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Phenology and productivity in a montane bird assemblage: Trends and responses to elevation and climate variation

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Abstract

Climate variation has been linked to historical and predicted future distributions and dynamics of wildlife populations. However, demographic mechanisms underlying these changes remain poorly understood. Here, we assessed variation and trends in climate (annual snowfall and spring temperature anomalies) and avian demographic variables from mist-netting data (breeding phenology and productivity) at six sites along an elevation gradient spanning the montane zone of Yosemite National Park between 1993 and 2017. We implemented multi-species hierarchical models to relate demographic responses to elevation and climate covariates. Annual variation in climate and avian demographic variables was high. Snowfall declined (10 mm/year at the highest site, 2 mm at the lowest site), while spring temperature increased (0.045°C/year) over the study period. Breeding phenology (mean first capture date of juvenile birds) advanced by 0.2 day/year (5 days); and productivity (probability of capturing a juvenile bird) increased by 0.8%/year. Breeding phenology was 12 days earlier at the lowest compared to highest site, 18 days earlier in years with lowest compared to highest snowfall anomalies, and 6 d earlier in relatively warm springs (after controlling for snowfall effects). Productivity was positively related to elevation. However, elevation–productivity responses varied among species; species with higher productivity at higher compared to lower elevations tended to be species with documented range retractions during the past century. Productivity tended to be negatively related to snowfall and was positively related to spring temperature. Overall, our results suggest that birds have tracked the variable climatic conditions in this system and have benefited from a trend toward warmer, drier springs. However, we caution that continued warming and multi-year drought or extreme weather years may alter these relationships in the future. Multi-species demographic modeling, such as implemented here, can provide an important tool for guiding conservation of species assemblages under global change.

KEYWORDS

avian demography, climate, hierarchical model, MAPS program, mist-netting, phenology, productivity, Sierra Nevada, Yosemite

1 | INTRODUCTION

Climate variation and trends can be important drivers of phenology, demography, and dynamics of wildlife populations (Miller-Rushing, Høye, Inouye, & Post, 2010). Understanding effects of climate on populations is urgently needed to inform effective conservation and habitat management that promotes resilience to climate change. Climate change may disrupt synchrony between arrival on breeding territories (for migratory species) or initiation of breeding activities, and the availability of resources needed for successful reproduction (Burgess et al., 2018; Franks et al., 2018; Mayor et al., 2017; Møller, Rubolini, & Lehikoinen, 2008). These phenological mismatches, if they occur, could lead to reduced reproductive success and population declines (Dunn & Møller, 2014; Miller-Rushing et al., 2010; Møller et al., 2008). In some cases, wildlife populations may adapt to phenological shifts in food resources by tracking thermal niches in space (Chen, Hill, Ohlemüller, Roy, & Thomas, 2011) or time (Socolar, Epanchin, Beissinger, & Tingley, 2017). Although demographic mechanisms underlying such adaptations remain poorly understood, productivity of some species at upper ends of their thermal niches may benefit from warming trends (Meller, Piha, Vähätalo, & Lehikoinen, 2018; Scridel et al., 2018).

Studies along elevation gradients provide an ideal opportunity to understand demographic responses of species to climatic variation and trends (Chamberlain et al., 2012; Scridel et al., 2018). In the Sierra Nevada mountains of California, many breeding bird species have shifted elevation distributions (Tingley, Koo, Moritz, Rush, & Beissinger, 2012) or timing of reproduction (phenological shifts; Socolar et al., 2017) to track thermal niches over the past century. This thermal niche-tracking parallels other metrics that signal a trend toward earlier springs, such as recent declines in winter snowpack and earlier snowmelt (Cayan, Dettinger, Kammerdiener, Caprio, & Peterson, 2001; Lundquist et al., 2004; Mote, Li, Lettenmaier, Xiao, & Engel, 2018). However, annual climatic variation that can alter spring phenology or the quality of breeding habitat conditions is high (Cayan & Cayan, 1996). Years with heavy snow accumulation have been associated with reduced breeding bird abundance in subalpine and upper montane forests (DeSante, 1990; Hejl, Verner, & Balda, 1988; Raphael & White, 1984). In addition, lingering snowpack or late-season storms can delay initiation of breeding, result in fewer nesting attempts, lead to direct soaking by snow or disrupted parental care, and reduce reproductive success in high-elevation habitats (Hahn, Sockman, Breuner, & Morton, 2009; Morton, 2002; Pereyra, 2011; Verhulst & Nilsson, 2008; Whitmore, Mosher, & Frost, 1977). The extent that such variability affects birds at moderately lower elevations in the montane zone is poorly known. Understanding how montane bird populations in the Sierra Nevada respond to annual climate variation could help explain observed population trends or changes in distributions of birds (Tingley et al., 2012; Tingley, Monahan, Beissinger, & Moritz, 2009), as well as enable better predictions of future population changes in the region (Siegel et al., 2014; Stralberg et al., 2009).

Here, we analyze a historical modeled climate data set (ClimateNA) and mist-net capture data from 25 bird species at six Monitoring Avian Productivity and Survivorship (MAPS) stations (DeSante, Saracco, O'Grady, Burton, & Walker, 2004) along an elevation gradient spanning the montane zone of Yosemite National Park between 1993 and 2017. Yosemite, like many other national parks, provides an excellent reference site for assessing climate effects on wildlife populations because confounding changes in local land use are small compared with other landscapes (Ray et al., 2017; Simons, Farnsworth, & Shriner, 2000), and such areas may provide important refugia from the most severe effects of climate change (Wu, Wilsey, Taylor, & Schuurman, 2018). We assessed annual variation and trends in climate variables (annual snowfall and spring temperature) and avian demographic parameters related to breeding (timing of juvenile bird captures and an index of productivity) and implemented multi-species hierarchical models to test relationships among demographic parameters, climate covariates, and elevation. We hypothesized that years with heavy snowfall and cool spring temperatures would result in later breeding (later first capture dates of young birds) and depressed productivity (lower probability of capturing juvenile birds), while light snowfall years and relatively warm spring temperatures would yield earlier breeding and higher productivity. Finally, to explain species variation in productivity responses to elevation, we conducted a *post hoc* analysis of elevation effects as a function of recent species range shifts in the central Sierra Nevada (Tingley et al., 2012).

2 | MATERIALS AND METHODS

2.1 | Study areas

Our study included six mist-netting stations between 1,311 and 2,402 m above sea level in Yosemite National Park, on the western slope of the Sierra Nevada (Table 1; Figure 1). In Yosemite, the montane ecological zone transitions to subalpine at approximately 2,700 m, and to foothill habitats below approximately 900 m, so the six stations collectively spanned most of the montane zone (Fites-Kaufman, Rundel, Stephenson, & Weixelman, 2007; Keeler-Wolf et al., 2012). Each mist-netting station was situated at a montane meadow–forest ecotone and comprised 10 or 14 12 × 2.5-m, 30-mm mesh, four-tier nylon mist nets, some of which were placed within the meadow and some of which were within the adjacent forest. The six meadows varied somewhat in plant species composition, but all were dominated by graminoids and forbs, and all except White Wolf (WHWO; Table 1) also contained substantial patches of riparian deciduous shrubs, including willow (*Salix* spp.) and mountain dogwood (*Cornus nuttallii*). Forests at the stations ranged from Sierran mixed conifer forest (Allen, 1988) at lower elevations to red fir (*Abies magnifica*; Barrett, 1988) and lodgepole pine (*Pinus contorta*; Bartolome, 1988) forests at higher elevations, and were interspersed with montane chaparral in varying proportions. Portions of most of the stations have burned in one or more wildfires during the 25-year study period. Each mist-netting station comprised a sampling area of about 20 ha.

TABLE 1 Elevation and major habitats of six mist-netting stations operated between 1993 and 2017 at Yosemite National Park, California

Station name (code)	Elev. (m)	Habitat	Years operated
White Wolf (WHWO)	2,402	Wet montane meadow surrounded by red fir (*Abies magnifica*) and lodgepole pine (*Pinus contorta*) forest.	1993–2017
Gin Flat East Meadow (GFEM)	2,073	Wet montane meadow with small willow (*Salix* spp.) thickets surrounded by red fir (*Abies magnifica*) and lodgepole pine (*Pinus contorta*) forest.	1998–2017
Tamarack Meadow (TAME)	2,024	Wet montane meadow with small willow (*Salix* spp.) thickets surrounded by red fir (*Abies magnifica*) and lodgepole pine (*Pinus contorta*) forest.	1993–1996
Crane Flat (CRFL)	1,875	Wet montane meadow with small willow (*Salix* spp.) thickets surrounded by Sierran mixed conifer and red fir forest.	1993–2017
Hodgdon Meadow (HODG)	1,408	Wet montane meadow with willow and dogwood (*Cornus nuttallii*) thickets, surrounded by Sierran mixed conifer forest.	1993–2017
Big Meadow (BIME)	1,311	Riparian willows surrounded by montane meadow and Sierran mixed conifer forest.	1993–2017

2.2 | Field methods

We operated mist-netting stations following protocols established by the Monitoring Avian Productivity and Survivorship (MAPS) program (DeSante & Kaschube, 2009; DeSante et al., 2004). Four stations were operated for 25 years (1993–2017); one station was operated for 20 years (Gin Flat East Meadow [GFEM]: 1998–2017); and one station was operated for 4 years (Tamarack Meadow [TAME]: 1993–1996). Ten or 14 (Hodgdon Meadow [HODG] only) net sites were established within the central 8 ha of each station. For all stations except HODG, we operated nets on a single day within each of 5–8 (fewer at higher elevations) 10-day periods between 21 May and 8 August. This sampling window represented a compromise between providing adequate coverage of the postfledging period at all sites while trying to avoid late-season samples that could include large numbers of upslope postbreeding dispersers or transients in fall migration. At HODG, mist-netting was typically spread across two days within each 10-day period, with half of the nets operated on one day and the remaining nets operated on the second day. At the three highest stations (>2,000 m), the first mist-netting period was typically 31 May–9 June (with the exception of 2015, when conditions were snow-free early enough to begin operating all stations during the 10-day period beginning on 21 May). Additional early netting periods were missed at the four stations ≥1,875 min years of heavy snowpack, due to logistical difficulties of accessing sites and operating mist nets in areas with lingering snow and subsequent flooding. Despite annual variation in initiation of station operation at higher elevation stations, operation was always initiated by the fourth 10-day period (20–29 June). Even at stations that were operated earlier, young were rarely captured during the first three periods (~2% of young for target species for all years and stations combined).

On each day of station operation, we erected four-tier nylon 12 × 2.5-m, 30-mm mesh, mist nets at each net site and opened them for approximately six morning hours beginning at local sunrise. We occasionally closed individual nets (or did not open them) due to inclement weather, unmanageably high capture rates, or for other logistical reasons. The mean annual number of net-hours completed ranged from a low of 253 net-hours at TAME to a high of 610 net-hours at HODG. We checked nets and extracted birds at ca. 40-min intervals. With few exceptions, we identified all birds captured in mist nets to species, age (young = hatching year; adult = after hatching year), and sex (based on Pyle, 1997) and banded them with US Geological Survey—Biological Resources Division numbered aluminum leg bands if not already banded. We carefully recorded band numbers of all recaptures. All field data collection was conducted under US federal bird banding permit 22,423 and a research permit from Yosemite National Park in compliance with the Guidelines to the Use of Wild Birds in Research (http://www.nmnh.si.edu/BIRDNET/guide/).

2.3 | Climate data

We characterized annual variation in climatic conditions for 1993–2016 (2017 data not yet available) using variables extracted from the ClimateNA database (ver. 5.50; https://sites.ualberta.ca/~hamann/data/climatena.html). ClimateNA uses bilinear interpolation of monthly gridded climate data and local elevation adjustments to provide "scale-free" climate metrics for individual point locations (Wang, Hamann, Spittlehouse, & Carroll, 2016; Wang, Hamann, Spittlehouse, & Murdock, 2012). To characterize spring conditions believed to be important in driving avian nesting phenology and productivity, we used anomalies from the 24-year station averages of two variables: (a) annual precipitation as snow (mm) from August of the previous year to July of the current year (PAS) and (b) mean spring (March–May) temperature (°C; TSP). Because these two variables were highly correlated ($r = -0.595$; $df = 142$; $p < 0.001$), we entered TSP into demographic models (see below) as residuals of a regression of TSP on PAS (Graham, 2003). The PAS anomaly variable was strongly correlated with May snow water equivalent data from an automated snow monitoring station operated by the California Department of Water Resources at the GFEM station (http://www.nps.gov/yose/naturescience/hydrology-data.htm) for each of the six MAPS stations ($r = 0.89$–0.93; $df = 22$; all $p < 0.001$) and for all stations combined ($r = 0.72$; $df = 142$; $p < 0.001$).

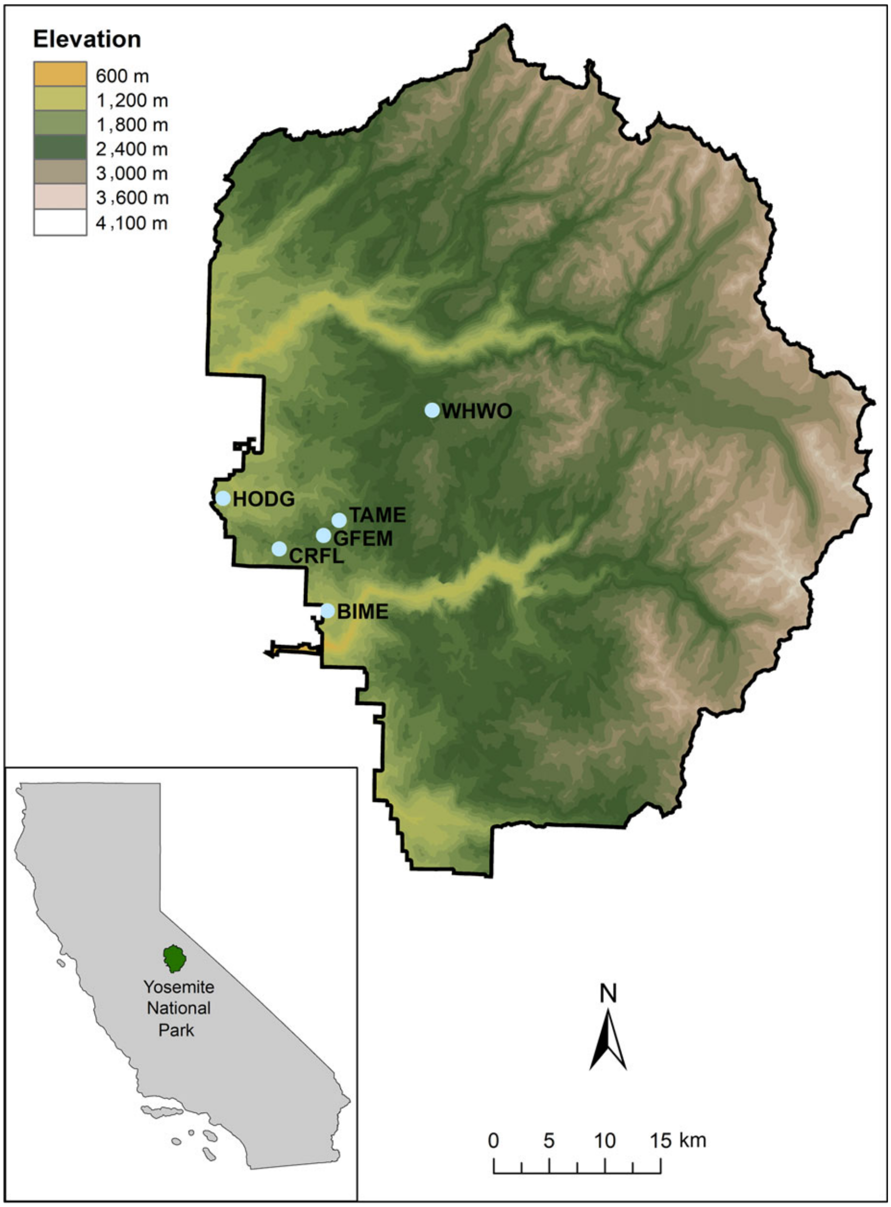

FIGURE 1 Locations of the six Monitoring Avian Productivity and Survivorship (MAPS) stations in Yosemite National Park. Station codes are defined in Table 1

2.4 | Statistical analyses

We implemented linear models to estimate temporal trend in climate variables. We modeled snowfall anomaly with a mixed model as follows: $Y_{j,t} \sim \mathrm{Norm}(\mu_{j,t}, \sigma^2)$, where the $Y_{j,t}$ represent snowfall anomaly values for station j and year t. We then modeled $\mu_{j,t}$ based on the linear relationship:

$$\mu_{j,t} = \beta_{0,j} + \beta_{1,j} \times (t - t*), \tag{1}$$

where the βs represent zero-mean random station-varying intercepts and slopes and t*represents a midpoint year for centering the year covariate. For spring temperature anomaly and drought anomaly models, we did not include station effects, as there was little variation in responses among stations.

We implemented multi-species hierarchical models to assess temporal variation and climate covariate relationships for two avian demographic response variables: day-of-year of capture for individual young birds (first capture for individuals that were captured more than once in a given year) and probability of a captured bird being a young bird (the latter providing an index of productivity). We included data for 25 bird species with ≥125 individual young (hatching year) birds captured (i.e., mean of ≥5 young per year) (Table 2; see Supporting Information Figure S1 for distribution of species captures by station and age). We only included data for a species at a given station if the species was known to have attempted to breed in at least one year of the study at the station (based on observational data similar to those used in breeding bird atlases, as well as on the breeding condition of captured adults and multiple within-season captures of individual adults).

We assessed temporal variation and trends in breeding phenology based on the model $Y_{i,s,j,t} \sim Norm(\mu_{i,s,j,t}, \sigma^2)$, where the $Y_{i,s,j,t}$ represent earliest capture date of hatching-year bird i of species s at station j and year t. We then modeled the mean young capture dates following:

TABLE 2 Numbers of year-specific young and adult captures summed across years for 25 target bird species captured at six Monitoring Avian Productivity and Survivorship (MAPS) stations in Yosemite National Park, 1993–2017

Species	Code	No. of young	No. of adult
Red-breasted Sapsucker (*Sphyrapicus ruber*)	RBSA	231	387
Hammond's Flycatcher (*Empidonax hammondii*)	HAFL	201	119
Dusky Flycatcher (*Empidonax oberholseri*)	DUFL	160	677
Pacific-slope Flycatcher (*Empidonax difficilis*)	PSFL	184	216
Black Phoebe (*Sayornis nigricans*)	BLPH	154	78
Warbling vireo (*Vireo gilvus*)	WAVI	266	1,021
Mountain Chickadee (*Poecile gambeli*)	MOCH	278	375
Red-breasted nuthatch (*Sitta canadensis*)	RBNU	366	183
Brown Creeper (*Certhia americana*)	BRCR	552	278
Golden-crowned kinglet (*Regulus satrapa*)	GCKI	1,069	308
Purple finch (*Haemorhous purpureus*)	PUFI	309	541
Pine Siskin (*Spinus pinus*)	PISI	218	327
Lesser Goldfinch (*Spinus psaltria*)	LEGO	154	218
Song Sparrow (*Melospiza melodia*)	SOSP	938	741
Lincoln's Sparrow (*Melospiza lincolnii*)	LISP	1,042	1,489
Dark-eyed junco (*Junco hyemalis oregonus*)	ORJU	3,059	2,392
Nashville Warbler (*Oreothlypis ruficapilla*)	NAWA	366	225
MacGillivray's Warbler (*Geothlypis tolmiei*)	MGWA	995	1,530
Yellow Warbler (*Setophaga petechia*)	YEWA	133	206
Yellow-rumped Warbler (*Setophaga coronata auduboni*)	AUWA	2,073	1,413
Hermit Warbler (*Setophaga occidentalis*)	HEWA	992	627
Wilson's Warbler (*Cardellina pusilla*)	WIWA	128	155
Western Tanager (*Piranga ludoviciana*)	WETA	152	407
Black-headed Grosbeak (*Pheucticus melanocephalus*)	BHGR	250	507
Lazuli Bunting (*Passerina amoena*)	LAZB	246	572

Note. Species are listed in taxonomic order.

$$\mu_{i,s,j,t} = \beta_{0,s} + \beta_{1,s} \times (t - t*)_j + \beta_{2,s} \times \text{ELEV}_j + \gamma_{s,t}, \tag{2}$$

where the $\beta_{1,s}$ is a linear trend effect multiplied by the difference between year t and a fixed midpoint year t^* = 13, $\beta_{2,s}$ is a station elevation effect, and $\gamma_{s,t}$ is a zero-mean random species × year effect.

Using 1993–2016 data, we then modeled climate and elevation effects on mean young capture dates by replacing linear year and random year effects with spatio-temporally varying climate covariates:

$$\mu_{i,s,j,t} = \beta_{0,s} + \beta_{1,s} \times \text{ELEV}_j + \beta_{2,s} \times \text{PAS.dev}_{j,t} + \beta_{3,s} \times \text{TSP.resids}_{j,t}, \tag{3}$$

where $\beta_{2,s}$are the species regression coefficients for standardized snowfall anomaly effects ($\text{PAS.dev}_{j,t}$) and $\beta_{3,s}$ are the species regression coefficients for standardized spring temperature anomaly residual effects ($\text{TSP.resids}_{j,t}$). Model coefficient inferences for both the trend and covariate models were not sensitive to whether extreme dates were included in analysis. Thus, we included all observations in these models.

To model productivity, we used overdispersed multi-species binomial models of the form: $N.hy_{s,j,t} \sim \text{Bin}(p_{s,j,t}, N.tot_{s,j,t})$, where $N.hy_{j,s,t}$ is the number of young (hatching year) birds of species s captured at station j in year t, $N.tot_{s,j,t}$ is the total number of birds captured, and $p_{s,j,t}$ is the probability of a captured bird being a young bird. To examine temporal patterns in productivity, we used the model:

$$\text{logit}(p_{s,j,t}) = \beta_{0,s} + \beta_{1,s} \times (t - t*) + \beta_{2,s} \times EF_{j,t} + \gamma_{s,t} + \alpha_{s,j} + \varepsilon_{s,j,t}, \tag{4}$$

where the $\beta_{0,s}$ and $\beta_{1,s}$ are species intercept and trend effects (as above for the breeding phenology models), $\beta_{2,s}$are species coefficients to control for effort $EF_{j,t}$ effects on productivity, the $\gamma_{s,t}$ and $\alpha_{s,j}$ are zero-mean random species × year and species × station effects, and the $\varepsilon_{s,j,t}$ is an additional error term to accommodate evidence of overdispersion (see below). We modeled station effects on productivity with the random effect, $\alpha_{s,j}$, rather than with an elevation covariate as we did with the breeding phenology model, so as not to impose any particular structural relationship between elevation and productivity. The $EF_{j,t}$ covariate above represents the proportion of total mist-netting effort (net-hours) occurring during periods when young birds were typically captured (Supporting Information Figures S2 and S4b). The first period of young captures for calculating the effort covariate for each station and year and was defined as the first period of young captures, excluding the first 2.5% of young captures to remove outlier observations.

To assess covariate effects on productivity, we considered a model analogous to the one used to assess covariate effects on timing of young captures:

$$\begin{aligned}\text{logit}(p_{s,j,t}) = {} & \beta_{0,s} + \beta_{1,s} \times EF_{j,t} + \beta_{2,s} \times \text{ELEV}_j + \beta_{3,s} \\ & \times \text{PAS.dev}_{j,t} + \beta_{4,s} \times \text{TSP.resids}_{j,t} + \beta_{s,5} \\ & \times \text{ELEV}_j \times \text{TSP.resids}_{j,t} + \varepsilon_{s,j,t}\end{aligned} \tag{5}$$

The only new term introduced in this equation is $\beta_{5,s}$, which estimates an interaction between elevation and temperature. We included this term to assess the hypothesis that relatively warm springs would increase productivity at higher elevations but potentially depress productivity at lower elevations, similar to the contrasting temperature effects observed for species in warm v. cool portions of their ranges (Socolar et al., 2017).

For all linear and logit-linear models, we assumed species-varying intercepts and regression covariates (β_s) to be distributed according to $\text{Norm}(\mu_\beta, \sigma_\beta^2)$. We used vague prior distributions for hyperparameters of the intercepts, covariates, and model random effects. We implemented models in JAGS (Plummer, 2003) using the jagsUI package (Kellner, 2015) in R (R Core Team, 2015). We obtained posterior distributions by sampling the full conditional distributions using Markov chain Monte Carlo (MCMC) methods (Gilks, Richardson, & Spiegelhalter, 1996) as implemented in JAGS (Plummer, 2003). Posteriors were based on four chains of 40,000 iterations after an adaptive phase of 20,000 iterations and a "burn-in" phase of 10,000 iterations and thinning by three. This resulted in a total of 40,000 posterior samples for each model. We determined models to have successfully converged based on all $\hat{R}$ values < 1.1 (Gelman & Hill, 2006). We assessed goodness-of-fit (GoF) of breeding phenology models by comparing squared residuals from the model fit to data to squared residuals from simulated data generated at each iteration of the MCMC chain. For productivity models, we assessed GoF based on differences in chi-square statistics between observed data and data generated for each MCMC iteration (Kéry & Royle, 2016). For all models, Bayesian *p*-values suggested adequate fit ($0.3 < p < 0.6$). We present all posterior parameter estimates as means with 95% credible intervals in parentheses or brackets.

3 | RESULTS

Posterior distribution means (±95% credible intervals) for all parameters and hyperparameters included in models of climate and avian demographic response variables are presented in Supporting Information Table S1.

3.1 | Climate variables

Annual climate variation from 1993 to 2016 was high (Figure 2). Snowfall tended to decline overall (Equation (1): $\hat{\mu}_{\beta_{j,1}} = -4.34$ [−9.03, 0.48]; Figure 2a). This decline was strongest at the highest station, WHWO ($\hat{\beta}_1 = -10.14$ [−14.37, −5.58]), and weakest at the lowest station, BIME ($\hat{\beta}_1 = -1.77$ [−5.38, 1.98]). Spring temperature ($\hat{\beta}_1 = 0.05$ [0.02, 0.07]) increased over the study period (Figure 2b).

3.2 | Breeding phenology

Mean capture dates of young birds decreased by about 5 days over the 25-year study period (Equation (2): $\hat{\mu}_{\beta_{s,2}} = -0.20$ [−0.30, −0.11]; Figure 3a). Annual trend estimates in breeding phenology for individual species ranged from a low of −0.37 (−0.64, −0.13) for Pacific-slope Flycatcher (~9 days earlier over the 25 years) to a high of −0.01 (−0.23, 0.22) for warbling vireo (~0.15 days earlier over the 25 years; Supporting Information Figure S3a).

From our model including climate covariates, elevation had the strongest effect on breeding phenology (Equation (3): $\hat{\mu}_{\beta_{s,1}} = 3.77$ [2.54, 5.00]) with mean capture date of young birds occurring about 12 days earlier at the lowest versus highest sites (~1,100 m gradient; Figure 3b). Elevation effects on breeding phenology were highly variable among species. Golden-crowned kinglet showed the strongest response to elevation ($\hat{\beta}_{s,1} = 8.01$ [6.93, 9.08]) with an estimated mean HY capture date that was 23 days (20–26 days) earlier at the lowest station for this species (HODG at 1,408 m; 28 Jun) compared

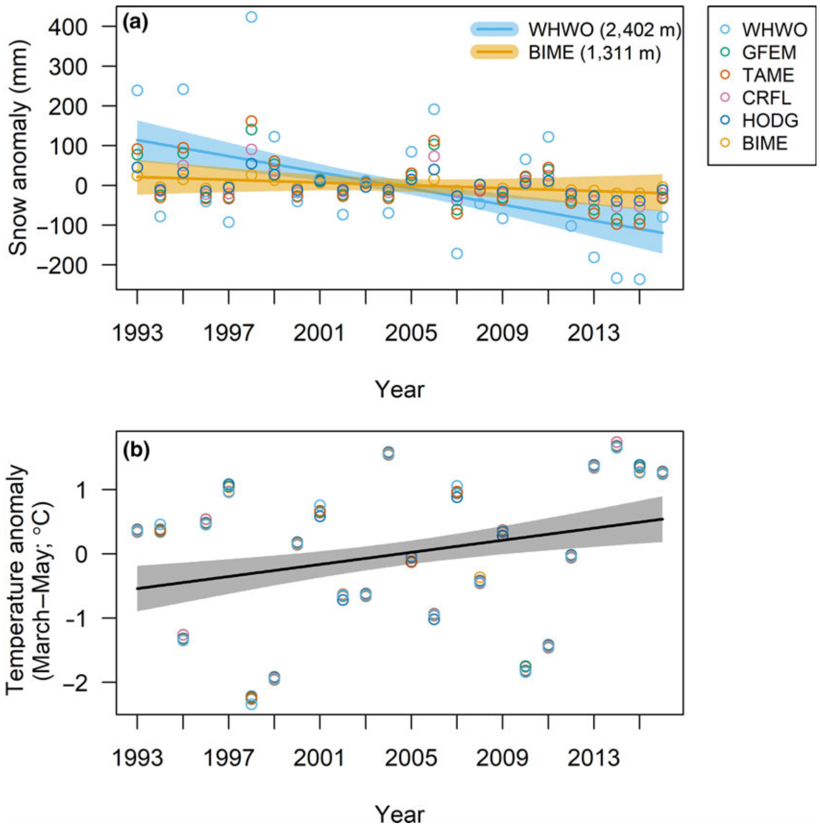

FIGURE 2 Temporal variation and trends in climate covariates at the six MAPS stations. (a) Annual precipitation as snow anomaly (mm) and (b) spring (March–May) temperature anomaly. Station values are distinguished by color, and differing snowfall trends between highest (WHWO) and lowest (BIME) stations are indicated in (a)

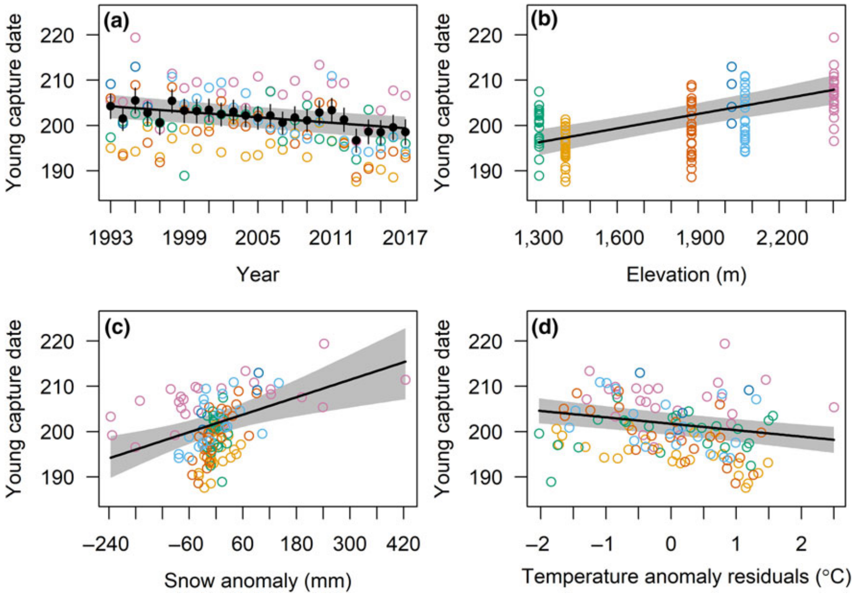

FIGURE 3 Temporal patterns and covariate relationships for the capture date of young (hatching year) birds response variable. (a) Temporal variation and trend in young capture date over the 25-yr study period. Black points represent model annual mean estimates (±95% cred. int.). Relationships between young capture date and (b) elevation, (c) annual precipitation as snow anomaly, and (d) spring (March–May) temperature anomaly residuals. Open circles in all panels show sample means (across all individuals) for each station (colors corresponding to Figure 2) and year. Annual trend in a and predicted covariate relationships in b–d are indicated by solid lines; gray polygons delineate 95% credible boundaries

to the highest station (WHWO at 2,402 m; 23 Jul). A few species showed virtually no evidence of later breeding at higher sites (e.g., $\hat{\beta}_{s,1} < 0$ for warbling vireo and purple finch; Supporting Information Figure S3b).

Breeding phenology also depended on snowfall anomaly (Equation (3): $\hat{\mu}_{\beta_{s,2}}$ = 1.95 [0.83, 2.94]), with the average day of capture for a young bird~18 days earlier at extreme low snowfall anomaly values compared to highest snowfall anomaly values (Figure 3c). As was the case for elevation, responses were variable among species. Negative snowfall effects were strongest for red-breasted nuthatch, golden-crowned kinglet, and purple finch (all with $\hat{\beta}_{s,2} > 4$) with estimated differences of 37–39 days in young capture timing between lowest and highest observed snowfall anomalies. Yellow Warbler showed weakest evidence of snowfall effects ($\hat{\beta}_{s,2}$ = −3.66[−10.48, 1.16]; Supporting Information Figure S3c), although at the highest station (WHWO) this species was only captured in a single year.

Spring temperature, after accounting for snowfall effect, also affected breeding phenology (Equation (3): $\hat{\mu}_{\beta_{s,3}}$ = −1.23 2 [−1.78, −0.65]), with young capture dates about 6 d earlier in relatively warm springs (Figure 3d). Strongest temperature effects ($\hat{\beta}_{s,2} < -2$) were observed for Yellow-rumped Warbler, Song Sparrow, dark-eyed junco, golden-crowned kinglet, and Brown Creeper, with estimated mean young capture dates 11–14 days earlier in the warmest compared to coldest springs (Supporting Information Figure S3d).

3.3 | Avian productivity

Mean productivity increased by ~20% over the 25-year study period (0.8%/year; Equation (4): $\hat{\mu}_{\beta_{s,1}}$ = 0.01[0.00, 0.02]; Figure 4a). The most positive trend estimate was an increase of about 48% over the study period ($\hat{\beta}_{s,1}$ = 0.02 [0.00, 0.05]) for Dusky Flycatcher, and the least positive trend effect estimate was ~10% over the study period for Lincoln's Sparrow ($\hat{\beta}_{s,1}$ = 0.01 [−0.02, 0.02]; Supporting Information Figure S4a).

Productivity was higher, on average, at higher elevation stations (Equation (5): $\hat{\mu}_{\beta_{s,2}}$ = 0.19[−0.02, 0.39]; Figure 4b). However, there was substantial variation in elevation response among species ($\hat{\sigma}_{\beta_{s,2}}$ = 0.45 [0.30, 0.65]), ranging from the strongest positive response by Hammond's Flycatcher ($\hat{\beta}_{s,2}$ = 1.17 [0.72, 1.64]) to the most negative response by Lazuli Bunting ($\hat{\beta}_{s,2}$ = −0.56 [−1.05, −0.09]; Supporting Information Figure S4c). Hammond's Flycatcher only bred at the highest five stations (~1,000 m range) and, of these, productivity was approximately 214% (92%, 415%) higher at the highest station (WHWO) compared to the lowest station (HODG). Lazuli Bunting only bred at the lowest three stations and, of these, estimated productivity was ~90% (9%, 219%) higher at the lowest (BIME) compared to the highest station (CRFL). Variation in productivity responses to elevation corresponded closely to elevation range shifts (i.e., changes to the elevational extent of the range) reported in Tingley et al. (2012). A regression of posterior estimates of species elevation effects on range shifts showed a strong negative relationship (slope est.: −0.0003 [−0.0005, −0.0001]; $\hat{R}^2$ = 0.20 [0.04, 0.38]; Figure 4c; Supporting Information Table S2). Species with highest productivity at low elevation tended to have expanding elevation ranges (i.e., broadened breeding elevation extents), while species with highest productivity at high elevation had shrinking ranges (i.e., narrowed breeding elevation extents).

Productivity was weakly negatively related to snowfall (Equation (5): $\hat{\mu}_{\beta_{s,3}}$ = −0.06[−0.14, 0.02]), with productivity approximately 31% higher at lowest snowfall anomaly values compared to highest values (Figure 4d). Productivity showed a stronger positive relationship with spring temperature anomalies (Equation (5): $\hat{\mu}_{\beta_{s,4}}$ = 0.15 [0.07, 0.23]), with productivity approximately 50% higher at warmest compared to coolest temperature anomaly values after controlling for snowfall effects (Figure 4e). Snowfall and temperature effects showed little variation among species ($\hat{\sigma}_{\beta_{s,3}}$ = 0.06 [0.00, 0.16]; Supporting Information Figure S4d; $\hat{\sigma}_{\beta_{s,4}}$ = 0.09 [0.00, 0.20]; Supporting Information Figure S4e). We found only weak support for the hypothesis that

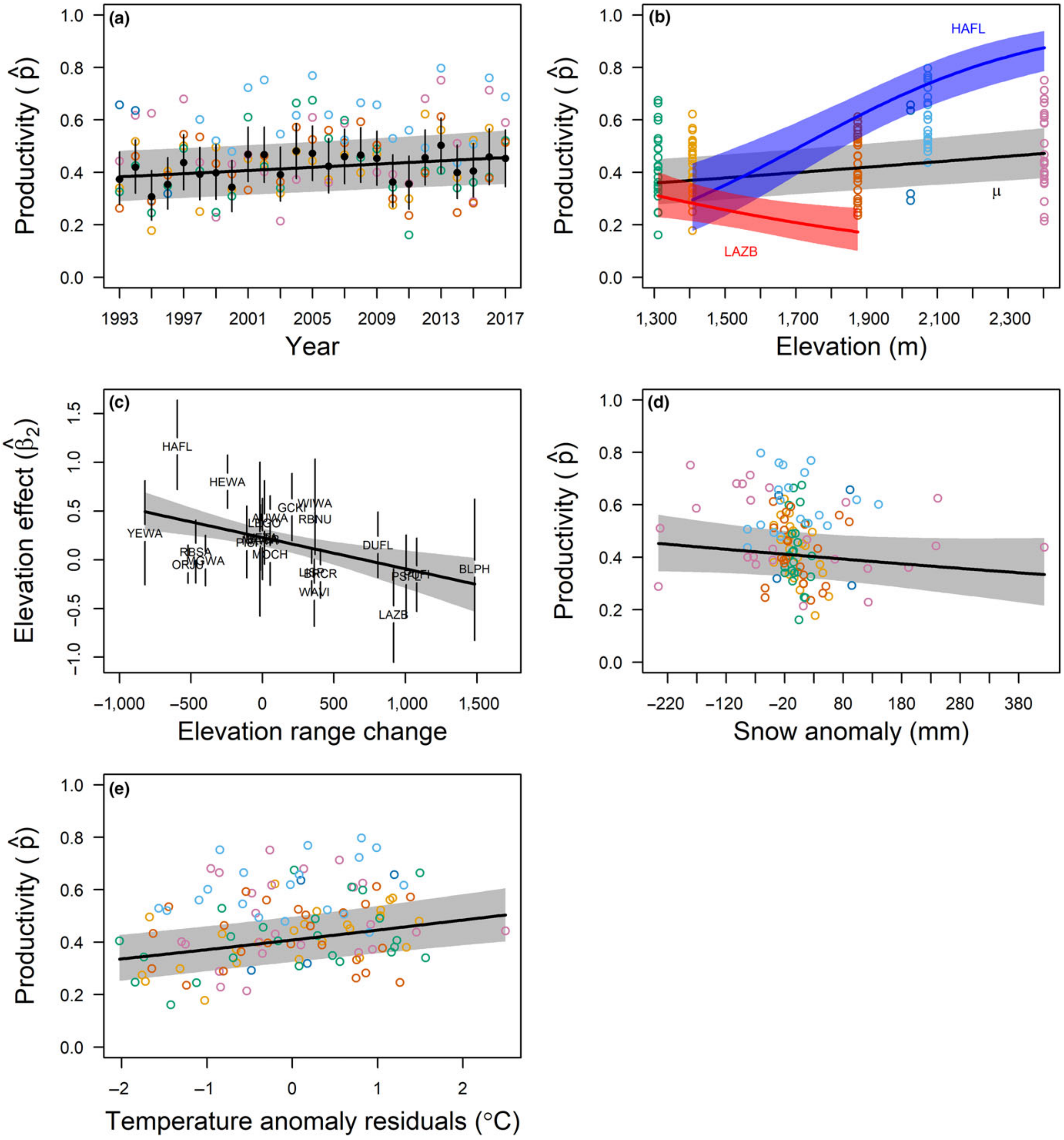

FIGURE 4 Summary of results for productivity (proportion young) models. (a) Temporal variation and trend in productivity. Black circles represent model mean estimates (±95% cred. int.). (b) Relationship between productivity and elevation. Species variation in B is highlighted with the species showing the most positive productivity–elevation relationship in blue (Hammond's Flycatcher; HAFL) and most negative relationship in red (Lazuli Bunting; LAZB). (c) Estimated relationship between productivity–elevation effects and species range shifts reported in Tingley et al. (2012). Points are represented by species codes in Table 2 (± 95% cred. ints.). Relationships between mean productivity and (d) snowfall anomaly and (e) spring (March–May) temperature anomaly residuals. Open circles in a, b, d, and e show sample means (across all individuals) for each station (colors corresponding to Figure 2) and year. Annual trend and predicted covariate relationships are indicated by solid lines; polygons delineate 95% credible boundaries

productivity responses to temperature varied by elevation, and the direction of interaction effect (stronger response to temperature at low elevation) was opposite to our expectation (Equation (5): $\hat{\mu}_{\beta_{s,5}}$ = −0.06 [−0.14, 0.02]; Supporting Information Figure S4f).

4 | DISCUSSION

Snowfall has declined and spring temperatures have increased at our study sites in the montane zone of Yosemite in recent decades. This pattern is consistent with studies from across the Sierra Nevada and mountainous western United States (Mote et al., 2018; Rapacciuolo et al., 2014), and further warming and reductions in snowpack are expected to continue under climate change scenarios (Hayhoe et al., 2004). Our analysis of the timing of captures of juvenile birds suggests that breeding phenology has advanced to match climate trends. Moreover, correspondence between avian demographic responses and elevation and climate variables, combined with an overall increasing productivity trend, suggests that birds have successfully tracked thermal niches and resource shifts related to climate trends.

On average, our index of productivity was higher at high elevations, likely reflecting augmentation of local productivity with upslope movements of young birds to some extent. Although we are unable to distinguish the relative spatial scales of sampling at our monitoring stations, higher elevation sites may provide high-quality late-season habitat for both postfledging young birds and adults when habitats at lower elevations are relatively hot and dry (Gaines, 1988; Wiegardt, Wolfe, Ralph, Stephens, & Alexander, 2017). Despite an overall tendency for productivity to increase with elevation, responses varied widely among species, and productivity of some species, such as warbling vireo and Lazuli Bunting, declined at higher elevations. Of these two species, only warbling vireo bred across the entire elevation gradient, and for this species our findings are consistent with Purcell (2006) who found relatively high nesting success in habitats and elevation similar to our lower montane stations.

Variation in productivity across elevation may have profound consequences for species resilience to climate change. For example, we found close correspondence between productivity–elevation relationships and changes in the extent of elevation ranges of individual species in the central Sierra Nevada over the past century (Tingley et al., 2012). Species for which we estimated higher productivity at high elevation in the montane zone have experienced range retractions. This finding could reflect limited available area for expansion into new habitat above the upper montane zone, which drops off precipitously above 2,000 m (Elsen & Tingley, 2015), possibly combined with altered biotic interactions or opposing climatic forces at higher elevations (Tingley et al., 2012). In contrast, species with higher productivity at low elevations have generally exhibited range expansions largely defined by increased maximum elevational limits. This latter pattern is consistent with these species tracking thermal niches upslope as average temperatures increase.

Birds appeared to track climate variation by breeding later at sites and in years with positive snowfall and negative spring temperature anomalies. Late-lingering snowpack in high snowfall years can delay breeding due to lower availability of snow-free substrates (particularly for ground- or shrub-nesting species) or less plant material available for constructing or lining nests early in the season (Pereyra, 2011; Smith & Andersen, 1985). Cooler temperatures may further delay nesting due to later insect emergence (Finn & Poff, 2009; Marshall, Cooper, DeCecco, Strazanac, & Butler, 2002) or reduced leaf cover for concealing nests (Briskie, 1995). Climate models generally predict that an increasing proportion of the Sierra Nevada's precipitation will fall as rain rather than snow in the future (Das, Dettinger, Cayan, & Hidalgo, 2011), and the snowpack that does accumulate will melt earlier in the year, at least in the montane zone (Cayan & Cayan, 1996; Howat & Tulaczyk, 2005; Maurer, Stewart, Bonfils, Duffy, & Cayan, 2007). Thus, we expect that timing of breeding will continue to advance.

Although we found snowfall to be negatively related to productivity, the estimated effect size was relatively small with 95% credible interval overlapping zero. Complex abiotic and biotic interactions could play a role in ameliorating potential negative snowfall effects on productivity. For example, at a higher subalpine site in the central Sierra Nevada, DeSante (1990) reported similar levels of avian productivity between years of early and late snowmelt. He suggested that smaller clutches and fewer nesting attempts in years with late-lingering snowpack were offset by lower nest predation rates because of weather-related reductions in mammalian predator populations (chipmunks and ground squirrels). Similarly, Martin and Maron (2012) suggested that nest predation at a montane site in Arizona in low snowpack years was facilitated by greater overwinter elk herbivory in those years.

After accounting for snowfall effects, we found a positive relationship between avian productivity and spring temperature. It could be argued that sampling biases may have contributed to this finding due to either under-sampling of young birds in late years or age-related differences in upslope movements that may have depended on climatic conditions. However, a variety of evidence suggests that these factors likely had minimal effect on results. For example, nest-monitoring data from nearby sites (DeSante, 1990; Pereyra, 2011) and lack of pattern in timing of captures of young birds between the last two sampling periods in early and late years both suggest that unavailability of late fledglings in late years would have been unlikely to have affected inferences. In addition, DeSante (unpubl. data) found that relatively large-scale upslope movements adjacent to the eastern boundary of Yosemite National Park extended to about 3,000 m for only two species included in this analysis, dark-eyed junco (ORJU) and Yellow-rumped Warbler (AUWA), perhaps reflecting the large numbers of these two species captured at the WHWO, GFEM, and CRFL stations (Supporting Information Figure S2). Nevertheless, these two species did not appear to be consistently exceptional in any of the species effect estimates for any of the productivity models (Supporting Information Figure S4), further suggesting that postfledging movements of adults and young likely had little effect on our results.

Our finding of a positive productivity–temperature relationship is consistent with larger scale reports of positive avian productivity–temperature responses (Meller et al., 2018; Socolar et al., 2017) and suggests that projected climate trends may bode well for montane breeding birds in this region. Mild winter and spring temperatures may facilitate overwinter survival of insect prey and yield abundant early-season insects (Bale et al., 2002). This, in turn, likely has positive effects on nesting success. Although we found an overall positive productivity–temperature relationship, reported mixed responses of species distributions to warming indicate that demography and population dynamics under a warmer, drier climate regime may be complex (Rapacciuolo et al., 2014; Tingley et al., 2012). In addition, multi-year extreme drought scenarios, which are historically rare and only observed in several of the later years of our study (2013–15), may become increasingly common (Griffin & Anchukaitis, 2014). Such conditions may ultimately have broader ecological consequences, including alteration of plant communities (e.g., through increased tree mortality; Aubry-Kientz & Moran, 2017; van Mantgem & Stephenson, 2007), insect dynamics, and fire regimes that disrupt observed productivity–climate relationships.

Climate trends have been implicated in altered species distributions and biodiversity loss around the globe and can have profound consequences for ecosystem functioning (Hooper et al., 2012). An expanding array of metrics has been proposed to assess species vulnerability to future climate change (Bellard, Bertelsmeier, Leadley, Thuiller, & Courchamp, 2012; Pacifici et al., 2015; Ruegg et al., 2018). Demographic parameters are key among these because they provide a mechanistic link between population processes, climate covariates, and population dynamics (Grosbois et al., 2008). Studies that link demographic rates to climate are still relatively rare (Amburgey et al., 2018; Kleinhesselink & Adler, 2018; Scridel et al., 2018). We suggest that multi-species demographic monitoring combined with directed research relating climate to demographic parameters can provide an important tool for guiding conservation of species assemblages in the face of climate change (Saracco, Fettig, San Miguel, Mehlman, & Albert, 2018).

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AUTHORS' CONTRIBUTIONS

J.F.S. and R.B.S. conceived the analysis. D.F.D. initiated the MAPS program at Yosemite National Park. D.F.D, L.H., and S.L.S. contributed data and oversaw data collection. J.F.S. analyzed the data and wrote the paper with input from all co-authors. All authors approved the submitted version.

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SUPPORTING INFORMATION

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

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