


The effects of climate change and fluctuations on the riparian bird communities of the arid Intermountain West

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Abstract

Riparian corridors are critical refuges for biodiversity in arid regions like the southwestern US. Birds in particular rely on these habitats for breeding and as migratory stopover sites within a resource-scarce landscape. Climate change is likely to affect the distribution of resources across such landscapes and how birds use riparian zones. In this study, we used 15 years of bird-banding data (1994–2008) from eight riparian sites across the state of Utah to examine the effects of variation in climate and vegetation on birds at the community and population level. We used generalized linear mixed models to analyze the effects of temperature, precipitation, El Niño Southern Oscillation (ENSO) and Normalized Difference Vegetation Index (NDVI) on daily total captures, species richness and community composition. We found that total captures and species richness increased in hotter, drier, less green years and in El Niño years, and the relationships were more pronounced for non-riparian species than for species breeding in riparian zones. We also found changes in community composition in relation to temperature and precipitation. At the population level, we used capture–mark–recapture (CMR) models to analyze the effects of these covariates on the rates of population growth, recruitment and apparent survival. We found that population growth rates were negatively associated with temperature and ENSO for roughly half of the focal species. This pattern was almost entirely due to lower recruitment, likely caused by the combination of fewer resources and increased competition from the influx of non-riparian birds into riparian oases. Our results have important implications for arid areas which are expected to become hotter and drier. Reducing other anthropogenic threats to riparian corridors, such as cattle grazing and water management, is likely to increase the resilience to climate change of riparian habitats and their avian residents.

Introduction

Riparian corridors represent critical habitat for biodiversity (Naiman, Decamps & Pollock, 1993; Sabo *et al.*, 2014), providing resources, landscape connectivity and refugia for many taxa (Seavy *et al.*, 2009; Friggens & Finch, 2015), and often harboring disproportionate levels of diversity given their relatively small geographic footprint (Szaro, 1980). Riparian habitats are particularly important within arid landscapes (Szaro, 1980; Szaro & Jakle, 1985) where water availability is low and resources are generally scarce (Gaur & Squires, 2017). For birds, many species are highly dependent upon riparian zones as breeding grounds, with the

unique assemblage of riparian plants and insects providing essential habitat for nesting and offspring provisioning (Knopf, 1985; Sabo *et al.*, 2014). Birds also rely heavily on riparian corridors during migration, especially in temperate arid regions (Szaro, 1980; Strong & Bock, 1990; Parrish *et al.*, 2007). Riverine habitats serve as important stopover sites during migration when birds' energetic expenditure rises dramatically (Skagen *et al.*, 2008; Carlisle *et al.*, 2009; Fischer, Valente & Guilfoyle 2015). Riparian corridors also connect bird populations and their ecosystem services, and this connectivity is especially critical for non-migrating, sedentary bird species in fragmented landscapes (Şekercioğlu *et al.*, 2015).

Riparian zones face many anthropogenic threats. Urbanization lowers the water table and alters plant communities (Groffman *et al.*, 2003), while livestock grazing (Belsky, Matzke & Uselman 1999; Tewksbury *et al.*, 2002) reduces habitat quality and vegetative health through plant removal and soil compaction (Kauffman & Krueger, 1984). In addition to these issues, climate change is an increasing threat to birds and other biodiversity (Parmesan, 2006; Miller-Rushing *et al.*, 2008; Rosenzweig *et al.*, 2008; Wormworth & Şekercioğlu, 2011; Sheldon, 2019; Román-Palacios & Wiens, 2020). Under a changing climate, riparian corridors are predicted to become more important in connecting landscapes, allowing species to shift in response to a changing climate, and providing ecosystem services by protecting watersheds and reducing erosion (Şekercioğlu, 2009). However, climate change also threatens the riparian corridors themselves (Capon *et al.*, 2013). In addition to altering precipitation regimes and snowpack, climate change may lead to changes in the magnitude and timing of streamflow and sediment transport dynamics (Khatri *et al.*, 2019), alter riverine habitat (Hinojosa-Huerta, Zamora & Calvo-Fonseca, 2013; Friggens & Finch, 2015) and impact the biodiversity that depends on it (Seavy *et al.*, 2009). In an era when bird populations are in general decline (Rosenberg *et al.*, 2019) and the conservation status of migratory birds is declining much faster than that of sedentary species (Şekercioğlu, 2007; Horns & Şekercioğlu, 2018), there has never been a more critical time to understand the effects of climate change on riparian avifauna.

Despite their importance for avian diversity, riparian corridors are relatively understudied, particularly in the American West (Carlisle *et al.*, 2009). This region is the driest in the US (Newman *et al.*, 2015) and native bird communities are consequently dependent on these few ecological oases (Szaro, 1980; Szaro & Jakle, 1985; Skagen *et al.*, 2005; Seavy *et al.*, 2009; Sabo *et al.*, 2014). Little is known about how breeding and migratory birds in riparian habitat may be affected by climate change. Migrant and breeding birds are influenced by the availability of suitable vegetation, food resources and water (Hutto, 1985; Yong *et al.*, 1998; Kelly, Finch & Yong, 2000; Moore, 2000; Sapir *et al.*, 2004; Hinojosa-Huerta *et al.*, 2008). These resources in turn are likely to be modified by climate change (Hinojosa-Huerta *et al.*, 2013; Friggens & Finch, 2015). In particular, the southwestern US is projected to become increasingly hot and dry (Seager & Vecchi, 2010; Garfin *et al.*, 2013; Seager *et al.*, 2013) and these trends could lead to a reduction in habitat and resource availability across the landscape (Hinojosa-Huerta *et al.*, 2013; Friggens & Finch, 2015). For birds, a drying climate may negatively impact obligate riparian species (Hinojosa-Huerta *et al.*, 2013), concentrating them in a more optimal habitat (Skagen *et al.*, 2005; Banville *et al.*, 2017) where they face increased competition (Hutto, 1985; Moore & Yong, 1991). On the other hand, we could observe more birds from other habitats utilizing riparian areas (Hinojosa-Huerta *et al.*, 2013) as resources in other habitats decline. In addition to long-term climate trends, fluctuating climatic events, such as extreme droughts or El Niño events, can affect bird communities (Sillert, Holmes &

Sherry, 2000; LaManna *et al.*, 2012; Hinojosa-Huerta *et al.*, 2013), and the responses of birds to climate variability could be used to predict their responses to long-term climate change.

In order to enable informed and effective conservation of riparian habitats and their species, it is imperative that we understand how birds in riparian areas are responding to climate change and climate variability. At the community level, it is important to measure levels of species richness and abundance in relation to climate change (Blake & Loiselle, 2015; Banville *et al.*, 2017; Iknayan & Beissinger, 2018; Stouffer *et al.*, 2020). For example, in the surrounding desert habitats of the southwest, long-term increases in temperature and aridity have negatively impacted desert bird communities (Iknayan & Beissinger, 2018). Yet, community-level patterns are emergent properties of the demographic processes of individual populations. It is, therefore, critical to monitor the demographic rates of birds in relation to climate change (Santisteban *et al.*, 2012; Dybala *et al.*, 2013; Cruz-Mcdonnell & Wolf, 2016; Neate-Clegg *et al.*, 2021) and climate variability (Sillert *et al.*, 2000; Robinson, Baillie & Crick, 2007; Grosbois *et al.*, 2008; LaManna *et al.*, 2012).

To investigate the effects of climate change and climate variability on the riparian bird communities of the Intermountain West, we analyzed 15 years of bird banding data from eight sites across the state of Utah to assess changes in bird diversity, community structure and demographic rates. We examined changes in daily total captures, species richness and community composition between 1994 and 2008 in relation to interannual variation in temperature, precipitation, climate oscillations and landscape greenness. We also separated species into those that breed primarily in riparian habitat and those that do not, and compared their responses to the environmental variables. Finally, for a subset of riparian species we used capture–mark–recapture (CMR) models to analyze changes in the rates of population growth, recruitment and apparent survival in relation to the same environmental variables. The results presented in this study provide crucial information on the relationships between climate and riparian bird diversity and demography in the southwestern US. This information may help to predict future effects of climate change on the avifauna of western North America and can help to inform conservation management decisions for riparian ecosystems in the region.

Materials and methods

Locations and bird banding

In the early 1990s, the landbird conservation group Partners in Flight raised concerns that riparian bird populations were declining at an alarming rate. In response, the Utah Division of Wildlife Resources (UDWR) initiated a riparian bird-monitoring program in 1992. In 1994, UDWR added mist netting operations to selected existing point-transect survey sites. Potential survey sites were distributed randomly along non-ephemeral river and stream segments across the state.

Sites were selected preferentially if they were situated on publicly managed and accessible land, with sufficient vegetation to conceal the nets. Between 1994 and 2008, the agency ran a total of 14 banding stations, varying in duration from 1 to 15 years. All stations were located along perennial streams and were placed in habitat representative of the riparian area as a whole. For this study, we analyzed data from eight of these banding stations (Fig. 1, Supporting Information Table S1) that had ≥ 8 years of data. These eight stations were representative of two physiographic regions that display broad-scale differences in habitat driven by differences in elevation and latitude. The Utah Mountains region (sites: DUTC, SLC1, RUSH and NEPH) in north-central Utah is high in elevation (1777–1936 m) while the Southern Deserts region (sites: MOAB, MONT, SMOK and STGE) is lower in elevation (1041–1550 m), hotter, drier and less green (Supporting Information Figure S1). All sites experience summer troughs in precipitation, but sites varied in the occurrence of peak rainfall (Supporting Information Figure S2).

At each banding station, UDWR followed and contributed to the Monitoring Avian Productivity and Survivorship Program (MAPS, Desante, Williams & Burton 1993; <https://www.birdpop.org/pages/mapsMap.php>) during the breeding season (Apr–Sep). MAPS is a nationwide standardized bird-banding collaboration that monitors bird populations across hundreds of bird-banding stations. In this study, birds were handled and banded following the Bander's Code of Ethics and authorized under a Federal Bird Banding and Marking Permit (#21673) provided by the Bird Banding Laboratory (USGS). The stations were operated for 10–27 days per year (median = 12) spread out over the season. Each banding day consisted of 6 h of sampling with a uniform number of nets. All birds were identified to species level, aged and sexed if possible, and a number of body size and condition metrics were taken.

Climate and greenness

To represent local climate, we used data from Parameter-estimation Regressions on Independent Slopes Model (PRISM,

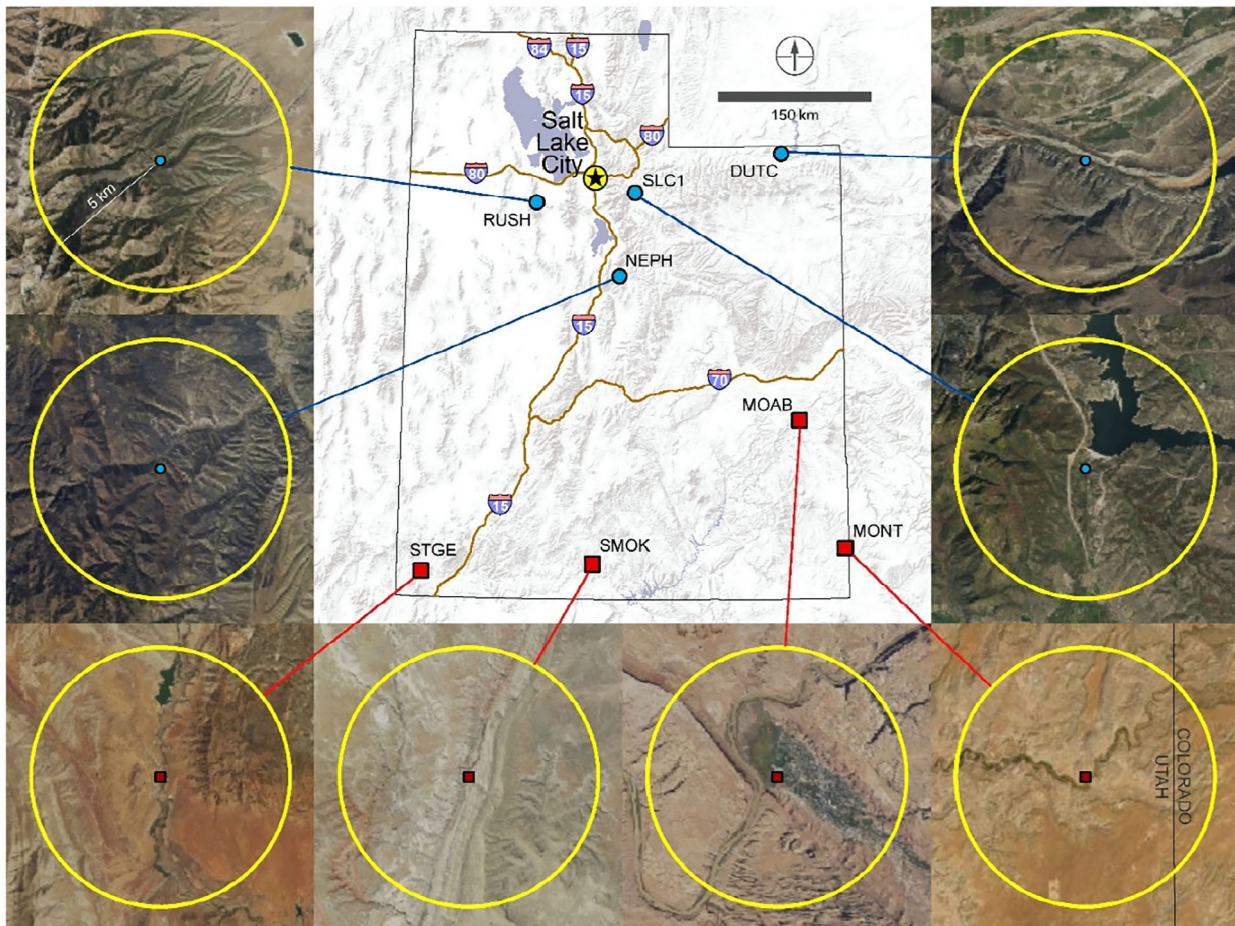


Figure 1 A map of eight riparian bird-banding stations located within Utah, US, surveyed over 15 years (1994–2008). Four stations (blue circles) were located within the northern mountains of Utah. Four stations (red squares) were located within the southern deserts. Subsets show aerial imagery of each station at 5-km radii. Aerial imagery (2018) is from the US Department of Agriculture's NAIP program. The terrain base map is from ESRI.

2004). PRISM provides monthly interpolated mean temperature and total precipitation data (AN81m data elements tmean and ppt) for the US at a pixel resolution of 2.5 arc seconds (~ 4 km at the latitude of our study sites). We computed mean temperature and precipitation around each sampling site, for each month from 1993 through 2008, by sampling all pixels whose centroids fell within a 5-km radius of the site using the Buffer and Zonal Statistics tools in ArcGIS Pro v2.4.0 (ESRI, 2019). Buffers were generated in the NAD83 UTM 12N coordinate system. Sampled pixel counts per 5-km buffer ranged from 4 to 6 due to registration effects (i.e. alignment of sampling site with the PRISM grid). From these sampled values, we calculated the mean of monthly mean temperatures (hereafter 'temperature') and the total of monthly precipitations (hereafter 'precipitation') for the 12-month period (October through September) preceding and including the bird survey periods. We used these annual-resolution climate variables rather than higher temporal-resolution variables as we were concerned with interannual dynamics pertinent to conservation trends and management actions, as opposed to the seasonal dynamics associated with intra-annual processes such as migration. In preliminary analyses, we tried different temporal windows (e.g. 6 mo, April–September; 9 mo, January–September) but these data were highly correlated (12-mo temp ~ 9-mo temp, $r \approx 1$; 12-mo temp ~ 6-mo temp, $r = 0.98$; 12-mo precip ~ 9-mo precip, $r = 0.98$; 12-mo precip ~ 6-mo precip, $r = 0.88$) and led to qualitatively similar results. We opted for the October to September period in order to capture the annual water and vegetation phenocycle that defines the landscape of resource availability for birds in each annual season, including winter precipitation and summer rains.

Most of the bird species in this study do not remain in Utah year-round, but in winter migrate south to Central or South America. Their fitness can, therefore, be affected by weather across the annual cycle in different regions. To represent transcontinental variation in climate, we investigated the effects of the El Niño Southern Oscillation (ENSO), a multi-annual periodic fluctuation in winds and sea surface temperature across the tropical Pacific which affects global weather patterns (NOAA, 2021). We used the Multivariate ENSO Index (hereafter 'ENSO'), available at monthly resolution from the Physical Sciences Laboratory (NOAA, 2020). ENSO values are anomalies fluctuating about 0. Positive ENSO values correspond to El Niño events (high sea surface temperature and low pressure in the eastern Pacific) while negative values correspond to La Niña events (low sea surface temperature and high pressure in the eastern Pacific). Although ENSO cycles occur over many years, there were multiple El Niño events during the 15-year study period. Previous studies have used ENSO values (or similar indices, e.g., Southern Oscillation Index) to assess changes in various metrics including apparent survival (Mazerolle *et al.*, 2005; LaManna *et al.*, 2012; Wolfe, Ralph & Elizondo, 2015), avian productivity (Sillert *et al.*, 2000; Nott *et al.*, 2002; Mazerolle *et al.*, 2005), recruitment of males (Ryder & Sillert, 2016), numbers of breeding pairs (Marchant, Guppy & Guppy, 2016), species richness (Jaksic & Lazo, 1999) and

arthropod abundance (Lister & Garcia, 2018). The effects of ENSO vary across the globe. El Niño events are known to produce hot, dry conditions in South America, but in the southwestern US, El Niño events correspond to higher-than-average precipitation. As with our local climate variables, we averaged ENSO values over the 12 months from October through September.

To represent resource availability (food and habitat), we used the Normalized Difference Vegetation Index (NDVI), a measure computed from reflectance in red and near-infrared wavelengths of remotely sensed imagery that correlates with the amount of healthy green vegetation (Carlson & Ripley, 1997). We used the 30-m Landsat-derived NDVI data product developed by Robinson *et al.* (2017) and represented landscape greenness each year with data from two 16-day composites starting respectively at day-of-year (DOY) 129 and 157. These DOYs begin 16-day Landsat revisit periods (09–24 May and 14–30 Sep respectively) most closely representing the months of May and September, when migration peaks. As described by Robinson *et al.* (2017), for the majority of our study period – April 1999 through December 2008 – both Landsat 5 and Landsat 7 satellites were operational, guaranteeing at least two observations per 16-day window from which to composite the highest quality observation. Independent of the number of satellites, at the mid-latitudes of our study area there is significant overlap (~ 30%) between adjacent Landsat orbital paths, so a given point will be imaged multiple times on successive overpasses of the same satellite. In practice, the combination of these two characteristics of the Landsat record typically provides multiple candidate observations of our study sites from which to composite a 'best' pixel value, even when restricting temporal support to a span as short as the nominal 16-d revisit period. Where the Landsat archive does not provide any viable observations for a given pixel, Robinson *et al.*'s methodology composites that pixel using climatology-driven temporal interpolation.

The NDVI values range theoretically between -1 and 1 , typically transformed to integer values between -100 and 100 allowing for storage and transmission as lower bit-depth raster imagery. Negative NDVI values are characteristically associated with cloud and snow (corrected via compositing in Robinson *et al.*'s data product), and standing or open water characteristically have NDVI values near zero. Non-snow-covered terrestrial surfaces display increasing NDVI with increasing leaf area index, although NDVI response saturates over areas where biomass is high (Huete *et al.*, 2002). Because our focus is on the impact of interannual variability in riparian (and adjacent) habitat resources, we masked out water (whose NDVI signature correlates negatively with that of vegetation in response to environmental water abundance) prior to computing mean NDVI. Because our focus is on the entire avifaunal suite observed in the study area and not only riparian specialists, we reasoned it is important to consider variation in upland resource availability when analyzing population and community dynamics. We, therefore, measured aggregate NDVI throughout the entire 5-km buffer and not only within the

riparian zone. For each composite scene, we computed the mean value of all pixels with centroids within 5 km of each sampling site, using the Zonal Statistics tool in ArcGIS Pro v2.4.0 (ESRI, 2019). Once we had compiled NDVI estimates at each site and year for the May and September composite windows, we averaged the two to produce a value more representative of the whole banding season.

To assess changes in climate and greenness across years, we regressed temperature, precipitation and NDVI against year. As these were all site-specific variables, we included physiographic region as a fixed effect and site as a random effect in linear mixed models (package 'lme4' v1.1-26, Bates *et al.*, 2015). We did not look for trends in ENSO as it is a cyclical phenomenon.

Captures, species richness and community composition

We calculated community-level metrics based on each standardized 6-h day of mist netting at each banding station (hereafter 'banding day'). For each banding day, we calculated the total captures and species richness, and these were used as response variables in generalized linear mixed models with Poisson errors (package 'lme4', Bates *et al.*, 2015). In each model, we included six fixed explanatory variables. As environmental covariates, climate was represented by temperature, precipitation and ENSO, and greenness was represented by NDVI. We also included year to account for long-term trends (Ballard *et al.*, 2003; Blake & Loiselle, 2015; Sauer *et al.*, 2017; Horns, Adler & Şekerciöğlü, 2018) that might result from a variety of reasons, including factors other than climate. Finally, we included a factor coding for our two physiographic regions (Utah Mountains and Southern Deserts; Supporting Information Table S1) to account for regional-level differences in elevation, climate and habitat (Supporting Information Figure S1). In addition to the six fixed effects, all models contained banding station as a random intercepts effect to account for site-level differences in community composition.

Sites varied greatly in temperature, precipitation and NDVI (Supporting Information Figure S1), but we were more concerned with temporal variation in environmental variables than spatial variation. We, therefore, scaled these three variables at the site level by subtracting the site mean over the 15 years and dividing by the site standard deviation. Response variables were thus modelled as a function of variation in climate across years about the local mean, not as a function of variation in climate between sites. Following this, all numerical variables including year were scaled to have a mean of 0 and a standard deviation of 1 in order to make their effect sizes comparable. Due to some moderate correlation among explanatory variables, we checked for potential issues of multicollinearity by calculating the variance inflation factors (VIF) of every variable in each model (package 'car' v3.0-10, Fox, Friendly & Weisberg, 2013), but we found no evidence of multicollinearity (all VIFs <2.5; Zuur, Ieno & Elphick, 2010). We plotted the fitted model values against the residuals to ascertain that the data met the

assumptions of the models. We also tested for overdispersion in the Poisson models using the *dispersion_glm* function from the package 'blme4' (v1.4; Korner-Nievergelt *et al.*, 2015). After constructing the models, we extracted the covariate coefficients and their associated confidence intervals. Covariates were deemed significant when the 95% confidence intervals on the coefficients did not overlap 0. Because we found that the models of total captures were overdispersed, we used the function *quasi_table* (Bolker, 2021) which adjusts the model coefficients table by multiplying the standard errors by the square root of the dispersion factors. We also used the package 'MuMIn' (v1.43.17; Bartoń, 2015) to calculate the marginal R^2 ($R^2_{GLMM(m)}$) and conditional R^2 ($R^2_{GLMM(c)}$) for each model as estimates of model fit.

Many of the bird species captured in this study breed principally in riparian areas while the rest may only pass through riparian areas on migration. To test whether different groups of birds responded differently to climate fluctuations, we used a report on the habitat usage of Utah avifauna to categorize birds as either riparian or non-riparian species. Riparian birds (~75% of captures, ~40% of species – see Results) comprised species whose primary breeding habitat is either lowland or mountain riparian. The remaining species either breed primarily in non-riparian habitat or do not breed in Utah at all, and these species were categorized as non-riparian. It is important to note that riparian breeding species do not necessarily breed at the banding stations but do breed in similar habitat. After separation, we recalculated total captures and species richness for each banding day and category and reran the models with the same model structure as above.

To examine species composition, we conducted a principal coordinate analysis (PCoA), on a Bray–Curtis dissimilarity matrix (package 'VEGAN' v2.5-6, Dixon, 2003) which measures the abundance-weighted community dissimilarity between banding days across sites and years. A PCoA extracts the greatest orthogonal axes of variation in community composition, plotting them in multidimensional space. We used the first two axes of the PCoA, which contain the greatest amount of variation, to represent community composition (hereafter Axis 1 and Axis 2). To analyze variation in community composition, we took a two-step approach. We first characterized spatial gradients in community composition. To do this, we calculated the correlation coefficients between each axis and temperature, precipitation and NDVI. In this instance, the variables were not scaled so as to capture the geographical variation in the variables. For the second step, we analyzed temporal variation in community composition. We ran a linear mixed model for each axis (package 'lme4', Bates *et al.*, 2015) with the same fixed and random effects as the captures and richness models where temperature, precipitation and NDVI were again scaled at the site level. This two-step approach allowed us to first describe spatial gradients in community composition before testing for temporal variation and relating that temporal variation to the spatial gradients.

Demographic rates

To analyze changes in the demographic rates of riparian species in relation to environmental variation, we employed CMR models (package 'RMark' v2.2.7, Laake & Rexstad, 2006) which estimate demographic parameters from individual capture histories while controlling for imperfect encounter probabilities (P). For each individual bird (identified by their unique bird band), we constructed a capture history consisting of a series of 1s and 0s based on whether that individual was captured (1) or not (0) in a given year. We then compiled the capture histories for each species which serve as the data for CMR models. Cormack–Jolly–Seber (CJS) models are the standard framework used to estimate apparent survival rates (ϕ), the rate at which individuals remain in the population (Cormack, 1964; Jolly, 1965; Seber, 1965; Lebreton, Burnham & Anderson, 1992), while accounting for P . In addition, Pradel models (Pradel, 1996; Nichols *et al.*, 2000) use a reverse time approach to estimate either recruitment rates (F , the rate at which new individuals join the population) or realized population growth rates (λ , the combination of survival and recruitment). Pradel models also simultaneously estimate ϕ and P .

For every species, we ran a separate CMR model for each of the three demographic parameters of interest (ϕ , F and λ). In these models, the parameter of interest was modeled as a linear function (on the logit or log scale for probabilities and rates respectively) of four covariates: temperature, precipitation, ENSO and NDVI. As with the community-level analyses, temperature, precipitation and NDVI were scaled at the site level before being combined with other sites to focus on temporal variation rather than spatial variation. All covariates were then scaled to have a mean of 0 and a SD of 1. In the Pradel models, either F or λ was modeled as a function of the covariates while ϕ was held constant. We made this decision as (i) very few species showed an association between ϕ and the covariates (see Results), (ii) it is redundant to model ϕ as a function of the covariates twice in each of the Pradel models, and (iii) modeling ϕ as a function of the 4 covariates in the same model as F or λ involves the estimation of 11 parameters which greatly reduces the number of species that can be analyzed. For every model, we extracted the covariate coefficients and their associated 95% confidence intervals. We again deemed a covariate to be significant if the confidence intervals did not overlap 0.

Initially, we ran these models for all species in the dataset. We then removed species for which our models failed to estimate one or more of the parameters, where parameter estimates had standard errors of 0, or where confidence limits on ϕ converged on range limits (0 or 1). In preliminary analyses, we also modelled encounter probabilities, P , as a function of temperature, precipitation, ENSO and NDVI, but we found so few significant results (2 out of a possible 120) that we did not consider variation in P any further.

All analyses were carried out in R version 3.2.4 (R Core Team, 2020).

Results

Climate and greenness

Overall, temperatures did not change significantly across years (coefficient: $+0.01^\circ\text{C}/\text{year}$, CI -0.01 – 0.04 ; Fig. 2a), but were significantly cooler in the Utah Mountains sites (6.82°C , CI 6.67 – 6.98 ; Supporting Information Figure S1) than in the Southern Deserts sites (13.12°C , CI 12.67 – 13.57 ; Supporting Information Figure S1). Precipitation decreased by 4.74 mm/year (CI -9.37 to -0.11 ; Fig. 2b) and was significantly higher in the Utah Mountains sites (525 mm/year, CI 476 – 573 ; Supporting Information Figure S1) than in the Southern Deserts sites (266 mm/year, CI 240 – 292 ; Supporting Information Figure S1). NDVI did not change significantly across years (coefficient: -0.07 , CI -0.15 – 0.00 ; Fig. 2d) but was significantly higher in the Utah Mountains sites (35.37 , CI 33.78 – 36.96 ; Supporting Information Figure S1) than in the Southern Deserts sites (16.64 , CI 16.04 – 17.24 ; Supporting Information Figure S1).

Before scaling, temperature, precipitation and NDVI were all moderately correlated (maximum $r = -0.79$ for temperature \sim NDVI). After site-level scaling there was little correlation between the three variables, except between precipitation and temperature ($r = -0.59$) and precipitation and NDVI ($r = 0.52$), suggesting that drier years also tended to be hotter and less green. However, when included in the community-level models, variance inflation factors for these variables were small (<2.5) suggesting no issues of multicollinearity (Zuur *et al.*, 2010). When averaging climate variables across sites, ENSO was poorly correlated with temperature ($r = -0.18$), precipitation ($r = 0.41$) and NDVI ($r = 0.33$).

Captures, species richness and community composition

In total, 31 788 birds of 148 species were captured over 1247 banding days. These captures included 23 402 (74%) riparian birds of 58 (39%) species and 8386 (26%) non-riparian birds of 90 (61%) species. Daily total captures (30.97 , CI 29.48 – 32.47) and species richness (11.07 , CI 10.75 – 11.38) were higher in the Utah Mountains compared with the Southern Deserts (captures: 17.75 , CI 16.67 – 18.84 ; richness: 8.22 , 7.90 – 8.55).

The model for total captures ($R^2_{\text{GLMM(m)}} = 0.41$, $R^2_{\text{GLMM(c)}} = 0.79$) contained significant coefficients (confidence intervals on the coefficients did not overlap 0) for all fixed explanatory variables except precipitation while the model for species richness ($R^2_{\text{GLMM(m)}} = 0.19$, $R^2_{\text{GLMM(c)}} = 0.30$) contained significant coefficients for all six fixed explanatory variables. Total captures and species richness increased across years (Fig. 3a). Both total captures and species richness were positively associated with temperature and ENSO but negatively associated with precipitation and NDVI (Figs 3a and b and 4) such that total captures and species richness tended to be higher in hotter years, drier years, El Niño years and less green years. The model coefficients for

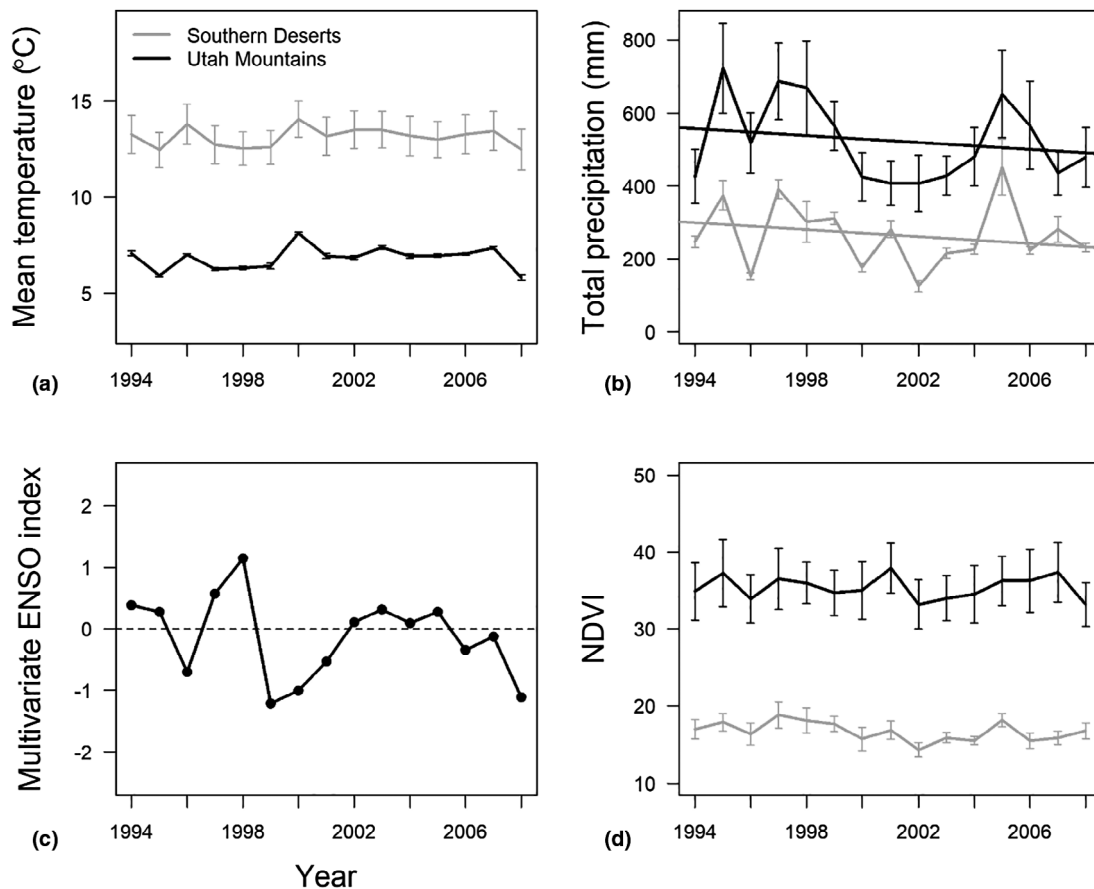


Figure 2 Changes in environmental covariates over 15 years (1994–2008) including (a) mean temperature, (b) total precipitation, (c) multivariate ENSO index and (d) NDVI. For temperature, precipitation and NDVI, values were extracted from 5-km radii surrounding eight bird-banding stations across Utah and were then grouped into two geographic regions: Utah Mountains (black) and Southern Deserts (gray). Mean and standard errors are shown for each region and year based on monthly data. ENSO values are international indices (NOAA). Values were calculated over 12-month periods (Oct–Sep) prior to and including the survey periods. A trend line is shown for precipitation, the only covariate that changed significantly across years.

non-riparian species tended to be larger than the coefficients for riparian species (Fig. 3) while the intercepts for non-riparian species (captures: 1.98, CI 1.75–2.20; species richness: 1.28, CI 1.16–1.41) were smaller than those of riparian species (captures: 2.25, CI 1.84–2.66; species richness: 1.52, CI 1.27–1.76), suggesting that the covariates had a greater effect on non-riparian species. In particular, for riparian species richness the association with year, temperature and precipitation was not significant (Fig. 3b) and for riparian species captures the association with precipitation was not significant (Fig. 3a). The associations with ENSO and NDVI were also reduced for riparian species captures and species richness. However, the model fit for non-riparian species tended to be lower (captures: $R^2_{\text{GLMM}(m)} = 0.16$, $R^2_{\text{GLMM}(c)} = 0.37$; species richness: $R^2_{\text{GLMM}(m)} = 0.06$, $R^2_{\text{GLMM}(c)} = 0.10$) than for riparian species (captures: $R^2_{\text{GLMM}(m)} = 0.42$, $R^2_{\text{GLMM}(c)} = 0.85$; species richness: $R^2_{\text{GLMM}(m)} = 0.20$, $R^2_{\text{GLMM}(c)} = 0.41$).

Community composition was separated along Axis 1 by region, with the Southern Deserts (0.19, CI 0.18–0.20) having

higher values than the Utah Mountains (−0.14, CI −0.15 to −0.13; Fig. 5). Across the eight sites, Axis 1 and 2 described a spatial gradient in temperature, precipitation and NDVI (Fig. 5). Axis 1 values were positively correlated with temperature ($r = 0.68$), and negatively correlated with precipitation ($r = -0.34$) and NDVI ($r = -0.72$) while Axis 2 values were negatively correlated with temperature ($r = -0.46$), and positively correlated with precipitation ($r = 0.38$) and NDVI ($r = 0.27$). However, the environmental gradients were not consistent within physiographic regions. In the Utah Mountains, both Axis 1 values ($r = 0.34$) and Axis 2 values ($r = 0.30$) were positively correlated with precipitation although the correlation was weak. In the Southern Deserts, Axis 1 values were negatively correlated with temperature ($r = -0.26$) and NDVI ($r = -0.24$) while Axis 2 values were negatively correlated with temperature ($r = -0.38$), precipitation ($r = -0.18$) and NDVI ($r = -0.35$), although, again, the correlation was weak.

After scaling the environmental variables at the site level, community composition shifted across years along both axes

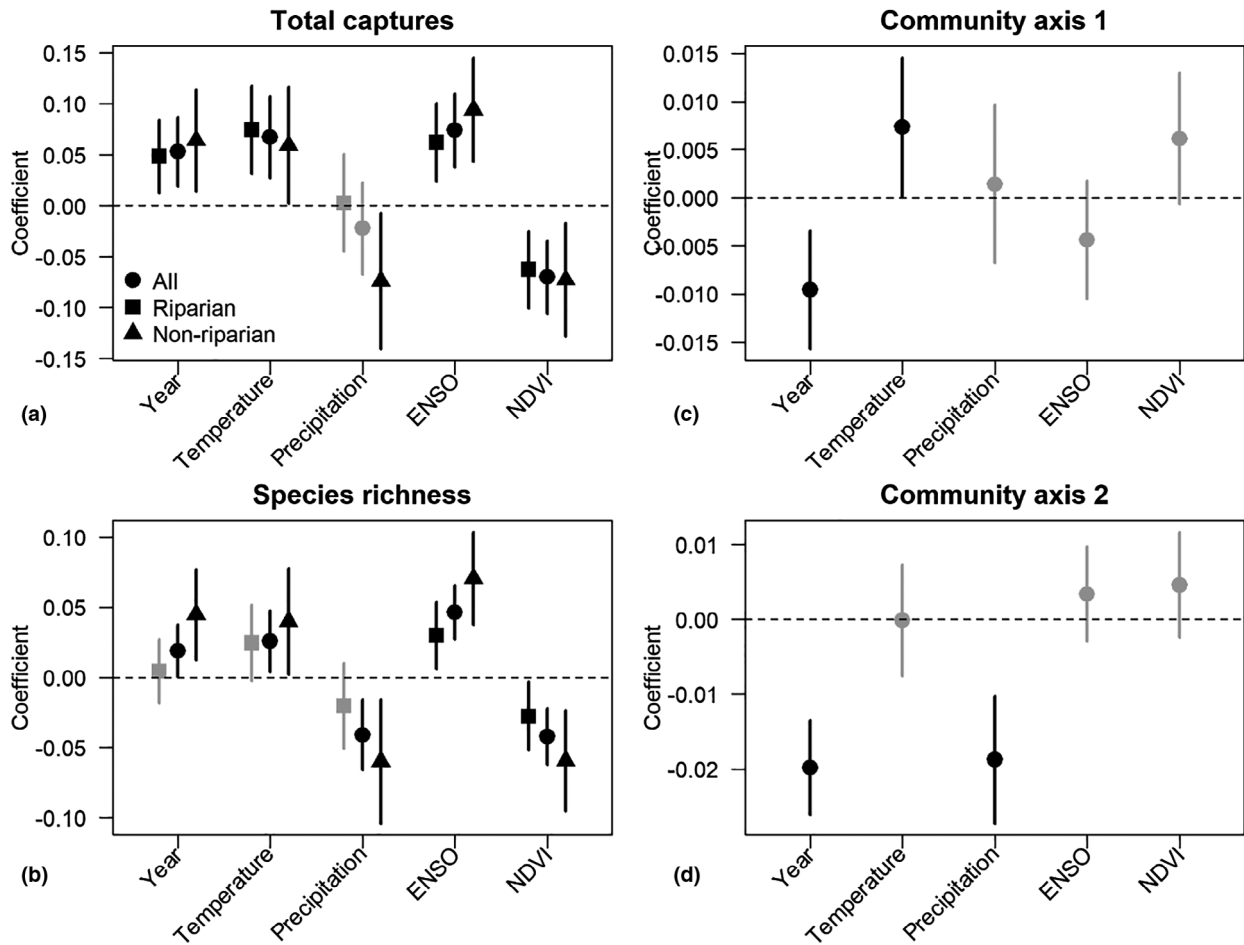


Figure 3 Coefficients for the effects of five covariates on four bird community metrics from 15 years of bird banding at eight riparian bird-banding stations in Utah. Four models regressed (a) daily total captures, (b) species richness and (c and d) the first two axes of a Principal Coordinate Analysis of community composition against year, mean temperature, total precipitation, multivariate ENSO index and NDVI. Community metrics were modeled in either generalized linear mixed models with Poisson errors (total captures/species richness) or linear mixed models (community composition), with banding station as random intercepts. Mean temperature, total precipitation and NDVI were extracted from 5-km radii around the banding stations, summarized at annual resolution and scaled at the station level. ENSO values are international indices (NOAA). For total captures and species richness, results are given for all birds, riparian birds and non-riparian birds. Coefficients and 95% confidence intervals are black when significant (not overlapping 0).

(Fig. 3c and d). In the Utah Mountains, the community shifted toward that found at SLC1 while in the Southern Deserts the community shifted toward that found at STGE (Fig. 5). In addition, Axis 1 values were more positive in hotter years ($R^2_{LMM(m)} = 0.56$, $R^2_{LMM(c)} = 0.77$; Fig. 3c) while Axis 2 values were more negative in wetter years ($R^2_{LMM(m)} = 0.16$, $R^2_{LMM(c)} = 0.74$; Fig. 3d).

Demographic rates

The CMR models were conducted successfully (see Methods) for 30 species (20% of all species; Table 1) and each of these species had either ≥ 100 captured individuals or encounter probabilities (P) ≥ 0.1 . All 30 species breed in and around the riparian zones featured in this study. Below, we

report positive or negative coefficients when significant (i.e. confidence intervals on the coefficients did not overlap 0). On average, realized population growth rates (λ) were negatively associated with temperature (mean coefficient = -0.13 ± 0.03 SE), with a negative coefficient for 14 species (47%), and a positive coefficient for 1 species (Fig. 6a). There was no consistent association between λ and precipitation (mean coefficient = -0.02 ± 0.03 SE), with a positive coefficient for three species (10%) and a negative coefficient for six species (20%; Fig. 6a). On average, λ was negatively associated with ENSO (mean coefficient = -0.12 ± 0.03 SE), with a negative coefficient for 16 species (53%) and a positive coefficient for 1 species (Fig. 6a). There was no consistent association between λ and NDVI (mean coefficient = -0.02 ± 0.02 SE), with a positive

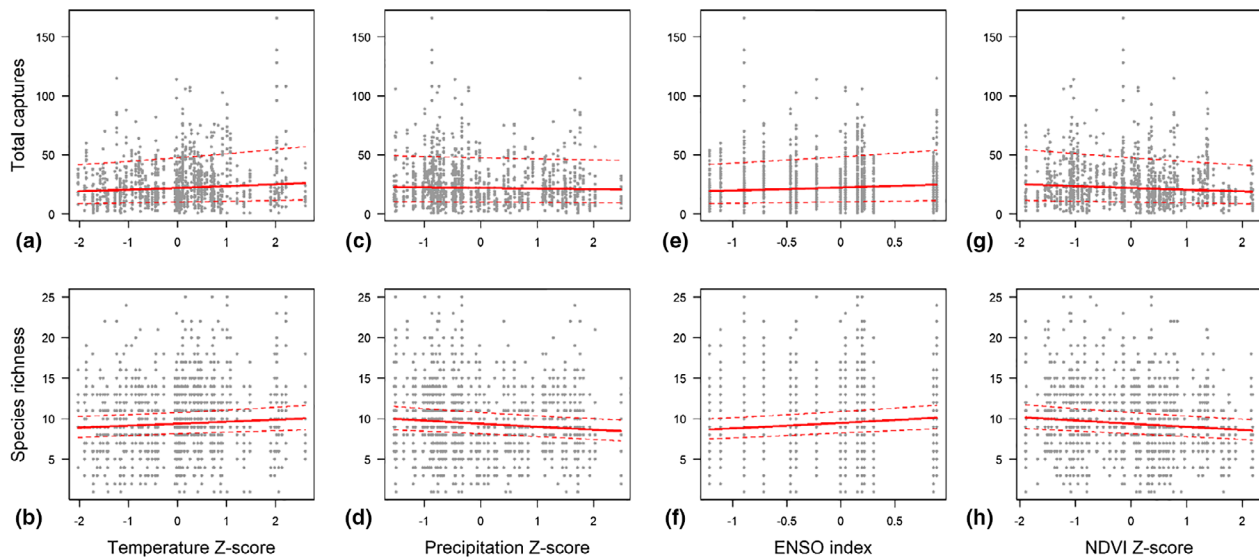


Figure 4 Significant relationships between (a and b) mean temperature, (c and d) total precipitation, (e and f) multivariate ENSO index and (g and h) NDVI, and total captures and species richness over 15 years (1994–2008) at eight riparian bird-banding stations in Utah. Mean temperature, total precipitation and NDVI were extracted from 5-km radii around the banding stations, summarized at annual resolution and scaled at the station level. ENSO values are international indices (NOAA). The response variables were modeled in generalized linear mixed models with Poisson errors and banding station as random intercepts.

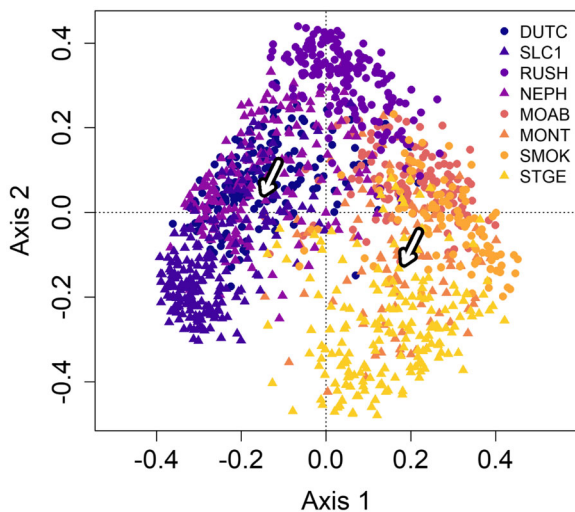


Figure 5 Community composition of eight riparian bird-banding stations in Utah over 15 years (1994–2008), based on a Principal Coordinate Analysis of a Bray–Curtis dissimilarity matrix of daily captures of each species. Each point represents the community composition of a banding day and proximity between points equates to the level of similarity. Banding stations are colored from north (DUTC) to south (STGE). The arrows are based on coefficients predicting average community composition values along both axes between 1994 (base of arrow) and 2008 (tip of arrow). Arrows are shown separately for the Utah Mountains (darker points) and Southern Deserts (paler points).

coefficient for six species and a negative coefficient for six species (Fig. 6a). In general, the effect sizes (coefficient values) were greatest for the temperature covariates, suggesting that temperature was the strongest predictor of population growth rates. Species affected by at least one covariate tended to be affected by multiple covariates. Of 30 species, 25 (83%) had ≥ 1 significant coefficient. Of these 25 species, 80% had ≥ 2 significant coefficients, with 28% having ≥ 3 significant coefficients.

On average, recruitment rates (F) were negatively associated with temperature (mean coefficient = -0.20 ± 0.06 SE), with negative coefficients for 13 species (43%) and a positive coefficient for 2 species (Fig. 6b). There was no consistent association between F and precipitation (mean coefficient = -0.02 ± 0.06 SE), with a positive coefficient for five species (17%) and a negative coefficient for five species (Fig. 6b). On average, F was negatively associated with ENSO (mean coefficient = -0.20 ± 0.05 SE), with negative coefficients for 15 species (50%) and a positive coefficient for 1 species (Fig. 6b). The associations between F and NDVI were variable (mean coefficient = -0.04 ± 0.04 SE) with positive coefficients for six species and negative coefficients for five species (Fig. 6b).

There was little association between apparent survival and the four covariates, with significant coefficients present only for two to three species per covariate (Fig. 6c). These results strongly suggest that the changes in population growth rates were driven by the changes in recruitment rates.

Table 1 Thirty riparian bird species included in capture–mark–recapture analyses, with associated number of captures, number of individuals and recapture rate in Utah

Alpha code	English name	Binomial name	Captures	Individuals	Recapture rate
RSFL	Red-shafted Flicker	<i>Colaptes cafer</i>	133	120	0.10
RNSA	Red-naped Sapsucker	<i>Sphyrapicus nuchalis</i>	149	115	0.23
ATFL	Ash-throated Flycatcher	<i>Myiarchus cinerascens</i>	272	219	0.19
BLPH	Black Phoebe	<i>Sayornis nigricans</i>	186	157	0.16
COFL	Cordilleran Flycatcher	<i>Empidonax occidentalis</i>	230	207	0.10
DUFL	American Dusky Flycatcher	<i>Empidonax oberholseri</i>	859	772	0.10
WAVI	Warbling Vireo	<i>Vireo gilvus</i>	2302	1921	0.17
PLVI	Plumbeous Vireo	<i>Vireo plumbeus</i>	193	154	0.20
BCCH	Black-capped Chickadee	<i>Poecile atricapillus</i>	754	544	0.28
HOWR	House Wren	<i>Troglodytes aedon</i>	234	198	0.15
BEWR	Bewick's Wren	<i>Thryomanes bewickii</i>	575	443	0.23
GRCA	Grey Catbird	<i>Dumetella carolinensis</i>	622	458	0.26
SWTH	Swainson's Thrush	<i>Catharus swainsoni</i>	352	225	0.36
HETH	Hermit Thrush	<i>Catharus guttatus</i>	559	445	0.20
AMRO	American Robin	<i>Turdus migratorius</i>	1410	1255	0.11
AMGO	American Goldfinch	<i>Spinus tristis</i>	412	356	0.14
GTTO	Green-tailed Towhee	<i>Pipilo chlorurus</i>	269	250	0.07
SPTO	Spotted Towhee	<i>Pipilo maculatus</i>	725	628	0.13
SOSP	Song Sparrow	<i>Melospiza melodia</i>	1751	1246	0.29
YBCH	Yellow-breasted Chat	<i>Icteria virens</i>	521	378	0.27
BUOR	Bullock's Oriole	<i>Icterus bullockiorum</i>	205	185	0.10
BHCO	Brown-headed Cowbird	<i>Molothrus ater</i>	160	124	0.23
LUWA	Lucy's Warbler	<i>Leiothlypis luciae</i>	361	284	0.21
VIWA	Virginia's Warbler	<i>Leiothlypis virginiae</i>	1060	959	0.10
MGWA	MacGillivray's Warbler	<i>Geothlypis tolmiei</i>	1845	1413	0.23
COYE	Common Yellowthroat	<i>Geothlypis trichas</i>	109	89	0.18
YWAR	American Yellow Warbler	<i>Setophaga petechia</i>	5265	3817	0.28
BHGR	Black-headed Grosbeak	<i>Pheucticus melanocephalus</i>	697	611	0.12
BLGR	Blue Grosbeak	<i>Passerina caerulea</i>	100	81	0.19
SUTA	Summer Tanager	<i>Piranga rubra</i>	117	85	0.27

Bird banding took place over 15 years (1994–2008) and across eight stations. Recapture rate is the proportion of captures that were recaptures. Taxonomy follows Handbook of the Birds of the World and BirdLife International, 2020.

Discussion

In arid regions around the world, riparian corridors provide critical habitat for breeding and migratory birds. Yet, climate change has the potential to alter riparian ecosystems and the diversity that depends on them. This study reveals two important patterns for birds in the riparian areas of Utah: in hotter and less green years, avifaunal captures and richness increased in riparian corridors, but in hotter years the population growth rates of 47% of focal riparian species declined. It is important to note that, although much of the riparian habitat featured in this study is short in stature, these results are based on data from mist nets, which only catch small birds within 2 m of the ground, potentially biasing the bird community sampled (Pagen, Thompson III & Burhans, 2002). Smaller birds are potentially more vulnerable to climate change in arid environments (Albright *et al.*, 2017) so comparable datasets of point-count or transect data should be analyzed in a similar way to assess species not captured in mist nets.

Total captures increased in hotter and less green years and species richness also increased in hotter, drier, less green

years (Figs 3 and 4). In hotter, drier years, resources may decrease across the landscape (Hinojosa-Huerta *et al.*, 2013), particularly along ephemeral streams (Banville *et al.*, 2017). We hypothesize that this drying and reduction in resources means that more birds use habitats along more constant sources of water (Skagen *et al.*, 2005), such as the perennial streams where our banding stations were located. We, therefore, captured more birds of greater diversity in hotter, drier, less green years. In particular, the relationships between climate and community metrics were more pronounced for non-riparian species, with the negative effect of precipitation becoming significant, indicating an influx into riparian areas of migrants and species from other habitats in those years. However, it is worth noting that model fit was lower for non-riparian species, perhaps reflecting the greater variation in the number of non-riparian birds using riparian areas.

Conversely, population growth rates of our focal breeding species decreased in hotter years (Fig. 6a). These changes were almost entirely due to changes in recruitment rates rather than changes in survivorship (Fig. 6b), that is, relatively fewer birds joined the population in hotter years. The species included in the CMR analyses represent a subset of

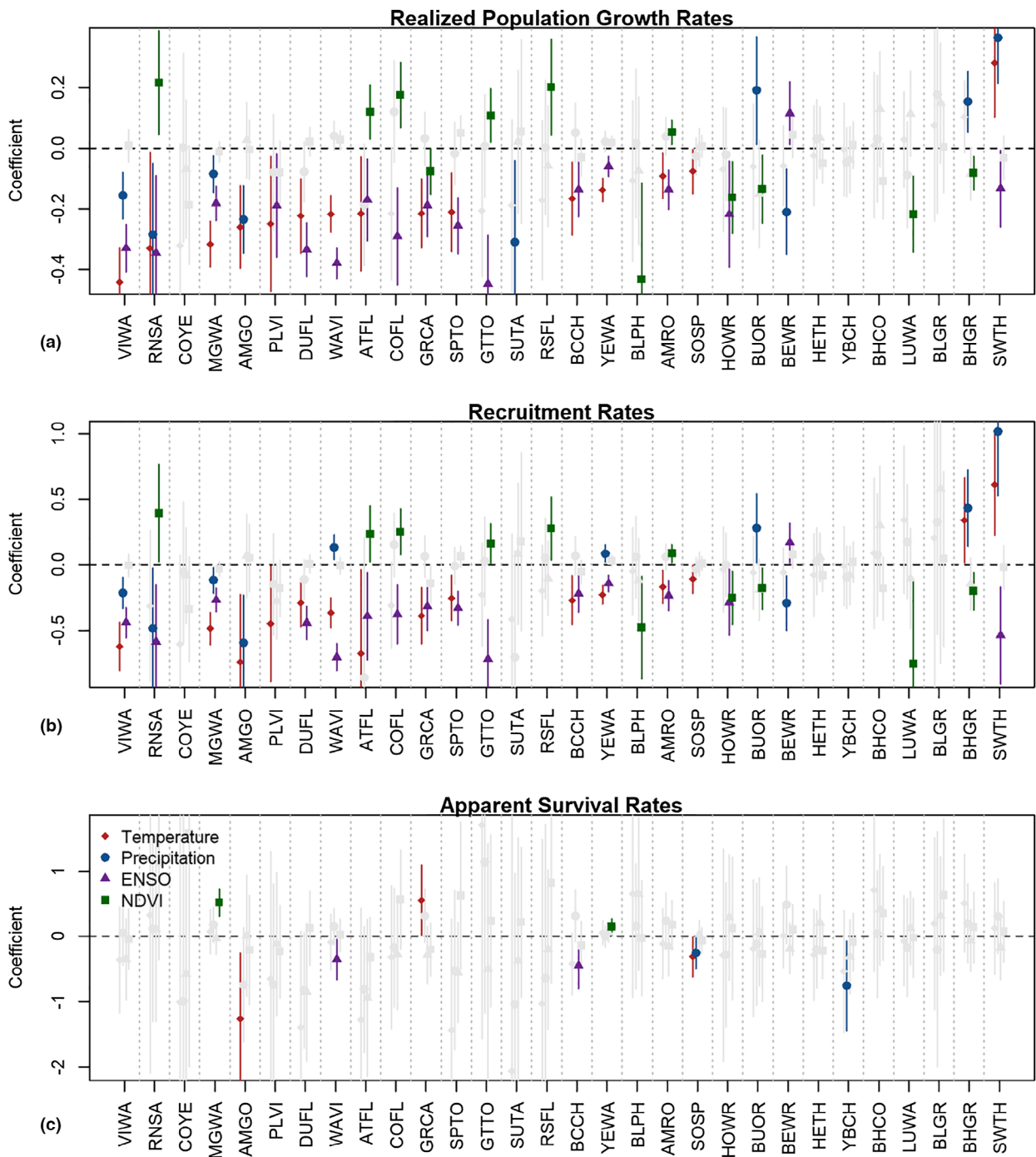


Figure 6 The effects of mean temperature, total precipitation, multivariate ENSO index and NDVI on rates of (a) realized population growth (λ), (b) recruitment (F) and (c) apparent survival (ϕ) for 30 riparian bird species estimated from capture–mark–recapture data collected over 15 years (1994–1998) at eight riparian banding stations in Utah. Mean temperature, total precipitation and NDVI were extracted from 5-km radii around the eight banding stations, summarized at annual resolution and scaled at the station level. ENSO values are international indices (NOAA). Species names and alpha codes are given in Table 1. The points and bars are the covariate coefficients, with 95% confidence intervals, extracted from Cormack–Jolly–Seber and Pradel models where the parameter of interest was modeled as a function of the covariates. Points and bars are light gray when not significantly different from 0. Species are ordered according to their λ -temperature coefficients.

the bird community that necessarily had high capture and recapture rates and that are typically common local breeding species. Their demographic responses may, therefore, differ from more transient species such as passage migrants and non-riparian species. Higher temperatures may place thermal stress on riparian birds (Wolf, 2000; Albright *et al.*, 2017), forcing them to adopt certain behaviors or physiological responses that trade-off with other activities such as foraging efficiency (du Plessis *et al.*, 2012; Smit *et al.*, 2016; Pattinson & Smit, 2017), and this could result in reduced nestling body condition (Oswald *et al.*, 2021). In addition, although the association between recruitment and precipitation was inconsistent, temperature and precipitation were moderately correlated, meaning that hotter years also tended to be drier. Precipitation can be an important driver of food availability for birds (Leech & Crick, 2007; Dybala *et al.*, 2013) which affects nest initiation phenology and provisioning rates to offspring. In hotter, drier years, adults may delay nesting (McCreedy & Van Riper, 2015) or reduce provisioning rates leading to a decline in nesting or fledging success. Similarly, fledglings may find it more difficult to acquire food for themselves (Wheelwright & Templeton, 2003), affecting juvenile survival rates (Robinson *et al.*, 2007; Streby *et al.*, 2015). Furthermore, if hotter, drier weather leads to more birds from other habitats entering perennial riparian areas, there may be increased competition for resources (Hutto, 1985; Moore & Yong, 1991), once again reducing food availability for immature birds. Finally, climate change may also affect nest predation rates (Martin & Maron, 2012; Cox, Thompson & Reidy 2013; DeGregorio *et al.*, 2015) or host-parasite interactions (Møller, 2010; McCreedy & Van Riper, 2015; McNew *et al.*, 2019).

Temporal variation in temperature was positively associated with Axis 1 values of community composition, indicating that in hotter years, assemblages were more likely to resemble those found in the hotter Southern Deserts. Temporal variation in precipitation also had a strong association with community composition where wetter years tended to have more negative values along Axis 2 (i.e. toward STGE; Fig. 5). This was somewhat counter to expectation because more negative values along Axis 2 were more typical of community composition at drier sites, so why would wetter years result in community composition more typical of drier, southern environments? When we separated community composition by physiographic region, we found that for sites in the Southern Deserts the precipitation gradient increased rather than decreased from north to south (Supporting Information Figure S1b). In other words, even though STGE was the hottest, most southerly site, it was also the wettest and greenest of the Southern Deserts sites. This result, therefore, supports the hypothesis that increased precipitation in the Southern Deserts leads to community composition in riparian corridors more typical of wetter sites (e.g. STGE). Among the Utah Mountains sites, community composition in wetter years moved toward that of SLC1. Although SLC1 is not the wettest of the sites in terms of local precipitation, it is located below the dam of a reservoir (Fig. 1). At this site, flow of water from the

dam might be a more important predictor of local resources than local precipitation.

El Niño Southern Oscillation also had a contrasting effect on community metrics and demographic parameters where total captures and species richness were positively associated with ENSO (Figs 3 and 4), but population growth rates and recruitment rates were negatively associated with ENSO. Positive ENSO values correspond to El Niño events which, in the southwestern US, mean wetter conditions. However, the effects of ENSO are felt across the globe and vary geographically (NOAA, 2021). In western Mexico, El Niño events correspond to cooler, wetter conditions, but in the Caribbean, southern Central America and northern South America, El Niño events correspond to hotter, drier conditions. Thus, the effects of ENSO on demographic rates likely depend on where a species overwinters and migrates. Most of our focal species (63%) are Neotropical migrants, with the majority wintering in Mexico and northern Central America. El Niño events have been shown to reduce body condition and survival in both resident Neotropical birds (Wolfe *et al.*, 2015; Ryder & Sillett, 2016) and Nearctic migrants (Sillett *et al.*, 2000; Strong & Sherry, 2000; Nott *et al.*, 2002; Mazerolle *et al.*, 2005; Wolfe & Ralph, 2009), and the North Atlantic Oscillation has a disproportionate effect on immature birds compared to adults (Robinson *et al.*, 2007). A reduction in body condition during the non-breeding season may lower the survival probability of immature birds and force them to be more selective in habitat choice when migrating through the arid Intermountain West (Skagen *et al.*, 2005).

Three species of short-distance migrants (Red-naped Sapsucker, Spotted Towhee, American Robin) showed a strong negative association with ENSO, suggesting that El Niño also has an important effect locally (although no year-round Utah residents showed this association). One possible explanation is that El Niño events produce higher-than-average winter snowfall in the Southwest US (Kunkel & Angel, 1999) which negatively impacts overwintering birds. In particular, harsh winters (Robinson *et al.*, 2007) and spring snow storms (Chmura *et al.*, 2018) could reduce resource availability and offspring survival.

Across years, total captures increased (Fig. 3a), corroborating increases in bird abundance on point count surveys in riparian zones across the state. Elsewhere in the American West, bird abundances have declined in the riparian zones of Phoenix, Arizona (Banville *et al.*, 2017). However, declines in urban areas are likely driven by invasive species and human development along or nearby riparian areas (Miller *et al.*, 2003; Banville *et al.*, 2017). In this study, increases in total captures cannot be attributed to increases in introduced bird species, as we caught just two House Sparrows *Passer domesticus* and two European Starlings *Sturnus vulgaris* during the entire study period. Additionally, the riparian areas included in this study were in largely undeveloped areas (Fig. 1) on public land and thus are unlikely to have been affected by local urbanization. Positive trends in total captures and species richness may instead indicate a decline in habitat quality across the wider landscape, leading more

birds to use riparian corridors along perennial streams for migration and breeding. Declines in habitat quality elsewhere may result from increased agriculture, disturbance by livestock (Tewksbury *et al.*, 2002) or climate stress in desert habitats (Iknayan & Beissinger, 2018).

Community composition also changed significantly across years, shifting toward that found in warmer and less green environments. This result is corroborated by the increase across years in the species richness and diversity of non-riparian species. Within the Southern Deserts, the community composition trend moved toward species found in the lower elevation STGE site. The Southern Deserts, which are located principally on the Colorado Plateau, may be incorporating more southerly desert species more typical of the neighboring Sonoran or Mojave Desert (Johnson, 1994). Within the Utah Mountains, the trend in community composition was toward the community of SLC1, a site located near the resort town of Park City. This is not the lowest elevation site of the mountain sites but it is close to urban areas as well as a large reservoir, so it is possible that other mountain sites are gaining species more typical of developed areas (Miller *et al.*, 2003; Banville *et al.*, 2017).

Our results indicate a dynamic response of riparian birds to interannual fluctuations in climate conditions. In particular, years of higher temperature, lower precipitation and El Niño years appear to concentrate birds along riparian corridors, increasing the numbers and diversity of birds, particularly of non-riparian species, but reducing the recruitment and population growth rates of common riparian species. Precipitation decreased over the study period for sites in both regions (Fig. 2b), indicating that Utah became progressively drier. Although not significant, there was also a trend toward decreasing greenness across years. Utah is already one of the driest states in the US and riparian areas there are vital for migrating birds (Szaro, 1980; Naiman *et al.*, 1993; Sabo *et al.*, 2014). Moreover, hot and dry regions are predicted to become hotter and drier as a result of climate change (Trenberth, 2011; Zhou, Chen & Dai, 2015; Donat *et al.*, 2016). In this changing world we may see more diverse bird communities utilizing perennial riparian corridors but at the expense of the bird populations that rely most heavily on these zones for breeding. Future studies could further test our hypotheses by monitoring birds in more ephemeral habitats (Banville *et al.*, 2017) or by tracking the decisions of birds on migration (Horns *et al.*, 2016; Buechley *et al.*, 2018; Mckinnon & Love, 2018; Humple *et al.*, 2020).

The negative impacts of climate change on bird populations are projected to increase rapidly (Abolafya *et al.*, 2013; Friggens & Finch, 2015). Tackling climate change is an international problem yet local land owners, policy makers and conservation biologists all have a role to play in facilitating the resilience of ecosystems to climate change (Seavy *et al.*, 2009). In addition to the threat of climate change, riparian areas in the western US are heavily utilized and managed systems, and anthropogenic changes such as livestock grazing, invasive plant species and altered fluvial processes, have greatly affected native ecosystems (Poff *et al.*, 2011). Resilience to climate change could, therefore, be

increased by reducing these threats, protecting and restoring riparian areas (Seavy *et al.*, 2009; Friggens & Finch, 2015; Selwood *et al.*, 2018), and ensuring that sufficient resources are available to migratory birds (Hinojosa-Huerta *et al.*, 2008). In addition, managing land use across the wider landscape (Martin *et al.*, 2006) could create more opportunities for migrants by providing additional oases in the arid west (Skagen *et al.*, 2008). Successful conservation of riparian communities will require managers of wildlife, land and water to work together to keep water flowing in perennial streams (Richter & Richter, 2000; Hinojosa-Huerta *et al.*, 2008) and to conserve and restore suitable native habitat growing along the banks (Stromberg, 2001; Seavy *et al.*, 2009; Friggens & Finch, 2015). Improving nesting success and reducing fledgling mortality by ensuring the persistence of climate change-resilient riparian habitat is key to the successful conservation of these communities.

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Supporting information

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

Table S1. Data on eight MAPS bird-banding stations in Utah.

Figure S1. Annual mean temperature, total precipitation, and mean NDVI across eight riparian bird-banding stations in Utah.

Figure S2. Monthly total precipitation across eight riparian bird-banding stations in Utah.