RESEARCH ARTICLE

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Drought influences habitat associations and abundances of birds in California's Central Valley

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Abstract

Aim: As climate change increases the frequency and severity of droughts in many regions, conservation during drought is becoming a major challenge for ecologists. Droughts are multidimensional climate events whose impacts may be moderated by changes in temperature, water availability or food availability, or some combination of these. Simultaneously, other stressors such as extensive anthropogenic landscape modification may synergize with drought. Useful observational models for guiding conservation decision-making during drought require multidimensional, dynamic representations to disentangle possible drought impacts, and consequently, they will require large, highly resolved data sets. In this paper, we develop a two-stage predictive framework for assessing how drought impacts vary with species, habitats and climate pathways.

Location: Central Valley, California, USA.

Methods: We used a two-stage counterfactual analysis combining predictive linear mixed models and N-mixture models to characterize the multidimensional impacts of drought on 66 bird species. We analysed counts from the eBird participatory science data set between 2010 and 2019 and produced species- and habitat-specific estimates of the impact of drought on relative abundance.

Results: We found that while fewer than a quarter (16/66) of species experienced abundance declines during drought, nearly half of all species (27/66) changed their habitat associations during drought. Among species that shifted their habitat associations, the use of natural habitats declined during drought while use of developed habitat and perennial agricultural habitat increased.

Main Conclusions: Our findings suggest that birds take advantage of agricultural and developed land with artificial irrigation and heat-buffering microhabitat structure, such as in orchards or parks, to buffer drought impacts. A working lands approach that promotes biodiversity and mitigates stressors across a human-induced water gradient will be critical for conserving birds during drought.

KEYWORDS
birds, citizen science, climate change, drought, N-mixture model, relative abundance

1 | INTRODUCTION

The frequency of hot, dry periods constituting ecological drought is increasing in many parts of the globe (Crausbay et al., 2017, 2020; Dai, 2013; Diffenbaugh et al., 2015; Vicente-Serrano et al., 2020). Conservation management during drought requires careful study, as ecological impacts are multifaceted and species- and habitat-specific. Reduced precipitation during drought can impact wildlife directly through water stress-induced mortality or indirectly by altering the availability of food resources (Cahill et al., 2013). When high temperatures and dry periods occur simultaneously, synergistic impacts occur, especially increased cooling costs in the form of higher water or food requirements (Cahill et al., 2013; Kearney et al., 2009; Mantyka-Pringle et al., 2012; Riddell et al., 2019, 2022). Ultimately, a species' vulnerability to drought is a combination of its level of exposure (the degree to which regional climatic change is experienced by individuals of the species) and its sensitivity (the degree to which a species' abundance changes per unit change in exposure to drought) (Williams et al., 2008).

Previous studies have established that extreme drought can have a major impact on bird abundance (Albright et al., 2010a, 2010b; Bennett et al., 2015; Mac Nally et al., 2009; Nimmo et al., 2016; Prugh et al., 2018; Selwood et al., 2018). A variety of mechanisms explaining which species decline, and where, have been investigated in isolation and in tandem. Certain habitats, especially natural ones, have been shown to promote species resilience via increased availability of food or microhabitat (Bennett et al., 2015; George et al., 1992; Jackson et al., 2016; Nimmo et al., 2016; Riddell et al., 2022). Likewise, species traits may influence drought sensitivity. Birds' cooling costs correlate with body mass, so larger-bodied birds may be more sensitive to water deficits (Riddell et al., 2019); on the other hand, smaller-bodied birds experience greater relative evaporative water loss, so extreme heat might more strongly impact smaller species (Albright et al., 2017). Trophic niche may determine sensitivity to indirect effects of drought, as the availability of food in response to drought changes differently in different habitats for herbivores and carnivores (Prugh et al., 2018). Resource pressure may lead to density-dependent relationships between drought and bird abundance (Cady et al., 2019; Prugh et al., 2018). Behavioural plasticity and mobility may play a role in structuring sensitivity; for example, migratory species may have greater spatial flexibility in choosing breeding sites but may be more phenologically restricted (Furnas & McGrann, 2018; McGrann & Furnas, 2016). The timing of drought events in relation to the breeding season may moderate which species are more exposed (Riggio et al., 2023). Species with more suitable habitat may also be better equipped to seek out new territory during drought.

Habitat composition and structure both moderate the extent to which birds are affected by climatic extremes. The availability of resources, including water, varies differently during drought in different habitats within a region, and diversity in habitat structure can allow animals to moderate exposure to extreme heat by using microclimates. The role of human-modified habitat in moderating species' exposure to drought is especially difficult to predict. Human modification and temperature increases are likely to interact in their impacts on species. Human-modified habitats tend be more open with less microhabitat complexity, leading to more thermal variation. As a result, species may be more sensitive to climate extremes, including drought, in human-dominated landscapes (Lauck et al., 2023). Evidence suggests that human-modified habitat tends to support species that are further from their thermal limits (Williams & Newbold, 2020). Agricultural lands support smaller populations than natural lands, especially during hot periods, and especially for less drought-tolerant species (Hendershot et al., 2020; Williams & Newbold, 2020, 2021). Species that are more sensitive to drought may become more vulnerable to habitat degradation as the availability of natural lands decreases (Travis, 2003). On the other hand, human activity may buffer smaller-scale climate impacts on heavily used lands by providing artificial sources of water in agricultural and domestic settings. Understanding how species respond to drought in heavily modified landscapes requires a holistic modelling framework that considers interacting effects of habitat type and drought.

In this paper, we investigated the impact of droughts on birds' abundances and their relative use of different habitats in the Central Valley ecoregion in California, USA. Like much of western North America, this region has experienced a number of severe droughts in recent decades (Diffenbaugh et al., 2015) and contains a wide variety of human-modified and natural habitats, making it a relevant study system. We characterized changes in counts of 66 common Central Valley birds from 2010 to 2019 reported to the participatory science platform eBird, taking advantage of the density of eBird activity to achieve a high degree of spatiotemporal resolution. Using N-mixture models and linear mixed models, we asked (1) whether each of 66 species' overall abundance changed with drought severity, and whether those overall changes were related to species traits; (2) whether the effect of drought on each species varied meaningfully between habitat types; and (3) which individual climate or environmental variables were responsible for overall species abundance changes during drought.

2 | METHODOLOGY

2.1 | Study region

Comprising the Sacramento Valley in the north and the San Joaquin valley in the south, the Central Valley is a predominantly developed and agricultural system with remnant riparian and natural grassland habitat. Despite the relative lack of unmodified habitat, the Valley serves as an important breeding habitat for many birds and a migratory habitat for more (DeLuca et al., 2021). Climate change is expected to increase the frequency of extreme droughts in California as the probability of co-occurring dry and warm periods increases (Diffenbaugh et al., 2015), so understanding birds' responses to drought in this area is crucial for their conservation. This region has a high density of eBird sampling activity spread across a variety of habitats and climatic conditions. It has experienced multiple periods of severe drought and non-drought in recent years (Figure 1). This
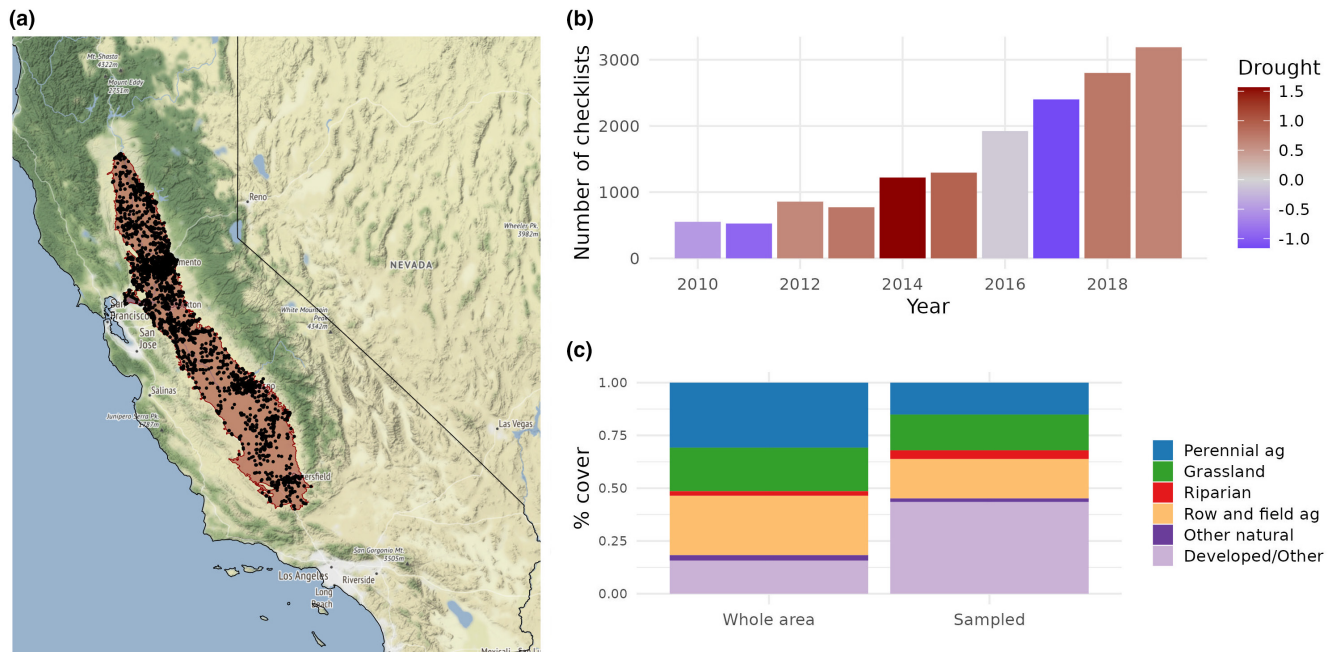
FIGURE 1 (a) Locations of eBird checklists (black points) in the Central Valley ecoregion (red polygon) of California. Checklists were densest near developed areas but distributed throughout the region, with some gaps in the southern Central Valley. (b) Due to increases in eBird activity over time, more recent years were better represented in the data set. Bar colours indicate annual average drought as defined by the standard precipitation-evapotranspiration index where positive values indicate drier conditions and negative values indicate wetter conditions. Our study period comprised two relatively wet periods and two drought periods. (c) Land cover proportions of the entire study region (left bar) compared to the areas sampled in the data (right bar). The developed/other category was overrepresented in the data, comprising 16% of the Central Valley region but 43% of sampled area.

combination of features makes the ecoregion an ideal study area for resolving the effect of drought on species in different habitats and via different mechanisms. To delineate the study area we used the 'Central California Valley' ecoregion as defined by the USGS (Griffith et al., 2016).

2.2 | Bird count and trait data

eBird is a participatory science birding data repository where volunteer observers report checklists comprising counts of bird species detected on discrete sampling occasions (Strimas-Mackey et al., 2020; Sullivan et al., 2009, 2014). Reported counts from eBird have been used in the past in the Central Valley to inform conservation planning (Golet et al., 2018; Reynolds et al., 2017) and assess species status (Robinson et al., 2020). eBird data are semi-structured, meaning that most checklists are associated with sampling metadata describing effort. Checklists may also be tagged as 'complete' (meaning all detected birds were reported, and any non-reported bird was not observed). These two features make it possible to model eBird counts while partially controlling for sampling variation. However, eBird data also contain heterogeneity, especially heterogeneity in area sampled, that precludes inferring absolute abundance from these data (Goldstein & de Valpine, 2022). We therefore focus our interpretations on relative abundance while accounting for variation in detection, rather than the absolute abundance of birds.

We analysed eBird checklists in the Central Valley region in California, USA (Figure 1a). We extracted all eBird complete checklist data for observations that took place in California's Central Valley in the years 2010–2019 during the months of April, May and June. This date range was selected as a rough approximation of the breeding season in this region. From each checklist, we retrieved the following metadata: date of year, time of day, duration of sampling event and number of observers in the observation group. Any checklist missing one or more of these metadata was excluded. We also excluded checklists other than those that followed the 'stationary sampling' protocol, which specifies that all birds were detected from a single point in space, and excluded any checklists with a recorded duration of more than 3 hours or with more than eight observers to minimize unmodeled heterogeneity and spatial error in the data (Johnston et al., 2021). Of 73,853 eBird checklists conducted in the Central Valley during the study period, 15,522 eBird checklists met all quality criteria and were admitted to analysis. Because each checklist included was 'complete', each was associated with either a count or a nondetection (count of 0) for all species, meaning that all single-species models were fit to observations from all checklists. We chose to model 66 species that were detected on at least 500 (or 3%) of admitted eBird checklists (Table S1).

For each species, we retrieved its trophic niche (i.e., diet category) and whether or not it is migratory from AVONET (Tobias et al., 2022). We also retrieved each species' taxonomic order and grouped species into two groups for comparison (Passerines and non-Passerines).

2.3 | Landscape covariate data

Observations were assigned to spatiotemporal cell-year units according to a grid of $1\,km \times 1\,km \times 1\,year$ covering the Central Valley ecoregion over the period 2010–2019. A spatial resolution of 1 km was chosen to maximize resolution while allowing eBird checklists conducted very nearby one another to be associated. Checklists were distributed across a total of 4821 cell-years each containing between 1 and 190 checklists (mean = 3.2 checklists; median = 1 checklist; 90th quantile = 5 checklists; 95th quantile = 10 checklists.).

For each cell, habitat covariates were produced representing the proportion of each cell covered by each of six habitat types. Crop types were retrieved from the California Statewide Crop Mapping data set for 2018. At the time this work was initiated, only cropping data for 2016 and 2018 were available, so we opted to use the 2018 data set only under the expectation that aggregated land use categories at the 1-km scale were constant during the study period (Of Water Resources, C. D, 2020). Gaps in the Statewide Crop Mapping data set were filled in with land cover data from the Functional Vegetation LANDFIRE data set (LANDFIRE, 2020). Land cover classes were aggregated into six categories: row and field crops, perennial crops, grassland and pasture, natural riparian habitat, other natural and semi-natural habitat and developed/other. The 'developed/other' category comprised 91.4% urban habitat.

We retrieved four environmental variables of interest in each grid cell: temperature, precipitation, the normalized differential water index (NDWI) and the enhanced vegetation index (EVI). We retrieved daily precipitation and temperature data from the PRISM climate group (Hart & Bell, 2015). We computed the average maximum daily temperature in the sampling period April–June in each cell-year and calculated the amount of precipitation in the preceding year (July of the previous year through June of the sampling year). We retrieved EVI, an index of vegetative productivity (Justice et al., 1998; Vermote & Wolfe, 2023), at 500 m daily resolution and NDWI, a measure of the amount of standing water in an area (USGS, 2022), at 30 m bi-weekly resolution. For both EVI and NDWI, we computed averages within each cell-year during the months April–June.

We used the standardized precipitation-evapotranspiration index (SPEI) as a continuous measure of drought severity. SPEI represents the effects of both water availability and evaporative demand and is calculated based on remotely sensed temperature and precipitation (Beguería et al., 2010). The standardized precipitation-evapotranspiration index has been used in previous studies of birds to quantify drought (Cady et al., 2019; Iknayan & Beissinger, 2018). We obtained monthly measures of SPEI from the global SPEI database at 1° resolution (roughly 85 km in central California), which are derived from monthly temperature and precipitation averages at that scale (Beguería, 2022). We interpret SPEI as a regional measure of drought. For each cell-year, we extracted SPEI on April 1, the beginning of the sampling period for that year. However, we do not use multiple measures of preceding drought or an average over the previous period to avoid making an assumption about the duration of drought impacts. We investigate potential longer-term and lagged

effects separately (see section 'N-mixture models for bird counts'). The standardized precipitation-evapotranspiration index is parameterized such that lower SPEI indicates drier conditions, so a positive effect of SPEI on occupancy means a negative effect of drought on occupancy. We selected two levels of SPEI to represent a typical wet year and a typical extremely dry year in this system based on the lowest and highest median annual SPEI (in 2014 and 2017, respectively). These two representative levels were used to predict environmental conditions and bird abundance in a characteristic drought and non-drought year.

2.4 | Predicting bird abundance in drought and non-drought conditions

2.4.1 | Overview of two-stage model framework

Our primary objective was to understand how the abundance of 66 Central Valley bird species changed between non-drought and drought conditions, which we accomplished with a novel two-stage model framework (Figure 2). To estimate how bird counts varied with various habitat and environmental covariates we developed single-species N-mixture models (Dénes et al., 2015). Rather than including a single drought index, we estimated the effects of four environmental variables that collectively represent the local conditions hypothesized to influence bird abundance. This allowed us to differentiate between correlated but distinct pathways of drought impacts, and to estimate complexity in these relationships in the form of habitat–environment interactions. In the imperfect detection submodel, we accounted for variation in eBird sampling, non-independence between checklists, and overdispersion in the data.

Generating predictions under drought and non-drought conditions required selecting representative levels of each environmental variable in each grid cell. To choose these representative levels, we developed a set of linear mixed models to explore the relationship between overall drought (as represented by SPEI) and each variable in each habitat type. From these models, we predicted site-specific environmental conditions under representative levels of SPEI. We then used these predicted distributions as inputs to predict from N-mixture models of bird counts, propagating uncertainty. Ultimately, this method yielded predictions of bird abundance corresponding to specific drought levels while accommodating the multidimensionality of drought events. We interpret these predictions to ask how birds' abundances changed overall during drought (Q1), how their relative habitat use changed (Q2), and whether abundance changes were attributable to particular dimensions of drought (Q3).

2.4.2 | N-mixture models for bird counts

We analysed eBird reported counts using single-species N-mixture models (Royle, 2004). Since N-mixture models are somewhat sensitive to unmodeled variation in counts (Link et al., 2018), and since
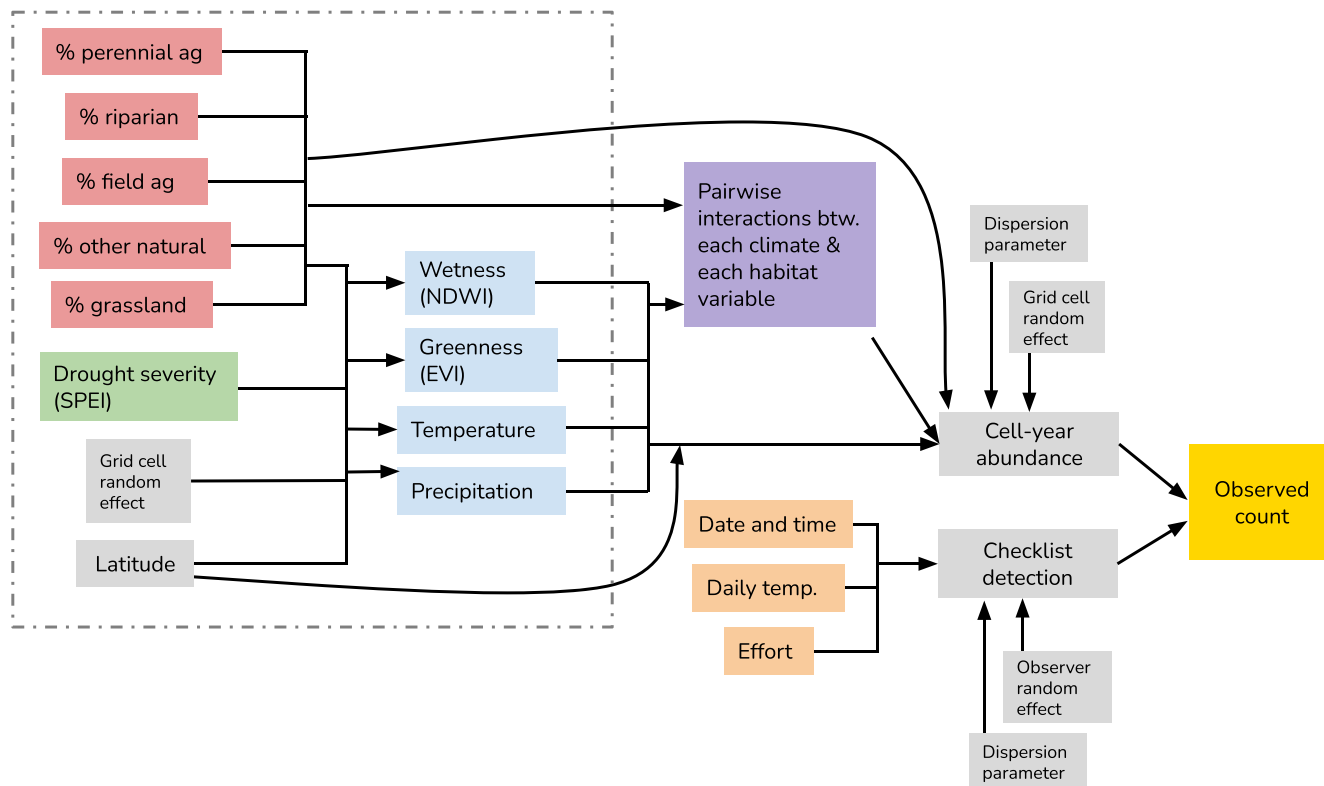
FIGURE 2 A conceptual diagram illustrating relationships between variables in the model. Linear mixed models (LMMs), delineated by the dotted grey box, were used to explore how four environmental variables (NDWI, EVI, maximum temperature, annual precipitation) changed with change in a drought index differently in different habitat types. Posterior predictions of the four environmental variables under drought and non-drought conditions were generated with linear mixed models. N-mixture models were used to estimate the effect of covariates on eBird counts, and included two random effects and two layers of possible overdispersion. Posterior predictions of environmental variables from LMMs were then used as input data to predict posterior distributions of bird counts under drought and non-drought conditions.

eBird data are sampled heterogeneously, we accounted for two layers of potential overdispersion with a beta-binomial detection submodel and a negative binomial abundance submodel and included two types of random effects. The N-mixture models were defined as

$$y_{ijt} \mid N_{it} \sim \text{BetaBinomial}\left(N_{it}, p_{ijt}, \theta_1\right)$$
$$N_{it} \sim \text{NegativeBinomial}\left(\lambda_{it}, \theta_2\right)$$
$$logit\left(p_{ijt}\right) = \mathbf{x}_{ijt}\boldsymbol{\beta} + \alpha_{o(ijt)}$$
$$\log\left(\lambda_{it}\right) = \mathbf{w}_{it}\boldsymbol{\Upsilon} + \alpha_i$$
$$\alpha_{o(ijt)} \sim \mathcal{N}\left(0, \sigma_{\alpha_o}\right)$$
$$\alpha_i \sim \mathcal{N}\left(0, \sigma_{\alpha_i}\right)$$

The datum y_{ijt} is the observed count of the species for the jth checklist submitted in grid cell i and year t. These counts follow a beta-binomial distribution with size N_{it}, a cell-year-level latent variable representing the expected count under perfect detection; probability p_{ijt}, the detection probability of each individual on the jth observation event at grid cell i, year t; and overdispersion parameter θ_1 to account for extra-binomial variation in counts within a cell-year due to unobserved heterogeneity. N_{it} follows a negative binomial distribution with expected value λ_{it} representing the mean abundance in grid cell i in year t and overdispersion parameter θ_2 representing extra-Poisson variation in underlying counts across

cell-years (parameterized such that the variance of the negative binomial distribution is $\lambda_{it} + \theta_2 \lambda_{it}^2$). The values λ_{it} and p_{ijt} are log- and logit-linear functions of checklist-level and cell-year-level covariates $\mathbf{x}_{ijt}$ and $\mathbf{w}_{it}$, respectively, with corresponding coefficient vectors $\boldsymbol{\beta}$ and $\boldsymbol{\Upsilon}$. We include a random effect of grid cell, α_i, on abundance to account for potential nonindependence between counts in each grid cell in different years. A random effect of observer (grouping checklists submitted by the same eBird user), $\alpha_{o(ijt)}$, on detection is also included, where $o(ijt)$ gives the observer ID for the jth checklist submitted in grid cell i and year t. Each of the random effects is normally distributed with standard deviation parameters σ_{α_i} and σ_{α_o}.

The following checklist-level covariates were included in the detection submodel (as $\mathbf{x}_{ijt}$) to account for variation in effort and detectability: sampling duration, time of day, time of day squared, day of year, day of year squared and number of observers in group. Maximum daily temperature as retrieved from PRISM was also included because birds vocalize differently depending on temperature (McGrann & Furnas, 2016).

Ten cell-year-level covariates were included in the abundance submodel (as $\mathbf{w}_{it}$): latitude; categorical effect of year (nine levels); habitat type percentages (0–1 values for each of perennial agriculture, row and field agriculture, grassland, riparian, and other natural habitat); and four continuous environmental variables (EVI, NDWI,

average daily temperature, and annual precipitation). We also included 20 pairwise interactions between each habitat variable and each climate variable and an interaction between wetness (NDWI) and average daily maximum temperature. We identified collinearity between EVI and NDWI (correlation of 0.74) and between some EVI and NDWI interaction terms (3 of 5 pairs EVI and NDWI interaction terms showed correlation >0.7). In the context of the Bayesian posterior predictive method used throughout, we judged that collinearity between variables would not inhibit predicting changes in overall abundance, so we retained both EVI and NDWI in the model. A model with explicit spatiotemporal dynamics, allowing for density-dependent abundance changes, was beyond the scope of our study for a few reasons. Separating demography from movement is not feasible with eBird data, 10 years is a short period for estimating time series effects, and such a model would introduce computational challenges. We therefore limited our approach to predicting bird abundances under drought and non-drought conditions based on simple year-to-year differences.

eBird data arise from a nonrandom sampling process driven by observer behaviour (Johnston et al., 2021). We attempt to mitigate bias in estimates of drought effects via model-based inference, explicitly modelling variation in the sampling process (Cressie et al., 2009). By including observer-level random effects to accommodate differences in sampling as the observer pool turns over (Johnston et al., 2022), as well as site-level random effects on abundance, and a number of meaningful effort and habitat covariates, we are able to estimate the effects of drought and habitat on abundance in the presence of heterogeneous sampling. In addition to model-based inference approaches, we apply data filtering to standardize the checklists modelled. By only including stationary point counts, we eliminate the possibility that birders track birds while conducting their checklists. Bias in estimated drought impacts may still arise if eBird observers choose sites with higher counts of birds within grid cells in a way that is drought-correlated (i.e., if eBird observers seek out bird-rich microsites during non-drought periods, but do not exhibit this preferential sampling during droughts) and if this behaviour is not represented in effort metadata or observer identity. An interaction between drought and observer behaviour is impossible to check with the data. However, we believe that the many steps taken to mitigate the impact of unmeasured variation, including data filtering, multiple measures of effort, and random effects, have minimized the impact of observer behaviour on the results we report.

All covariates in both submodels were centered and scaled.

We expected that drought impacts on abundance would coincide with the drought events themselves. Since it is possible that ecological drought leads to worse breeding outcomes and reduced populations after the drought event has concluded, the impact of drought on abundance may occur on a delay. To test whether predicted changes in abundance were robust to the choice to use year-of environmental variables, we replicated the N-mixture modelling and posterior predictive steps for all species with one year lags for the drought index and four drought-related environmental variables (see Supplemental Materials for full details).

We implemented single-species N-mixture models in NIMBLE v0.12.2 (De Valpine et al., 2017). We chose all priors to be minimally informative on their relevant scales (Northrup & Gerber, 2018). For the detection intercept β_0, we used a logistic prior. For all other coefficients in **b** and **g**, we used normal priors with mean 0 and standard deviation 2.25. For both random effect standard deviation priors, we used uniform distributions from 0.001 to 10. For priors on beta-binomial and negative binomial overdisperion parameters, we used uniform distributions from 0.0001 to 25. Models were estimated with MCMC using custom sampler assignments for improved mixing. For each species, we ran three chains of 15,000 iterations with 5000 iterations of burn-in and a thinning interval of 10. We checked whether each model had a minimum effective sample size of 100 for all stochastic parameters, and ran additional chains for each species until this condition was met.

2.4.3 | Linear mixed models of environmental covariates

To predict the impact of drought on each species' abundance, we needed to understand how each of the four drought-related environmental variables (EVI, NDWI, average daily temperature, and annual precipitation) vary between a typical drought and non-drought year, for different habitat types. We assessed how SPEI, an accepted index of drought, predicted several environmental variables in each habitat type, treating SPEI as a predictor variable in the context of the larger model framework. After using SPEI to predict each variable, we could then generate posterior predictions of each environmental variables for a given location in the study area under a typical dry or wet year.

We used explanatory linear mixed models (LMMs) to estimate how each of the four climate covariates varied with SPEI. For a given climate variable $_C$, we fit LMMs defined by the equations

$$C_{it} \sim \mathcal{N}\left(\mu_{it}, \sigma_\epsilon\right)$$
$$\mu_{it} = \beta_0 + x_{it}\beta_c + \alpha_i$$
$$\alpha_i \sim \mathcal{N}\left(0, \sigma_\alpha\right)$$

where the value of the climate variable at cell i in year t, C_{it}, was normally distributed with mean μ_{it} and residual variation σ_ϵ. The mean climate variable at each cell-year μ_{it} was a linear combination of covariates x_{it} with coefficients β_c. Covariates included were SPEI, five habitat types (as in N-mixture models), and interactions between SPEI and each habitat type. We included a normally distributed additive random effect of grid cell, α_i. All covariates were centered and scaled. Data for the years 2010–2019 for all 2566 grid cells containing eBird data were included.

Linear mixed models were estimated with the R package 'brms' (Bürkner, 2017). We used normal priors with mean 0 and standard deviation 5 for all β covariates, and half-Cauchy priors with scale parameter 2 for the prior on σ_α. We ran three chains of 15,000 iterations with 5000 iterations of burn-in. We then obtained posterior

predictions of each climate variable at each cell-year in the study area using actual habitat values and the two reference levels of SPEI, representing a distribution of potential climate conditions under drought and non-drought scenarios.

Parameter estimates from linear mixed models are presented and interpreted in the Supplemental Materials.

2.4.4 | Question 1: Do species' overall counts change with drought?

We combined the N-mixture models and LMMs in a joint posterior predictive framework to estimate changes in bird counts during drought (Figure 2). Using predicted levels of environmental variables from LMMs and posterior samples of abundance coefficients from single-species N-mixture models, we computed an expected abundance λ_i for each species at each cell-year in each MCMC iteration. We drew random negative binomial counts using these expected abundances and draws of the overdispersion parameter, θ_2, ultimately yielding posterior predictive distributions of underlying counts of each species in both drought and non-drought conditions. To evaluate whether each species declined or increased during drought, we predicted the difference in overall count (summed across cell-years) between representative drought and non-drought conditions at each iteration for each species. If the 95% credible interval of this distribution did not overlap zero, we interpreted this as evidence that the species had either a positive or negative association between drought and reported counts. We used chi-squared tests to ask whether changes in species counts were associated with trophic niche, whether or not a species is migratory, and taxonomic group (comparing Passerines and non-Passerines). We corrected p-values obtained from chi-squared tests across both Question 1 and Question 2 by controlling the false discovery rate (Benjamini & Hochberg, 1995).

2.4.5 | Question 2: Do species' habitat associations change during drought?

Whether species' habitat associations—their predicted relative abundance in each habitat type—varied between drought and non-drought conditions was a major question of this study. In a linear modelling context, the question 'does the effect of covariate 1 on the response variable change with the level of covariate 2?' can be represented by including an interaction term and testing whether that term is different from zero. In the two-stage model presented above, we estimate an interaction effect of drought and habitat on the four climate variables and an interaction effect of those climate variables with habitat on bird counts. This structure creates multiple pathways through the model by which both habitat and drought can influence abundance and multiple opportunities for interaction effects to occur (Figure 2). This means that a simple interaction term is not estimated. However, we can use partial derivatives to analytically derive the quantity the interaction term represents—the rate of change of the effect of covariate 1 on the

response variable with respect to covariate 2—in our two-stage model. We estimate an interaction between drought and each habitat type term for each species. This interaction represents how the effect of drought on species' abundances varied across habitat types. Because habitat composition is represented as the percent of each of six habitat types, we can calculate six such interaction terms for each species, one per habitat. We computed posterior predictive distributions of the derived interaction terms for each species-habitat type combination. If the 95% CI of the posterior distribution of the interaction term between drought and one or more habitat variable did not overlap zero, we interpreted that as evidence that the species shifted its overall use of habitat types during drought.

Please see the Supplemental Materials Section S1 for an in-depth discussion of this method. A posteriori, we developed a summary generalized linear model to characterize whether species' tolerance for developed habitat in non-drought periods explained habitat shifts, which we present in Supplemental Materials Section S6.

2.4.6 | Question 3: Are species' changes with drought attributable to changes in environmental variables?

To estimate the effect of each climate variable's change during drought on the count of each species, we adapted the counterfactual count generation workflow. To understand the impact of each climate variable in isolation, we instead predicted counterfactual counts with only one climate variable drawn from predictions in drought conditions, while the others were predicted in non-drought conditions. By comparing these new count distributions with counts under non-drought conditions, we were able to identify the amount of change in each species' abundance attributable to change in each climate variable. We refer to these tests as 'one-variable counterfactual scenarios'.

If the 95% credible interval of the difference in predicted count between each one-variable counterfactual scenario and the non-drought baseline scenario did not overlap zero, we interpreted this as evidence of that variable's importance in driving the species' overall abundance during drought.

Figures 1, 3, and 4 were created using the R packages ggplot2 v3.3.6, ggtern, and urbnmapr (Hamilton & Ferry, 2018; Strochak et al., 2022; Wickham, 2016). MCMC samples were processed using the package MCMCvis (Youngflesh, 2018).

3 | RESULTS

3.1 | Summary of eBird coverage

More recent years are represented by more checklists in the data than years further into the past, mirroring trends in eBird usage overall (Sullivan et al., 2014) (Figure 1). This weakens our ability to identify trends in time relative to early (low-information) years, but recent years contain both wet and dry conditions, so inference on drought effects should be robust to this pattern. Coverage of habitat

types was comparable to the distribution of habitat types across the landscape, with the major exception that developed habitats were strongly overrepresented. We explicitly estimate habitat-specific abundances and drought effects on bird abundance using covariates at various points in the model, so we do not assume that sampling across habitat types is representative. However, this oversampling could mean that the effect of developed habitat types on species abundance may be better informed than that of other habitat types.

3.2 | Do species' overall counts vary during drought?

We estimated posterior distributions of the change in overall abundance of each of 66 bird species between drought and non-drought conditions. Of these, 22 species had 95% credible intervals of change in abundance that did not overlap zero. We infer that counts of six species increased during drought, while counts of 16 species decreased (Figure 3).

Chi-squared tests indicated that there was no evidence of associations between species traits (i.e., foraging guild and body size) or taxonomic group (Passerines vs. non-Passerines) and whether the species' overall abundance changed during drought (see Figure S2).

To test whether year-of drought effects were appropriate, we replicated the models including drought variables on a one-year lag (Supplementary Materials S1). Results of these models were nearly identical to results produced by the main year-of models (see Figure S5). Under these models, 15 species decreased and five increased their overall abundance, with all but two species effects being the same direction as in the primary models. This suggested that the choice to use year-of models did not obfuscate a lagged

effect of drought, and we proceed with interpreting year-of model results.

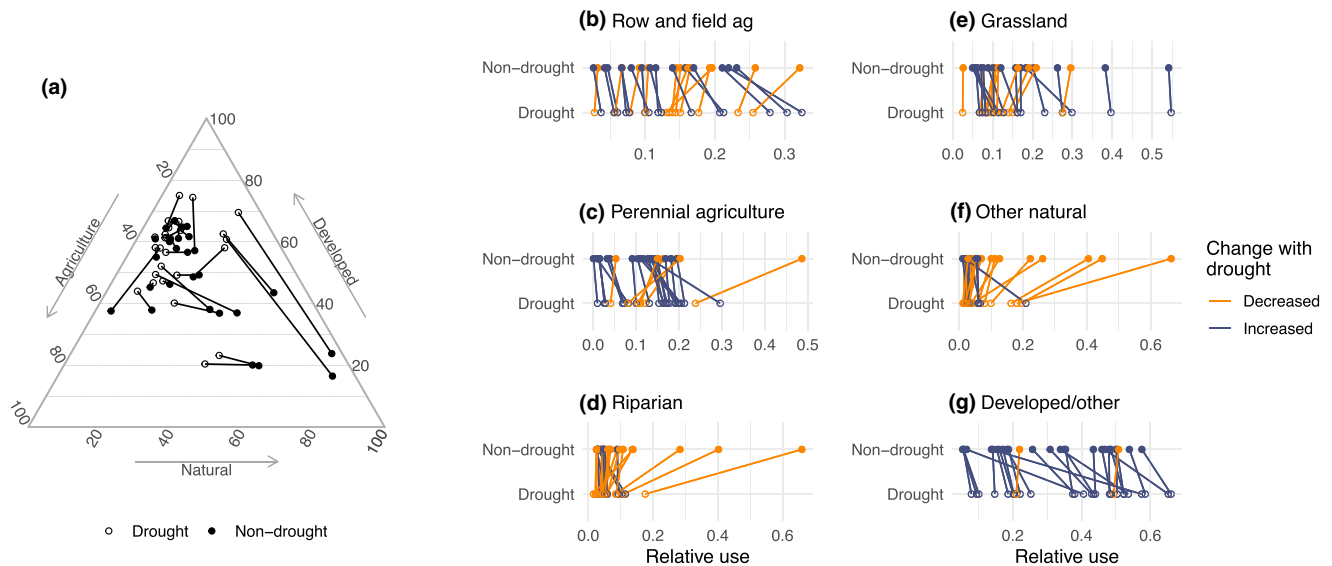## 3.3 | Do species' habitat associations change during drought?

We estimated posterior distributions of interaction terms representing how abundance changed differently for each species in each of five habitats during drought. Across 66 species, 27 species had one or more credibly nonzero interaction terms. We infer that associations between counts of those species and habitat type changed with drought level, suggesting that species used habitat types in different proportion during drought. We did not identify patterns in habitat shifts with taxonomy or any functional traits. We provide a table indicating which species were associated with statistically clear habitat shifts in the Supplemental Materials (Table S6).

To characterize multispecies patterns in habitat–drought relationships, we visualize how the proportion of each species in each habitat shifts between drought and non-drought conditions (Figure 4). Across the 27 species with habitat shifts, chi-squared tests indicated that birds were more likely to increase than decline in developed habitat (25/27 species increased use; adjusted p-value < 0.001) and in perennial agricultural habitat (21/27 species increased use; adjusted p-value < 0.05). Relative increases in use of perennial agriculture and developed habitats were offset by decreases in the other four habitat types. More species declined than increased use of riparian habitat (19/27 decreased) and other natural habitat (17/27 decreased), but chi-squared tests did not indicate that these patterns were statistically different from an even
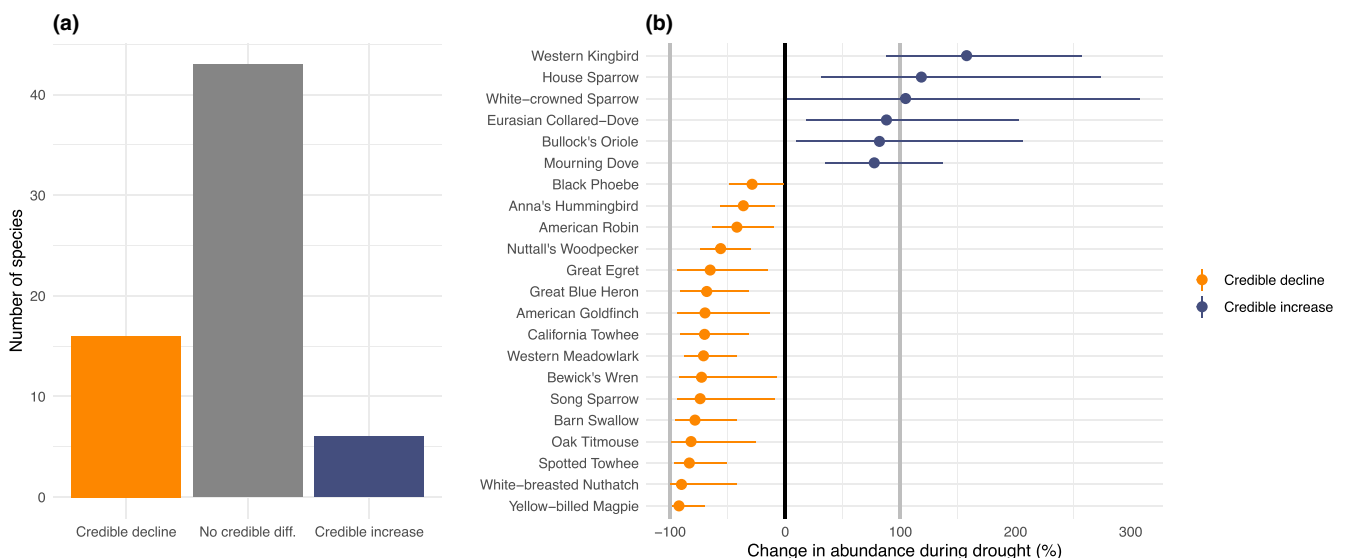
FIGURE 3 Summary of shifts in overall abundance by species. (a) Counts indicating the rate at which species decreased, increased, or showed no relationship between overall abundance and drought. 16 species declined in abundance with drought, 6 increased, and the remaining 44 species showed no relationship between overall abundance and drought. (b) Percent change in abundance with 95% credible intervals for 22 species with credibly nonzero relationships between overall abundance and drought. See Figure S1 for a plot including species for which we detected no overall change in abundance.

FIGURE 4 Visualizing how 27 species shifted their habitat associations during drought. Only the 27 species that credibly shifted their distributions are shown; the 39 species that did not change their relative use of habitat with drought are excluded. (a) A ternary plot shows how species shift in three-dimensional habitat space. Each point pair represents one species for which a habitat shift was estimated. Habitats have been aggregated into three categories: agriculture (combining perennial and row/field agriculture), natural (riparian, grassland, and other natural) and developed. Species overall show shifts away from natural habitat and toward developed and agricultural habitat during drought (moving from filled to empty circles, species largely shift up and to the right). (b–g) The shift in use of each species in each habitat. Colours indicate whether each species' median posterior predicted proportional use increased or declined in the drought condition. We identify a pattern of increase agriculture and developed habitat, while species declined at the greatest rate in riparian and other natural habitats. Both plots visualize median posterior predicted proportional habitat use.

pattern of increases and decreases after controlling for false detection. Grassland and row and field agricultural habitats also showed a roughly even mix of increases and declines in use (11/27 and 12/27 species declined, respectively).

Chi-squared tests indicated that there was no evidence of associations between species traits or taxonomic group (Passerines vs. non-Passerines) and whether the species changed its relative use of habitat types during drought (see Figure S3).

Finally, we investigated the possibility that species already affiliated with human-modified habitats were more likely to shift their habitat affiliations to increasingly utilize developed areas and perennial agriculture during drought. We did not find an association between species' non-drought use of developed habitat and the probability of habitat shifts (see Supplemental Section S5). We note that this null result does not represent evidence that such a relationship does not exist, as it may be the result of limited power arising from the relatively small number of species (66) and the many sources of uncertainty in eBird data.

3.4 | Are species' changes with drought attributable to changes in environmental variables?

Among 16 species that exhibited an overall decline during drought, seven declined in a temperature-only one-variable counterfactual scenario, and two species declined in a precipitation-only counterfactual scenario (see Figure S4). Among five species that increased

overall during drought, three species increased in a temperature-only and three species increased in a precipitation-only drought counterfactual; one species with an overall increase declined in the precipitation-only scenario. Additionally, we find very low rates of marginal counterfactual difference among species with no overall change (four species of 45). No species declined in EVI-only or NDWI-only counterfactual scenarios, which is explained by the finding in the LMM phase that EVI and NDWI did not vary with drought to a relevant degree.

We chose a posteriori to predict abundance changes under an additional counterfactual scenario where precipitation and temperature were both allowed to vary with drought, but EVI and NDWI were not. Under this scenario, 15 species declined in abundance and five increased, indicating that the combination of change in temperature and precipitation were jointly responsible for nearly all abundance changes predicted by the model.

4 | DISCUSSION

Birds' responses to drought depend on habitat type. Using a novel two-stage modelling framework to analyse eBird data, we provide the strongest evidence to date that changes in the relative importance of habitats may be a more common and immediate consequence of drought than changes in overall abundance. Nearly half of a set of common Central Valley species, including many species whose overall abundances did not change during

drought, changed their relative use of habitats during drought. We also found that the abundance of a moderate number of species declined meaningfully during severe drought, a pattern comparable to that identified in previous research (Mac Nally et al., 2009; Nimmo et al., 2016; Prugh et al., 2018; Selwood et al., 2018). However, the rate of abundance declines was lower across species than the rate of habitat shifts.

In California's Central Valley, birds used human-modified habitat more during periods of drought compared to non-drought periods. This pattern contrasts with research in other systems indicating that natural habitat supports greater biodiversity and promotes resilience during drought (Nimmo et al., 2016). This discrepancy might be explained by the intensity and character of human activity in the region. The Central Valley is dominated by irrigated agricultural land, and the distribution of water between 'environmental' applications (including river flow, wildlife habitat maintenance, and scenic waterways) is highly regulated and varies dramatically between drought and non-drought periods. As an illustration, in one characteristic dry year, 2014, the allocation of water for environmental use was cut to a quarter of its allocation compared to a characteristic wet year, 2006, while the allocation for agriculture actually increased slightly to offset precipitation deficits (Mount & Hanak, 2016). In addition to driving short-term changes in relative abundance, changes in water availability were a major driver of avian community composition change in the Central Valley over the last 100 years, supporting the idea that water is a major factor determining species distributions (MacLean et al., 2018). However, the effect of water availability on bird abundance may be dwarfed by effects of climate change and land use change over longer timescales (Beissinger et al., 2023). Agricultural and developed habitats, which may be less preferable for species in normal climate conditions, experience less change in water availability due to human intervention compared with natural landscapes, which may dry entirely as intermittent streams stop flowing.

Of the 16 species whose overall abundance declined during drought, the yellow-billed magpie experienced the greatest decline. The yellow-billed magpie is a species of conservation concern whose range is restricted almost entirely to the Central Valley. Yellow-billed magpies use developed and perennial agricultural habitats such as orchards, where they take advantage of open foraging habitat in proximity to large nesting trees (Koenig et al., 2023). This species declined with drought and did not shift its use of habitat, in contrast to three other generalist corvids in this study (common raven, American crow, and California scrub-jay) that shifted their use of habitat but did not decline. This difference suggests that habitat plasticity and drought sensitivity are species-specific. For the yellow-billed magpie in particular, we suspect that drought impacts compounded with other drivers of recent population decline in yellow-billed magpies, including habitat loss and West Nile virus, which limited the species' capacity for adaptation and behavioural plasticity. (Crosbie et al., 2008; Koenig et al., 2023).

Predicted abundance declines during drought were similar when considering effects of drought on a one-year lag, suggesting that

the year-of model was appropriate. The rapid response by birds is more consistent with the hypothesis that observed habitat shifts are driven by individuals moving across the landscape as opposed to by habitat-dependent mortality gradients, which would be more evident over longer timescales. While our use of SPEI as a drought index accommodates the possibility that accumulating dryness in the environment is responsible for driving changes in bird distributions, our model is unable to estimate cumulative effects of steady drought on bird populations. Our model ultimately cannot differentiate between animal movement and mortality gradients. Another limitation in this study was the lack of information on annual change in habitat type. Over time, turnover in crop types could lead to longer-term shifts in bird responses. Similarly, future studies could investigate whether annual variation in fallowing on agricultural lands could influence birds' responses. Interestingly, we did not find greenness to be an important influence on bird abundances during drought, suggesting that fallowing may not be an important factor in this system. This may be due to the relatively inelastic demand for water in the region.

We found that nearly half of overall drought-related species declines in this system were attributable to the extreme temperature dimension of drought, and all changes were attributable to a combination of high temperature and low precipitation. Birds' sensitivity to drought is in large part driven by heat stress (Riddell et al., 2019, 2022), and we predicted few species declines when temperatures were normal. The importance of temperature is consistent with the fact that species increased their use of perennial agriculture—fruits, nuts and vineyards that provide year-round shaded microhabitats in the form of vegetative structure—but not row and field crops during drought.

Conserving birds in the Central Valley requires balancing the needs of wildlife with the reality of extensive human modification of the landscape. As extremely high temperatures synergize with water deficits to produce abundance declines among birds, habitats with stable sources of water and sufficient microrefugia may support the persistence of some sensitive species. Our results, which show that species' relative use of developed and perennial agricultural habitat is greater during periods of drought, indicate that birds are likely already buffering some effects of anthropogenic climate change by tracking human-induced gradients in water availability across suitable habitats. Conservation managers can work with this trend by placing a stronger emphasis on conservation in working landscapes during drought (Kremen & Merenlender, 2018). Agricultural and developmental practices that promote biodiversity in the context of human modification, such as crop diversity and remnant natural habitat, could have a greater proportional effect on birds during drought when modified habitats are of greater relative importance (Beillouin et al., 2021; Garibaldi et al., 2021; Rich et al., 2017). However, a conservation paradigm that ties the persistence of birds during extremely hot, dry periods to agricultural and developed land poses potential problems. Increasing human-wildlife interactions can expose birds to additional stressors such as disturbance, noise, and pollution,

which could constitute an ecological trap in which species prefer human-modified habitat despite having worse demographic outcomes there (Robertson & Hutto, 2006). Negative impacts on human systems must also be considered, such as increased consumption of crops by birds, although birds may also predate pests and provide other ecosystem services. A conservation plan that emphasizes working lands in this system should focus on mitigating the impacts of human disturbance on birds and promoting biodiversity on human-dominated habitat during drought.

While this study is a step towards a comprehensive picture of drought impacts on birds, tailored conservation decision-making will require careful observational study of individual systems of interest to clarify the extent to which demographic processes and species movement separately contribute to changes in relative habitat use during drought. We suggest that ecologists emphasize interactions between habitat type and drought in future studies and experimental interventions. eBird data likely contain observer variation, cell variation and overdispersion, all of which we accounted for in the model but which potentially limited our power to detect changes in abundance. Higher statistical power may be achieved via more targeted sampling in future studies. Because this study was restricted to the 66 most commonly detected birds in the Central Valley, our ability to identify impacts on rare species was limited. eBird data may be insufficient for understanding how rare species respond to drought, so ecologists may wish to prioritize targeted monitoring of rare species. We note also that while the N-mixture approach is an effective way to account for between- and within-site variation such as that generated by detection heterogeneity (Royle, 2004), it is possible that additional unmeasured variation in the detection process beyond that accounted for with covariates and random effects can introduce bias in parameter estimates or lead to misattribution of variation. For instance, if eBird observer behaviour differed systematically during periods of extreme temperature (as might occur during drought) beyond what was accounted for by effort covariates and observer-level random effects, we may infer biological relationships from detection-driven variation. We attempted to account for observer behaviour throughout the modelling workflow, but it is possible that some drought-correlated observational effects are present and impossible to disentangle from biological processes.

Our ability to identify changes in bird abundance during drought, and isolate those changes to particular environmental variables and habitat types, depended on the new model framework presented in this manuscript. By hierarchically structuring the impacts of drought and habitat on abundance, we were able to estimate parameters across a complex set of ecological relationships for a large number of species. We propose that joint posterior predictive methodology will be a valuable tool for ecologists and environmental scientists seeking to leverage high-volume data sets to understand such systems.

Shifting habitat associations, more than abundance declines, define birds' responses to drought. Patterns in 10 years of eBird data suggest that species respond rapidly to severe drought, and that individuals are likely able to track gradients of habitat suitability to meet temperature and water needs. This pattern is part of a global trend of increased human-wildlife interaction driven by climate change (Abrahms et al., 2023). When human-induced resource gradients lead species onto agricultural and developed land, conservation managers must be prepared to follow. Conservation planning for such species should adopt a working lands approach that considers species' habitat associations not as fixed properties but as dynamic and climate-dependent (Kremen & Merenlender, 2018).

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ddi.13827.

DATA AVAILABILITY STATEMENT

All data used in this study were obtained from publicly available data sets. Sources for all data sets have been cited in the main manuscript. Code used to process data and conduct analyses is available via Dryad (doi: 10.6078/D1GB02). The code is also available on Github at https://github.com/dochvam/drought_CV_eBird_reproducible.

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REFERENCES

Abrahms, B., Carter, N. H., Clark-Wolf, T. J., Gaynor, K. M., Johansson, E., McInturff, A., Nisi, A. C., Rafiq, K., & West, L. (2023). Climate change as a global amplifier of human–wildlife conflict. *Nature Climate Change*, 13, 224–234.

Albright, T. P., Pidgeon, A. M., Rittenhouse, C. D., Clayton, M. K., Wardlow, B. D., Flather, C. H., Culbert, P. D., & Radeloff, V. C. (2010a). Combined effects of heat waves and droughts on avian communities across the conterminous United States. *Ecosphere*, 1, art12. https://doi.org/10.1890/ES10-00057.1

Albright, T. P., Pidgeon, A. M., Rittenhouse, C. D., Clayton, M. K., Flather, C. H., Culbert, P. D., Wardlow, B. D., & Radeloff, V. C. (2010b). Effects of drought on avian community structure. *Global Change*

Biology, 16, 2158–2170. https://doi.org/10.1111/j.1365-2486.2009.02120.x

Albright, T. P., Mutiibwa, D., Gerson, A. R., Smith, E. K., Talbot, W. A., O'Neill, J. J., McKechnie, A. E., & Wolf, B. O. (2017). Mapping evaporative water loss in desert passerines reveals an expanding threat of lethal dehydration. *Proceedings of the National Academy of Sciences of the United States of America*, 114, 2283–2288. https://doi.org/10.1073/pnas.1613625114

Beguería, S. (2022). *sbegueria/SPEIbase: Version 2.7*. https://doi.org/10.5281/zenodo.5864391

Beguería, S., Vicente-Serrano, S. M., & Angulo-Martínez, M. (2010). A multiscalar global drought dData set: The SPEIbase: A new gridded product for the analysis of drought variability and impacts. En. *Bulletin of the American Meteorological Society*, 91, 1351–1356. https://doi.org/10.1175/2010BAMS2988.1

Beillouin, D., Ben-Ari, T., Malézieux, E., Seufert, V., & Makowski, D. (2021). Positive but variable effects of crop diversification on biodiversity and ecosystem services. *Global Change Biology*, 27, 4697–4710. https://doi.org/10.1111/gcb.15747

Beissinger, S. R., MacLean, S. A., Iknayan, K. J., & de Valpine, P. (2023). Concordant and opposing effects of climate and land-use change on avian assemblages in California's most transformed landscapes. *Science Advances*, 9, eabn0250. https://doi.org/10.1126/sciadv.abn0250

Benjamini, Y., & Hochberg, Y. (1995). Controlling the false discovery rate: A practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society: Series B: Methodological*, 57, 289–300. https://doi.org/10.1111/j.2517-6161.1995.tb02031.x

Bennett, J. M., Clarke, R. H., Horrocks, G. F. B., Thomson, J. R., & Mac Nally, R. (2015). Climate drying amplifies the effects of land-use change and interspecific interactions on birds. *Landscape Ecology*, 30, 2031–2043. https://doi.org/10.1007/s10980-015-0229-x

Bürkner, P.-C. (2017). Brms: An R package for Bayesian multilevel models using Stan. *Journal of Statistical Software*, 80, 1–28.

Cady, S. M., O'Connell, T. J., Loss, S. R., Jaffe, N. E., & Davis, C. A. (2019). Species-specific and temporal scale-dependent responses of birds to drought. En. *Global Change Biology*, 25, 2691–2702. https://doi.org/10.1111/gcb.14668

Cahill, A. E., Aiello-Lammens, M. E., Fisher-Reid, M. C., Hua, X., Karanewsky, C. J., Yeong Ryu, H., Sbeglia, G. C., Spagnolo, F., Waldron, J. B., Warsi, O., & Wiens, J. J. (2013). How does climate change cause extinction? *Proceedings of the Royal Society B: Biological Sciences*, 280, 20121890. https://doi.org/10.1098/rspb.2012.1890

Crausbay, S. D., Betancourt, J., Bradford, J., Cartwright, J., Dennison, W. C., Dunham, J., Enquist, C. A. F., Frazier, A. G., Hall, K. R., Littell, J. S., Luce, C. H., Palmer, R., Ramirez, A. R., Rangwala, I., Thompson, L., Walsh, B. M., & Carter, S. (2020). Unfamiliar territory: Emerging themes for ecological drought research and management. *One Earth*, 3, 337–353. https://doi.org/10.1016/j.oneear.2020.08.019

Crausbay, S. D., Ramirez, A. R., Carter, S. L., Cross, M. S., Hall, K. R., Bathke, D. J., Betancourt, J. L., Colt, S., Cravens, A. E., Dalton, M. S., Dunham, J. B., Hay, L. E., Hayes, M. J., McEvoy, J., McNutt, C. A., Moritz, M. A., Nislow, K. H., Raheem, N., & Sanford, T. (2017). Defining ecological drought for the twenty-first century. *Bulletin of the American Meteorological Society*, 98, 2543–2550. https://doi.org/10.1175/BAMS-D-16-0292.1

Cressie, N., Calder, C. A., Clark, J. S., Hoef, J. M. V., & Wikle, C. K. (2009). Accounting for uncertainty in ecological analysis: The strengths and limitations of hierarchical statistical modeling. *Ecological Applications*, 19, 553–570. https://doi.org/10.1890/07-0744.1

Crosbie, S. P., Koenig, W. D., Reisen, W. K., Kramer, V. L., Marcus, L., Carney, R., Pandolfino, E., Bolen, G. M., Crosbie, L. R., Bell, D. A., & Ernest, H. B. (2008). Early impact of West Nile virus on the yellow-billed magpie (*Pica nuttalli*). *The Auk*, 125, 542–550. https://doi.org/10.1525/auk.2008.07040

Dai, A. (2013). Increasing drought under global warming in observations and models. *Nature Climate Change*, 3, 52–58. https://doi.org/10.1038/nclimate1633

de Valpine, P., Turek, D., Paciorek, C. J., Anderson-Bergman, C., Lang, D. T., & Bodik, R. (2017). Programming with models: Writing statistical algorithms for general model structures with NIMBLE. *Journal of Computational and Graphical Statistics*, 26, 403–413. https://doi.org/10.1080/10618600.2016.1172487

DeLuca, W. V., Meehan, T., Seavy, N., Jones, A., Pitt, J., Deppe, J. L., & Wilsey, C. B. (2021). The Colorado River Delta and California's Central Valley are critical regions for many migrating north American landbirds. *Ornithological Applications*, 123, duaa064. https://doi.org/10.1093/ornithapp/duaa064/6119082

Dénes, F. V., Silveira, L. F., & Beissinger, S. R. (2015). Estimating abundance of unmarked animal populations: Accounting for imperfect detection and other sources of zero inflation. *Methods in Ecology and Evolution*, 6, 543–556. https://doi.org/10.1111/2041-210X.12333

Diffenbaugh, N. S., Swain, D. L., & Touma, D. (2015). Anthropogenic warming has increased drought risk in California. *Proceedings of the National Academy of Sciences*, 112, 3931–3936. https://doi.org/10.1073/pnas.1422385112

Furnas, B. J., & McGrann, M. C. (2018). Using occupancy modeling to monitor dates of peak vocal activity for passerines in California. En. *The Condor*, 120, 188–200. https://doi.org/10.1650/CONDOR-17-165.1

Garibaldi, L. A., Oddi, F. J., Miguez, F. E., Bartomeus, I., Orr, M. C., Jobbágy, E. G., Kremen, C., Schulte, L. A., Hughes, A. C., Bagnato, C., Abramson, G., Bridgewater, P., Carella, D. G., Díaz, S., Dicks, L. V., Ellis, E. C., Goldenberg, M., Huaylla, C. A., Kuperman, M., ... Zhu, C.-D. (2021). Working landscapes need at least 20% native habitat. *Conservation Letters*, 14, e12773. https://doi.org/10.1111/conl.12773

George, T. L., Fowler, A. C., Knight, R. L., & McEwen, L. C. (1992). Impacts of a severe drought on grassland birds in Western North Dakota. *Ecological Applications*, 2, 275–284. https://doi.org/10.2307/1941861

Goldstein, B. R., & de Valpine, P. (2022). Comparing N-mixture models and GLMMs for relative abundance estimation in a citizen science data set. *Scientific Reports*, 12, 12276. https://doi.org/10.1038/s41598-022-16368-z

Golet, G. H., Low, C., Avery, S., Andrews, K., McColl, C. J., Laney, R., & Reynolds, M. D. (2018). Using ricelands to provide temporary shorebird habitat during migration. *Ecological Applications*, 28, 409–426. https://doi.org/10.1002/eap.1658

Griffith, G. E., Omernik, J. M., Smith, D. W., Cook, T. D., Tallyn, E., Moseley, K., & Johnson, C. B. (2016). *Ecoregions of California (poster): U.S. Geological Survey open-file report*. Series: Open-File Report.

Hamilton, N. E., & Ferry, M. (2018). Ggtern: Ternary diagrams using ggplot2. *Journal of Statistical Software, Code Snippets*, 87, 1–17.

Hart, E. M., & Bell, K. (2015). *prism: Download data from the Oregon prism project*. https://github.com/ropensci/prism

Hendershot, J. N., Smith, J. R., Anderson, C. B., Letten, A. D., Frishkoff, L. O., Zook, J. R., Fukami, T., & Daily, G. C. (2020). Intensive farming drives long-term shifts in avian community composition. *Nature*, 579, 393–396. https://doi.org/10.1038/s41586-020-2090-6

Iknayan, K. J., & Beissinger, S. R. (2018). Collapse of a desert bird community over the past century driven by climate change. *Proceedings of the National Academy of Sciences*, 115, 8597–8602. https://doi.org/10.1073/pnas.1805123115

Jackson, M. C., Loewen, C. J. G., Vinebrooke, R. D., & Chimimba, C. T. (2016). Net effects of multiple stressors in freshwater ecosystems: A meta-analysis. En. *Global Change Biology*, 22, 180–189. https://doi.org/10.1111/gcb.13028

Johnston, A., Matechou, E., & Dennis, E. B. (2022). Outstanding challenges and future directions for biodiversity monitoring using

citizen science data. *Methods in Ecology and Evolution, 14*, 103–116. https://doi.org/10.1111/2041-210X.13834

Johnston, A., Hochachka, W. M., Strimas-Mackey, M. E., Ruiz Gutierrez, V., Robinson, O. J., Miller, E. T., Auer, T., Kelling, S. T., & Fink, D. (2021). Analytical guidelines to increase the value of community science data: An example using eBird data to estimate species distributions. *Diversity and Distributions, 27*, 1265–1277. https://doi.org/10.1111/ddi.13271

Justice, C. O., Vermote, E., Townshend, J. R. G., Defries, R., Roy, D. P., Hall, D. K., Salomonson, V. V., Privette, J. L., Riggs, G., Strahler, A., Lucht, W., Myneni, R. B., Knyazikhin, Y., Running, S. W., Nemani, R. R., Wan, Z., Huete, A. R., van Leeuwen, W., Wolfe, R. E., ... Barnsley, M. J. (1998). The moderate resolution imaging Spectroradiometer (MODIS): Land remote sensing for global change research. *IEEE Transactions on Geoscience and Remote Sensing, 36*, 1228–1249.

Kearney, M., Shine, R., & Porter, W. P. (2009). The potential for behavioral thermoregulation to buffer "coldblooded" animals against climate warming. *Proceedings of the National Academy of Sciences, 106*, 3835–3840. https://doi.org/10.1073/pnas.0808913106

Koenig, W. D., Reynolds, M. D., & Airola, D. A. (2023). In S. M. Billerman, B. K. Keeney, P. G. Rodewald, & T. S. Schulenberg (Eds.), *Birds of the world*. Cornell Lab of Ornithology. https://birdsoftheworld.org/bow/species/yebmag/2.0/introduction

Kremen, C., & Merenlender, A. M. (2018). Landscapes that work for biodiversity and people. *Science, 362*, eaau6020. https://doi.org/10.1126/science.aau6020

LANDFIRE. (2020). *LANDFIRE remap 2016 existing vegetation type (EVT) CONUS tech. Rep.* Earth Resources Observation and Science Center (EROS), U.S. Geological Survey.

Lauck, K. S., Ke, A., Olimpi, E. M., Paredes, D., Hood, K., Phillips, T., Anderegg, W. R. L., & Karp, D. S. (2023). Agriculture and hot temperatures interactively erode the nest success of habitat generalist birds across the United States. *Science, 382*, 290–294. https://doi.org/10.1126/science.add2915

Link, W. A., Schofield, M. R., Barker, R. J., & Sauer, J. R. (2018). On the robustness of N-mixture models. *Ecology, 99*, 1547–1551. https://doi.org/10.1002/ecy.2362

Mac Nally, R., Bennett, A. F., Thomson, J. R., Radford, J. Q., Unmack, G., Horrocks, G., & Vesk, P. A. (2009). Collapse of an avifauna: Climate change appears to exacerbate habitat loss and degradation. *Diversity and Distributions, 15*, 720–730. https://doi.org/10.1111/j.1472-4642.2009.00578.x

MacLean, S. A., Rios Dominguez, A. F., de Valpine, P., & Beissinger, S. R. (2018). A century of climate and land-use change cause species turnover without loss of beta diversity in California's Central Valley. *Global Change Biology, 24*, 5882–5894. https://doi.org/10.1111/gcb.14458

Mantyka-Pringle, C. S., Martin, T. G., & Rhodes, J. R. (2012). Interactions between climate and habitat loss effects on biodiversity: A systematic review and meta-analysis. En. *Global Change Biology, 18*, 1239–1252. https://doi.org/10.1111/j.1365-2486.2011.02593.x

McGrann, M. C., & Furnas, B. J. (2016). Divergent species richness and vocal behavior in avian migratory guilds along an elevational gradient. En. *Ecosphere, 7*, e01419. https://doi.org/10.1002/ecs2.1419

Mount, J., & Hanak, E. (2016). *Water use in California tech. Rep.* PPIC Water Policy Center.

Nimmo, D. G., Haslem, A., Radford, J. Q., Hall, M., & Bennett, A. F. (2016). Riparian tree cover enhances the resistance and stability of woodland bird communities during an extreme climatic event. *Journal of Applied Ecology, 53*, 449–458. https://doi.org/10.1111/1365-2664.12535

Northrup, J. M., & Gerber, B. D. (2018). A comment on priors for Bayesian occupancy models. *PLoS One, 13*, e0192819. https://doi.org/10.1371/journal.pone.0192819

Of Water Resources, C. D. (2020). 2018 *Statewide Crop Mapping GIS Map Service*. https://gis.water.ca.gov/arcgis/rest/services/Planning/i15_Crop_Mapping_2018/MapServer

Prugh, L. R., Deguines, N., Grinath, J. B., Suding, K. N., Bean, W. T., Stafford, R., & Brashares, J. S. (2018). Ecological winners and losers of extreme drought in California. *Nature Climate Change, 8*, 819–824. https://doi.org/10.1038/s41558-018-0255-1

Reynolds, M. D., Sullivan, B. L., Hallstein, E., Matsumoto, S., Kelling, S., Merrifield, M., Fink, D., Johnston, A., Hochachka, W. M., Bruns, N. E., Reiter, M. E., Veloz, S., Hickey, C., Elliott, N., Martin, L., Fitzpatrick, J. W., Spraycar, P., Golet, G. H., McColl, C., ... Morrison, S. A. (2017). Dynamic conservation for migratory species. *Science Advances, 3*, e1700707. https://doi.org/10.1126/sciadv.1700707

Rich, L. N., Beissinger, S. R., Engilis, A., Jr., Brashares, J. S., & Furnas, B. J. (2017). *An evaluation of avifaunal diversity in California's Great Valley tech. Rep.* Department of Environmental Science, Policy & Management, University of California.

Riddell, E. A., Iknayan, K. J., Wolf, B. O., Sinervo, B., & Beissinger, S. R. (2019). Cooling requirements fueled the collapse of a desert bird community from climate change. *Proceedings of the National Academy of Sciences, 116*, 21609–21615. https://doi.org/10.1073/pnas.1908791116

Riddell, E. A., Iknayan, K. J., Hargrove, L., Tremor, S., Patton, J. L., Ramirez, R., Wolf, B. O., Beissinger, S. R. (2022). Exposure to climate change drives stability or collapse of desert mammal and bird communities. En. *Science, 371*, 633–636. https://doi.org/10.1126/science.abd4605

Riggio, J., Engilis, A., Cook, H., de Greef, E., Karp, D. S., & Truan, M. L. (2023). Long-term monitoring reveals the impact of changing climate and habitat on the fitness of cavity-nesting songbirds. *Biological Conservation, 278*, 109885. https://doi.org/10.1016/j.biocon.2022.109885

Robertson, B. A., & Hutto, R. L. (2006). A framework for understanding ecological traps and an evaluation of existing evidence. *Ecology, 87*, 1075–1085. https://doi.org/10.1890/0012-9658%282006%2987%5B1075%3AAFFUET%5D2.0.CO%3B2

Robinson, O. J., Ruiz-Gutierrez, V., Reynolds, M. D., Golet, G. H., Strimas-Mackey, M., & Fink, D. (2020). Integrating citizen science data with expert surveys increases accuracy and spatial extent of species distribution models. *Diversity and Distributions, 26*, 976–986. https://doi.org/10.1111/ddi.13068

Royle, J. A. (2004). *N*-mixture models for estimating population size from spatially replicated counts. *Biometrics, 60*, 108–115. https://doi.org/10.1111/j.0006-341X.2004.00142.x

Selwood, K. E., McGeoch, M. A., Clarke, R. H., & Mac Nally, R. (2018). High-productivity vegetation is important for lessening bird declines during prolonged drought. En. *Journal of Applied Ecology, 55*, 641–650. https://doi.org/10.1111/1365-2664.13052

Strimas-Mackey, M., Hochachka, W. M., Ruiz-Gutierrez, V., Robinson, O. J., Miller, E. T., Auer, T., Kelling, S., Fink, D., & Johnston, A. (2020). *Best practices for using eBird data. Version 1.0.* Cornell Lab of Ornithology. https://cornelllaboffornithology.github.io/ebird-best-practices/

Strochak, S., Ueyama, K., & Williams, A. (2022). *urbnmapr: State and county shapefiles in sf and tibble format*. https://github.com/Urban Institute/urbnmapr

Sullivan, B. L., Aycrigg, J. L., Barry, J. H., Bonney, R. E., Bruns, N., Cooper, C. B., Damoulas, T., Dhondt, A. A., Dietterich, T., Farnsworth, A., Fink, D., Fitzpatrick, J. W., Fredericks, T., Gerbracht, J., Gomes, C., Hochachka, W. M., Iliff, M. J., Lagoze, C., La Sorte, F. A., ... Kelling, S. (2014). The eBird enterprise: An integrated approach to development and application of citizen science. *Biological Conservation, 169*, 31–40. https://doi.org/10.1016/J.BIOCON.2013.11.003

Sullivan, B. L., Wood, C. L., Iliff, M. J., Bonney, R. E., Fink, D., & Kelling, S. (2009). A citizen-based bird observation network in the biological sciences. *Biological Conservation, 142*, 2282–2292. https://doi.org/10.1016/j.biocon.2009.05.006

Tobias, J. A., Sheard, C., Pigot, A. L., Devenish, A. J. M., Yang, J., Sayol, F., Neate-Clegg, M. H. C., Alioravainen, N., Weeks, T. L., Barber,

R. A., Walkden, P. A., MacGregor, H. E. A., Jones, S. E. I., Vincent, C., Phillips, A. G., Marples, N. M., Montaño-Centellas, F. A., Leandro-Silva, V., Claramunt, S., … Schleuning, M. (2022). AVONET: Morphological, ecological and geographical data for all birds. *Ecology Letters*, 25, 581–597. https://doi.org/10.1111/ele.13898

Travis, J. M. J. (2003). Climate change and habitat destruction: A deadly anthropogenic cocktail. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 270, 467–473. https://doi.org/10.1098/rspb.2002.2246

USGS. (2022). *USGS Landsat 7 Collection 1 Tier 1 and Real-Time data Raw Scenes [Data set]*. https://www.usgs.gov/landsat-missions/landsat-collection-1

Vermote, E., & Wolfe, R. (2023). MOD09GA MODIS/Terra Surface Reflectance Daily L2G Global 1kmand 500m SIN Grid V006 [Data set] 2015. https://doi.org/10.5067/MODIS/MOD09GA.006

Vicente-Serrano, S. M., Quiring, S. M., Peña-Gallardo, M., Yuan, S., & Domínguez-Castro, F. (2020). A review of environmental droughts: Increased risk under global warming? *Earth-Science Reviews*, 201, 102953. https://doi.org/10.1016/j.earscirev.2019.102953

Wickham, H. (2016). *ggplot2: Elegant graphics for data analysis*. Springer-Verlag. https://ggplot2.tidyverse.org

Williams, J. J., & Newbold, T. (2020). Local climatic changes affect biodiversity responses to land use: A review. En. *Diversity and Distributions*, 26, 76–92. https://doi.org/10.1111/ddi.12999

Williams, J. J., & Newbold, T. (2021). Vertebrate responses to human land use are influenced by their proximity to climatic tolerance limits. *Diversity and Distributions*, 27, 1308–1323. https://doi.org/10.1111/ddi.13282

Williams, S. E., Shoo, L. P., Isaac, J. L., Hoffmann, A. A., & Langham, G. (2008). Towards an integrated framework for assessing the vulnerability of species to climate change. *PLoS Biology*, 6, 2621–2626. https://doi.org/10.1371/journal.pbio.0060325

Youngflesh, C. (2018). MCMCvis: Tools to visualize, manipulate, and summarize MCMC output. *Journal of Open Source Software*, 3, 640.

BIOSKETCH

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SUPPORTING INFORMATION

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