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A century of climate and land-use change cause species turnover without loss of beta diversity in California's Central Valley

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Abstract

Climate and land-use changes are thought to be the greatest threats to biodiversity, but few studies have directly measured their simultaneous impacts on species distributions. We used a unique historic resource—early 20th-century bird surveys conducted by Joseph Grinnell and colleagues—paired with contemporary resurveys a century later to examine changes in bird distributions in California's Central Valley, one of the most intensively modified agricultural zones in the world and a region of heterogeneous climate change. We analyzed species- and community-level occupancy using multispecies occupancy models that explicitly accounted for imperfect detection probability, and developed a novel, simulation-based method to compare the relative influences of climate and land-use covariates on site-level species richness and beta diversity (measured by Jaccard similarity). Surprisingly, we show that mean occupancy, species richness and between-site similarity have remained remarkably stable over the past century. Stability in community-level metrics masked substantial changes in species composition; occupancy declines of some species were equally matched by increases in others, predominantly species with generalist or human-associated habitat preferences. Bird occupancy, richness and diversity within each era were driven most strongly by water availability (precipitation and percent water cover), indicating that both climate and land-use are important drivers of species distributions. Water availability had much stronger effects than temperature, urbanization and agricultural cover, which are typically thought to drive biodiversity decline.

KEYWORDS
Bayesian, bird, climate, drought, global change, land use, occupancy, resurvey

1 | INTRODUCTION

Global climate and land-use changes are projected to be the greatest threats to biodiversity over the coming century (Sala et al., 2000), with implications for community functions and ecosystem services (Cardinale et al., 2012). The effects of climate and land use on the geographic structuring of biodiversity have largely been studied independently (Ibáñez-Álamo, Rubio, Benedetti, & Morelli, 2017; Karp et al., 2012; Newbold et al., 2015; Thomas et al., 2004; Tingley & Beissinger, 2013). However, realistic scenarios must consider the simultaneous effects of these two drivers (Ferger et al., 2017; Hof, Araújo, Jetz, & Rahbek, 2011; Parmesan et al., 2013; Travis, 2003). Some studies suggest that climate is more important than land use in determining species distributions (Bucklin et al., 2015; Sohl, 2014; Thuiller, Araújo, & Lavorel, 2004), but the continental scale of these analyses could underestimate the importance of land use in regions of intense urban or agricultural development.

Species demonstrate heterogeneous distributional responses to both climate and land-use (Carrara et al., 2015; McKinney, 2002; Tingley, Koo, Moritz, Rush, & Beissinger, 2012; Walther, Post, Convey, & Menzel, 2002), although these two drivers may favor species with similar ecological traits (Frishkoff et al., 2016). Climate and land-use changes are associated with decreased occupancy for a wide range of species, particularly those with low mobility or specialized habitat requirements (Carrillo-Rubio et al., 2014; Distler, Schuetz, Velásquez-Tibatá, & Langham, 2015; Tingley & Beissinger, 2013). At the same time, occupancy typically increases in species tolerant to altered habitats, particularly habitat generalists (Carrara et al., 2015; MacLean & Beissinger, 2017; McKinney, 2002; Rahel, 2002). Thus, the combined effects of climate and land-use change should cause a loss of species richness and increased homogenization at the community level (Bonebrake et al., 2016; Frishkoff et al., 2016; Karp et al., 2017). There is, however, considerable debate on whether local species richness has declined globally (Gonzalez et al., 2016; Newbold et al., 2015), as some studies demonstrate a surprising lack of diversity loss despite climate or land-use change (Dornelas et al., 2014; Vellend et al., 2017).

We quantified the influence of climate and land-use on community composition by comparing early 20th-century bird communities to their contemporary counterparts in the California Central Valley, a 47,000 km^2 region that has undergone intensive agricultural and urban expansion, as well as heterogeneous climate change. Since the early 1900s, the Central Valley has been converted from seasonal wetlands and alkali scrub to one of the most intensely developed agricultural regions in the world, interspersed with several large urban centers (Frayer, Peters, & Pywell, 1989; Nelson, Lasagna, Holtgrieve, & Quinn, 2003). Concurrently, the valley has undergone spatially heterogeneous changes in temperature and precipitation patterns (Rapacciuolo et al., 2014). We used unique historic resources—early 1900s systematic bird surveys and land-use maps—paired with modern resurveys and measures of land cover and climate to quantify bird species occupancy. We asked the following: (a) How have community-level occupancy, richness and diversity changed over the past century?; (b) how has species-level occupancy changed and to what extent can these changes be explained by species' traits?; and (c) what is the relative importance of climatic and land-use covariates to occupancy, species richness and beta diversity (as measured by Jaccard similarity) within each survey period? We predicted that more bird species would decrease than increase in occupancy, and that contemporary bird communities would contain fewer species and be more homogeneous than their historic counterparts. We also predicted that species-level changes in occupancy would be related to body mass, clutch size, habitat breadth and diet breadth. Finally, we predicted that land use would have a greater influence on site-level occupancy, richness and diversity than climate, especially during the modern resurvey period due to the dominance of human-altered habitats.

2 | MATERIALS AND METHODS

2.1 | Study area

We resurveyed bird diversity in the Central Valley of California at 41 sites surveyed prior to 1925 by Joseph Grinnell and seven collaborators from the Museum of Vertebrate Zoology at UC Berkeley (Figure 1). The valley extends approximately 640 km north to south and on average 64 km across, bordered on the east by the Sierra Nevada foothills and on the west by the Coast Ranges. The natural vegetation of this ecoregion is a mosaic of riparian belts and seasonal wetlands within a flat grassland matrix, with limited coverage of oak woodland along the foothills and saltbrush scrub in the southern valley (Nelson et al., 2003).

Although localized agricultural development was well under way as early as the 1890s (Sumner, Bervejillo, & Kuminoff, 2003), large-scale expansion occurred after an extensive networks of canals and reservoirs were constructed as part of the Central Valley Project in the 1930s and the California State Water Project in the 1950s (Gilmer, Miller, Bauer, & Ledonne, 1982). By the early 2000s, the valley had lost over 90% of its original four million acres of wetland (Frayer et al., 1989), and approximately 70% of the valley was under cultivation (Sleeter, 2007). This agricultural land continues to be one of the most productive regions in the United States (Sumner et al., 2003), and urban areas currently have one of the fastest population growth rates in California (US Census Bureau, 2010). Historic maps and descriptions suggest that habitat loss over the past century has been primarily from conversion of a natural type to urban or agriculture, or from loss/construction of waterways and reservoirs, with limited transitions among natural land cover types (Nelson et al., 2003; Sleeter, 2007). Field notebooks kept by Grinnell and colleagues do not provide detailed maps of vegetation cover, but do describe the dominant natural plant communities, which have not changed qualitatively at any of our sites.

2.2 | Bird surveys

Collection of historic and modern bird survey data followed established protocol for the Grinnell Resurvey Project (Tingley & Beissinger, 2013; Tingley et al., 2012; Tingley, Monahan, Beissinger, & Moritz, 2009). Field journals kept by historic researchers provide detailed descriptions and maps of survey routes, as well as systematic lists of bird species observed each day. Historic surveys occurred between 1912 and 1923 (late March through June). Each site had an average of 3.7 consecutive days of surveys (minimum 1, maximum 11).

We conducted modern resurveys during the breeding seasons (April through June) of 2015 and 2016. At each site, we created a transect of 10 point count stops placed 250 m apart, corresponding as closely as possible to the route followed by the historic surveyors and the habitats that they visited. We recorded all birds seen or heard using variable-distance point counts lasting 7 min. Counts began at dawn, and sites were surveyed daily over three consecutive

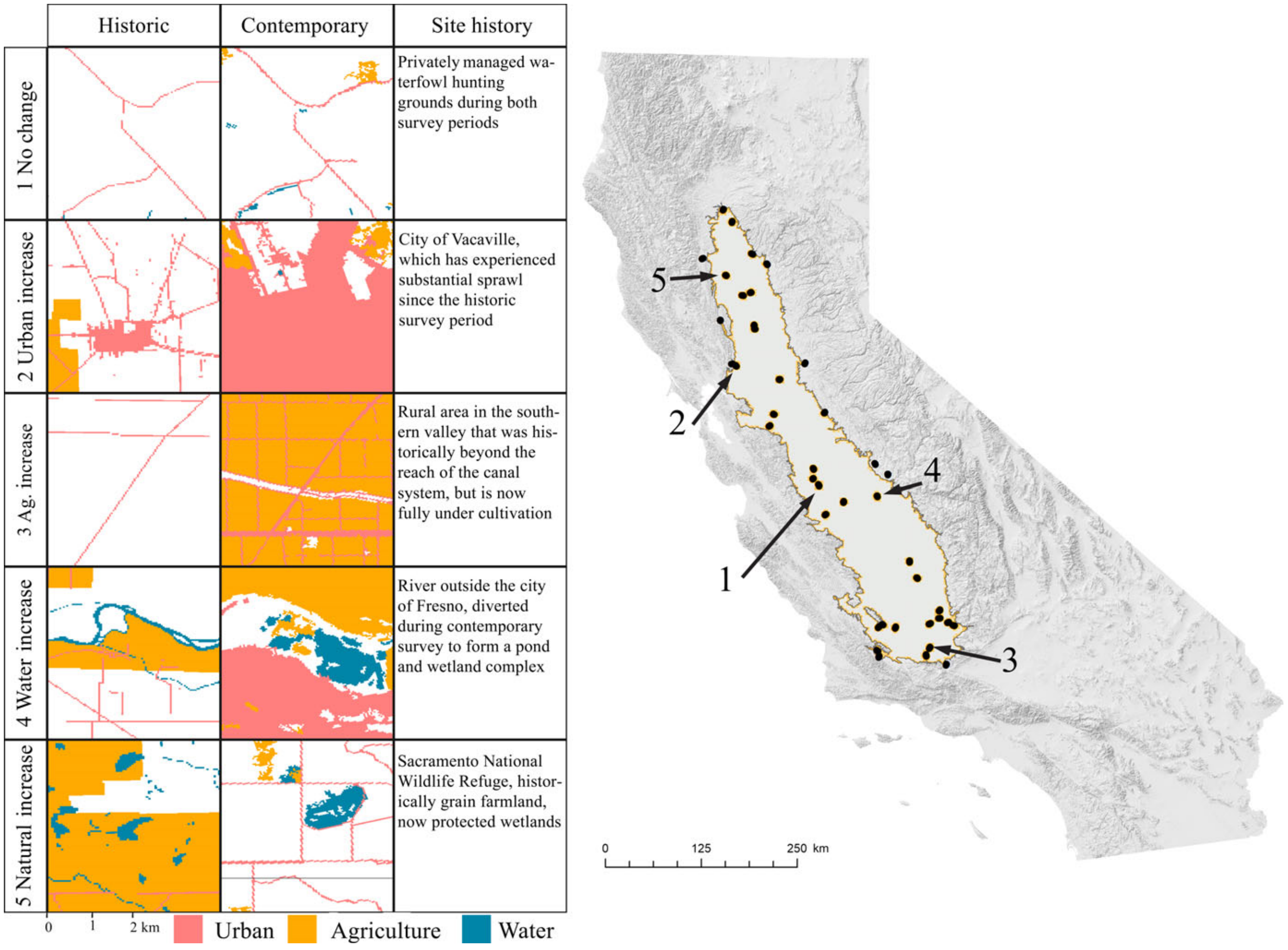

FIGURE 1 Map of survey locations. Outlined area represents the extent of the Central valley ecoregion. Panel provides examples of change in urban, agriculture, and water coverage at five survey sites with varying land-use change histories, to demonstrate the efficiency of our historic mapping methods. Modern land-use data were obtained from the National Land Cover Database [Colour figure can be viewed at wileyonlinelibrary.com]

days to allow estimation of detection probability (Dorazio, Royle, Söderström, & Glimskär, 2006).

We included bird species in our analyses if they were known to breed in the Central Valley (NatureServe, 2017). We excluded two species of breeding shorebirds (American avocet and black-necked stilt), one species of wading bird (white-faced ibis), and eight species of breeding waterfowl (wood duck, northern pintail, gadwall, cinnamon teal, ruddy duck, western grebe, Clark's grebe, and pied-billed grebe) from our analysis (see Supporting Information Table S1 for scientific names of all species), because they have highly localized distributions near large bodies of open water and were not adequately sampled by historic survey locations. During modern resurveys, these species were almost exclusively recorded flying overhead away from transects toward unknown areas. Flyover species that remained reasonably within the observable area (e.g., circling or flying low over the vegetation) were included as detections. The final dataset consisted of 110 species in the historic survey period and 107 species in the modern survey period.

2.3 | Historic land cover mapping

Digital maps of historic land use in California were not available at a suitable resolution or spatial extent, and historical map products created by the Wieslander Project (Kelly, Ueda, & Allen-Diaz, 2008) or the San Francisco Estuary Institute (Whipple, Grossinger, Rankin, Stanford, & Askevold, 2012) do not include most of the Central Valley. We created maps of land cover within 1 km of our survey transects by hand-digitizing historic maps from sources discussed below using ArcMap (Figure 1). While it would have been ideal to map different natural land covers present historically in the Central Valley (i.e., grassland, wetland, scrub, riparian, and oak woodland), we were unable to find corresponding historic vegetation maps. Instead, we focused our analysis on land-use categories associated with habitat conversion in the Central Valley. These categories were (a) urban, (b) agriculture, and (c) water. We found no evidence for shifts among natural habitat types based on site descriptions in the historic field notes, and no strong evidence based on the coarse-resolution historic map series developed by the Central

Valley Historic Mapping Project (Nelson et al., 2003). In line with this evidence, our three focal land-use change categories capture the processes of habitat conversion most relevant to changes in bird occupancy.

Cover of water and urban area were mapped using historic USGS topographic maps (ca. 1906–1932). Water bodies were outlined directly as polygons. Urban area was mapped as buildings (area of the building icon on the topographic map plus a buffer of 50 m) and roads (digitized as line features from the topographic map, then given a width of 30 m). Area of historic agriculture was delineated using a series of three maps of irrigated land in the state of California published by the US Department of Agriculture (USDA, 1922). We converted our digitized historic land cover from vector format to raster format at 30 m resolution per pixel, corresponding to the National Land Cover Database used for contemporary sites (Jin et al., 2013).

2.4 | Multispecies occupancy model

Multispecies occupancy models use a hierarchical framework to produce estimates of species' occupancy while accounting for heterogeneity in detection probability (Dorazio & Royle, 2005; Iknayan, Tingley, Furnas, & Beissinger, 2014). We modeled historic and resurveyed sites separately using two single-season occupancy models (MacKenzie et al., 2002; Tingley & Beissinger, 2009). This approach is useful when survey periods are separated by sufficient time to satisfy the assumption of independence (Iknayan et al., 2014; Moritz et al., 2008; Tingley & Beissinger, 2009), and when colonization and extinction parameters in a multi-season model have difficulty converging due to data limitations (MacKenzie, Nichols, Hines, Knutson, & Franklin, 2003). After estimating models formulated from a priori assumptions, we conducted a sensitivity analyses of whether results were robust to violations of those assumptions by estimating a set of alternative models.

Probabilities of occupancy and detection were modeled as linear combinations of site- and survey-level covariates. Following previous models of birds in California (Tingley & Beissinger, 2013), detection probability was modeled as a function of season, defined as the Julian day (jday = 1 on 1 January). Probability of detection for the i-th species at the j-th site on the k-th visit was modeled as follows:

$$\text{logit}\left(p_{i,j,k}\right) = \alpha_{0,i} + \alpha_{1,i}\text{jday}_{j,k}$$

where $\alpha_{0,i}$ and $\alpha_{1,i}$ are coefficients for detectability for species i. Avian surveys were mostly performed in the first half of the breeding season before singing tends to decline, so we omitted a quadratic term for Julian day from the a priori model but assessed robustness to this assumption in the sensitivity analysis.

Occupancy was modeled as a linear function of site-level temperature (temp) and precipitation, percent cover of water (water), percent cover of built-up area (urban), and percent cover of agriculture (ag). In a multispecies occupancy model, the effects of covariates on individual species occupancy are allowed to vary, as should be expected due to differences in behavior and life history, but species-specific effects are assumed to come from a common community-level hyperdistribution (Iknayan et al., 2014). Occupancy was modeled as follows, where $\beta_{0,i,\ \ldots\ ,5,i}$ are species-specific model coefficients for occupancy:

$$\text{logit}\left(\psi_{i,j}\right) = \beta_{0,i} + \beta_{1,i}\text{temp}_j + \beta_{2,i}\text{precip}_j + \beta_{3,i}\text{water}_j + \beta_{4,i}\text{urban}_j + \beta_{5,i}\text{ag}_j$$

Covariates were centered at 0 and normalized to a standard deviation of 1 prior to analysis. Climate covariates (mean maximum temperature and mean total precipitation) were obtained from 800 m resolution interpolated maps produced by the PRISM climate group (Daly, Gibson, Taylor, Johnson, & Pasteris, 2002), and averaged over 30-year periods corresponding to the historic (1900–1929) and modern (1987–2016) surveys. We used second quarter climate data since it corresponded closely to the breeding season when our surveys were conducted (Tingley et al., 2009). We used mean total precipitation because it is a commonly used metric of precipitation for modeling species distributions (Illán et al., 2014; Stralberg et al., 2009; Tingley et al., 2009). Mean, maximum, and minimum temperature, and change in these parameters were all highly correlated at our sites and throughout the state of California (Rapacciuolo et al., 2014; Tingley et al., 2009). We used maximum temperature because it is a common metric for modeling distributions of birds and other taxa in California and elsewhere (Dobrowski et al., 2011; Illán et al., 2014; Stralberg et al., 2009; Tingley et al., 2009), affects energetic costs and hydric stress associated with thermal limits of birds (Khaliq et al., 2014; Mckechnie, Wolf, Mckechnie, & Wolf, 2010), and displayed slightly more heterogeneity across sites than did the other two metrics, although it has changed less than minimum and mean temperatures in California during the 20th century (Rapacciuolo et al., 2014).

Land cover covariates were calculated for a 200 m buffer around the modern survey transects, which correspond to the maximum distance at which birds were detected during the modern surveys. We reasoned that smaller survey buffer would fail to sample habitats in which birds were detected, and a larger buffer would potentially sample habitats that were not representative of our survey transects. Percent natural land cover was not explicitly included as a covariate in the model, as it is the complement of the sum of the other three land cover categories. Modern land cover data were obtained from the National Land Cover Database (Jin et al., 2013). Historic land cover data were obtained from the hand digitized maps described above.

We examined whether outcomes of our occupancy model were sensitive to a priori assumptions by estimating models with alternative assumptions and comparing parameter estimates and credible regions to those from the a priori model. To assess sensitivity to spatial scale of land cover covariates, we fit models using buffers of 100, 500, and 1,000 m around the modern survey transects to compare with the a priori 200 m scale. To assess sensitivity to the assumption of linear trend of detection probability (on the logit scale) across Julian date, we included a quadratic Julian date term in the models for each spatial scale. This approach avoids the statistical uncertainty inherent to model selection and the difficulties of post-selection inference by instead evaluating whether conclusions were robust to alternative assumptions. The mean coefficient values and occupancy change across mean species-level posteriors were similar regardless of the buffer distance or detection model used (Supporting Information Table S2). For simplicity, we limit our presentation in the main text to the a priori model (i.e., linear detection for Julian date and 200 m buffer).

We specified two community-level measures in the model that were direct functions of estimated parameters. They were calculated from posterior draws of the Markov Chain Monte Carlo runs. Species richness at the *j*-th site, N_j, was calculated as.

$$N_j = \sum_{i=1}^{n} z_{i,j}$$

where $z_{i,j}$ is the model-estimated matrix of true occurrence for each species at a site (0 or 1; for a more detailed description of $z_{i,j}$ and its calculation, see Dorazio & Royle, 2005) and *n* is the total number of potential species within each survey period ($n_{\text{modern}} = 107$, $n_{\text{historic}} = 110$).

Similarity in species composition between two sites was calculated using the Jaccard Index (Real & Vargas, 1996). Within each survey period, we estimated Jaccard similarity, *J*, between two sites as.

$$J_{a,b} = \frac{\sum_{i=1}^{n} z_{i,\,a} z_{i,\,b}}{N_a + N_b - \sum_{i=1}^{n} z_{i,\,a} z_{i,\,b}}$$

for sites, $a = 1, 2, \ldots, 41$ and $b = 1, 2, \ldots, 41$, where *n* is the total number of potential species within each survey period. This yielded a total of 820 unique site pairs for each survey period.

Beta diversity between sites may reflect two different processes—spatial turnover and nestedness—that may change independently in response to climate or land-use change, even if their sum (i.e., overall diversity) remains the same (Baselga, 2010). We calculated mean multi-site species turnover and nestedness for each survey period using the package “BETAPART.”

Bayesian parameter estimation was run with WINBUGS (Lunn, Thomas, Best, & Spiegelhalter, 2000) via R using the package “R2WINBUGS” (Sturtz, Ligges, & Gelman, 2005). We used uninformative priors for the means and variances of the hyper-parameters. The full model code is provided in the Supporting Information. We ran three parallel chains of length 50,000, discarding the first 40,000 as burn-in, and used a thinning rate of 10. This resulted in a posterior distribution consisting of 3,000 samples for each parameter. Convergence was assessed by visual inspection of traceplots and by using the Gelman–Rubin convergence diagnostic (Gelman & Hill, 2007), with all diagnostic values <1.1. Adequacy of the model was assessed using Bayesian *p*-values (Gelman, Meng, & Stern, 1996; Zipkin, Dewan, & Andrew Royle, 2009). Values closer to 0 or 1 indicate that the model was inadequate. For our dataset, Bayesian *p*-values were estimated at 0.49 for the historic surveys and 0.47 for the modern surveys, indicating that our models provided adequate description of the data.

2.5 | Species’ traits

Species’ functional and life history traits mediate sensitivity and ability to move in response to climate and land-use change (Buckley & Kingsolver, 2012; Estrada, Morales-Castilla, Caplat, & Early, 2016). Thus, traits may explain heterogeneity in observed distributional changes (Angert et al., 2011; Auer & King, 2014), although a recent meta-analysis revealed that only habitat breadth has been a consistent predictor of range shifts of several frequently analyzed traits (MacLean & Beissinger, 2017). We tested whether traits explained variation in species-specific change in mean occupancy between the historic and modern survey period. Body size (mean adult mass) and clutch size (average per female) data were obtained from the online Encyclopedia of Life (Parr et al., 2014). Diet breath (number of food types consumed) was obtained from Elton Traits (Wilman et al., 2014). Habitat preference was obtained from The Birds of North America Online (Rodewald, 2015) and included seven habitat categories: generalist, developed, open, riparian, scrub, wetland, and woodland. Because we used two separate single-season models, the effects of species’ traits on change in occupancy could not be estimated directly within our modeling framework, so we conducted a secondary analysis using the output from our occupancy models. We used linear mixed models to analyze change in species occupancy as a function of traits, with species as a random effect. To incorporate uncertainty from our occupancy models, we weighted the mean change in occupancy across sites for each species by the corresponding inverse variance in occupancy change, so that species with smaller variance in occupancy change were given more weight. The full model set consisted of all single trait models ($n = 4$) and all combinations of two traits ($n = 6$), which were compared using AIC_c.

2.6 | Covariate effects on community similarity and species richness

The effects of covariates on species richness and similarity were not directly estimated within the occupancy model, so we developed a method to approximate these effects in a secondary analysis using posterior distributions from the model output. Both species richness and Jaccard similarity are functions of the occupancy states, $z_{i,j}$, but these occupancy states were random variables in the model, with probabilities that depended on covariates. Therefore, we calculated expected species richness and expected Jaccard similarity based on the model's predicted probabilities of occupancy. The expected values are averages over every species’ occupancy status in every site for species richness, or in each of two sites for Jaccard similarity. We then calculated the partial derivatives of expected species richness and similarity with respect to each of the covariates ($dE[J_{j1,j2}]/\text{dcov}$ and $dE[N_j]/\text{dcov}$, respectively), where cov refers to temperature, precipitation, water, urban, or agriculture. A larger derivative (i.e., a steeper slope) indicated a covariate had greater relative influence on expected richness or similarity, relative to other covariates.

For species richness, the expected richness at a hypothetical site *j*, $E[N_j]$, was related to the species-specific coefficients as follows:

$$E[N_j] = \sum_{i=1}^{n} \text{expit}(\beta_{0,i} + \beta_{1,i}\text{temp}_j + \beta_{2,i}\text{precip}_j + \beta_{3,i}\text{water}_j + \beta_{4,i}\text{urban}_j + \beta_{5,i}\text{ag}_j),$$

where $\beta_{0,i,\ \ldots\ ,5,i}$ are species-specific coefficients estimated by the occupancy model. We calculated d$E[N_j]$/dcov from this function directly using the grad() function from the "NUMDERIV" package.

While the expected species richness can be calculated analytically, this cannot be done for expected Jaccard similarity. This is because the expected Jaccard similarity is a summation of a nonlinear function of occupancy status over all possible values of occupancy status at each pair of sites. Since the occupancy status for a site includes the occupancy of each species, the expected value is a very high dimensional summation, so we implemented the calculation and its derivative using Monte Carlo methods. The goal of this approach was to simulate the relationship between expected Jaccard similarity and each covariate (while holding all other covariates constant at their mean standardized covariate value of 0), and then calculate the derivatives of the resulting curves.

Since Jaccard similarity is calculated between pairs of sites, we considered how similarity changed as a covariate value varied at one site, while the second site was held constant at a reference value (i.e., the mean value). We began by calculating occupancy probability at the reference site for each species. For each occupancy probability, we then simulated 1,000 vectors of occupancy (0 or 1 for each species).

For each covariate being tested, we calculated the occupancy probability for each species across the full range of the covariate's observed (standardized) values at our survey sites, using intervals of 0.05, and setting other covariates to their mean standardized value of 0. For each covariate value, we then simulated 1,000 vectors of occupancy for each species. We calculated Jaccard similarity between the 1,000 vectors of occupancy for each test covariate value and the 1,000 vectors of occupancy for the reference site, resulting in 1,000 values of simulated Jaccard similarity for each value across the covariate's range.

We then used the simulated Jaccard similarity values to estimate the derivative of expected Jaccard similarity with respect to the covariate. We did this by fitting a smooth function, for which we chose simply a cubic function since it was adequate to the task. We fit one cubic regression across all the simulated Jaccard values as a function of the covariate, using the lm() function in R. We then calculated the derivative of this function at the mean covariate value (i.e., 0) using the grad() function from the "NUMDERIV" package in R. To account for uncertainty in our occupancy model output, we repeated this entire process across all 3,000 posterior values of the model coefficients.

We also calculated the partial derivatives of richness with respect to each of the covariates using the Monte Carlo method described for Jaccard similarity. We did this to verify that the Monte Carlo results would match the analytic results, and to provide assurance that the Monte Carlo calculations for Jaccard were correct. The partial derivatives of richness with respect to each covariate were similar, regardless of whether they were calculated analytically or with our Monte Carlo method. We present results for species richness based on the Monte Carlo method to maximize comparability with results for Jaccard similarity. Sample code for this analysis is provided in Supporting Information Appendix S2.

3 | RESULTS

3.1 | Climate and land-use change over the past century in the Central Valley

Sites represented a broad range of climate and land-use values within each survey period, as well as experienced heterogeneous changes in climate and land use over the past century (Supporting Information Figure S1). The average (±1 *SE*) maximum temperature across all sites did not change significantly (historic: 31.9 ± 1.5°C; modern: 31.7 ± 1.5°C), but change varied greatly among sites from +1.1°C to −2.3°C. Both patterns were similar to trends in maximum temperature that occurred throughout California during the 20th century (Rapacciuolo et al., 2014). Mean annual precipitation increased slightly from 3.4 ± 2.9 to 4.1 ± 3.3 cm, which was less than the increase of 2.7 cm average across the entire state. While most sites got wetter, a few got drier (range: −0.9 to +3.9 cm). Water cover at sites decreased on average from 5.4% ± 6.5% to 2.9% ± 6.0% (range: −25% to +10%), urban cover increased from 7.7% ± 6.6% to 22.8% ± 17.6% (range: −4% to +55%), and agricultural cover increased from 13.1% ± 25.5% to 25.5% ± 29.3% (range: −67% to +78%).

3.2 | Species-level changes in occupancy

Bird species varied greatly in their responses to climate and land-use change in the Central Valley. Of the 122 species analyzed, 27 significantly decreased in occupancy, 35 significantly increased in occupancy, and 60 showed no significant change (Figure 2 and Supporting Information Table S1). Because the distribution of species increasing and decreasing was roughly equal, there was no overall change in mean occupancy across all species (mean ± 1*SE* = 0.01 ± 0.02).

Changes in occupancy for individual species were highly heterogeneous (Figure 2 and Supporting Information Table S1). Species with the largest significant increases in occupancy (>33%) were predominantly exotics and human adapters, including the Eurasian collared-dove (EUCD), brown-headed cowbird (BHCO), European starling (EUST), northern mockingbird, Anna's hummingbird (ANHU), great egret, common raven (CORA), rock pigeon (ROPI), and mourning dove. Species with the largest significant decreases in occupancy (>33%) were the American kestrel (AMKE), western meadowlark (WEME), burrowing owl (BUOW), American goldfinch, loggerhead shrike (LOSH), chipping sparrow, Bell's sparrow, turkey vulture (TUVU), and northern flicker. Fifteen species disappeared from our study sites over the past century; nine of these had low (<0.15) historic occupancy (mountain bluebird, bank swallow, Hammond's

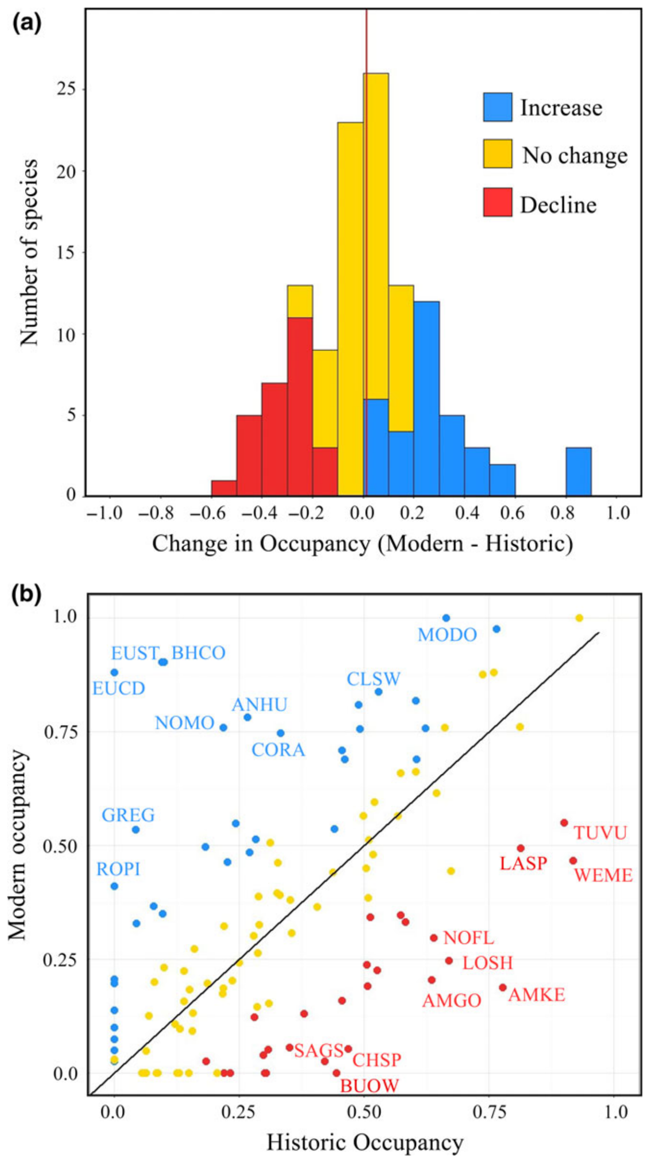

FIGURE 2 (a) Change in the proportion of sites occupied between historic (1912–1923) and modern (2015–2016) survey periods for bird species of the Central Valley, with colors indicating significant increases, significant decreases, or no change; (b) Comparison of historic and modern occupancy for all species, colored as in panel (a); species with >33% decreases or increases are labeled and discussed in the main text (also see Supporting Information Table S1 for guide to species four-letter codes) [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 1 AICc rankings for linear mixed effects models of traits as predictors of occupancy change, weighted by variance in occupancy change

Model	*k*	AIC$_c$	ΔAIC$_c$	AIC$_c$ weight	Log likelihood
Habitat	9	−50.44	0.00	0.42	35.02
Habitat + Mass	10	−49.83	0.61	0.31	35.91
Habitat + Clutch	10	−48.34	2.10	0.15	35.16
Habitat + Diet	13	−47.89	2.55	0.12	38.63
Mass	4	17.06	67.50	0.00	−4.36
Null	3	17.22	67.66	0.00	−5.51
Diet	7	17.68	68.12	0.00	−1.35
Diet + Mass	8	18.18	68.62	0.00	−0.45
Clutch	4	19.19	69.63	0.00	−5.43
Mass + Clutch	5	19.24	69.68	0.00	−4.36
Diet + Clutch	8	19.97	70.41	0.00	−1.35

flycatcher, black-chinned sparrow, Allen's hummingbird, Le Conte's thrasher, Costa's hummingbird, Lewis' woodpecker, and purple martin), but six of the species were relatively common (>0.20 occupancy) historically (Bell's vireo, Brewer's sparrow, BUOW, hairy woodpecker, hermit thrush, and ruby-crowned kinglet). Of the 12 species new to the modern survey period, six were rare (occupancy <0.15) colonizers from neighboring ecoregions on the edges of the Central Valley (brown creeper, pileated woodpecker, white-tailed kite, common ground dove, Steller's jay, and osprey), two were exotic species occurring at low occupancy (ring-necked pheasant and rose-ringed parakeet), and four were well-known expanders in California including three exotic (EUCD, ROPI, and wild turkey) and one native (great-tailed grackle) species.

Species-level changes in occupancy were primarily associated with habitat preferences (Table 1). Habitat preference explained the greatest amount of variation in occupancy change (AIC$_c$ weight = 0.42 for single-covariate model). It had a ΔAIC$_c$ score that was 67 less than body mass and diet, which were barely more descriptive than the null model. Habitat generalists and species that utilized human-modified habitats were more likely to increase in occupancy than were species specializing in natural habitats, which tended to remain stable overall in their occupancy (Figure 3). When modeled with habitat preference, body mass did describe some additional variation in species' responses and was slightly positively related to occupancy change (beta <0.001), but this and other two-factor models were less informative than habitat preference alone (Table 1).

3.3 | Avian community change

Both species richness per site and Jaccard similarity between sites changed little on average over the past century (Figure 4). Richness increased slightly by 1.91 species per site on average (95% credible interval = −14.17 to 17.76; Figure 4a). Jaccard similarity between sites (which ranges from 0 to 1) also increased only slightly by 0.06 on average (95% CI = −0.11 to 0.23; Figure 4b). Species turnover and nestedness, as described by Baselga (2010), changed little between the historic and modern survey periods (mean ± *SD* turnover = 0.88 ± 0.003 vs. 0.86 ± 0.002; mean nestedness = 0.03 ± 0.002 vs. 0.04 ± 0.001, respectively).

Community-level occupancy was driven primarily by precipitation and water cover in both the historic and modern periods (Figure 5a). Precipitation had the greatest mean effect across all species-level coefficients followed closely by the percent cover of water; both

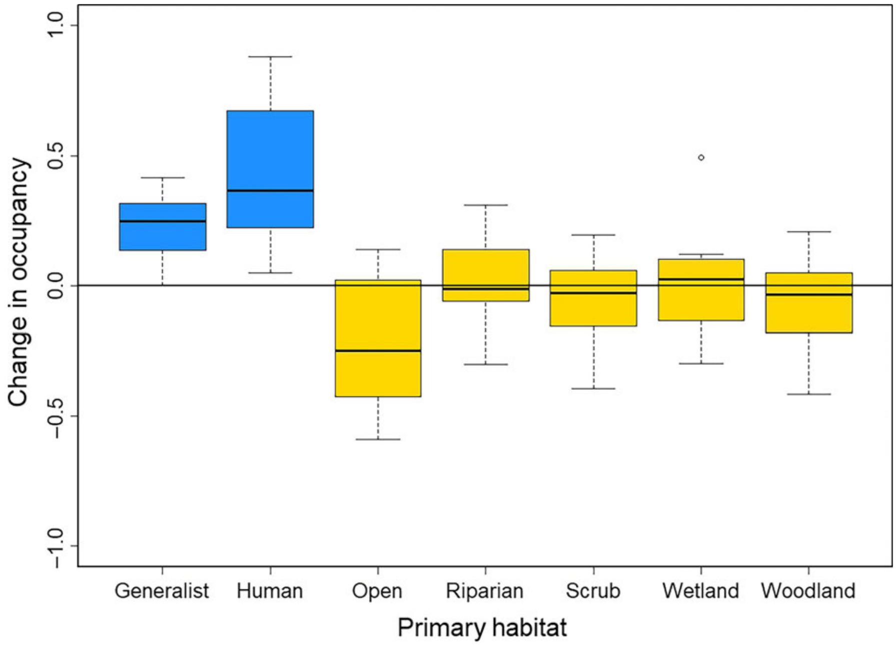

FIGURE 3 Changes in occupancy (modern – historic) by habitat preference [Colour figure can be viewed at wileyonlinelibrary.com]

effects were positive. Temperature had a strong negative effect on occupancy in the modern survey period, but had a minimal effect during the historic survey period. Urban and agricultural land use had no significant community-level effects on occupancy during either survey period. Species-level coefficient effects showed similar patterns (Supporting Information Tables S4 and S5, Figures S3 and S4).

Covariates had strikingly similar effects on expected species richness (Figure 5b) and Jaccard similarity (Figure 5c) as on community occupancy (Figure 5a). It is logical that the number of species in common between independent sites responds to variables in a way similar to the expected number of species at one site, but on very different scales. Figure 5, however, only presents the first derivatives of species richness and expected Jaccard similarity at the mean value of each covariate. Relationships for expected species richness across covariate values were roughly linear (Supporting Information Figure S2a,b), so the slopes were similar across all covariate values. Expected Jaccard similarity displayed stronger nonlinearity (Supporting Information Figure S2c,d). This resulted in differing slopes, but primarily at more extreme covariate values (>1–2 standard deviations from the mean). Thus, focusing on derivatives at mean value provides a reasonable method to quantify and compare these metrics.

4 | DISCUSSION

Over the past century, birds of the Central Valley responded heterogeneously to climate and land-use change. Occupancy increased for predominantly generalist and exotic species, while declines were more common in species with more specialized habitat preferences (Figure 3). Nevertheless, species-level changes were surprisingly well balanced, resulting in unexpected stability in community richness and beta diversity (Figure 4). Occupancy, richness, and diversity were determined in both survey periods predominantly by water

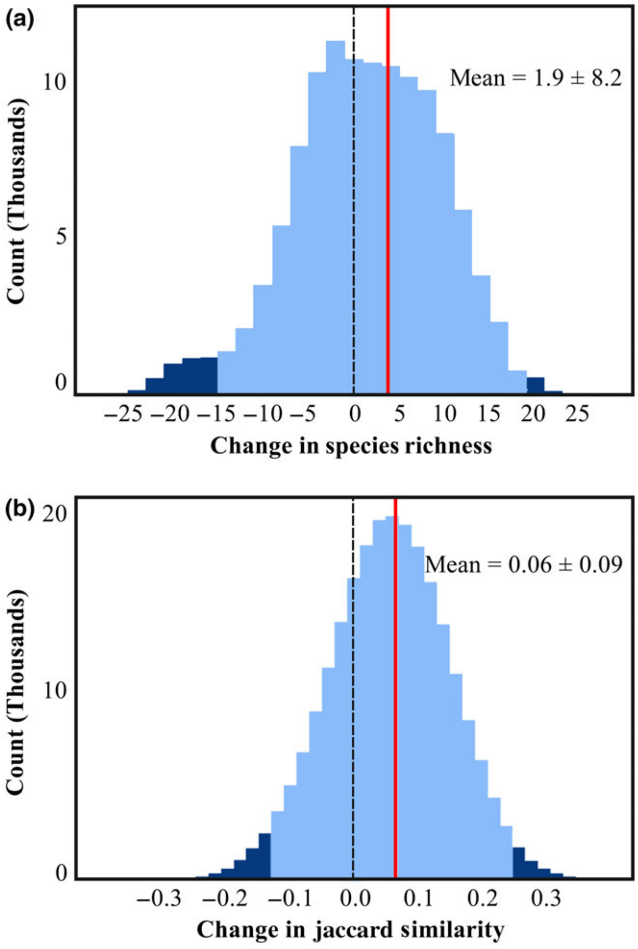

FIGURE 4 Histogram showing the posterior distribution for change (modern-historic) in (a) species richness per site and (b) Jaccard similarity between sites. Light blue regions indicate the 95% credible interval. Mean and one standard deviation are given for each distribution [Colour figure can be viewed at wileyonlinelibrary.com]

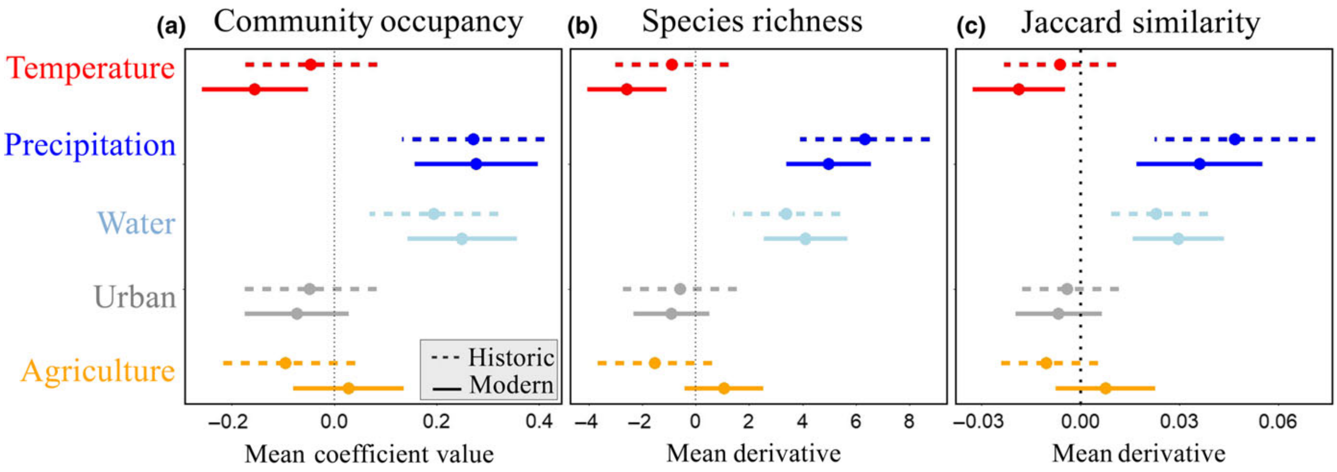

FIGURE 5 Effects of climate and habitat covariates on (a) community-level avian occupancy, (b) site-level species richness, and (c) Jaccard similarity between sites (c) in the historic (dashed) and modern (solid) survey periods. Lines represent 95% credible intervals. Panel (a) shows the community hyperdistribution (mean coefficient values of all species) from the occupancy model output. Panels (b) and (c) show the derivative at mean value for the effect of each covariate on expected species richness and similarity, approximated by the Monte Carlo method described in text [Colour figure can be viewed at wileyonlinelibrary.com]

availability—precipitation and the percent cover of surface water (Figure 5)—suggesting that the dichotomy between climate and land use as drivers of biodiversity may be an oversimplification.

4.1 | Bird species change driven by habitat preference

Despite site-level changes in climate and land use in California's Central Valley, the majority of species exhibited stable or increasing occupancy over the past century (Figure 2). Unsurprisingly, occupancy increased the most for exotic species that have become well established in California since the historic surveys, including the EUCD, EUST, and ROPI. Another top expander, the wild turkey, was purposefully introduced to California by the Department of Fish and Game several times throughout the 1900s (Gardner, Blankinship, & Decker, 2004). However, we also found large increases in occupancy of several native North American bird species that are known to favor human-modified habitats, including ANHU (Greig, Wood, & Bonter, 2017), CORA (Kristan & Boarman, 2007), BHCO (Rothstein, Verner, & Stevens, 1980), and great-tailed grackle (Wehtje, 2003). Overall, increases in occupancy predominantly occurred in species with a generalist or developed habitat association (Figure 3).

Large decreases in occupancy occurred for several bird species with well-documented population declines within and beyond California, including the AMKE (Smallwood et al., 2009) and BUOW (Klute et al., 2003). Other top decliners were predominantly species with relatively specialized habitat preferences, including scrub-specialists such as the California thrasher, wetland specialists such as the common yellowthroat, and open habitat specialists such as LOSH, TUVU, lark sparrow, and WEME. Species that were fairly common during the historic survey period but completely or nearly absent during modern surveys included the state endangered Bell's vireo and several Species of Special Concern, such as the yellow-breasted chat (California Department of Fish & Wildlife, Natural Diversity Database 2017). The yellow-billed magpie, one of California's two endemic bird species, showed no change in occupancy, though the extremely low probability of occupancy in both survey periods (~0.02) should be taken into account before comparing this result to apparent population declines documented by other studies (Crosbie, Souza, & Ernest, 2014).

4.2 | Community stability and the absence of biotic homogenization in response to a century of climate and land-use change

At the community level, we found no significant change in average occupancy (Figure 2) or in species richness per site (Figure 4a). This result contradicts expectations that occupancy and richness should decrease at sites experiencing anthropogenic land-use and climate change (Distler et al., 2015; McKinney, 2002; Newbold et al., 2015; Wiens, Stralberg, Jongsomjit, Howell, & Snyder, 2009). We were also surprised to find that the Central Valley had a greater proportion of species with significant increases in occupancy (29%) compared to similar resurvey efforts in far less modified regions of the California Sierra Nevada (7%; Tingley et al., 2012) and the Mojave desert (3%; Iknayan & Beissinger, 2018). The Central Valley also had proportionally fewer species with significant decreases (22%) than the Mojave Desert (29%). This counterintuitive pattern of stable or increased site-level species richness has been documented elsewhere (Dornelas et al., 2014; Sax & Gaines, 2003) but is unusual for a study region like ours that has undergone dramatic increases in urbanization and agriculture during the century between our surveys (Cardinale, 2011; Frishkoff et al., 2016; Karp et al., 2017; Karp, Ziv, Zook, Ehrlich, & Daily, 2011).

Despite the increasing prevalence of generalists and human adapters in the Central Valley since Grinnell conducted surveys, Jaccard similarity changed little between the historic and modern survey periods (Figure 4b). This result contradicts the expectation that climate and land-use change should result in biotic homogenization over time (Bonebrake et al., 2016; Frishkoff et al., 2016; Ibáñez-Álamo et al., 2017; Karp et al., 2012; McKinney, 2002). It is encouraging that avian diversity has persisted over the past century in one of the most heavily modified landscapes on the planet (Galloway & Riley, 1999). We suspect that bird communities are being maintained by the stark contrast between the agricultural matrix and preserved riparian corridors (McKinney, Raposa, & Cournoyer, 2011), and by human landscape modifications that increase food, such as feeding stations and irrigated landscaping (Beissinger & Osborne, 1982; Marzluff, Bowman, & Donnelly, 2001) in an otherwise arid region. Further research is needed to explore these relationships. It will also be important to determine whether similar stability in occupancy is shared by bird species that were not sampled by our surveys, namely, migrants and wintering waterfowl that are highly dependent on localized habitats undergoing conversion within the valley (Cormier, Gardali, & Wood, 2013; Gilmer et al., 1982).

Species richness at a site may be stable or even increase when generalist and invasive species replace more sensitive species (Kerr, 1997; McKinney, 2002; Prendergast, Quinn, Lawton, Eversham, & Gibbons, 1993). This occurred in the Central Valley over the past century, given the results of our trait analysis (Figure 3) and the identities of our top increasing species (Figure 2b). However, the lack of biotic homogenization in our study is a puzzling result, although it could be related to our choice of diversity metric. While species diversity is a hallmark metric of conservation (Ibáñez-Álamo et al., 2017), recent studies have revealed important effects of land-use change on functional and phylogenetic diversity (Frishkoff, Karp, M'Gonigle, Hadly, & Daily, 2014; Karp et al., 2011; Sol, Bartomeus, González-Lagos, & Pavoine, 2017), and these metrics deserve consideration in future work.

Nevertheless, climate change is expected to produce non-analog communities throughout California and elsewhere (Stralberg et al., 2009; Williams & Jackson, 2007), which could act to counter biotic homogenization. Diversity, however, remained stable within the Central Valley, but the increased prevalence of exotic species could be indicative of homogenization at larger scales (Cardinale, Gonzalez, Allington, & Loreau, 2018). The mean temperature warmed more in the Central Valley over the past century than most other California ecoregions (Rapacciuolo et al., 2014). However, there was little change in maximum temperature or in annual precipitation, although individual sites experienced a range of climate change similar to elsewhere in the state (Rapacciuolo et al., 2014). Caution should be taken before generalizing our results to other regions with different histories of climatic change.

4.3 | Water availability drives occupancy in the Central Valley

Community-level occupancy, richness, and similarity were driven primarily by water availability—precipitation and the percent cover of surface water in the vicinity of the survey sites—in both centuries that we surveyed (Figure 5). We were surprised by the low importance of urban and agricultural cover in structuring avian communities, given the large extent of land-use change in our study area and the strong influence of human habitat association on species-level occupancy changes. These conclusions were unaffected by quantifying land cover covariates at smaller or larger buffer distances, or by the addition of a quadratic term to the detection model (Supporting Information Table S2).

Water availability represents a combination of climate and land-use impacts that affect avian occupancy in the Central Valley, challenging previous findings that climate alone is the primary determinant of bird distributions (Bucklin et al., 2015; Sohl, 2014; Thuiller et al., 2004). Precipitation had the largest influence on avian occupancy in the arid environment of the Central Valley, while temperature had a small influence in the modern survey period (Figure 5). We found little effect on occupancy of the two most commonly analyzed drivers of land use, urban and agricultural cover. However, water cover—an anthropogenic land-use driver influenced by highly-managed canals and reservoirs in the Central Valley—had an influence similar to precipitation. Since the early 1900s, the Central Valley has lost over 1.9 million acres of wetland and gained at least 3.3 million acres of agricultural and urban land (Nelson et al., 2003). This region is naturally hot and arid, and biodiversity was historically associated with riparian corridors and seasonal wetlands (Frayer et al., 1989; Nelson et al., 2003). The link between water and bird communities has persisted despite massive anthropogenic landscape alterations.

Our finding that precipitation and secondarily temperature are more influential to community-level metrics than the extensive agriculture and urban cover in the Central Valley provides evidence for the severe threat posed to future biodiversity by climate change, particularly in a region susceptible to drought. At the same time, anthropogenic habitat modification clearly plays an important role in bird communities of the Central Valley, given the influence of water cover to occupancy, as well as the importance of generalist tendencies and human habitat tolerance to species' level occupancy change. Addition of water to this arid landscape may create anthropogenic refugia that ameliorate the effects of climate change (Morelli et al., 2012, 2016). It will be important to continue to study the combined effects of these drivers on species distributions to better understand how their influence may vary by scale and geographic context.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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