relative benefits and costs of songbirds in vineyards merits further study. Here, we document comparatively little damage caused by songbirds to winegrapes in Napa Valley, California. On the other hand, birds can conceivably contribute substantively to pest control in winegrape vineyards. Several studies involving sentinel pests suggest birds can deliver insect-removal services in vineyards (Jedlicka et al. 2014), but little work has documented whether songbirds actually eat known pests (Jedlicka et al. 2017), nor whether they are capable of actually reducing pest abundance. While we documented low levels of grape damage from birds, fruit-growers in California have more negative perceptions of songbirds than other farmers (Kross et al. 2018), and a fear that conservation practices such as planting hedgerows or retaining uncultivated habitats may cause more damage is a barrier to avian conservation efforts. Future research is needed to investigate these questions and to examine the possible effects of nest box deployment on bird and pest abundance. We hope this work prompts additional investigations of the full role (net-effect) of birds in winegrape vineyards in California and elsewhere.

ACKNOWLEDGMENTS

We would like to thank the 20 participating vineyards for allowing us access to conduct research on their lands. We especially appreciate the coordinating vineyard and winery managers who provided us with invaluable information related to winegrape growing and processing that was helpful for developing our study design and sampling methods. We thank M. Cooper and J. Roncoroni for guidance and support. Funding was provided by the Agricultural Research Institute, Napa County University of California Cooperative Extension, and Fulbright Germany.

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