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Increased drought drives avian community declines in the warm deserts of the United States

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A B S T R A C T

The frequencies, intensities, and durations of extreme weather are increasing under climate change, furthering biodiversity loss. In the Southwestern USA, rising drought frequencies and intensities are anticipated to increasingly affect wildlife and their habitat. Particularly in highly arid regions, where species live closer to the limit of physiological tolerances, increasing drought emerges as a major threat to biodiversity. Using North American Breeding Bird Survey data (1998–2022) in combination with the Standardized Precipitation-Evaporation Index (SPEI), we estimated the effects of short-term (3-month), annual (12-month), and prolonged (36-month) drought on avian abundance and apparent species richness in the warm deserts of the USA. We assessed community-level drought effects using six Bayesian relative abundance and apparent species richness models. Our results indicate declines in avian community abundance and richness under multiple drought durations, with the strongest effects associated with annual droughts. Our models estimated that in years where annual drought met the threshold of 'severe', 9 out of 38 species would have 18–34 % declines in relative abundance compared to a year with long-term average conditions, and apparent species richness would decline by 10 %. Availability of open water slightly mitigated negative drought effects on the avian community. Our results suggest drought will increasingly contribute to the collapse of aridland avian communities through declines in habitat generalist and obligate aridland species. Beyond mitigating future climate change, developing local adaptation strategies in arid regions, such as the conservation of water sources, appear necessary for biodiversity conservation.

1. Introduction

Anthropogenic climate change is altering global patterns of extreme weather events such as megafires, heatwaves, storms, floods, and drought, with potentially grave impacts on biodiversity (Parmesan et al., 2000; IPCC, 2023). As global warming alters precipitation and evapotranspiration dynamics, many regions are predicted to see increases in the frequency, severity, and duration of drought (Dai, 2013; IPCC, 2023). This environmental stressor, here defined as anomalously low precipitation and high evapotranspiration compared to a long-term historical average (Vicente-Serrano et al., 2010), can affect wildlife directly through physiological stress such as dehydration, or indirectly by altering habitat in ways that impede reproduction or survival (Hofmeister et al., 2010; Blaustein et al., 2010). Drought indirectly impacts species and biodiversity in several ways, including from forest die-off (Allen et al., 2015) and megafires (Ayars et al., 2023). It can also lead to mass mortality and reduced reproduction due to resource shortages, while shifts in competition and trophic dynamics may further drive species declines or even extirpation (Maron et al., 2015; Saracco et al., 2018; Prugh et al., 2018).

We are amid a biodiversity crisis that is likely to deepen as climatic change progresses (Lawler et al., 2009; Bellard et al., 2012; McElwee et al., 2023; IPBES, 2024). Of the more than 166,000 species assigned a conservation status by the International Union for the Conservation of Nature (IUCN), more than a quarter are considered threatened with extinction (IUCN, 2023). In the United States (USA), assessments by NatureServe indicate 40 % of animal species are at risk of extinction, with the same percentage of ecosystems at risk of wide-range collapse (NatureServe, 2023). The percentage of bird species considered by NatureServe to be at risk of extinction is 12 %, and the same percentage of global bird species is estimated to be at risk (IUCN, 2023). For many species, habitat loss and fragmentation remain the primary drivers of population declines. However, as climate change accelerates and climate-related stressors become more frequent and severe, species sensitive to these changing conditions are likely to see increasingly negative outcomes in the future (Travis, 2003; Bellard et al., 2012;

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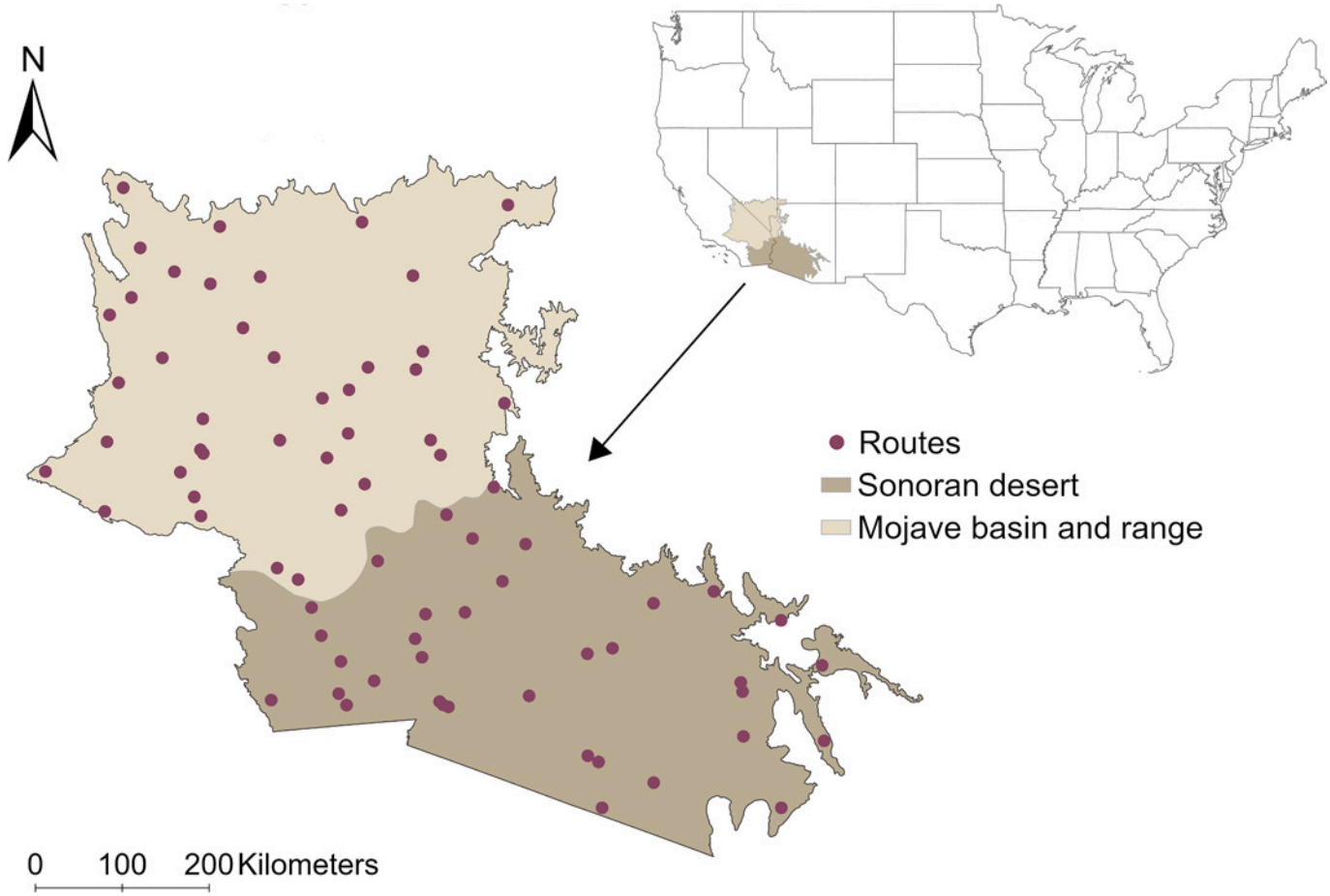

Fig. 1. Approximate route locations for North American Breeding Bird Surveys from 1998 to 2022 across two ecoregions which constitute the warm deserts of the southwestern USA. Dots represent routes, which consist of five point count locations each.

IPBES, 2024).

Drought affects birds through direct mechanisms, such as by causing dehydration and hyperthermia, and indirectly by affecting the availability of resources such as vegetation, insects, or fruit, and species-level drought impacts depend on drought duration and intensity (Prugh et al., 2018; Wilson et al., 2018). For example, birds reliant on moist soil to acquire invertebrate prey may respond strongly to short-term droughts which cause hardening of the topsoil and declining prey availability, while herbivorous and granivorous birds may be more strongly affected by reduced vegetation vigor associated with longer droughts (Cady et al., 2019). Similarly, a species may positively respond to short-term wetness because of increased resource availability, while long-term wetness may cause a negative response as increased vegetation vigor causes unsuitable habitat structure for certain species (Wilson et al., 2018). Contrastingly, it has been suggested that high vegetation vigor can mitigate prolonged drought effects on avian communities (Selwood et al., 2018). There is support for the idea that multi-year droughts and droughts of moderate durations (e.g. 6- or 12-month droughts) more strongly affect avian communities (Albright et al., 2010; Prugh et al., 2018; Cady et al., 2019) than short-term droughts (e.g. 1- or 3-month drought), whereby drought impacts accumulate over time.

To mitigate biodiversity loss caused by increased drought, knowledge is needed not only on the spatial overlap between expected drought increases and species distributions (drought "exposure"), but also on the sensitivity of individual species and ecological communities to drought. Climate change projections for the USA indicate large increases in the frequencies with which birds will be exposed to annual and multi-year droughts, with the largest increases projected for the southwestern USA (van den Bosch et al., 2024). The warm deserts of the USA are projected to see the highest increases in drought frequencies in the second half of the 21st century (van den Bosch et al., 2024), while 31 % of warm desert ecosystems in this country are at risk of range-wide collapse (NatureServe, 2023). Additionally, deserts are ecoregions defined by climate extremes in which many species live on the edge of their physiological tolerances and are suspected to be particularly vulnerable to increasing climate extremes (Hargrove and Rotenberry, 2011; Albright et al., 2017; Riddell et al., 2021). These regions nevertheless host substantial biodiversity with numerous endemic species (Ma et al., 2023). Therefore, assessing the drought vulnerability of desert bird communities emerges as a priority for species and ecosystem conservation. Simultaneously, this region provides an opportunity to isolate the effects of drought on avian communities, as it is relatively uniform in terms of land cover composition and topography, which may influence how birds are affected by drought (Albright et al., 2010; Goldstein et al., 2024).

We framed our study around the hypothesis that drought negatively affects bird abundance and species richness by reducing resource availability and through direct physiological stress. Both of these indirect and direct impacts may lower survival and reproduction resulting in fewer observed bird individuals and species. We investigated the effects of short-term (3-month), annual (12-month), and prolonged (36-month) drought conditions on an avian community in the warm deserts of the southwestern USA. We predicted drought calculated for these three timescales would negatively affect the relative abundance of individual bird species, overall community abundance, and community richness. We predicted that prolonged and annual drought would have stronger negative effects on community abundance and richness than short-term drought, as drought effects may accumulate over time, though we

Table 1
Results for three Bayesian Generalized Linear Mixed Models (GLMM), estimating the effects of a short-term (iSPEI-03), annual (iSPEI-12), and prolonged (iSPEI-36) drought index on relative abundance of birds of the warm deserts of the southwestern USA between 1998 and 2022. Parameters are shown for the community-level means, calculated across species. Rows of particular interest are italicized and gray.

	Posterior mean	Posterior Std. Dev.	95% CI-L	95% CI-U
Intercept	-1.38	0.18	-1.73	-1.03
iSPEI-03	*-0.06*	*0.02*	*-0.09*	*-0.02*
Water	0.02	0.07	-0.11	0.15
Shrubland	0.40	0.16	0.11	0.72
Ordinal day	0.06	0.04	-0.01	0.13
Year	*-0.08*	*0.03*	*-0.13*	*-0.02*
iSPEI-03 : Water	0.03	0.01	0.00	0.06
iSPEI-03 : Shrubland	0.00	0.02	-0.03	0.04
Intercept	-1.38	0.18	-1.73	-1.04
iSPEI-12	*-0.09*	*0.03*	*-0.14*	*-0.04*
Water	0.02	0.07	-0.10	0.15
Shrubland	0.41	0.15	0.12	0.74
Ordinal day	0.06	0.04	-0.01	0.13
Year	*-0.06*	*0.03*	*-0.11*	*-0.00*
iSPEI-12 : Water	0.04	0.01	0.01	0.06
iSPEI-12 : Shrubland	0.02	0.03	-0.04	0.09
Intercept	-1.38	0.18	-1.74	-1.04
iSPEI-36	*-0.05*	*0.03*	*-0.10*	*0.01*
Water	0.03	0.06	-0.09	0.16
Shrubland	0.41	0.16	0.12	0.73
Ordinal day	0.05	0.04	-0.02	0.12
Year	*-0.07*	*0.03*	*-0.13*	*-0.01*
iSPEI-36 : Water	0.03	0.02	-0.00	0.06
iSPEI-36 : Shrubland	0.00	0.04	-0.08	0.08

predicted this to vary by species. We further predicted that drought effects on community abundance would be more pronounced than those on community richness, in the form of larger percentual declines in relative abundance than apparent species richness, as abundance declines for individual species logically precede richness declines.

2. Methods

2.1. Study area

Our study area (246,059 km^2) comprises the warm deserts of the southwestern USA, the Mojave Basin and Range, and Sonoran Desert Level III ecoregions of the USA (Omernik and Griffith, 2014), which include parts of California, Arizona, Nevada, and Utah (Fig. 1). The average land cover composition at survey routes was 72.77 % shrubland, 8.04 % cropland, 7.45 % developed land, 7.05 % barren land, 2.32 % wetland and woody wetland, and 0.85 % water (USGS, 2025). Land cover was relatively consistent throughout the study period, with developed cover having the highest change across the study duration (σ = 0.91 %; Appendix A). Warm deserts have relatively arid conditions and average annual temperatures >17 °C (Kottek et al., 2006), and since 1950 the study area has seen increased frequencies of annual and multi-year droughts, a pattern expected to intensify throughout the 21st century (van den Bosch et al., 2024).

2.2. North American Breeding Bird Survey

The North American Breeding Bird Survey (BBS) was initiated in 1966 as annual avian transect surveys throughout North America, with data collected during the presumed breeding season of birds in a particular region. We compiled data collected by volunteer observers within our study area for 1998–2022, as point-specific count data were not available prior to this period. This totaled 25 years of data as no surveys were conducted in 2020 due to the COVID-19 pandemic. Of these data 96.06 % were collected in May and June, with the remainder collected in late April. Observers conduct 3-min point counts at 50 points along a ± 40 km transect, with point locations spaced approximately every 800 m along the transect. While the starting point and approximate transect paths are known, observers often deviate from the 800 m distance intervals or even route paths due to the need to safely park a vehicle at each location (Ziolkowski, pers. comm.). Uncertainty in point count locations therefore increases with distance along the transect, so we retained data from the first five count locations of each survey route (Cady et al., 2019). To reduce zero-inflation, we aggregated count data across the five points retained for each survey route. Hereafter, groups of five count locations are referred to as routes, and data from a particular year are called route-years. Of the 75 routes in our study area, we omitted routes with fewer than five route-years, so that the average route in our dataset had 15.5 years of data (σ = 5.7). To ensure models were based on sufficient data and to eliminate convergence problems, we retained only relatively common species which occurred in at least 10 % of route-years. We removed data for non-native (2) and nocturnal (3) species and Red-winged blackbird (*Agelaius phoeniceus*), as counts for the latter species were a strong positive outlier within the dataset. We retained data for 38 species counted across 47 routes by 87 unique observers.

2.3. Land cover

We extracted water, shrubland, and cropland cover from the North American Land Change Monitoring system, which together constitute about 90 % of land cover across the study area (USGS, 2025). We used annual land cover datasets spanning 1998–2022 to account for land cover change across the study period by matching bird survey data to its respective annual land cover dataset, though land cover change was low across the study period (Appendix A). For each route-year, we extracted land cover data for the combined 400 m buffers around the five approximate point count locations constituting a route, as observers are asked to record all birds within a 400 m radius from each location. We then calculated the percentage of each land cover type across the aggregated buffers for that route.

2.4. Drought index

We used the Standardized Precipitation-Evaporation Index (SPEI) as a measure of drought. SPEI is based on precipitation and potential evapotranspiration and is therefore relevant when assessing drought within the framework of climate change, which implies changing global surface temperatures (Beguería et al., 2014). SPEI values represent deviations in the climatic water balance from a long-term historical average and have $\bar{x} = 0$ and $\sigma = 1$. We inverted SPEI values (hereafter; iSPEI) for intuitive interpretation in regression models, whereby positive iSPEI values indicate drier conditions, so that positive effects of drought on a response variable (i.e. relative abundance) are expressed in positive numbers. iSPEI values are 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).

We extracted iSPEI data on a ± 5 × 5 km resolution from the nClimGrid-Monthly dataset (Vose et al., 2014) for June of the years 1998–2022. Values are fitted to a gamma distribution for standardization and then calibrated against a long-term average for the period 1895–2013. This dataset uses the Thornthwaite method to estimate potential evapotranspiration to construct iSPEI values. We considered iSPEI on three timescales representing short-term drought preceding the breeding season (3-month), annual drought (12-month) and prolonged

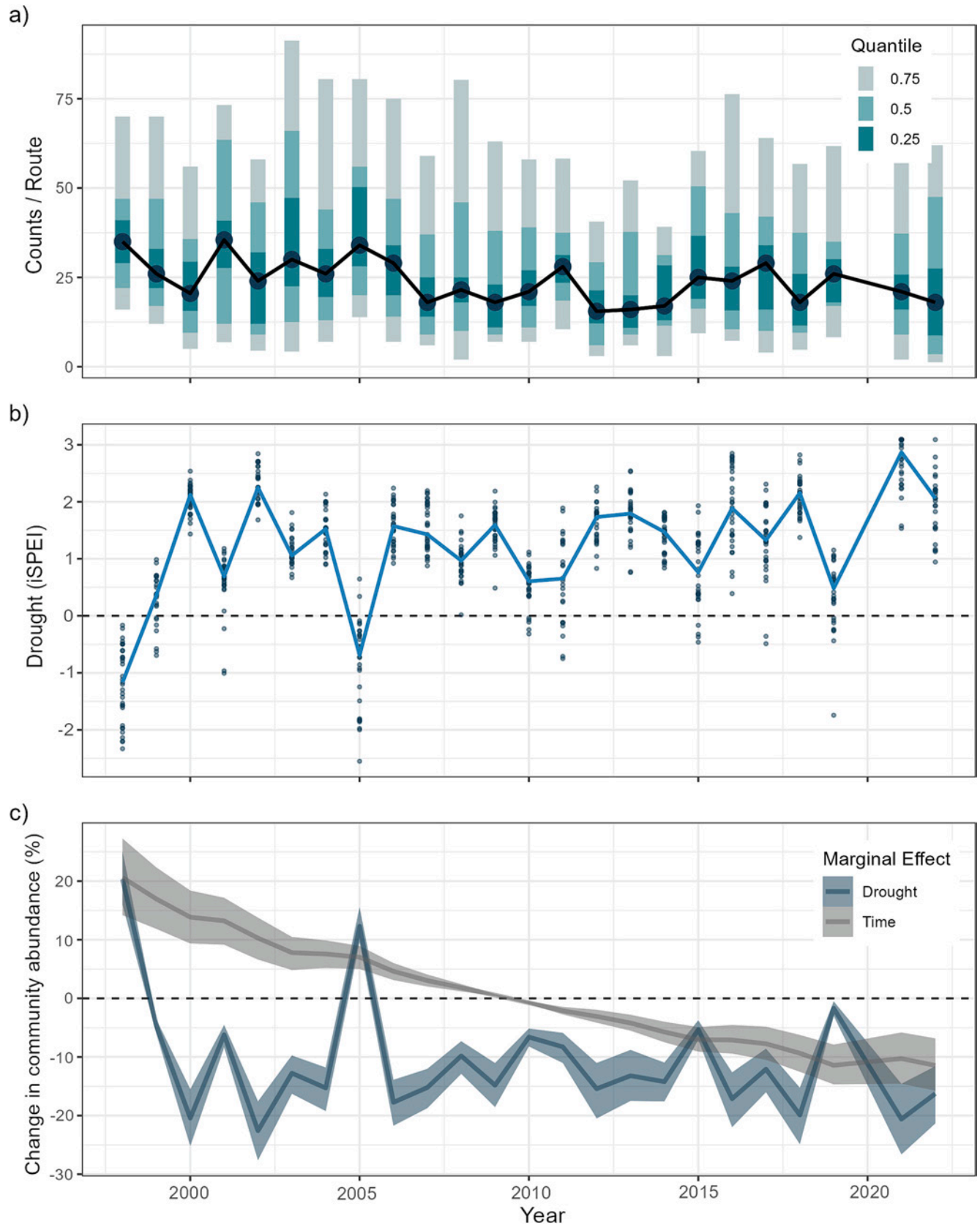

Fig. 2. (a) Aggregated bird counts across route-year combinations, shown as the median and 25–75 quantiles for routes surveyed that year. (b) Observed values for an annual drought index – iSPEI 12 – whereby positive values indicate drier conditions than the 1895–2013 average. Dots represent annual drought conditions at individual routes and the line represents the median condition among routes. (c) Predicted difference in the relative community abundance attributed to annual drought (observed iSPEI 12 – the 1895–2013 average) and time (Year – mean Year) with all other parameters held constant.

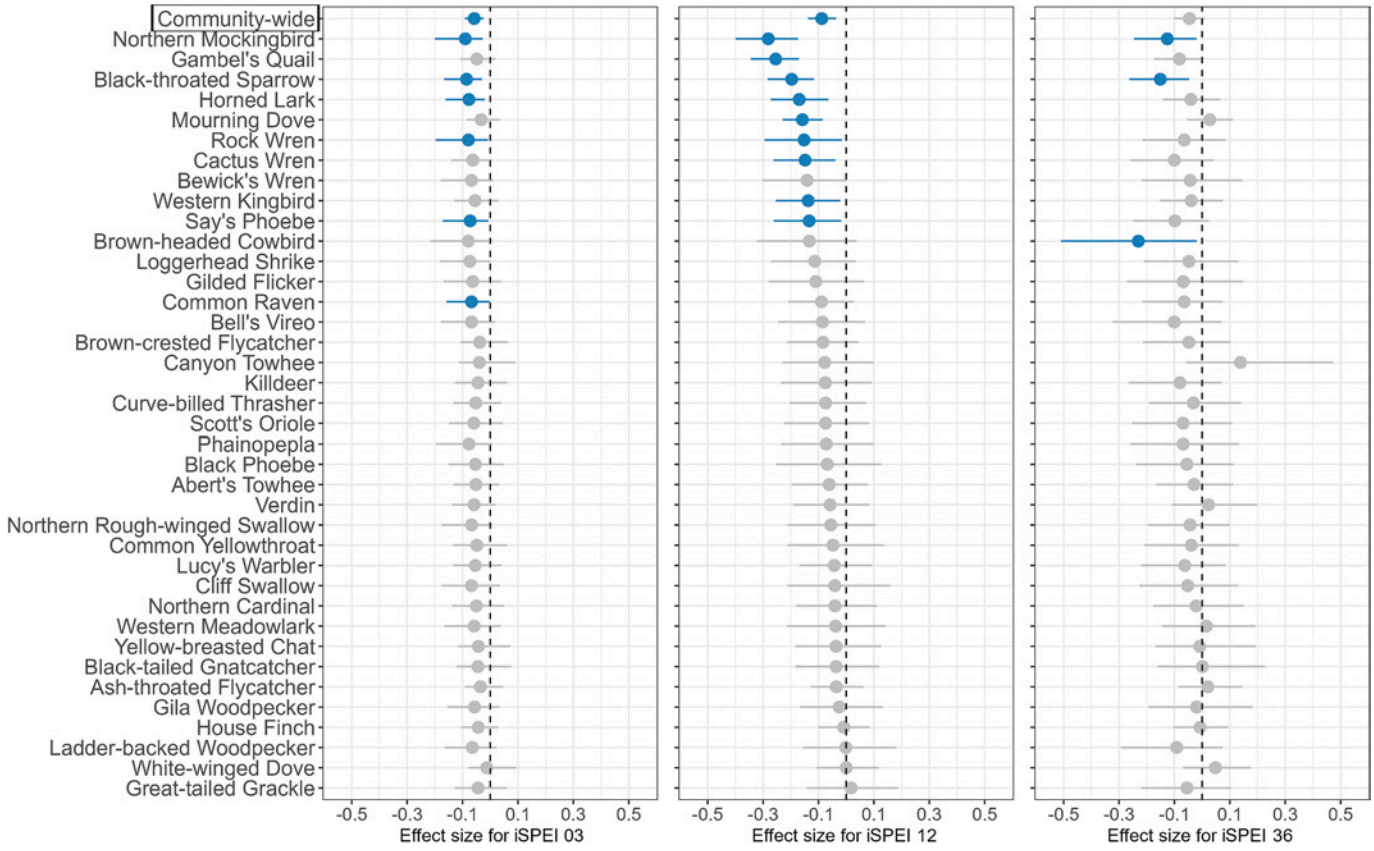

Fig. 3. Effect sizes of short-term (iSPEI 03), annual (iSPEI 12), and prolonged (iSPEI 36) drought on the relative abundance of 38 avian species of a warm desert community in the southwestern USA. Dots indicate median effect sizes for the community and individual species along with 95 % credible intervals. Effect sizes not overlapping with zero are colored blue. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

drought (36-month), as drought on different timescales can affect species differently (Prugh et al., 2018; Cady et al., 2019). iSPEI uses rolling time windows, representing the cumulative water balance over a particular number of months preceding the target month (Vicente-Serrano et al., 2010). iSPEI values were extracted for the aggregated 400-m buffers around the five point locations of each route. Because these values are spatially correlated, the variability introduced by routes intersecting multiple iSPEI cells is small (mean standard deviation between versus within routes was 0.43 versus 0.03). For route-years where polygons overlapped with multiple iSPEI cells, we therefore calculated weighted averages of these values.

2.5. Relative abundance and apparent richness models

Routes were sampled once annually, thus detection probability could not be modeled as this typically requires repeated samples within a short timeframe (e.g., Kéry and Royle, 2016). We therefore estimated the effect of droughts on the relative abundance and apparent species richness of birds, using Bayesian Generalized Linear Mixed Models (GLMM). Because we were interested in drought effects at different timescales, we created separate models for each iSPEI timescale (3, 12, and 36-month). This allowed us to assess the temporal scale which best captures drought responses without overparameterizing the models. Predictor variables included iSPEI on the relevant timescale, whereby an iSPEI coefficient reflects the effect of a one-standard-deviation anomaly at a particular timescale (Vicente-Serrano et al., 2010), percentual cover of shrubland and water, year, and ordinal day of each survey. We removed percentage of cropland from consideration as it was correlated with percentage of shrubland ($r = -0.77$), and there were no high correlations among other covariates ($r \leq 0.7$; Anderson and Burnham, 2002). We included year as a continuous fixed effect to account for long-term abundance changes in bird populations unrelated to iSPEI, and we included ordinal day to account for variation in counts due to the timing of the survey within the breeding season. We scaled all continuous variables ($\bar{x} = 0$ and $\sigma = 1$) and log-transformed land cover variables which are bound by zero.

We created three community relative abundance models using a negative binomial error distribution. iSPEI and the land cover variables were modeled in interaction, as birds may change habitat associations under drought conditions (Goldstein et al., 2024). Route-species combinations were included as random intercepts to account for species-specific variability in abundance among routes. Effects of all predictors were also allowed to vary by species as random slopes and community-level hyperparameters were estimated as the distribution of species-level parameters. Posterior distributions were sampled using 3 Hamiltonian Monte Carlo Markov Chains for a total of 6000 iterations (50 % warm-up). We utilized posterior draws to estimate species-specific and community-level responses. The three apparent species richness models employed a Poisson distribution, with the same fixed effects as the relative abundance models but route ID as a random factor to account for variability in species richness among routes. Posterior distributions for the species richness models were sampled identically to the relative abundance models. For all models, we used the following regulating priors on the log-scale (McElreath, 2018):

Intercept: $\text{norm}(\bar{x} = 0, \sigma = 5)$
Fixed effects: $\text{norm}(\bar{x} = 0, \sigma = 5)$
Random effects standard deviations: $\text{Exp}(1)$

Models were constructed using the *brms* package which uses Stan as a backend for Bayesian inference (Bürkner, 2017) in R 4.3.2 (R Core

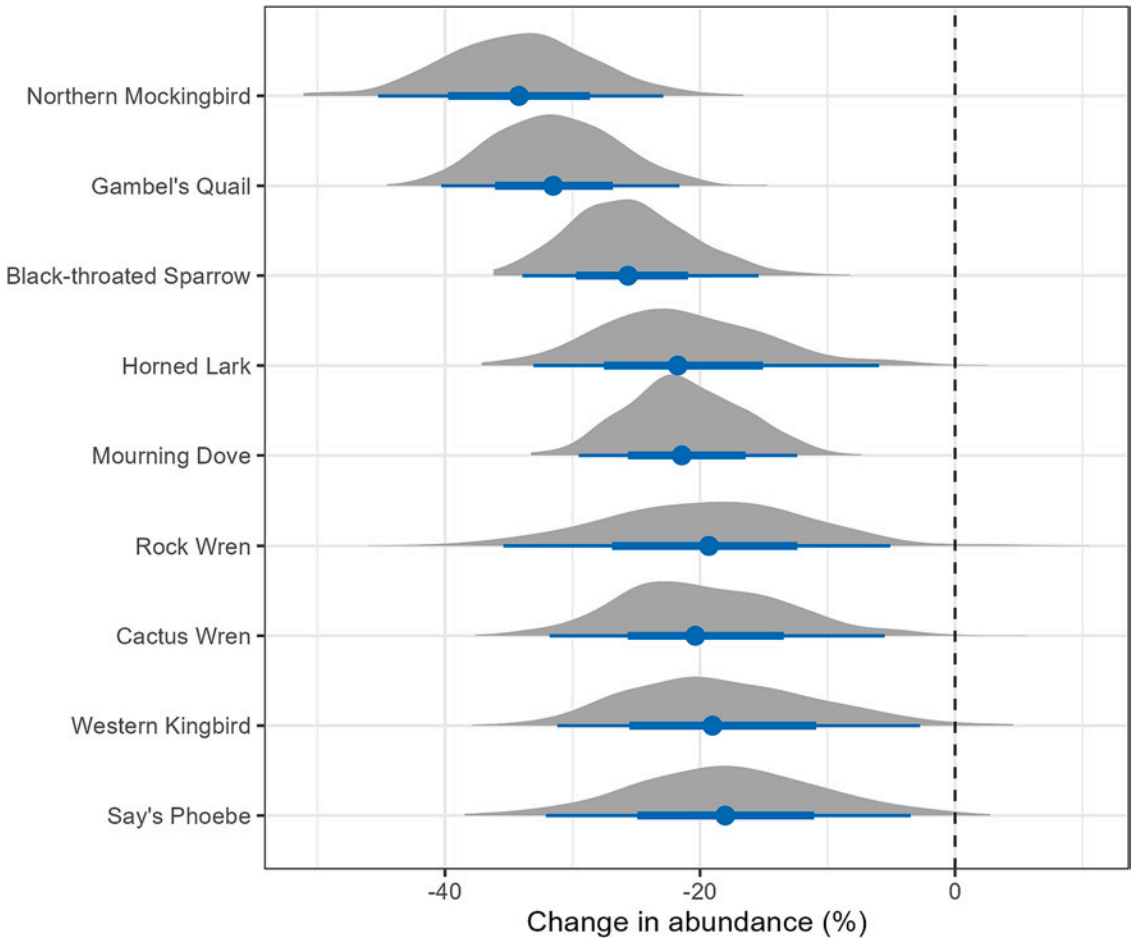

Fig. 4. Predicted change in relative abundance for selected bird species under conditions that meet the threshold of severe annual drought (iSPEI 12 = 1.5) compared to the average historical conditions (iSPEI 12 = 0) between 1895 and 2013. Predicted posterior probability densities in gray, with blue dots showing the species means along with 50 % (thick) and 95 % (thin) credible intervals. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Team, 2023). Traceplots and R-hat values were assessed for proper mixing and model convergence, and all R-hat values associated with parameter estimates were ≤ 1.01. In presenting and discussing results, we largely focus on results for which 95 % credible intervals did not overlap with zero, implying a 97.5 % certainty of a positive or negative effect on relative abundances or apparent species richness.

3. Results

3.1. Relative abundance models

Drought on all timescales appeared to have a negative effect on bird community abundance, thus the mean abundance effect across species (Table 1). The negative effects of short-term and prolonged drought were smaller than those of annual droughts. The certainty of a negative effect of prolonged drought on relative abundance was 94.8 % (calculated as the percentage of posterior samples for which the estimated effect was negative), while it was greater than 99.9 % for short-term and annual drought. Additionally, each model suggested a negative relationship between the year of data collection and relative bird abundance, implying overall bird abundance declined across the duration of our study period. These temporal effects were about twice as strong as negative effects of short-term and prolonged drought, but weaker than the negative effect of annual drought on abundance. Under short-term and annual drought, abundance was found positively related to the percentage of open water (Appendix B), while in the prolonged drought model this effect had a slightly lower probability of 96.1 %. For individual species, the interactions between iSPEI and open water was estimated positively for nearly all species, implying a positive relationship between open water and abundance under increasing drought, though with probabilities below 95 % for all. Interactions between drought and the percentage of shrubland had no notable effect on bird abundance.

Most years in our study period had conditions of severe or extreme drought, with iSPEI 12 values averaged across routes >1.5 and > 2, respectively (Fig. 2). The wettest and driest year within the study period had average iSPEI values of little under −1 and nearly 3, respectively. The annual drought model predicted an approximate 40 % average decline in community abundance between these extremely wet and dry years (Fig. 2). Short-term conditions followed a similar pattern as annual conditions, whereby conditions were severely or extremely dry in most years with only a few years with short-term conditions wetter than the long-term average. This resulted in consistent, but smaller predicted abundance declines for the full community under iSPEI 03 compared to iSPEI 12 (Appendix C). The entire study period was drier than the long-term average when considering drought on a prolonged timescale (iSPEI 36 > 0), with predominantly severe or extreme prolonged drought conditions. This resulted in consistent declines in predicted abundance on the community level, though the magnitude of decline in community abundance resulting from this was highly uncertain (Appendix C).

The magnitude of drought sensitivity varied by species with 9 out of 38 species having a > 97.5 % probability of annual drought negatively

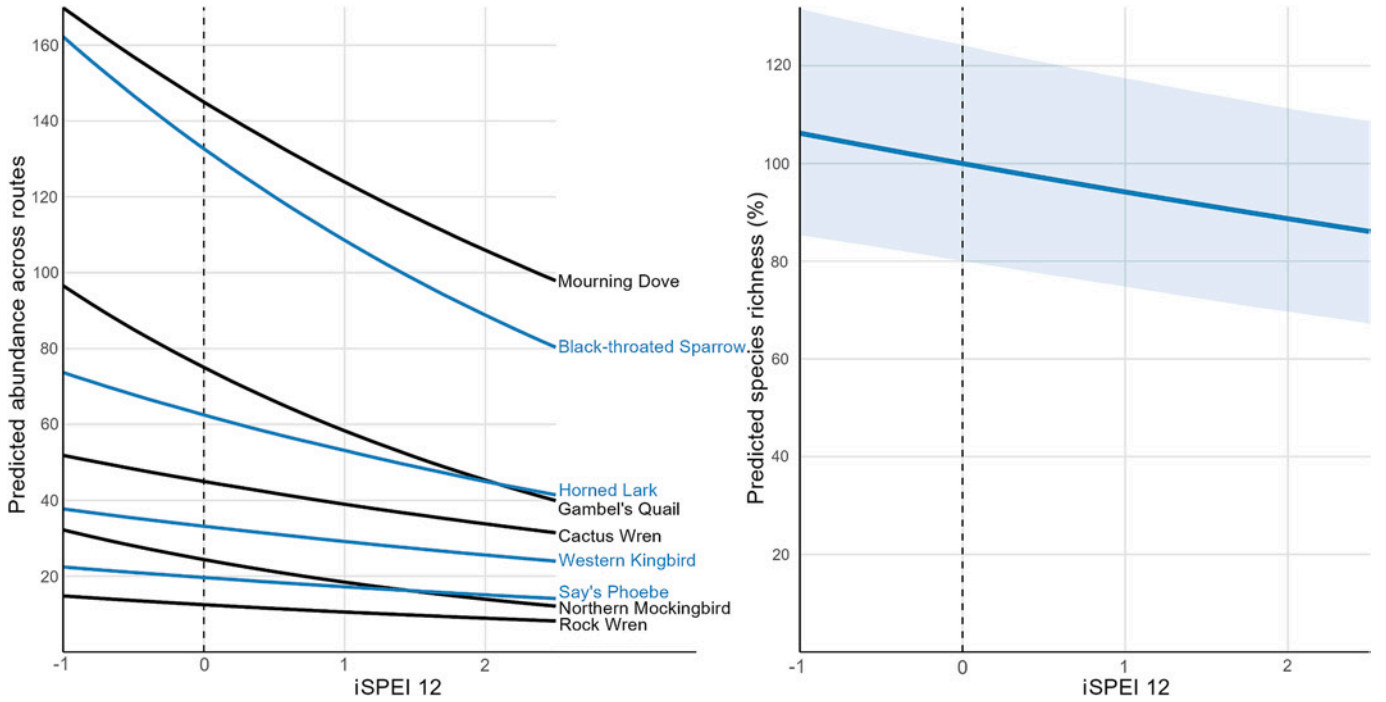

Fig. 5. Marginal effects of drought (iSPEI 12) on the relative abundance of selected bird species (left panel) and apparent species richness (expressed as a percentage of an average year; right panel) in the warm deserts of the United States. Model predictions are limited to the observed iSPEI 12 range between 1998 and 2022, which include moderately wet conditions compared to the historical average (−1) to extreme annual drought (2.5). Left panel: colorization used only to visually separate species with similar abundance trends, see appendix D for associated uncertainty estimates.

affecting abundance (Fig. 3). This number decreased to five and three species for short-term and prolonged drought, respectively. Two species, Northern mockingbird (*Mimus polyglottos*) and Black-throated sparrow (*Amphispiza bilineata*) responded negatively to iSPEI on all three timescales, while no species responded positively to higher aridity on any timescale.

For the nine species with the highest certainty of decline under annual drought, predicted declines in abundance for a year meeting the severe drought threshold (iSPEI 12 = 1.5) compared to the average long-term conditions (iSPEI = 0) ranged from 18 % (Say's phoebe, *Sayornis saya*) to 34 % (Northern mockingbird) (Fig. 4). For the six and three species with the highest certainty of decline under short-term and prolonged drought, respectively, median abundance declines were smaller under short-term drought, compared to annual drought, and smaller or associated with high degrees of uncertainty under prolonged drought (Appendix D). The variability in estimated effect size for the three species most likely affected by prolonged drought varied strongly, while estimated short-term drought effects were smaller but varied little among species (Fig. 3). Due to the varying baseline abundance across species, bird species most sensitive to drought did not necessarily contribute to the greatest absolute declines (Fig. 5; Appendix D).

3.2. Apparent species richness models

Similar to the relative abundance models, arid conditions on all timescales appeared to negatively affect avian species richness in the warm deserts of the southwestern USA (Table 2). The negative effects of short-term and prolonged drought were smaller than those of annual droughts, and the certainty of a negative effect of prolonged drought was lower at 91.8 %. Additionally, each model suggested a negative relationship between the year of data collection and species richness, implying overall richness declined across the duration of our study period. These temporal effects were slightly stronger than the negative effects of short-term and prolonged drought, and slightly weaker than the negative effects of annual drought. No notable interactions were found between aridity on any timescale and the percentage of either water or shrubland in their effects on species richness.

The predicted decline in apparent species richness in a year considered severely dry (iSPEI 12 = 1.5) compared to conditions representing the long-term average (iSPEI 12 = 0) was 12 % (Fig. 5), though when considering conditions on a short-term and prolonged timescale, the predicted declines under drought dropped to about 5 % (Appendix D).

4. Discussion

Particularly in aridland, where species live closer to the limit of physiological tolerances, increasing drought due to climate change emerges as a major threat to biodiversity. The bird communities of the warm desert ecoregions of the southwestern USA declined under droughts of various durations. The strongest declines in relative bird abundance and apparent species richness relate to year-long droughts, and abundance declines related to annual drought were estimated to be larger than the overall negative trend in abundances independent of drought. This suggests year-long droughts as a primary driver of avian abundance declines in aridland. While the stronger effects of annual droughts compared to short-term droughts aligns with our expectation, the smaller and less certain negative effects of prolonged drought did not. Our prediction that bird abundance declines would be more pronounced than declines in species richness was supported, regardless of drought duration. However, it is important to acknowledge this analysis only included relatively common species, while rarer species may have disproportionate effects on species richness. Most importantly, about 30 % of bird species in the community were highly certain to decline under droughts of at least one duration. Certain species were subject to 18–34 % declines under severe annual drought (iSPEI-12 = 1.5, while the maximum during the study period was 3.09), and higher declines in abundance could be expected under more extreme drought.

Previous analysis of Breeding Bird Survey data spanning 1966–2011 estimated declines for 88 % of birds in aridland of the western USA, with a 40 % composite abundance decline for 17 obligate aridland species

Table 2
Results for three Bayesian Generalized Linear Mixed Models (GLMM), estimating the effects of a short-term (iSPEI-03), annual (iSPEI-12), and prolonged (iSPEI-36) drought index on apparent avian species richness in the warm deserts of the southwestern USA between 1998 and 2022.

	Posterior Mean	Posterior Std. Dev.	95% CI-L	95% CI-U
Intercept	1.81	0.11	1.60	2.02
iSPEI-03	*-0.03*	*0.01*	*-0.06*	*-0.00*
Water	-0.10	0.09	-0.28	0.07
Shrubland	-0.02	0.08	-0.18	0.14
Ordinal day	0.01	0.02	-0.03	0.04
Year	*-0.06*	*0.02*	*-0.09*	*-0.03*
iSPEI-03 : Water	0.02	0.01	-0.01	0.05
iSPEI-03 : Shrubland	0.00	0.02	-0.03	0.03
Intercept	1.80	0.10	1.60	2.01
iSPEI-12	*-0.06*	*0.02*	*-0.09*	*-0.03*
Water	-0.11	0.09	-0.30	0.07
Shrubland	-0.01	0.08	-0.17	0.14
Ordinal day	0.02	0.02	-0.02	0.05
Year	*-0.04*	*0.02*	*-0.07*	*-0.01*
iSPEI-12 : Water	0.02	0.01	-0.01	0.05
iSPEI-12 : Shrubland	-0.01	0.02	-0.05	0.03
Intercept	1.80	0.10	1.61	2.00
iSPEI-36	*-0.02*	*0.02*	*-0.06*	*0.01*
Water	-0.10	0.09	-0.28	0.07
Shrubland	-0.01	0.08	-0.16	0.15
Ordinal day	0.01	0.02	-0.03	0.04
Year	*-0.05*	*0.02*	*-0.08*	*-0.02*
iSPEI-36 : Water	0.01	0.01	-0.02	0.04
iSPEI-36 : Shrubland	-0.00	0.02	-0.06	0.03

(Sauer et al., 2013). These findings were supported using data from various avian surveys for 1970–2024, with an average 41 % decline for 31 aridland specialists (NABCI, 2025). Moreover, together with shorebirds, the obligate aridland species were the only group without any species showing abundance increases (NABCI, 2025). Our results strongly aligned with these findings as we found abundance declines throughout time for both obligate and non-obligate aridland birds. In addition, our models show that drought is a primary driver of these declines for a variety of species, and that neither short-term nor long-term drought have a positive effect on the abundance of any species within this community.

Alarmingly, the frequencies to which this avian community is exposed to drought is projected to strongly increase. Between 2050 and 2080, the Mojave basin and Sonoran desert ecoregions are projected to be subject to four- and fivefold increases, respectively, in annual drought frequency compared to 1951–2005 (van den Bosch et al., 2024). Similarly, an approximately elevenfold increase in the frequency of prolonged droughts is predicted for both ecoregions. These projections combined with our results suggest future declines for this avian community are likely. This may prove particularly problematic for species our models show to experience moderate to larger declines under aridity levels that will frequently be surpassed in the future (Wahl et al., 2022; van den Bosch et al., 2024), such as Northern mockingbird (*Mimus polyglottos*), Gambel's quail (*Callipepla gambelii*), and Black-throated sparrow (*Amphispiza bilineata*).

Our analysis does not fully address all aspects of drought related to avian abundance and species richness, as in addition to drought duration and intensity, drought effects also depend on drought frequency. For example, species can recover from drought periods when these are followed by periods of less hostile conditions (Bennett et al., 2014; Selwood et al., 2015). Our data was not suited to assess this, as drought on all three timescales was prevalent throughout the study period. The greater uncertainty associated with prolonged drought effects may stem from low variability in 36-month SPEI across the study period, whereby conditions measured over 36 months were consistently drier than the average historical 3-year window. This does not necessarily indicate that prolonged droughts result in weaker ecological impacts, but that their effects may be harder to detect statistically due to consistent prolonged drought throughout our study period, and potentially due to the cumulative and smoothed nature of long-term drought indices. Secondly, our results do not pinpoint the drivers of negative drought effects, though they do indicate which species are more drought-sensitive and could be prioritized in investigating the relative importance of direct (e.g. dehydration, hyperthermia) and indirect (e.g. loss of prey availability, loss of nesting material) drought effects. Such knowledge can guide conservation decision making as, for example, artificial water sources may relieve direct stress resulting from drought (Albright et al., 2017; Rich et al., 2019) but are likely insufficient to restore drought-degraded habitat.

There were no discernable common denominators in life history traits for species most likely to decline under drought, as this group contained migrants (e.g. Western kingbird, *Tyrannus verticalis*) and year-round residents (e.g. Rock wren), habitat specialists (e.g. Cactus wren) and generalists (e.g. Northern mockingbird), herbivores (e.g. Mourning dove, *Zenaida macroura*) and insectivores (e.g. Say's phoebe), and small (e.g. Black-throated sparrow) to larger-sized birds (e.g. Gambel's quail). Contrasting findings of previous studies investigating the relationship between drought responses and life history traits stress the difficulty in generalizing species responses to drought (Albright et al., 2010; Iknayan and Beissinger, 2018; Goldstein et al., 2024). Similarly, why certain species are more strongly affected by drought on a particular timescale is often difficult to pinpoint (Cady et al., 2019). It is possible that while life history traits may in certain cases drive responses to drought, birds are particularly vulnerable to the direct effects of drought in the form of dehydration and hyperthermia (Albright et al., 2017).

The presence of open water appeared to mitigate the effects of drought on the abundance, but not richness, of an aridland avian community. Open water may provide relief from dehydration or hyperthermia and potentially cause higher resource availability in the form of increased vegetative or invertebrate food resources (Albright et al., 2017). These findings should be interpreted carefully as, firstly, we classified water availability as the percentage of 900 m^2 cells surrounding the surveying route that are open water, while smaller water sources may also be valuable to birds (Abdu et al., 2018; Rich et al., 2019). Secondly, the range of water availability across survey routes was 0–3.5 % of open water cover, thus no conclusions can be drawn on the importance of water in mitigating drought-caused bird abundance or richness loss beyond water-scarce environments. Our results suggest even limited water presence may benefit avian communities of aridland during drought, and while existing literature on the importance of artificial water sources for birds predominantly concerns waterfowl and wading birds (Sánchez-Zapata et al., 2005; Kloskowski et al., 2009), these could be of increasing importance for aridland birds, given the low water availability paired with high anticipated increases in drought (Rich et al., 2019; Gorta et al., 2021).

Our results indicate declines in avian community abundance and richness under multiple drought durations, with the strongest effects associated with annual droughts. The effects of prolonged drought on avian communities have not been studied within warm deserts of the USA, and while the negative impact of prolonged drought was less pronounced, this may be caused by the prevalence of prolonged drought throughout 1998–2022. The species found to have the strongest negative relationships with drought are currently not threatened with extinction, though several are experiencing range-wide population declines (IUCN, 2023), including three aridland specialists; Cactus wren

(*Campylorhynchus brunneicapillus*), Rock wren (*Salpinctes obsoletus*), and Black-throated sparrow (NABCI, 2025). Several other common bird species of the warm deserts of the USA, which drive the abundance of the avian community and may therefore disproportionally affect ecosystem functioning and services (Winfree et al., 2015), also declined under drought. This finding supports the idea that under climate change drought has and will increasingly drive avian community collapse (Iknayan and Beissinger, 2018). Furthermore, frequency and severity increases of not only extreme drought but also precipitation and heat are of conservation concern for vertebrates (Easterling et al., 2017; van den Bosch et al., 2025). Conservation action appears urgent, and artificial water sources and the conservation of habitat that provides thermal refuge may help mitigate the negative physiological effects of drought on birds (Albright et al., 2017; Riddell et al., 2019). However, long-term climate change mitigation in the form of greenhouse gas emission reductions will be crucial to preserve livable conditions for the specialized, diverse wildlife communities of warm deserts (Ma et al., 2023).

CRediT authorship contribution statement

M. van den Bosch: Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Data curation, Conceptualization. **Z.L. Steel:** Writing – review & editing, Visualization, Supervision, Methodology, Funding acquisition, Formal analysis, Conceptualization. **J.K. Costanza:** Writing – review & editing, Conceptualization. **K.F. Kellner:** Writing – review & editing, Methodology, Conceptualization. **R.A. Peek:** Writing – review & editing, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare no conflict of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2025.111393.

Data availability

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.866t1g229.

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