



Agricultural adapters from the vineyard landscape impact native oak woodland birds



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ARTICLE INFO

Keywords:

Species interactions
Biotic homogenization
Aves
Agriculture
California

ABSTRACT

Agricultural expansion changes wildlife communities. Some species adapt to working lands, increasing their relative abundance in these modified landscapes, and this may result in spillover effects for communities in adjacent wildlands. These effects remain largely undocumented, even though they can affect biodiversity conservation. We conducted bird surveys at 130 Mediterranean-climate oak woodland locations that exist across a gradient of nearby vineyard development. We used zero inflated Poisson (ZIP) N-mixture models to analyze the relationships among detected bird species, local vegetation, and surrounding vineyard land cover. We used joint species distribution modeling (JSDM) to measure species co-occurrence patterns and account for the influence of the surrounding agricultural land in order to explore indirect effects between bird communities associated with vineyard expansion and oak woodland remnants. We identified 10 species as agricultural adapters based on their positive association with vineyard land cover. Co-occurrence patterns suggested that i) agricultural adapter species may negatively interact with certain species associated with oak woodlands in adjacent wildlands, so competition with agricultural adapters may be an important driver of biotic homogenization of the community, and (ii) some positive species interactions were detected, especially among insectivore foliage gleaners, which may be facilitated by niche partitioning. Continued examination of spillover effects from agricultural land into adjacent natural areas is warranted in light of global species declines and biotic homogenization.

1. Introduction

Agriculture has fundamentally altered both the spatial configuration and function of ecosystems globally, often resulting in a mosaic of residual natural habitat patches surrounded by agricultural development and associated roads and infrastructure (Cameron et al., 2014; Curtis et al., 2018). The impacts of agricultural land use may depend on species requirements crop type, agricultural management, and the extent of agricultural development across the landscape (Assandri et al., 2017a; Bosco et al., 2019; Doxa et al., 2012; Gonthier et al., 2014; Kremen and Merenlender, 2018; Puig-Montserrat et al., 2017; Rollan et al., 2019). Changes in bird community composition can also impact ecosystem services (Assandri et al., 2017b; Brambilla et al., 2017; Jedlicka et al., 2011). Agriculture can have impacts within and beyond the farm limits, influencing wildlife communities at the local farm or parcel scale and across the larger landscape scale, such as within an entire river basin (Assandri et al., 2016; Karp et al., 2012).

It is well documented that the wildlife species compositions in agricultural lands spanning various levels of intensification are different from those in natural areas (Assandri et al., 2018; Balmford et al., 2012; Guyot et al., 2017; Phalan et al., 2011). Some generalist species benefit from agricultural landscapes as habitat, and these are referred from here as agricultural adapters, while other species decline or become displaced and restricted to remnant natural areas where their persistence may be uncertain (Devictor et al., 2008). Far fewer studies have been able to examine how these changes in the abundance of agricultural adapters may affect community composition in adjacent natural areas, possibly leading to biotic homogenization on a landscape scale (Olden et al., 2004), and this is usually not considered as a potential ecosystem disservice (Garcia et al., 2018).

Biotic homogenization at a site is expressed as the loss of β diversity along with a gain in a small number of species tolerant to disturbance (Plas et al., 2016). This process is often associated with the replacement of native biotas by non-natives (Olden et al., 2004) and is driven by

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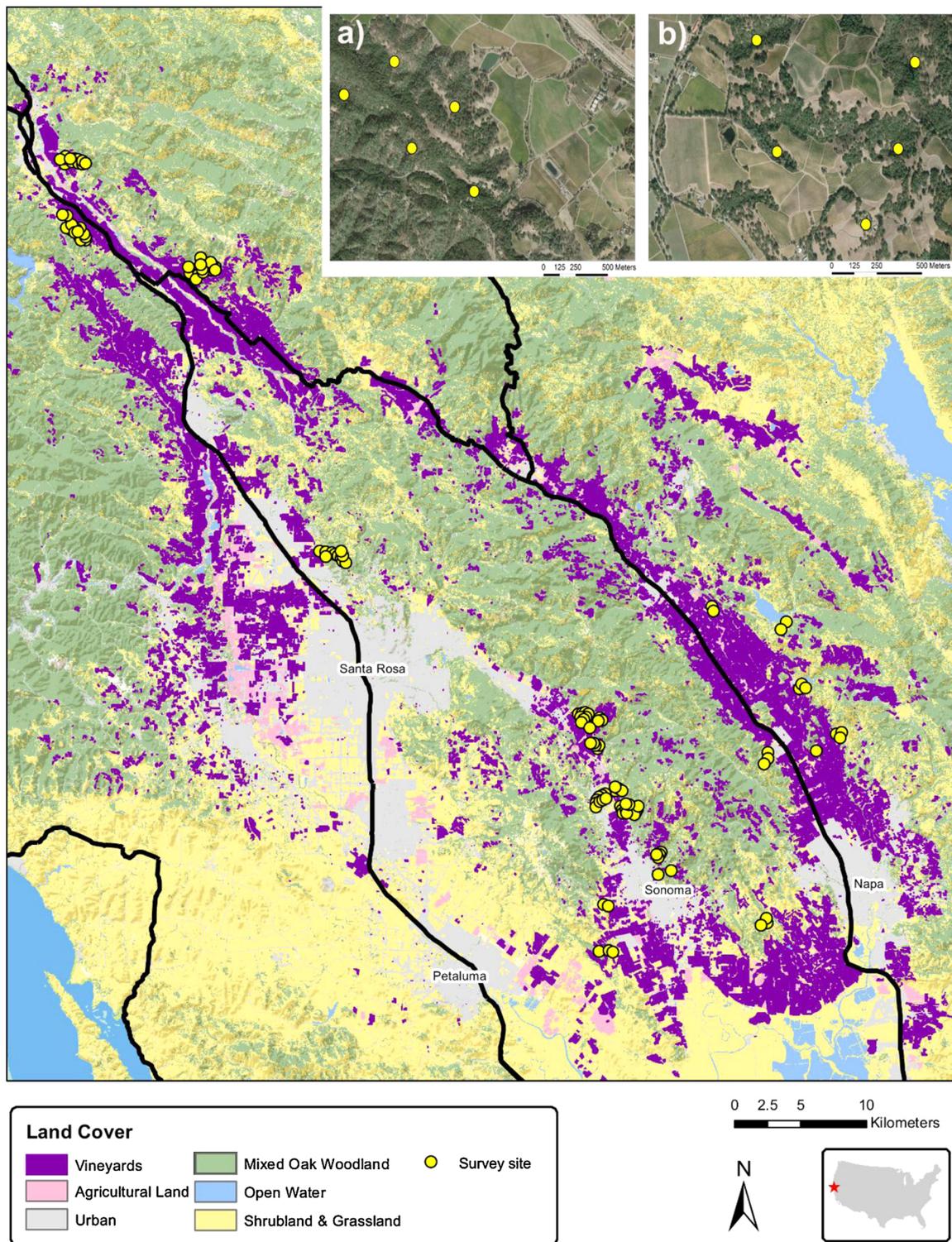


Fig. 1. Survey sites in northern California. N = 130 bird survey stations located 250 m apart from one another along a gradient of vineyard land cover from (a) low to (b) high.

local extinctions and colonization of alien species (Lambdon et al., 2008). An extended definition of biotic homogenization includes colonization by more disturbance-tolerant native species (McCune and Vellend, 2013). This biotic homogenization and its effects are often associated with agricultural intensification (Clavel et al., 2011; Pejchar et al., 2018).

Spillover effects are a part of the process of biotic homogenization; they are related to species that increase their abundances in the

working landscapes and can also colonize adjacent natural habitats (Blitzer et al., 2012; Driscoll et al., 2013). Recent studies have documented spillover effects of forest birds into adjacent agriculture (Boesing et al., 2017), bird spillover from surrounding non-forested lands into forested reserves (Häkkinen et al., 2018), and spillover effects from urban areas into natural areas (Spear et al., 2018). However, there is a dearth of studies that provide evidence of spill over from working landscapes into natural habitats (Blitzer et al., 2012; Spear et al., 2018).

In general, research on biodiversity in agroecosystems and adjacent areas typically focuses on species, guilds, or diversity indices (Maas et al., 2016). However, studies examining changes in co-occurrence patterns between species are less common (but see Lindenmayer et al., 2015), and how anthropogenic environments such as agriculture lead to these interactions and indirect effects between species remains relatively unknown.

Biotic interactions can shape the species distributions and communities (Wisiz et al., 2013). The direction and strength of interactions between species are likely to change depending on environmental conditions (Tikhonov et al., 2017); for example, changes in resource availability can regulate species composition through competition or facilitation (Barrio et al., 2013). While positive indirect interactions may be related to common-use habitat and niche partitioning, negative indirect interactions may be related to displacement of one species by another or different habitat preferences (D'Amen et al., 2018). These indirect interactions should be explored to improve species distribution models (Araújo and Luoto, 2007).

We investigated how local habitat and land cover at the landscape scale influence species abundance and presence across a gradient of vineyard development. We also explored the indirect effects of the surrounding agricultural landscape on woodland bird interactions. Indirect biotic interactions may play a role but are more difficult to observe and understand than direct interactions (Estes et al., 2013) and can make community dynamics difficult to predict (Wootton, 1994). Co-occurrence patterns in communities have been explained in several ways: by species interactions (e.g., community assembly rules), by use of null models in comparison with co-occurrence patterns expected by chance (e.g., null models), and more recently by joint species distribution modeling (JSDM) that uses a multivariate hierarchical model to describe association patterns (D'Amen et al., 2018). Progress has been made in recent years using various modeling methods to incorporate co-occurrence patterns into analysis of species distributions (Tikhonov et al., 2017; Warton et al., 2015). In particular, JSDM can reveal information about individual species distributions while accounting for habitat constraints and considering co-occurrence patterns (Ovaskainen et al., 2016).

We examined potential interactions among generalist bird species adapted to agricultural environments (hereafter referred to as “agricultural adapters”) and species associated with oak woodlands (hereafter referred to as “oak woodland birds”) by assessing patterns of species co-occurrence within natural areas adjacent to varying levels of vineyard development. We predicted that some species would be favored as the vineyard proportion of the landscape increased, due to their tolerance of anthropogenic environments. In addition, we expected patterns of co-occurrence between species to reflect negative interactions between agricultural adapters and oak woodland birds, due to dissimilar environmental niches and/or from indirect interactions (D'Amen et al., 2018; Ovaskainen et al., 2010). Exploring both the environmental and the residual correlations for detection rates across pairs of species enabled us to examine evidence for species co-occurrence and discuss different potential mechanisms that may be

operating. Our findings shed light on how agricultural landscapes influence Mediterranean-climate ecosystems that are a global conservation priority (Cox and Underwood, 2011). These findings are strongly needed given the relatively recent expansion of vineyards across Mediterranean-climate landscapes and the demand for empirical investigations of the influence of vineyards on the remaining native species (Viers et al., 2013).

2. Materials and methods

2.1. Study area

We conducted the study in eastern Sonoma County and western Napa County, California, USA (Fig. 1). The region is characterized by a Mediterranean climate with cool, wet winters and warm, dry summers (Viers et al., 2013). We established bird plot survey stations in oak woodland habitat in the internal Coast Ranges. Mixed oak woodland (*Quercus* spp., eight species in total) is the dominant cover type and is interspersed with chaparral, grassland, conifers, riparian woodland, and vineyards. Most valley bottoms are highly modified, having largely been converted from a mosaic of oak woodland, oak savannah, seasonal and perennial wetlands, riparian forest, and grassland to vineyards and rural residential development (Cameron et al., 2014). To minimize the confounding influence of urbanization on bird communities (Merlenlender et al., 2009), we avoided areas near moderate to high-density residential development, placing all sites more than 1 km from urban areas.

2.2. Bird surveys

We conducted bird counts in 130 survey stations in oak woodlands within a gradient from low to high amounts of vineyard development (Supplementary material, Figure S3). We registered all birds seen or heard within a radius of 50 m of the survey station for a period of 5 min (Farnsworth et al., 2002). We conducted bird counts between 6:00 and 10:00 AM, when birds are highly active. We repeated bird counts two to three times per breeding season (May and June in 2002 and 2003), totaling five to six surveys at each site. We located survey stations at least 250 m apart, which is recommended for an acceptable level of independence between survey stations (Ralph et al., 1993). We placed all survey stations within oak woodland habitat and distributed across a general gradient of vineyard development intensity (Fig. 1). We conducted all the bird counts on each site at least 10 days apart (Ralph et al., 1993).

2.3. Vegetation plot data

We collected data on vegetation structure and composition within circular plots with a 50 m radius for each survey station, following the method developed by Ralph et al. (1993). This method allowed us to determine the vegetation formation, association, and major structural characteristics that are known to have important relationships with

Table 1
Summary of environmental variables used in statistical analyses.

	Variable	Description	Scale (radius)	Measurement method
Plot scale	Oak woodland	Percentage cover of oak tree species	50 m	Field
	Shrub plot	Percentage cover of different shrub plant species	50 m	Field
	Tree height	Average height of tree canopy	50 m	Field
	Snags	Number of snags with diameter at breast height > 10 cm	50 m	Field
	Woody plant richness	Number of tree and shrub woody species	50 m	Field
Landscape scale	Vineyard	Proportion of vineyards	1000 m	GIS†
	Shrub	Proportion of shrubland	1000 m	GIS
	Road density	Road density (road meters by square meters × 10,000)	1000 m	GIS
		†Geographic Information System		

Table 2 Results of the ZIP N-mixture model average by species at two scales of analysis. Model coefficients, ± (Standard Error) estimates, and R-squared are shown. Significant values are represented in bold ($P < 0.05$). For species acronyms see Table S1.

Plot scale		Shrub plot		Woody plant richness		Snags		Oak woodland	
Species symbol	Tree height	(SE)	(SE)	(SE)	(SE)	(SE)	(SE)	(SE)	(SE)
WITU	-0.32	(0.25)	(0.32)	-0.22	(0.34)	0.49	(0.27)	-0.48	(0.22)
COHA	29.98	(267.06)	(293.43)	0.61	(84.76)	8.66	(301.17)	8.16	(208.16)
RTHA	1.06	(0.65)	(0.69)	-0.08	(0.46)	0.13	(0.24)	-0.95	(0.44)
WTKI	-10.24	(26)	(35.29)	10.74	(37.5)	-14.25	(61.84)	-2.87	(38.87)
ANHU	-0.14	(0.11)	(0.11)	0.06	(0.11)	-0.05	(0.12)	-0.05	(0.12)
ACWO	0.11	(0.07)	(0.12)	-0.18	(0.12)	0.12	(0.05)	0.14	(0.07)
NOFL	0.01	(0.23)	(0.27)	0.25	(0.21)	0.26	(0.22)	0.07	(0.22)
NUWO	0.10	(0.11)	(0.14)	-0.18	(0.11)	-0.17	(0.11)	0.13	(0.11)
PSFL	0.75	(0.19)	(0.15)	-0.03	(0.19)	-0.25	(0.17)	-0.19	(0.19)
WEKI	0.68	(0.26)	(0.33)	1.39	(0.31)	0.32	(0.19)	-0.93	(0.31)
WEWP	-0.01	(0.13)	(0.16)	-0.13	(0.13)	0.07	(0.09)	-0.08	(0.13)
CAVI	0.15	(0.22)	(0.39)	0.13	(0.18)	0.10	(0.15)	0.54	(0.21)
HUVI	0.07	(0.11)	(0.09)	-0.10	(0.1)	0.07	(0.09)	0.15	(0.12)
WAVI	0.35	(0.16)	(0.15)	0.28	(0.19)	0.09	(0.15)	0.29	(0.18)
AMCR	0.19	(0.23)	(0.13)	-0.27	(0.2)	0.07	(0.14)	0.15	(0.23)
CORA	-0.35	(0.48)	(1.07)	0.58	(0.57)	0.37	(0.23)	-0.71	(0.43)
OATI	-0.01	(0.04)	(0.04)	-0.02	(0.04)	0.09	(0.03)	-0.04	(0.04)
BUSH	-0.17	(0.08)	(0.08)	-0.03	(0.06)	-0.06	(0.09)	-0.21	(0.1)
WREN	-1.25	(0.68)	(0.56)	-0.31	(0.53)	0.44	(0.44)	-0.75	(0.83)
BEWR	-0.24	(0.12)	(0.12)	0.04	(0.11)	-0.13	(0.14)	-0.31	(0.14)
HOWR	-0.15	(0.19)	(0.21)	-0.02	(0.22)	-0.55	(0.26)	-0.43	(0.23)
BGGN	0.48	(0.25)	(0.25)	0.06	(0.24)	0.10	(0.26)	0.68	(0.22)
WBNU	-0.25	(0.12)	(0.14)	-0.07	(0.1)	-0.01	(0.07)	0.17	(0.11)
NOMO	0.08	(0.41)	(0.77)	0.46	(0.53)	1.06	(0.89)	-1.79	(0.74)
EUST	0.04	(0.14)	(0.26)	0.00	(0.19)	-0.25	(0.31)	-0.06	(0.13)
AMRO	-0.34	(0.19)	(0.31)	0.16	(0.15)	-0.22	(0.16)	0.44	(0.16)
SWTH	7.28	(175.83)	(492.08)	-1.42	(140.3)	-12.04	(252.6)	7.07	(109.25)
WEBL	-0.09	(0.2)	(0.38)	0.02	(0.22)	-0.16	(0.18)	-0.06	(0.19)
AMGO	-0.14	(0.24)	(0.23)	-0.02	(0.21)	0.11	(0.16)	-0.48	(0.26)
HOFI	-0.18	(0.16)	(0.27)	-0.12	(0.17)	0.06	(0.07)	0.03	(0.15)
LEGO	0.02	(0.06)	(0.07)	-0.08	(0.07)	0.05	(0.05)	-0.09	(0.06)
BTYW	0.37	(0.41)	(1.12)	0.75	(0.32)	-0.21	(0.3)	0.63	(0.33)
OCWA	-0.04	(0.1)	(0.1)	0.16	(0.09)	-0.06	(0.09)	0.06	(0.1)
WIWA	-35.61	(950.12)	(1567.56)	14.83	(621.69)	50.26	(1046.06)	-63.74	(1220.41)
BHCO	0.12	(0.4)	(0.73)	-0.04	(0.58)	0.33	(0.38)	0.28	(0.34)
BUOR	-0.10	(0.21)	(0.32)	0.19	(0.27)	0.37	(0.36)	-0.71	(0.34)
RWB1	-0.42	(0.52)	(1.96)	-1.59	(0.93)	0.15	(0.18)	-1.45	(0.49)
CAL1	0.13	(0.09)	(0.11)	0.15	(0.11)	-0.05	(0.09)	-0.38	(0.11)
CHSP	-0.34	(0.18)	(0.24)	0.23	(0.17)	0.07	(0.1)	-0.06	(0.18)
DEJU	0.04	(0.05)	(0.05)	0.12	(0.05)	0.16	(0.04)	0.04	(0.06)
SOSP	-0.32	(5148.57)	(4346.35)	0.19	(8540.03)	-11.06	(4111.55)	35.19	(7071.33)
SPTO	0.03	(0.08)	(0.07)	0.14	(0.08)	0.11	(0.08)	-0.12	(0.09)
LAZB	-0.06	(0.25)	(0.45)	-0.23	(0.35)	-0.25	(0.41)	-0.71	(0.33)

Plot scale		Landscape scale		Observation covariates				
Species symbol	Vineyard	(SE)	(SE)	Shrub landscape	Julian day	(SE)	Year	(SE)
WITU	0.60	(0.4)	(0.35)	-0.08	(0.25)	(0.19)	0.87	(0.22)
COHA	-20.55	(233.95)	(205.1)	25.03	(149.19)	(1.45)	-0.71	(0.76)
RTHA	0.33	(0.41)	(1.31)	-2.57	(1.31)	(0.2)	0.22	(0.18)
WTKI	8.20	(44.23)	(45.97)	-46.21	(102.78)	(0.5)	0.66	(0.56)

(continued on next page)

Table 2 (continued)

Plot scale	Landscape scale		Observation covariates							
ANHU	-0.03	(0.12)	0.30	(0.1)	0.34	(0.09)	-0.08	(0.09)	0.53	(0.1)
ACWO	-0.14	(0.06)	-0.73	(0.06)	0.46	(0.16)	0.13	(0.05)	-0.13	(0.05)
NOFL	0.44	(0.22)	-0.19	(0.19)	0.17	(0.31)	0.01	(0.16)	0.61	(0.18)
NUWO	-0.04	(0.11)	0.06	(0.1)	0.20	(0.12)	0.27	(0.09)	-0.18	(0.08)
PSFL	0.06	(0.2)	0.07	(0.18)	0.19	(0.19)	-0.02	(0.12)	-0.39	(0.12)
WEKI	0.46	(0.28)	-1.32	(0.25)	0.29	(0.55)	-0.06	(0.18)	0.38	(0.18)
WEWP	0.12	(0.11)	-0.42	(0.11)	0.18	(0.21)	-0.12	(0.09)	0.21	(0.09)
CAVI	-0.07	(0.16)	-3.43	(0.16)	0.35	(1.26)	0.01	(0.14)	0.13	(0.13)
HUVI	-0.08	(0.13)	0.20	(0.11)	0.19	(0.11)	-0.22	(0.09)	-0.17	(0.09)
WAVI	0.30	(0.16)	0.14	(0.14)	0.15	(0.19)	-0.17	(0.11)	-0.11	(0.1)
AMCR	0.58	(0.31)	0.51	(0.24)	0.20	(0.23)	0.29	(0.16)	0.42	(0.15)
CORA	0.23	(0.38)	1.60	(0.5)	0.25	(0.6)	-0.41	(0.33)	-0.28	(0.32)
OATI	0.00	(0.04)	0.04	(0.04)	0.27	(0.04)	0.10	(0.03)	0.11	(0.03)
BUSH	-0.13	(0.1)	-0.11	(0.1)	0.24	(0.09)	-0.16	(0.07)	0.18	(0.06)
WREN	-2.12	(1.2)	-2.82	(1.66)	0.32	(0.49)	0.27	(0.31)	0.29	(0.32)
BEWR	-0.64	(0.16)	-0.10	(0.12)	0.29	(0.11)	0.22	(0.1)	0.05	(0.09)
HOWR	-0.65	(0.21)	0.01	(0.14)	0.24	(0.51)	-0.09	(0.14)	0.34	(0.14)
BGGN	-1.03	(0.37)	1.02	(0.24)	0.39	(0.29)	-0.13	(0.17)	0.73	(0.21)
WBNU	-0.15	(0.09)	0.24	(0.08)	0.48	(0.13)	0.38	(0.08)	0.40	(0.08)
NOMO	1.55	(0.68)	1.11	(0.52)	0.27	(1.17)	0.10	(0.26)	-0.13	(0.24)
EUST	0.43	(0.2)	0.06	(0.15)	0.33	(0.44)	-0.59	(0.11)	-0.09	(0.1)
AMRO	0.22	(0.14)	-0.06	(0.16)	0.25	(0.37)	-0.14	(0.12)	0.27	(0.12)
SWTH	-4.20	(45.31)	-0.54	(105.38)	0.18	(544.31)	0.18	(0.08)	-0.30	(0.08)
WEBL	0.49	(0.21)	0.00	(0.23)	0.21	(0.19)	-0.08	(0.16)	-0.56	(0.18)
AMGO	0.24	(0.25)	0.15	(0.25)	0.35	(0.18)	-0.25	(0.18)	-1.46	(0.36)
HOFI	0.55	(0.15)	0.75	(0.17)	0.43	(0.22)	0.42	(0.12)	0.42	(0.12)
LEGO	0.23	(0.06)	-0.06	(0.06)	0.34	(0.08)	0.16	(0.05)	0.13	(0.05)
BTYW	1.39	(0.37)	-0.74	(0.34)	0.62	(0.43)	0.00	(0.25)	0.09	(0.24)
OCWA	-0.44	(0.12)	-0.20	(0.08)	0.31	(0.14)	0.02	(0.07)	0.15	(0.07)
WIWA	-58.34	(1851.19)	-62.68	(5487.16)	0.47	(4401.98)	0.25	(0.46)	40.32	(16326.1-5)
BHCO	1.14	(0.47)	-0.72	(0.29)	0.24	(1.57)	-0.15	(0.24)	-0.58	(0.24)
BUOR	1.07	(0.33)	0.62	(0.3)	0.29	(0.3)	-0.38	(0.19)	0.66	(0.21)
RWBL	0.72	(0.35)	1.09	(1.32)	0.44	(1.14)	-0.45	(0.24)	1.62	(0.51)
CALIT	0.08	(0.11)	0.19	(0.1)	0.17	(0.14)	0.11	(0.08)	0.11	(0.08)
CHSP	0.26	(0.15)	-0.68	(0.2)	0.29	(0.26)	-0.30	(0.11)	0.23	(0.11)
DEJU	0.02	(0.05)	0.06	(0.05)	0.29	(0.06)	0.01	(0.04)	0.18	(0.04)
SOSP	-26.67	(10125.4)	52.98	(6418.05)	0.43	(6071.17)	0.47	(0.51)	19.48	(35041.3-2)
SPTO	-0.23	(0.11)	0.03	(0.08)	0.41	(0.08)	0.21	(0.06)	0.20	(0.06)
LAZB	0.07	(0.32)	-0.38	(0.34)	0.21	(2.67)	-0.60	(0.28)	0.26	(0.26)

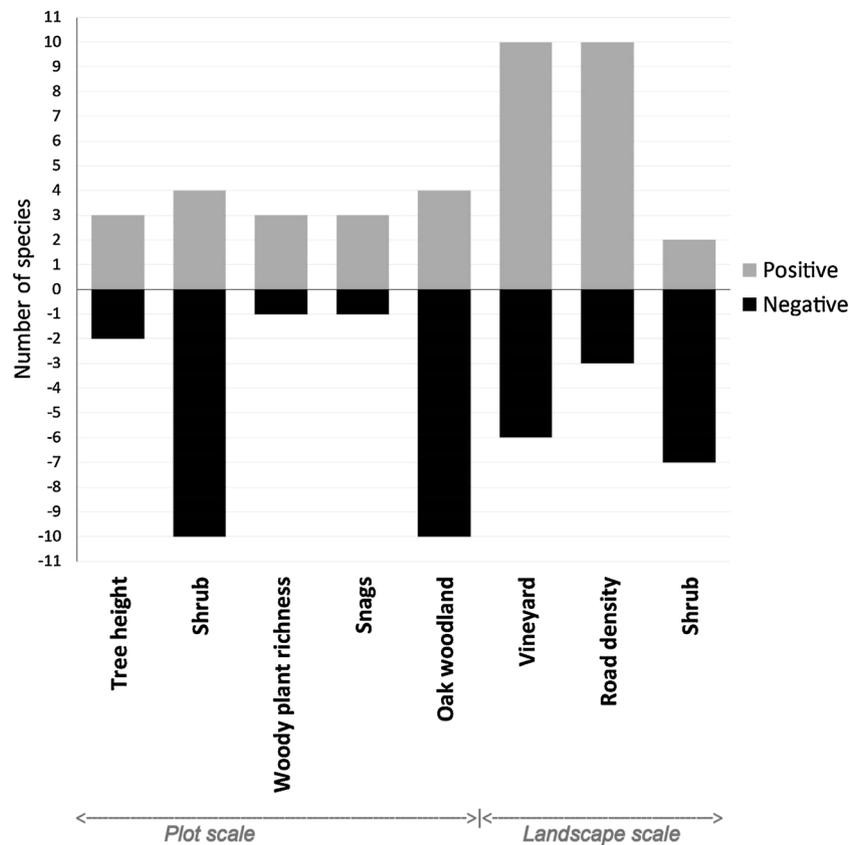


Fig. 2. Number of species significantly (positive and negative) influenced by environmental variables at two scales, based on the results of the ZIP N -mixture model average (see also Table 2).

birds' feeding and nesting requirements. We recorded the following measurements as described in (Ralph et al., 1993) and (Ballard, 2002): percentage of tree canopy cover by oak species ("oak woodland" in Table 1) and percentage of shrub cover ("shrub plot"). We identified all woody species and counted those with greater than 1% absolute cover ("woody plant richness"). We estimated visually the average height of the tree canopy ("tree height") and recorded the number of snags with diameter at breast height greater than 10 cm ("snags").

2.4. Landscape data

We measured all landscape data in circular plots at three landscape scales, that is, with 250 m, 500 m, and 1000 m radii, to adequately explore the influence of land cover on bird species (Pelosi et al., 2014). We digitalized all vineyard boundaries from orthorectified aerial photos overlapping with the period of bird sampling from 1993, 2000, 2002, and 2004. We calculated the proportions of vineyard within circular plots with radii of 250 m, 500 m, and 1000 m around each bird survey station (raster layer with a 25 m cell size). We derived the landscape-scale vegetation cover data from the California Land Cover Mapping and Monitoring Program (LCMMP), which used 1998 satellite imagery (Landsat Thematic Mapper) at a spatial resolution of 30m \times 30m (Levien et al., 2003) to classify vegetation. The LCMMP land cover was updated to 2002–2003–2004 period via manual classification on screen using the software ArcGIS 9 (ESRI, 2006). We used a GIS to calculate the proportion of shrub land cover and road density (measured as [m road/m²] \times 10,000) within circular plots of 250 m, 500 m, and 1000 m radii. We extracted all the landscape variables listed in Table 1 using ArcGIS 9. Previous analysis of our data showed that variables at different landscape scales (250 m, 500 m, and 1000 m radii) are highly correlated (Pearson correlation coefficient $|r| > 0.7$), so we removed scales of 250 m and 500 m radii from the analysis

(Guyot et al., 2017). Table 1 lists the plot- and landscape-scale environmental variables used in our analysis.

2.5. Statistical analysis

2.5.1. ZIP N -mixture models for species

We used ZIP N -mixture models to evaluate the relationship between birds species abundance and the predictor variables listed in Table 1 (Dénes et al., 2015; Guillerá-Arroita, 2017). Multiple field visits allowed us to take into account the imperfect nature of bird detections. The ZIP N -mixture modeling method can incorporate the uncertainty around imperfect detections and other phenomena that cause zero inflation and can induce error in the ecological patterns; hence this approach provides more accurate estimates of abundance than methods that do not explicitly address uncertainty in detections (Elsen et al., 2017). This approach accounts for three different sources of zeros i) detectability (e.g. how likely is to observe the species when it is actually there), ii) occupancy (e.g. how likely is the species to be present or absent), and iii) abundance (when the species is present, what are the factors that influence the number of individuals observed at that specific site) (Dénes et al., 2015). We also included Julian date and year when the data was collected as an observational covariate that could influence the probability of detection, occupancy, and abundance. We used eight main habitat variables that were not highly correlated (Pearson $|r| < 0.45$) (Bowen et al., 2009) to explore their influence on bird abundance at two scales (Table 1, Table S3). Previously, we standardized to a mean of 0 and standard deviation of 1 for all continuous variables used in the models (Kelly et al., 2016).

To correct for detectability, we compared the results across the multiple candidate models for each bird species (Burnham and Anderson, 2002). These candidate models included all the environmental variables. In addition, one also included the Julian date and the

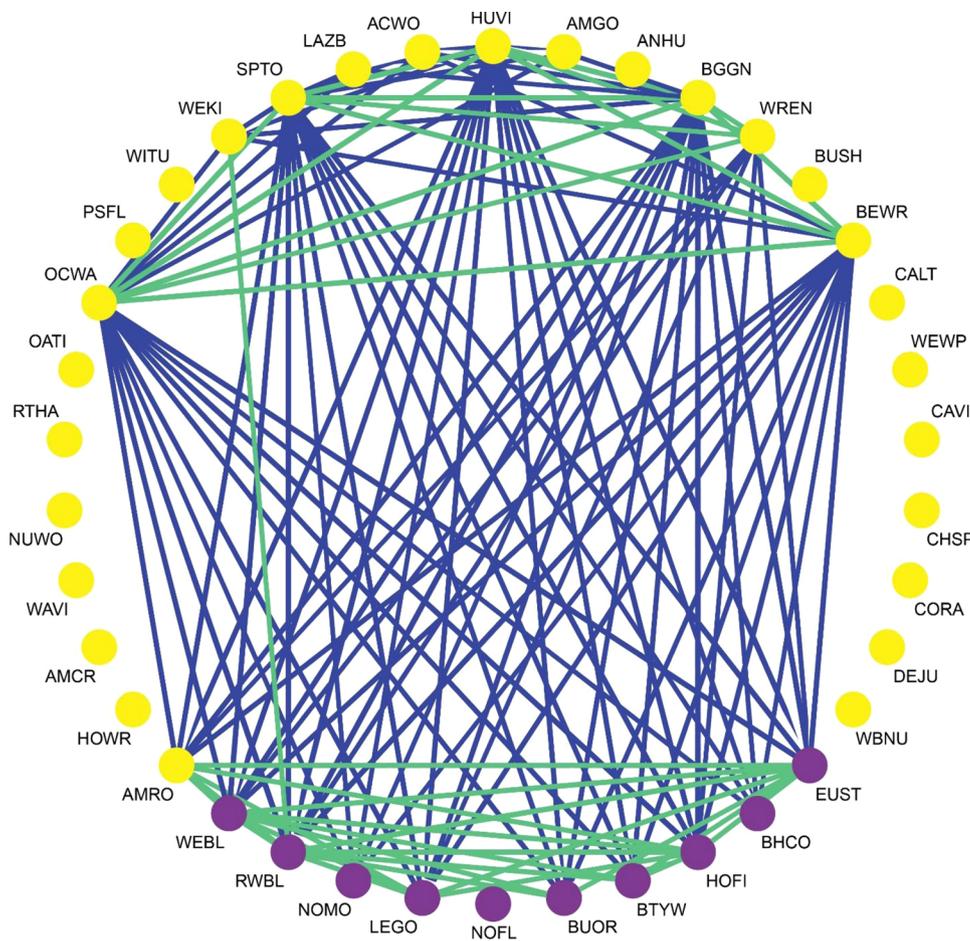


Fig. 3. Network diagrams for 38 species from JSDM results with vineyard land cover as the environmental variable. Blue lines represent negative correlations, and green lines represent positive correlations at $R_s > 0.85$ between species pairs. Purple circles indicate agricultural adapters; yellow circles are oak woodland birds. (See Figure S2 for a network diagram of residual correlation and Table S1 for species acronyms). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

Table 3

Summary of species pair associations in Figure S1. Quadrant “Q” (read counterclockwise) shows a positive-positive relationship between species (as in Q1, where species co-occurrence is promoted by vineyards and other non-measured variables), a negative-positive relationship (Q2), a negative-negative relationship (Q3), or a positive-negative relationship (Q4).

	Quadrant			
	Q1	Q2	Q3	Q4
Agricultural adapters-Agricultural adapters	76 %	0%	0%	24 %
Agricultural adapters-Oak woodland birds	41 %	15 %	21 %	24 %
Oak woodland birds-Oak woodland birds	33 %	22 %	23 %	22 %

year, another included just the Julian date, and a third included just the year. We compared these four approaches with a null model (without predictor variables) corresponding to a y-intercept of 1. We then compared these five models that vary in detectability parameters, in order to compose the candidate model set (Elsen et al., 2017). Finally, we averaged the resulting coefficients for each landscape and plot variable included in the bird species models, using the results from all models with $\Delta AICc < 4$ (Burnham and Anderson, 2002), and reported the R-squared value (Royle, 2017). With these model-averaged coefficients and standard errors, we assessed the relative importance of the predictor variables. We considered a modeled bird response to be significantly related to an environmental variable when the range of the 95 % model-averaged confidence interval did not contain zero (Elsen et al., 2017).

The statistical analyses we conducted for 72 species was performed using R 3.4.2 (R Development, 2017), including the use of the *pcount* function with the R packages “Unmarked” for fitting hierarchical

models of bird occurrence and abundance (Fiske and Chandler, 2011) and “AICcmodavg” to implement model averaging and selection based on Akaike’s information (AIC) and other criterion (Mazerolle, 2017). We included all birds that we could confidently identify to species and overflights were not included. The results are presented in Table 2 with the exception of those species where the null model were the best model ($N = 29$), as any differences that might exist among the alternative candidate models cannot be explained by the environmental variables (Burnham and Anderson, 2002). Also, we excluded three species that we could not reliably identify in the field (swallows and two similar-sounding jays). Finally, we tested for spatial autocorrelation using the R package DHARMA (function “*testSpatialAutocorrelation*”).

2.5.2. Joint species distribution model

To explore the possibility of co-occurrence interactions among the bird species, we analyzed the species that were present in more than 8 sites, as other studies suggest for this method (D’Amen et al., 2018), all of which had R-squared > 0.15 ZIP N-mixture model results. We selected 38 species for the co-occurrence analysis. A species was recorded as present if it was detected at least once (McCarthy et al., 2013). We used a hierarchical joint species distribution model (JSDM) to evaluate potential patterns of co-occurrence between pairs of species accounting for the influence of the surrounding vineyard as the key environmental variable of interest, and that was an important environmental predictor variable across the ZIP N-mixture model results (Table 2) (Pollock et al., 2014; Royan et al., 2016).

Hierarchical joint species distribution modeling assesses co-occurrence patterns based on species presence. Species are modeled using a probit hierarchical regression analysis for which the linear environmental predictors are related to a binary response (presence/absence matrix) variable using a latent variable (unobserved variable)

formulation. Here the probability of species occurrence at a site is determined by the latent variable (normal distribution, mean = 0, standard deviation = 1), positive values imply high probability of occurrence (presence), and negative values indicate low probability of occurrence (absence). The number of dimensions of the multivariate normal distribution is equal to the number of species being modeled. An inverse-Wishart prior is used to calculate the variance/covariance matrix made from the means of the normal distribution (Pollock et al., 2014). This allows reduction of the potential noise and bias introduced by non-independence in species responses, and it handles overdispersion between sites and species-specific residual variation (Stjernman et al., 2019). To calculate the correlation between species that is due to shared environmental response (surrounding vineyard landscape in our case), a second matrix is calculated as with other studies that used relevant predictors for modeling (D'Amen et al., 2018). This approach allows modeling of the dataset in an independent frame, in comparison with the previous ZIP *N*-mixture model, where the species classification among agricultural adapters and oak woodland birds was not included as a covariate in the JSDM. The output of JSDM includes predicted probability of species occurrence at each site, correlation between species and the environmental variable, regression coefficients, and residual correlations (Rohan et al., 2016). Additional details of the JSDM can be found in (Pollock et al., 2014) and (Rohan et al., 2016).

To execute the JSDM models, we used the Markov Chain Monte Carlo Bayesian software JAGS 4.2.0 package (Su and Yajima, 2015). We ran five chains for 100,000 iterations, with the first 10,000 discarded as burn-in and the remaining samples thinned by a value of 10 such that we retained 9000 samples for the analysis. We evaluated model convergence using a diagnostic plot, used vague normal priors (mean = 0, SD = 1) for all model parameters, and used network diagrams to visualize positive or negative patterns of species co-occurrence. To visualize how species pairs fall in relation to positive and negative interactions, we plotted the results along environmental (x axis) and residual correlation outputs (y axis). Network diagrams can also be used to represent the correlation patterns between species, as they indicate positive or negative interactions (Pollock et al., 2012; Rohan et al., 2016). Also, to present the relative concentration of the observed patterns based on their point density surface, we used a two-dimensional kernel density estimation (kde2d) function in the MASS package in R (Venables and Ripley, 2003) (Fig. S1). We conducted some sensitivity analyses and found that adding additional environmental variables had no effect on the results.

3. Results

3.1. Species models

In total, we recorded 6854 individuals from 750 observations belonging to 72 bird species, 43 of which had informative ZIP *N*-mixture model results to report (See Table S1 for species names and Table S2 for detailed ZIP model selection). We found that the proportion of vineyard at the landscape scale significantly affected the relative abundance of 37 % of these 43 species (10 of 43 species positively and 6 of 43 negatively; Fig. 2, Table 2). The following six species had significantly negative values for the vineyard cover in the ZIP *N*-mixture model: Acorn Woodpecker (ACWO), Bewick's Wren (BEWR), House Wren (HOWR), Blue-gray Gnatcatcher (BGGN), Orange-crowned Warbler (OCWA), and Spotted Towhee (SPTO) (See Supplementary material Table S1 for a complete list of scientific names). Ten species were significantly positively associated with vineyards and hence are considered here to be "agriculturally adapted" birds, as compared with "oak woodland" birds. These include Northern Flicker (NOFL), Northern Mockingbird (NOMO), European Starling (EUST), Western Bluebird (WEBL), House Finch (HOFI), Lesser Goldfinch (LEGO), Black-throated Gray Warbler (BTYW), Brown-headed Cowbird (BHCO),

Bullock's Oriole (BUOR), and Red-winged Blackbird (RWBL). Oak woodland structure and shrub proportion at the plot scale influenced 33 % of the species analyzed (4 positively and 10 negatively). At the landscape scale, the next most relevant variables were road density, with significant relationships for 30 % of species (10 species affected positively and 3 negatively), and shrub cover, with significant relationships for 19 % of bird species (2 affected positively and 7 negatively). The other environmental variables we examined explained observed differences for far fewer species (Fig. 2, Table 2). Only one species that is usually found in flocks (Chipping Sparrow) was significant for spatial autocorrelation (Table S4).

3.2. Co-occurrence analysis: JSDM

The results of the JSDM revealed potential interactions between species pairs, accounting for the influence of surrounding amounts of vineyard development. See Fig. 3 for network diagrams for 38 species from JSDM results with vineyard land cover as the environmental variable (Pollock et al., 2014; Rohan et al., 2016). Notably, nine of ten agriculturally adapted birds (European Starling (EUST), Western Bluebird (WEBL), Red-winged Blackbird (RWBL), Bullock's Oriole (BUOR), Black-throated Gray Warbler (BTYW), Lesser Goldfinch (LEGO), House Finch (HOFI), Brown-headed Cowbird (BHCO), and Northern Mockingbird (NOMO)) had a strong negative interaction with oak woodland bird species when the vineyard landscape environmental variable was accounted for (Fig. 3). All of these species use open natural habitats with exception of Black-throated Gray Warbler which is a migratory forest bird (Cornell Lab of Ornithology, 2020). The first five are insectivores, the following three are seed eaters, and the last one is an omnivore. The main oak woodland species that appear to be negatively interacting with agriculturally adapted birds were Orange-crowned Warbler (OCWA), SPTO, Hutton's Vireo (HUVI), Blue-gray Gnatcatcher (BGGN), Wren (WREN), and Bewick's Wren (BEWR) (Fig. 3). Only the American Robin (AMRO) was positively associated with multiple agriculturally adapted birds. Strong positive pair association between agricultural adapters and oak woodland birds was observed only between Western Kingbird (WEKI) and Red-winged Blackbird (RWBL) (Fig. 3). There were also positive relationships among pairs of oak woodland birds (Orange-crowned Warbler (OCWA), Spotted Towhee (SPTO), Hutton's Vireo (HUVI), Blue-gray Gnatcatcher (BGGN), Wren (WREN), and Bewick's Wren (BEWR)). These species were insectivore foliage gleaners except for Spotted Towhee (SPTO), which was considered an omnivore ground forager (Fig. 3).

Modeled environmental and residual correlations are plotted in Fig. S1 between all pairwise combinations for 38 bird species. Of the oak woodland bird pairs, all were evenly distributed (Table 3, Q1 Fig. S1A). Of the agricultural adapters–oak woodland pairs analyzed, 41 % co-occurred more than expected given the shared responses to vineyards as an environmental variable (Table 3, Q1 Fig. S1B), while 21 % of these pairs occurred less frequently than expected (Table 3, Q3 Fig. S1B). Of the agricultural adapter pairs, 76 % positively co-occurred with each other more frequently than expected (Table 3, Q1 Fig. S1C).

4. Discussion

Species co-occurrence patterns reveal certain oak woodland species are negatively associated with agricultural adapters and therefore extensive agricultural landscapes may be an important driver of biotic homogenization of adjacent wildlands. The amount and type of matrix surrounding natural areas can influence community composition within natural areas (Andrén and Andren, 1994; Phalan et al., 2011; Steel et al., 2017). Consistent with that notion, we observed that the extent of vineyard matrix partially explains the high abundance of agricultural adapters and lower abundance of oak woodland birds in adjacent patches of California oak woodlands. The species identified by our study as agricultural adapters were among the most commonly recorded species

in Californian vineyards (DeMars et al., 2010; Jedlicka et al., 2014). Not surprisingly, the majority of these species are known to occupy open habitat, this fact may help inform conservation, more generally, about which species may be more likely to adapt to agricultural conversion and potentially impact natural communities. Consistent with other studies (Devictor et al., 2008), we found that oak woodland birds were more affected by the agricultural matrix than generalists were.

The results from this study raise the concern that regional biotic homogenization of bird communities may be taking place in California's oak woodlands landscape. This finding was consistent with others that have documented increased homogenization associated with agricultural land use intensification (Karp et al., 2012). Our finding that detection of woodland birds within natural areas decreased as the amount of surrounding vineyard matrix increased reveals the potential for spillover effects from agricultural landscapes into adjacent wildlands. These types of spillover effects are not well documented in the literature to date. Noted exceptions come from exotic pine plantations and a few other land covers (Barnagaud et al., 2014; Häkkinen et al., 2018; Lindenmayer et al., 2015).

The ultimate influence of land use change on patterns of species co-occurrence in remaining natural areas may be associated with multiple factors that can influence species interactions and long-term persistence. Other studies have shown that adjacent working matrix is less relevant for habitat than reserve forest is (Häkkinen et al., 2018) or that the permeability of the agricultural matrix for species connectivity influences the spillover effect (Boesing et al., 2017). Edge effects and their role in modifying species interactions are also worth considering when assessing the impact of agriculture on adjacent wildlife communities. Recent research showed that edge effects have affected vertebrate communities globally by restructuring natural communities (Pfeifer et al. 2017). However, few studies have reported evidence for indirect interactions among agricultural adaptors and species more sensitive to disturbance, with the exception of predation and parasitism, near agroecosystems (Lindenmayer et al., 2015).

More work is required to get at the exact mechanisms that may be driving the observed spillover effects. However, the finding of negative co-occurrence patterns between well-known agriculturally adapted species and endemic woodland birds does raise concerns about spillover effects on habitat specialists, and it points to the need for future research on species interactions and potential mechanisms for these observed patterns. JSDM biotic interactions results were based on species residual correlations, which could be sensitive to missing predictors (D'Amen et al., 2018) or to the scale of the study (Stjernman et al., 2019). However previous non-reported analyses run with additional environmental variables (e.g., shrubs, oak woodland, roads) showed consistency with the reported results. In addition, more research is required to determine whether these negative interactions are sensitive to distance from the edge of the patch, in which case they might be attenuated by conservation of larger patches of habitat. The size range and configuration of the woodland patches that we studied did not allow us to detect an effect of distance from edge on the observed negative species co-occurrence patterns.

Mechanisms that can lead to negative co-occurrence patterns that have been documented in other field studies are useful to consider in interpreting our results. For example, the negative interactions that we found between European Starling (EUST) and multiple species coincide with its usurpation and/or depredation behavior on native species (Olsen et al., 2008). European Starling (EUST) is one of the most widespread invasive species in the world (Global Invasive Species Database, 2017). It is known to be aggressive in displacing other species from cavity nesting sites (Cabe, 2020) and to increase threats to other species (Bellard et al., 2016). In addition, studies in fragmented forest have reported higher parasitism by Brown-headed Cowbird (BHCO) than in continuous forests (Lowther, 1993; Wilcove, 1985). These species' biological traits can help to interpret patterns of co-occurrence.

In some cases, the mere presence of one bird can affect another's

feeding behavior (Peck et al., 2014), or the colonization of a new species can change the structure of the community (Betts et al., 2010). Indirect effects can also be associated with the spread of infectious diseases that are linked with agricultural intensification (Jones et al., 2013); for example, the effect of West Nile virus is amplified in some bird species and is associated with anthropogenic land use change (George et al., 2015). These negative interactions provide evidence that competition from species adapted to agricultural land use may be another driver of biotic homogenization, along with the habitat loss and fragmentation associated with habitat conversion.

Indirect effects can also have positive impacts on species (e.g., for bird flocks). Positive correlation between congeneric species and species with similar phenotypic traits (e.g., body size, foraging guild) was reported for bird flocks in different ecosystems (Sridhar et al., 2012). Sridhar et al. (and references therein) attribute positive interaction between species to the following advantages for individuals: i) acquisition of social and ecological information (foraging places, threats of predators), ii) facilitated foraging activities and protection (catching prey that other birds did not capture, having individuals that act as sentinels against bird predators), and iii) facilitated access to previously unexplored resources that become available when flocks forage together. Our results showed a strong (Fig. 3) positive interaction between the oak woodland birds that are insectivore foliage gleaners (Blue-gray Gnatcatcher (BGGN), Hutton's Vireo (HUVI), Orange-crowned Warbler (OCWA), Wrentit (WREN), and Bewick's Wren (BEWR)), supporting the idea that communities are assembled via positive interactions among species with similar foraging preferences. It may be that when resources are scarce, insectivorous communities can use alternative resources, probably through niche partitioning. This pattern of strongly associated species among oak woodland birds, as well as strongly associated species among agriculturally adapted birds (Fig. 3), suggests that vineyard expansion may promote species compartmentalization (Bascompte, 2009).

Although the mechanism of these interactions requires experimental verification, the underappreciated, indirect negative effects associated with agriculturally adapted species discussed here may have a real bearing on biodiversity conservation as vineyards continue to infringe on some of the last remaining native Mediterranean-climate habitat. In particular, impacts on species with declining populations, such as Spotted Towhee (SPTO), Orange-crowned Warbler (OCWA), and Bewick's Wren (BEWR) (Sauer et al., 2017), or on oak woodland specialist species, such as Nuttall's Woodpecker (NUWO), need to be addressed for species persistence. Changes in community composition can affect ecosystem services, for example increasing abundance of Western Bluebird (WEBL) and other insectivore birds enhance biological control of pest in vineyards (Assandri et al., 2017b; Bosco et al., 2019; Jedlicka et al., 2011), and increasing omnivore bird species such as European Starling (EUST) or Red-winged Blackbird (RWBL) can increase crop damage which is considered a disservice (Brugger et al., 1993; Dolbeer, 1990). In sum, continued examination of spillover effects from agricultural land into adjacent natural areas is warranted in light of global species declines, biotic homogenization, and our reliance on ecosystem services.

Declaration of interests

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.

Funding

The first author thanks Becas Chile (CONICYT) Fulbright (US Department of State) [grant #72110760], and UC Berkeley (ESPM) scholarships. We thank UCANR Integrated Hardwood Range Management Program, The Nature Conservancy, and Point Blue for

supporting field logistics and funding.

Declaration of competing interest

None.

Acknowledgments

We thank Paul Elsen for analysis advice and Leah Renwick and Lou Doucette for helping with manuscript clarity. We thank Gretchen LeBuhn and Kerry Heise for assistance with the field study.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.agee.2020.106960>.

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