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Long-Term Drought Exposure Shapes Declines and Range Shifts in Aridland Birds

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ABSTRACT

Climate change increases drought frequencies and intensities, posing risks to biodiversity. Species inhabiting arid regions may be vulnerable to drought because they live near their physiological limits, while species with low historical drought exposure may lack adaptations to cope with unprecedented drought. Using a breeding bird dataset and the Standardized Precipitation-Evaporation Index, we assessed drought vulnerability of 37 bird species across deserts of the western United States. We tested drought effects on community and species-level relative abundance, how species' long-term drought exposure influences these effects, and for drought-induced range shifts. Drought was associated with abundance declines and distributional shifts for over 40% of species, with shift directions reflecting regional drought patterns. Species with lower historical drought exposure declined more strongly, though several highly exposed species were among the most vulnerable. These findings demonstrate that climatic history modulates species' responses to increasing aridity. Under intensifying drought, incorporating regional drought dynamics and climatic legacies into climate change vulnerability assessments is essential for anticipating conservation issues.

1 | Introduction

Global environmental change alters ecosystems and their associated biological diversity through shifts in temperature, precipitation, and extreme weather patterns (Parmesan et al. 2000). These changes affect biodiversity directly when species experience conditions that exceed their physiological limits (Khaliq et al. 2014) and indirectly when habitats (Dirnböck et al. 2011) and resources (Twining et al. 2022) are altered. Such disruptions can lead to shifts in species distribution, local extirpation, and ultimately, extinction (Cohen and Jetz 2025). In many ecosystems, climate change causes increased drought frequencies and intensities (van den Bosch et al. 2025a), which have predominantly negative ecological effects (Maxwell et al. 2019).

Birds are often considered bioindicators of environmental change because they are present across all ecosystems, well-studied, and respond rapidly to environmental change (Carignan and Villard 2002). Alarmingly, widespread declines in both common and rare bird species have been observed, with an estimated 29% decline in total abundance across North American breeding birds between 1970 and 2020 (Rosenberg et al. 2019). While habitat loss and degradation are currently considered the primary threats to bird populations (Brooks et al. 2002), climate change has emerged as a multifaceted threat that can also reduce or degrade habitat (Lees et al. 2022). Increased drought, one such facet of climate change, can affect birds directly by increasing physiological stress (Albright et al. 2017) as well as by reducing habitat and resource availability (Goldstein et al. 2024).

The western interior of the United States is an already arid region expected to experience a rapid increase in drought frequencies for the remainder of this century (van den Bosch et al. 2024). In desert ecoregions, species are thought to live at the limits of their physiological tolerances, which may increase their vulnerability to drought (Albright et al. 2017). At the same time, it has been suggested that historical drought exposure may instill resilience to intensifying drought patterns (Backhaus et al. 2014), suggesting novel drought will disproportionately impact species in regions with lower historical exposure (Moss et al. 2024). Regardless, increased drought in the warm deserts of the southwestern United States has led to reduced reptile (Lovich et al. 2023) and amphibian (Zylstra et al. 2019) survival, as well as reduced mammal (Cárdenas et al. 2021) and bird abundance (van den Bosch et al. 2025b).

Because average global surface temperatures decrease toward the poles, climate warming is generally expected to cause poleward shifts in species distributions as they track their climate niche (Parmesan and Yohe 2003). Drought, which can be defined as anomalously low precipitation and high evapotranspiration, compared to long-term averages, is driven by both temperature and precipitation patterns (Vicente-Serrano et al. 2010). Shifts in precipitation and thus drought are more heterogeneous across space than shifts in temperature (IPCC 2021), leading to variable range contractions or expansions depending on regional climatic contexts (VanDerWal et al. 2013; Da Silva and Diamond 2024). Regional assessments of ecological responses to drought are thus crucial to discern geographic patterns of drought impacts (Da Silva and Diamond 2024).

To better understand the dynamics between drought and bird communities in arid environments, we investigated the effects of annual (12-month duration) drought conditions on an avian community of 37 species across three cold and two warm desert ecoregions of the western interior United States. We predicted that drought would negatively affect the relative abundance of individual bird species and the community they belong to. Because historical drought exposure may influence vulnerability, we assessed the interacting effects of annual drought and each species' long-term exposure to annual drought on relative abundance. Further, we assessed whether predicted abundance changes under drought conditions would lead to notable shifts in species distributions through changes in their geographic centroid of abundance.

2 | Methods

2.1 | Study Area

Our study area (748,674 km^2) comprises five level III ecoregions of the western United States (Figure 1; Omernik and Griffith 2014), of which two (the Mojave Basin and Range and Sonoran Desert) are classified as warm deserts and three as cold deserts (the Central and the Northern Basin and Range and the Snake River Plain). Ecoregions were used solely as a descriptive spatial framework for visualizing broad-scale environmental patterns (Figures 1 and 2) and were not included in statistical analysis. This study area includes parts of the US states of California, Arizona, Nevada, Utah, Oregon, and Idaho. The study area land cover composition was 73.3% shrubland, 6.5% grassland, 6.3% barren land, 5% coniferous forest, 4% cropland, and 1.8% developed land (USGS 2025). Warm and cold deserts both have relatively arid conditions but are subject to average annual temperatures above and below 18°C (Peel et al. 2007). Since 1950, the study area has seen a pattern of increasing drought frequencies and intensities, which is expected to exacerbate throughout the 21st century (van den Bosch et al. 2024).

The North American Breeding Bird Survey (BBS) comprises annual avian transect surveys throughout North America, with data collected during the breeding season. We retained data collected within our study area for 1966–2023 during May and June, which was 96.87% of all data from those years. Observers conduct 3-min point-counts at 50 points along a ± 40 km transect, with point locations spaced approximately every 800 m, with summed counts provided for each 10-point segment. While the starting point is known, uncertainty in point count locations increases with distance along the transect (Burner et al. 2024). To minimize spatial uncertainty, we retained summed counts from the first 10-point segment of each route, which constitutes the first ± 8 km of the route. When multiple routes overlapped in surveying years and had potential for spatial overlap (distance < 16 km), we retained only the first route in the dataset. We omitted routes with a sampling of < 10 route-years, so that the average route in our dataset had 25 years of data ($\sigma = 9$). To ensure models were based on sufficient data and to eliminate convergence problems, we excluded rarer species, which occurred in fewer than 10% of all route-years. We then omitted nocturnal, non-native, and waterfowl species. Finally, we omitted data for the red-winged blackbird (*Agelaius phoeniceus*) for which counts were a strong positive outlier, with a maximum count of 2060 birds, approximately 20 times higher than the mean maximum count across other species. Ultimately, we retained data for 37 out of 319 species counted across 161 of 689 routes in our study area (Table S1). We refer to this group of species as an avian community, where "community" denotes the set of species included in the hierarchical model, with species-specific parameters drawn from shared community-level hyperparameters (Stroud et al. 2015).

2.2 | Environmental Covariates

We used the Standardized Precipitation-Evaporation Index (SPEI) to measure drought. SPEI is based on precipitation and potential evapotranspiration and is useful when assessing drought within the framework of climate change (Beguería et al. 2014). Because evapotranspiration is partially determined through temperature, this index simultaneously captures precipitation and temperature changes associated with climatic change. SPEI values represent deviations in the climatic water balance from a long-term historical average and have means of zero and standard deviation of one.

We extracted SPEI data at a ± 5 × 5 km resolution from the nClimGrid-Monthly dataset (Vose et al. 2014) for each May and June between 1966 and 2023. Values are fitted to a gamma distribution for standardization and then calibrated against the mean for the period 1895–2014. We inverted SPEI values (hereafter, iSPEI) for intuitive interpretation in regression models, whereby positive iSPEI values indicate drier conditions (sensu van den

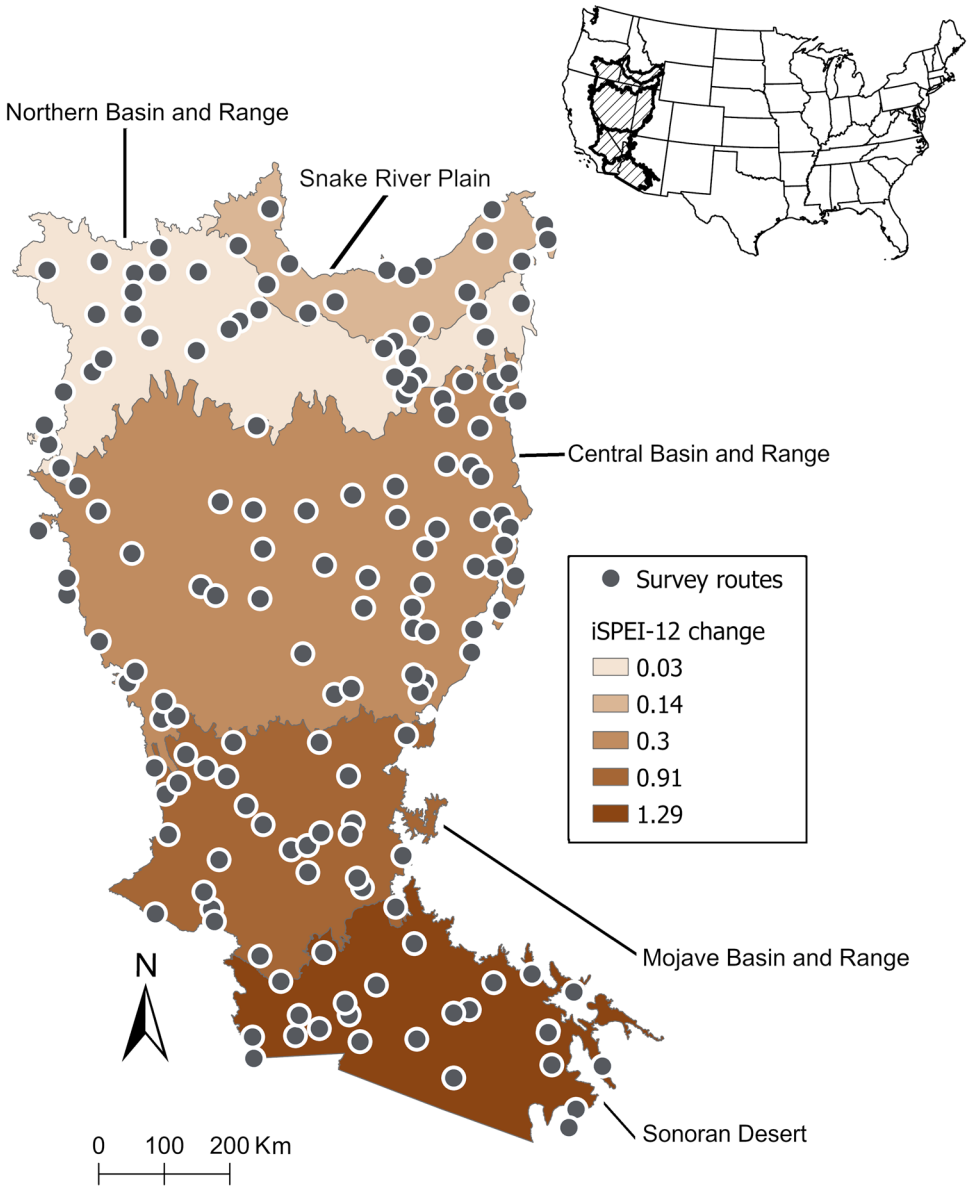

FIGURE 1 | Approximate route locations for North American Breeding Bird Surveys from 1966 to 2023 across two warm desert ecoregions (most southern) and three cold desert ecoregions (northern) in the western United States. Ecoregions are colored by the average pixel-level change in annual drought intensity (iSPEI-12) between 1966 and 1994 and 1995 and 2023, calculated across all pixels within each ecoregion. Positive iSPEI-12 change values indicate increasing drought intensity.

Bosch et al. 2025b). iSPEI values were categorized as −0.5–0.5 (normal), 0.5–1 (mild drought), 1–1.5 (moderate drought), 1.5–2 (severe drought), and > 2 (extreme drought) (Vicente-Serrano et al. 2010). iSPEI uses rolling temporal windows which represent the cumulative water balance over a particular number of months preceding the target month (Vicente-Serrano et al. 2010). We considered iSPEI on a timescale representing annual drought as measured in May and June (iSPEI-12; 12 months), which may have stronger or more traceable effects on aridland birds than short- or multiyear drought (van den Bosch et al. 2025b). We extracted the average iSPEI-12 in an 8 km radius of each route starting point (Cady et al. 2019).

To assess whether long-term exposure to annual drought influenced the effect of annual drought events, we calculated the mean iSPEI-12 values for May and June across each species' year-route combinations, weighted by each species' count of each year-route. Finally, we extracted average elevation in an 8 km radius around each route starting point (USGS 2008).

2.3 | Relative Abundance Model

We fit a community relative abundance model using Bayesian generalized linear mixed models (GLMM) with a negative binomial error distribution, where the response variable was the number of birds counted within the first 8 km of BBS routes. We estimated species-level responses from hyperparameters and species-level parameters. We were unable to model true abundance using hierarchical models because BBS data do not include

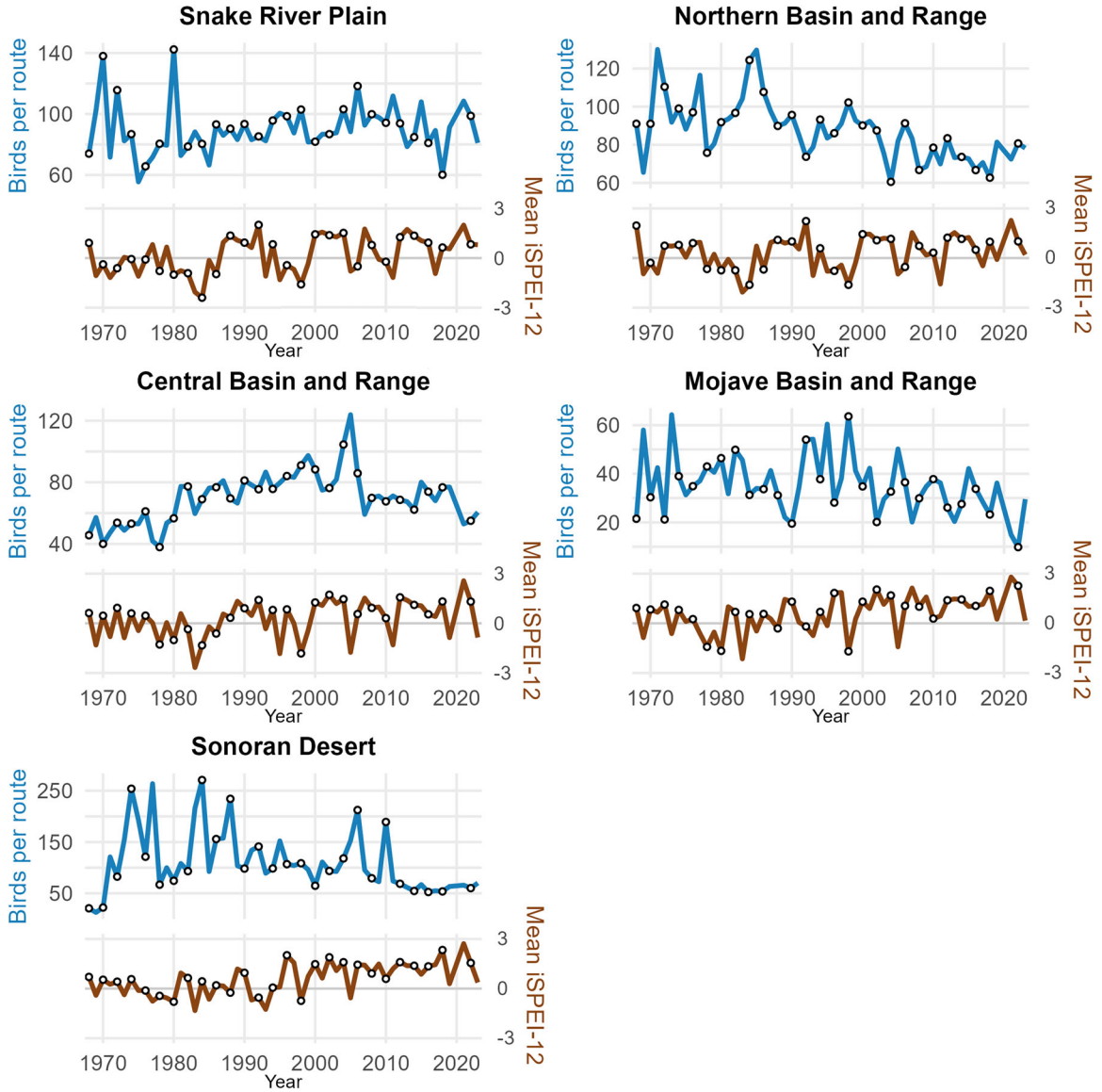

FIGURE 2 | Mean bird counts per route versus mean values of annual drought (iSPEI-12) per ecoregion across five desert ecoregions in the western United States for 1966–2023. Values for even years are indicated with white dots for visualization purposes.

multiple surveys within a season or distance estimates. BBS counts are likely lower than absolute abundance values but unlikely to systematically vary with drought conditions. Fixed effects included annual drought conditions (iSPEI-12), long-term drought exposure, and their interaction to test whether species-specific long-term drought adaptation modifies responses to interannual drought variability. Elevation was included as a broad-scale environmental effect associated with climatic conditions, and year was included as a continuous fixed effect to account for long-term changes in bird abundances unrelated to iSPEI-12. There were no strong correlations among covariates ($r \leq 0.7$). We scaled all continuous variables ($\bar{x} = 0$ and $\sigma = 1$).

Route-species combinations were included as random intercepts to account for species-specific variability in abundance among routes. Effects of predictors were allowed to vary by species as random slopes, and community-level hyperparameters were estimated as the distribution of species-level parameters. The model was fit using 3 Hamiltonian Monte Carlo Markov Chains with 4000 iterations (50% warm-up). We specified a weakly informative prior for the model intercept informed by raw bird counts and regularizing priors on slope and variance terms (McElreath 2018):

Intercept: norm($\bar{x} = 1.5, \sigma = 2$)
Fixed effects: norm($\bar{x} = 0, \sigma = 1$)
Random effects standard deviations: Exp(1)

Models were constructed using the *brms* package, which uses Stan as the backend for Bayesian inference (Bürkner 2017) in R 4.3.2 (R Core Team 2023). Traceplots and R-hat values were assessed for adequate mixing and model convergence, and R-hat values associated with parameter estimates were ≤ 1.01. Model residuals were aggregated across route-years and subjected to a spatial autocorrelation test, which indicated spatial dependence is adequately captured by our model structure (Moran's I = −0.02,

TABLE 1 | Fixed-effect estimates from a community-level Bayesian generalized linear mixed model (GLMM). The model relates annual drought to the relative abundance of 37 aridland breeding birds across desert ecoregions of the western United States between 1966 and 2023.

	Posterior mean	Posterior std. dev	95% CI-L	95% CI-U
Intercept	−0.31	0.15	−0.60	−0.00
iSPEI-12 (annual drought)	−0.06	0.01	−0.08	−0.03
Long-term drought exposure	−0.03	0.16	−0.35	0.28
Year	−0.03	0.01	−0.04	−0.02
Elevation	−0.04	0.03	−0.10	0.01
iSPEI-12 : Long-term drought exposure	0.03	0.02	0.00	0.06

$p = 0.998$). We assessed the certainty of parameter estimates by reporting the percentage of posterior samples consistent with the direction of the effect (McElreath 2018). Where 95% credible intervals excluded zero, this corresponds to at least 97.5% certainty. Code and data needed for analysis replication were stored in a Dryad repository (see Data Availability Statement).

2.4 | Effects of Increased Drought Between 1966 and 2023

Given the observed increases in drought in our study area (van den Bosch et al. 2024), we generated mean iSPEI-12 rasters for the first (1966–1994) and second half (1995–2023) of the study period. Using these rasters, we made two types of spatially explicit predictions. First, we predicted relative abundance across the full study area by generating predictions at each raster cell under the mean iSPEI-12 values of each period, holding all other covariates at their mean values. Second, we estimated abundance-weighted geographic centroids for each species by extracting the period-specific mean iSPEI-12 values at each survey route, predicting relative abundance at each route under each period's drought conditions, and computing the abundance-weighted mean across route coordinates. Centroid shifts between periods were then calculated as the difference in centroid position, converted to kilometers. In both cases, the differences in predictions reflect changes expected in a single year under drought conditions typical of each period rather than a cumulative change across all years.

3 | Results

3.1 | Drought Effects on Abundance

Years with intense drought (iSPEI-12) were generally associated with lower bird abundance (Figure 2). Despite large variation in absolute bird counts among ecoregions, this pattern was relatively consistent. Our model found > 99% certain negative effects of both annual drought and survey year on the relative abundance of the aridland bird community (Table 1). Additionally, there was a 95.5% certain interaction between annual drought and long-term drought exposure, indicating that birds with lower long-term exposure to annual drought were more sensitive to annual drought events. Elevation was negatively associated with community abundance with 93.6% certainty.

At the species-level, there was a > 97.5% certain negative effect of annual drought on the relative abundance of 15 out of 37 species (40.5%; Figure 3). Only one species (Common Raven, *Corvus corax*) was highly certain to have increased abundance under drier conditions. Considering species with 95% credible intervals that included zero, 31 out of 37 (80.5%) species were estimated to have lower relative abundances in drier conditions. Long-term exposure to annual drought positively interacted with the effect of annual drought on the relative abundance of 21 of 37 (56.8%) species, whereby species with lower historical drought exposure appeared more vulnerable to drought (Figure 4).

3.2 | Geographic Effects of Increased Drought Between 1966 and 2023

When all non-drought effects are held constant, our model estimated lower relative community abundance across the study region during a year representing average drought conditions of the latter half of our study period (1995–2023) relative to a year representing average conditions of the first half (1966–1994; Figure 5). Predicted declines due to changing drought patterns were of a higher magnitude (largest predicted decline: −7.3%, CI: −10.9%–−3.8%) than any predicted increases (largest increase: 1.2%, CI: 0.6%–1.9%), and declines were greater in the southern half than in the northern half of the study area.

Due to stronger relative abundance declines in southern ecoregions, the abundance-weighted geographic centroids of 16 out of 37 (43.2%) species were > 97.5% certain to be further northward in a year with average drought conditions of the second half of our study (Figure 6). The largest northward shifts ranged from 7.5 to 11.2 km in such a year, while the community-wide effect was a northward shift of 2.04 km (CI: 1.29–2.77 km). Only Common Raven had a highly certain southward shift estimated at 4.4 km. Longitudinally, the centroids of 12 out of 37 species were highly certain to be further westward under average conditions for the second half of the study period. However, the magnitude of longitudinal shifts was much lower than that of latitudinal shifts.

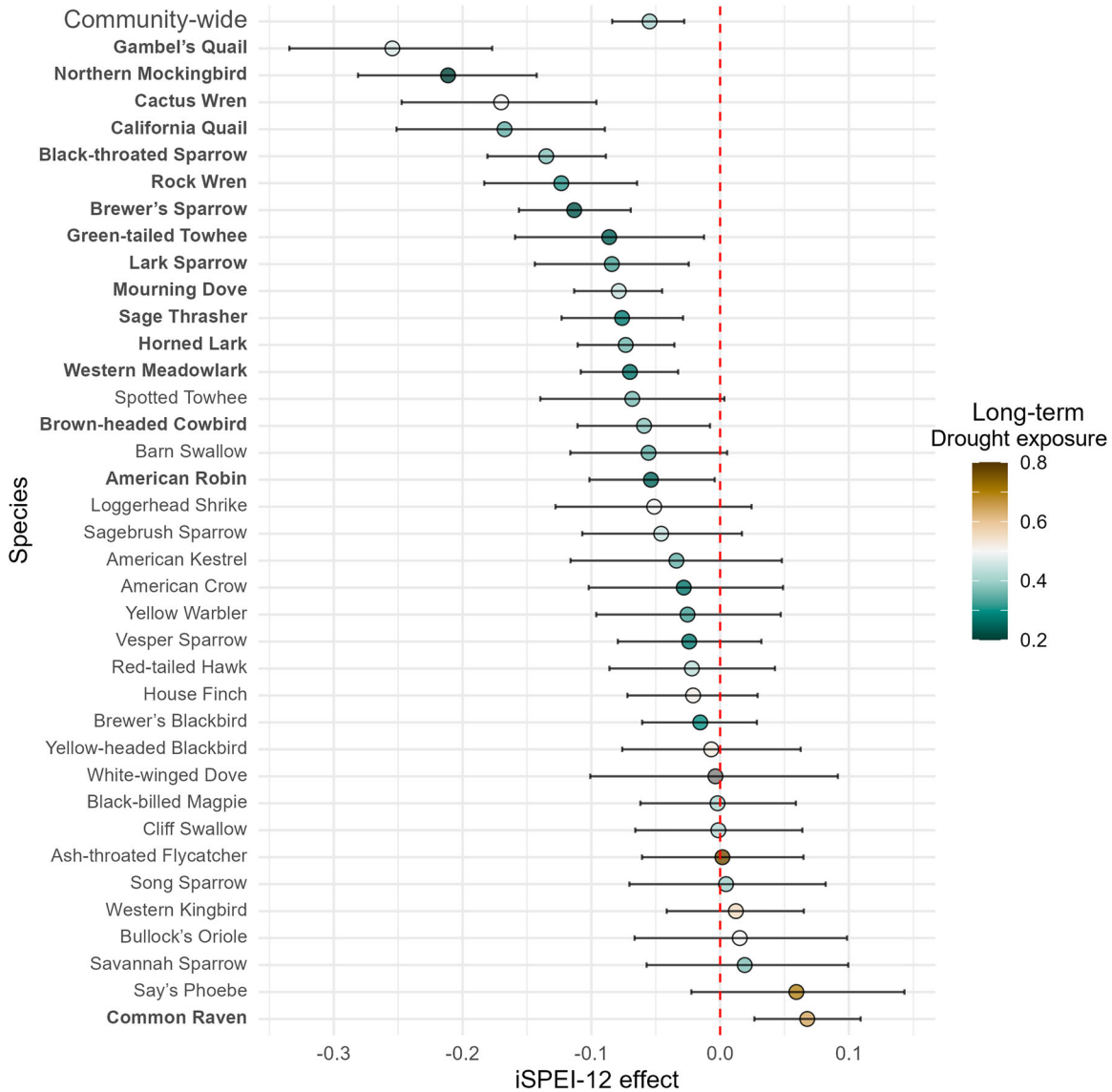

FIGURE 3 | Annual drought (iSPEI-12) effect estimates on the relative abundance of 37 avian species across five desert ecoregions in the western United States. Dots indicate median effect sizes for the community (top row) and individual species, along with 95% credible intervals. Species names are bolded when effect sizes do not overlap zero, and species estimates are colored according to their long-term exposure to annual drought between 1966 and 2023.

4 | Discussion

Our findings demonstrate drought as an increasingly important determinant of community structure for aridland birds in the western United States. Across five desert ecoregions, greater annual drought intensity was associated with reduced community abundance and shifts in the spatial distribution of drought-sensitive species. Moreover, these drought effects appear stronger than the long-term negative trend in community abundance over the study period. Globally, over 60% of bird species are known or suspected to be declining (Birdlife International 2025), with habitat loss and climate change considered dominant pressures (Lees et al. 2022). Our results highlight drought as a rapidly intensifying component of climate change threatening global biodiversity (Maxwell et al. 2019). By revealing abundance declines and directional range centroid shifts across diverse avian taxa, based on regional patterns of changing drought intensity, this study underscores the importance of incorporating drought dynamics into regional assessments of climate-driven biodiversity change.

These results align with previous findings that suggest the potential collapse of aridland bird communities in the United States due to increased drought (Iknayan and Beissinger 2018; NABCI 2025), particularly given anticipated further drought increases in this region throughout the century (van den Bosch et al. 2024). Further, this study indicates that only Common Raven abundance increased due to increasing drought, a generalist scavenger that may benefit from increased resource availability due to drought-induced macrofauna mortality (Barton et al. 2022). We found that increasing drought contributes to northward distribution shifts for over 40% of bird species in our study. Such shifts may take the

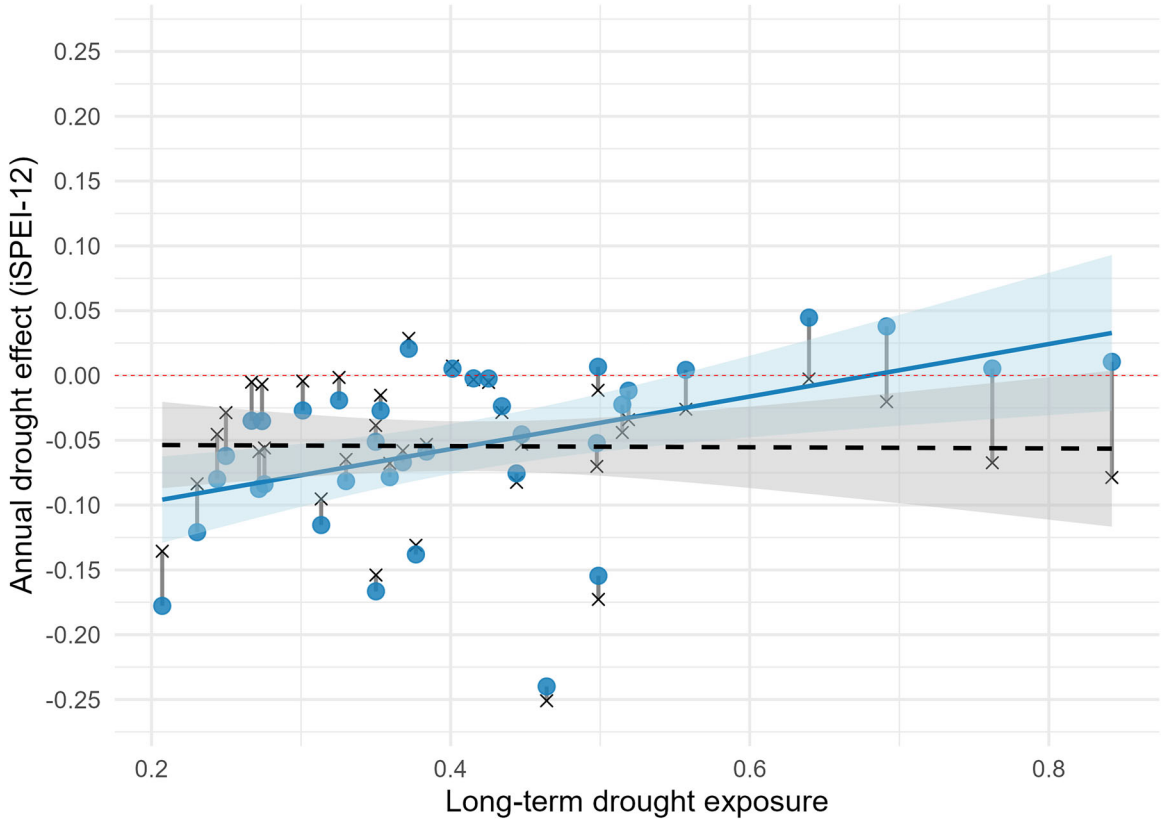

FIGURE 4 | The effect of annual drought (iSPEI-12) on the relative abundance of 37 avian species across five desert ecoregions in the western United States, shown with and without accounting for the interaction with species-specific long-term exposure to annual drought. Negative values indicate a negative relationship between annual drought and relative bird abundance. The lines represent community-level estimates (red: no drought effect, assuming species are insensitive to drought; black dashed: sensitivity of species to annual drought without accounting for their long-term exposure to annual drought; blue: sensitivity of species to annual drought while accounting for their long-term exposure to annual drought), while black crosses and blue dots show species-level drought effects excluding and including the interaction with long-term exposure to annual drought, respectively.

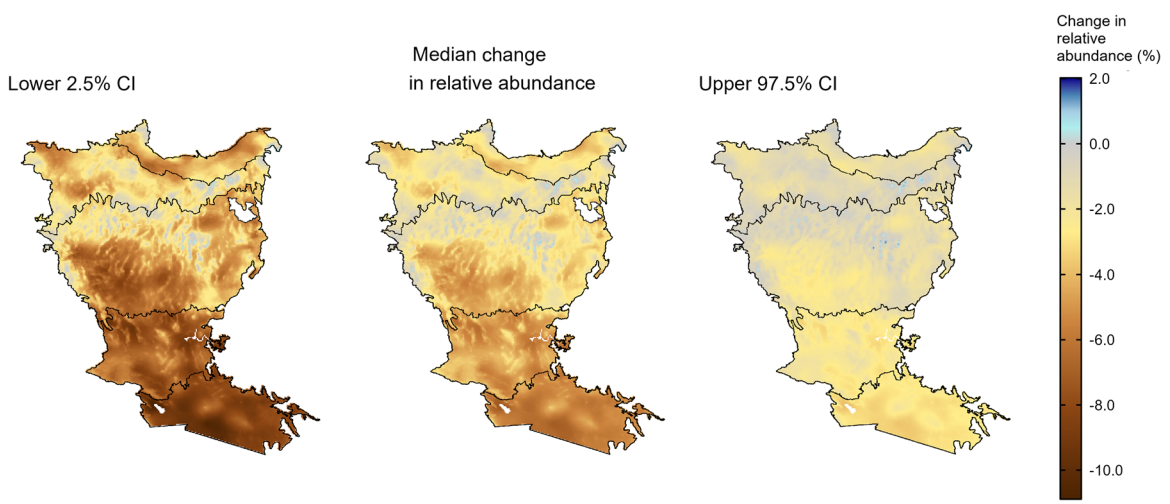

FIGURE 5 | Percentage marginal change in relative abundance due to drought for a community of 37 bird species. Change is calculated as the difference between a year with mean iSPEI-12 drought values of the early period (1966–1994) and a year with mean iSPEI-12 values of the late period (1995–2023). The center panel shows the median predictions, flanked by panels displaying the lower and upper credible intervals. Negative numbers represent percentual decline in bird abundance.

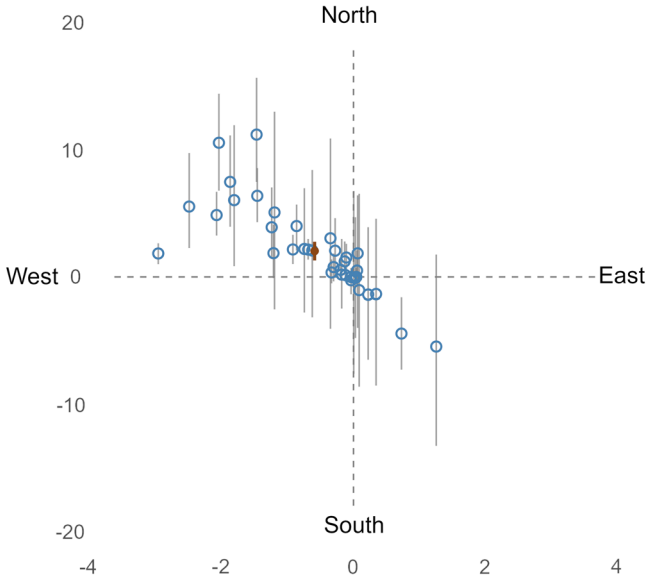

FIGURE 6 | Drought-induced marginal centroid shifts (in kilometers) of 37 bird species across five desert ecoregions in the western United States. For each species (blue) and the community (brown), values represent the modeled shift from zero (no change) in range centroid position attributable solely to the difference in estimated relative abundance under average drought conditions of the late period (1995–2023) versus the early period (1966–1994). Vertical bars represent 95% credible intervals for latitudinal shifts; intervals not overlapping the longitudinal axis indicate > 97.5% posterior certainty of a northward or southward shift. Note the wider range of values on the (latitudinal) y-axis.

form of range contractions and local extirpation when increasing drought erodes available habitat without evident compensation near the less arid part of their range.

Aridland species are considered particularly vulnerable to continued increases in drought frequencies and intensities because they live at the limits of their physiological capabilities and may be unable to adapt to further increases in drought (Albright et al. 2017). In the western United States, dryland specialist bird numbers have declined by about 40% since 1970 (NACBI 2025), and our results show drought as a primary driver of declines in several dryland specialists. Simultaneously, our results suggest species that historically have had relatively low drought exposure in our study area are more vulnerable to intensifying drought than species with high historical drought exposure. Drought vulnerability of aridland species may therefore be two-pronged, whereby species adapted to the driest environments may reach a tipping point when increased drought exceeds their physiological limits (Albright et al. 2017), while in historically more mesic areas, unprecedented drought frequencies and intensities can cause substantial declines due to a lack of drought adaptation (Bailey et al. 2022). These findings demonstrate the urgency of assessing drought effects on biodiversity in regions where exposure has historically been low (van den Bosch et al. 2024).

Due to data limitations, we assessed the effects of long-term drought exposure on drought vulnerability at the species level. Ideally, such differences would also be studied among populations of the same species with variable levels of historical drought exposure, as has been done with respect to changing surface temperatures (Bailey et al. 2022). Second, our estimates of distributional shifts aimed to isolate drought effects but do not account for other influential factors, such as changes in dispersal distance and biotic interactions (Brooker et al. 2007). Finally, more targeted studies investigating whether drought vulnerability is driven by direct drought effects, such as hyperthermia and dehydration (Albright et al. 2017), or indirect effects, such as loss of nesting opportunities or food sources (Cruz-McDonnell and Wolf 2016), would build upon this work.

As drought frequencies in the western United States are projected to accelerate throughout the 21st century (van den Bosch et al. 2024), greater declines potentially leading to range contractions and local extirpations may be expected. In our study area, drought-induced distribution shifts generally align with predictions of species moving poleward to track their climate niche as average temperatures rise. However, projected drought increases are spatially more heterogeneous than temperature increases, suggesting range shifts due to climate change will be more directionally variable than generally thought (VanDerWal et al. 2013). The forecasting of abundance declines, local extirpations, and distribution shifts under climate change therefore requires regional assessments incorporating local drought effects.

Our study exclusively used public data, and while historical and projected drought data are available globally, biodiversity monitoring schemes such as the North American BBS are currently unevenly distributed across the globe (Moussy et al. 2022). Besides the western United States, some of the world's biodiversity hotspots have seen large increases in drought, such as parts of the Amazon Basin, southern and tropical eastern Africa, southwestern China, and southeastern Australia (Vicente-Serrano et al. 2022), which together harbor significant proportions of the world's bird species. Because many of these areas are among the regions projected to face accelerating drought frequencies (van den Bosch et al. 2025a), regional assessments of species' drought vulnerability emerge as a global conservation priority. Understanding and anticipating the ecological consequences of intensifying drought may prove pivotal to safeguarding biodiversity.

Author Contributions

Merijn van den Bosch: conceptualization, methodology, formal analysis, data curation, writing – original draft, writing – review and editing, visualization. **Hailey M. Boone:**conceptualization, methodology, writing – review and editing. **Jennifer K. Costanza:**conceptualization, methodology, writing – review and editing. **Ryan A. Peek**: conceptualization, methodology, writing – review and editing**. Zachary L. Steel**: conceptualization, methodology, writing – review and editing, supervision, project administration, funding acquisition.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All data used are publicly available from the North American Breeding Bird Survey and the United States Geological Survey. Instructions on how to access these data and all code used for analysis are available through the Dryad repository at https://doi.org/10.5061/dryad.73n5tb3bf.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.

Supplementary Material: conl70069-sup-0001-TableS1.docx