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# The response of big sagebrush (*Artemisia tridentata*) to interannual climate variation changes across its range

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**Abstract.** Understanding how annual climate variation affects population growth rates across a species' range may help us anticipate the effects of climate change on species distribution and abundance. We predict that populations in warmer or wetter parts of a species' range should respond negatively to periods of above average temperature or precipitation, respectively, whereas populations in colder or drier areas should respond positively to periods of above average temperature or precipitation. To test this, we estimated the population sensitivity of a common shrub species, big sagebrush (*Artemisia tridentata*), to annual climate variation across its range. Our analysis includes 8,175 observations of year-to-year change in sagebrush cover or production from 131 monitoring sites in western North America. We coupled these observations with seasonal weather data for each site and analyzed the effects of spring through fall temperatures and fall through spring accumulated precipitation on annual changes in sagebrush abundance. Sensitivity to annual temperature variation supported our hypothesis: years with above average temperatures were beneficial to sagebrush in colder locations and detrimental to sagebrush in hotter locations. In contrast, sensitivity to precipitation did not change significantly across the distribution of sagebrush. This pattern of responses suggests that regional abundance of this species may be more limited by temperature than by precipitation. We also found important differences in how the ecologically distinct subspecies of sagebrush responded to the effects of precipitation and temperature. Our model predicts that a short-term temperature increase could produce an increase in sagebrush cover at the cold edge of its range and a decrease in cover at the warm edge of its range. This prediction is qualitatively consistent with predictions from species distribution models for sagebrush based on spatial occurrence data, but it provides new mechanistic insight and helps estimate how much and how fast sagebrush cover may change within its range.

**Key words:** *Artemisia tridentata*; climate change; climate variation; long-term data; population growth; sagebrush.

## INTRODUCTION

Global climate change is causing species to go extinct in locations where they once thrived and become common in areas where they never before occurred (Parmesan and Yohe 2003, Chen et al. 2011). Changing species distributions and abundances will have profound consequences for ecosystem functioning, the spread of diseases, and the future of biodiversity on Earth (Pachauri et al. 2015). To anticipate the future effects of climate change, we need not only a detailed species-specific understanding of how climate determines species occurrences, but also models to predict how much and how fast species' abundances will change within their current range (Ehrlén and Morris 2015).

Current approaches to this challenge generally use either species' distribution models fit to occurrence data at a large spatial scale or population models fit to annual observations of species performance at a single location. By coupling data on annual variation in species performance with data on annual variation in climate, population models can be used to estimate species' sensitivity to temperature and precipitation (e.g., Adler et al. 2012, Lunn et al. 2016). For many locations on the globe, the difference in temperature or precipitation

between two subsequent years can be nearly as great as the projected magnitude of long-term climate change at that location (Mora et al. 2013). This makes multi-year population data collected at a single site a potentially powerful tool for understanding how populations could respond to climate change in the future (Adler et al. 2012, Lunn et al. 2016).

Nevertheless, this approach has rarely been applied at the range-wide scale for broadly distributed species (but see Chen et al. 2010, Amburgey et al. 2018). This deficit can be attributed to the fact that long-term population data is usually collected at only a few locations and rarely across an entire species' distribution. Because widespread species often show important clinal and ecotypic variation in temperature and drought tolerance across their range (Kolb and Sperry 1999, Rehfeldt et al. 1999, Millien et al. 2006), having population models fit to only one site within a species distribution may not be a good indication of how that species as a whole will respond to climate change. In the context of understanding species' response to global climate change, this makes it all the more important to study many populations encompassing a broad range of conditions (Ehrlén and Morris 2015).

Species distribution models offer an alternative approach to predicting how wide-spread species will be affected by climate change, but they have their own shortcomings. Distribution models are generally used to predict species occurrence rather than abundance, and often assume that regional variation in occurrence is in equilibrium with regional variation in climate. However, this assumption may not

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be warranted if dispersal barriers and stochastic population extinctions have shaped where species occur. Species may even occur in areas outside of their climate niche due to immigration or because remnant populations do not immediately go extinct after climate change (Guisan and Thuiller 2005, Holt and Keitt 2005). Even if the underlying assumptions of distribution models are valid, without a population model that includes temporal dynamics, distribution models cannot tell us how fast populations will change in the short-term or how species abundances will change within a species' range. This missing information is often critical for management and conservation.

In theory, with enough multi-year population data collected at sites across a species' range, one could analyze population sensitivity to climate at the scale of species distribution models (Ehrlén and Morris 2015, Amburgey et al. 2018). For example, Ettinger et al. (2011) studied annual variation in growth in conifer species across a wide elevation range. Annual climate variation was strongly correlated with tree growth at the species' upper elevation range limit, but not at their lower elevation limit. This implied that climate limits the high elevation edge of these species' distributions but not necessarily their low elevation edge. This mechanistic insight into the role of climate would be incomplete if growth had only been studied at one site, and would be obscured by a species distribution model fit only to occurrence data.

We propose that comparing how a species responds to annual climate variation in multiple populations across its range can provide valuable insight into how that species' will be affected by long-term climate change. In particular, we expect that those species that which will be most affected by

long-term climate change will show a specific pattern of response across their range: in the hottest parts of their range, populations will decrease after warmer than average years, whereas in colder parts of the range, populations will increase after warmer than average years (Fig. 1A–C; see also Amburgey et al. 2018). Such a pattern can be tested statistically by examining whether the short-term effect of temperature anomalies on population growth rates changes from positive to negative with increases in the average temperature of each location (Fig. 1b). A similar pattern would be expected for precipitation or any other aspect of annual climate variation that limits a species' distribution. Finding such a pattern would suggest a strong link between the climate driver and the species' long-term abundance and distribution. On the other hand, if sensitivity to short-term climate variation is similar across sites with different average climate, this would indicate that while the climate variable may influence local population dynamics, it does not play an important role in determining the species' geographic distribution. Our expectation is founded on the assumption that short-term sensitivity of a species to annual climate variation can be a good indicator of how that species will respond to longer-term climate change (Ludwig et al. 2006).

#### Case study with big sagebrush (*Artemisia tridentata*)

Big sagebrush is a dominant shrub found across much of western North America, occurring from forest edges to prairies and from low elevation deserts to high elevation mountains (Kuchler 1970). Sagebrush provides unique and critical habitat for many endemic species of conservation concern

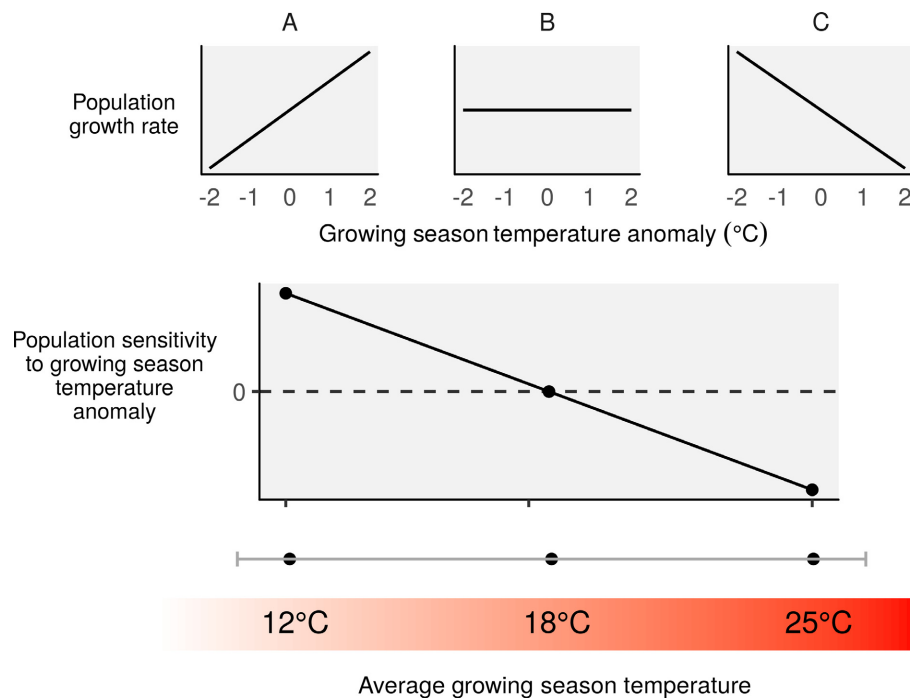


FIG. 1. Hypothetical effects of annual temperature variation on populations of a widespread species. Figures in the top row correspond to three sites, from coldest (A) to warmest (C), and show population growth rate on the y-axis and annual temperature anomalies on the x-axis. Years of above average temperature are expected to have a positive effect at the coldest site (A), a weak effect at sites in the center of the species' climatic range (B), and a negative effect at the warmest site (C). The lower figure plots the temperature sensitivity of each population against the average temperature at each site. A negative slope in the lower figure supports the hypothesis that temperature controls the species' distribution.

such as the Greater Sage-grouse (*Centrocercus urophasianus*) (Connelly et al. 2000). Distribution models for sagebrush typically indicate that climate change will cause large decreases in the total area suitable for sagebrush in the future (Neilson et al. 2005, Bradley 2010, Schlaepfer et al. 2012a, Still and Richardson 2015). Climate change could cause a decrease in snow cover and an increase in evaporation, both of which would lead to decreased soil moisture during the growing season and reduce sagebrush growth (Schlaepfer et al. 2012a, b).

Direct evidence for the effects of short-term climate variation on sagebrush comes from a multi-year global warming experiment and analysis of sagebrush growth rings. Harte et al. (2015) found that sagebrush cover increased substantially in response to 20 years of artificial warming at high elevation in the southern Rocky Mountains. This increase was linked to a longer snow-free growing season at higher elevations with warming (Perfors et al. 2003). In contrast, at lower elevation sites that are warmer and drier, sagebrush growth appears to decrease in response to warmer than average years (Poore et al. 2009, Apodaca et al. 2017).

Complicating detection of relationships between climate and sagebrush performance is the fact that sagebrush comprises many ecologically distinct subspecies or varieties. The three most common subspecies have more or less distinct climate niches: mountain big sagebrush (*A. t. ssp. vaseyana*) is found where snowfall is high, basin big sagebrush (*A. t. ssp. tridentata*) is found in warmer areas, and Wyoming big sagebrush (*A. t. ssp. wyomingensis*) is dominant in the most arid regions (Rosentreter 2001). These differences in distribution reflect underlying differences in germination (Meyer et al. 1990), drought adaptation (Kolb and Sperry 1999), phenology (Richardson et al. 2017), and response to temperature (Hansen et al. 2008, Brabec et al. 2017, Chaney et al. 2017).

Based on our conceptual model (Fig. 1), we predicted that sagebrush population growth rates will decrease during warmer than average years in the hottest parts of its range, whereas population growth rates will increase during warmer than average years in the coldest sites. Similarly, if sagebrush distribution is limited by precipitation, we expected sagebrush populations would respond positively to wetter than average years in drier areas but negatively to wetter than average years in wetter areas. We also expected that sagebrush subspecies might show distinct patterns of response to annual climate variation, with Wyoming big sagebrush showing a strong response to annual variation in precipitation, whereas mountain sagebrush, would show a stronger response to annual variation in temperature. Finding these patterns would support a link between local population dynamics and the climate niche of sagebrush and suggest that the future distribution and abundance of sagebrush will be sensitive to long-term climate change.

## METHODS

### *Multi-year sagebrush cover data sets*

We assembled multi-year data on sagebrush cover or sagebrush production through literature searches and by contacting scientists and natural resource managers at federal and state land management agencies. Only data sets that

directly measured big sagebrush (*Artemisia tridentata*) abundance in permanent monitoring plots for two or more consecutive years were included in the analysis. From each study, we extracted information on the exact plot location (latitude and longitude), the year of data collection, the plot size, the subspecies of sagebrush in the plot, the measurement type, and the measurement method (e.g., line-intercept, point intercept, visual estimate; Appendix S1: Table S1). Most sagebrush vegetative growth occurs before mid-summer (DePuit and Caldwell 1973) and most data sets measured sagebrush abundance between early and late summer. We excluded data from experimental treatments that would affect sagebrush cover, such as burning, herbicide application, irrigation, fertilization, or artificial warming. We included a small number of plots from Wyoming where harvester ants were experimentally removed using pesticide and we included a small number of plots within grazing enclosures (Appendix S1: Table S2).

For studies that reported multiple plots from multiple locations, we preserved plot groupings or location identifiers as reported by the original study authors. In our data set, only a small number of plots or transects included more than one subspecies, reflecting a tendency for co-occurring sagebrush subspecies to segregate on topographic gradients or soil types (Barker and McKell 1983). However, it is likely that some mixed stands in our data were recorded as a single subspecies, especially because sagebrush subspecies can be hard to distinguish (Rosentreter 2001). This could be a source of error for our individual subspecies models. A complete list of the data sources and references describing methods for each data set are included in the online supporting information (Appendix S2).

The full database of sagebrush cover and production estimates included 8,175 observations of annual changes in sagebrush cover or production from 1,066 plots, in 131 locations across the western United States (Fig. 2). The data captures most of the range of climate occupied by sagebrush, from sites with mean annual temperatures of 1° to 13°C and mean annual precipitation from 157 to 883 mm (Appendix S1: Figs. S1 and S2), although we had relatively fewer points from cold and wet regions (Appendix S1: Fig. S1). Sagebrush not identified to subspecies was the most common type in our data set, with Wyoming big sagebrush second, mountain sagebrush third and basin big sagebrush the least common (Appendix S1: Table S3).

### *Autoregressive model for sagebrush abundance*

We used a discrete time Gompertz population model to analyze the cover and production time-series and draw inference about the effects of interannual climate variation on sagebrush abundance (Ives et al. 2003). In this model, cover or production at the plot or transect level in year  $t$  is dependent on cover or production in the previous year  $t - 1$  via the following relationship

$$n_t = n_{t-1} \exp[a + (b - 1) \log n_{t-1}] \quad (1)$$

where  $n_t$  is the abundance (e.g., percent cover or density) in year  $t$ ,  $a$  is the intrinsic rate of increase, and  $b$  is the

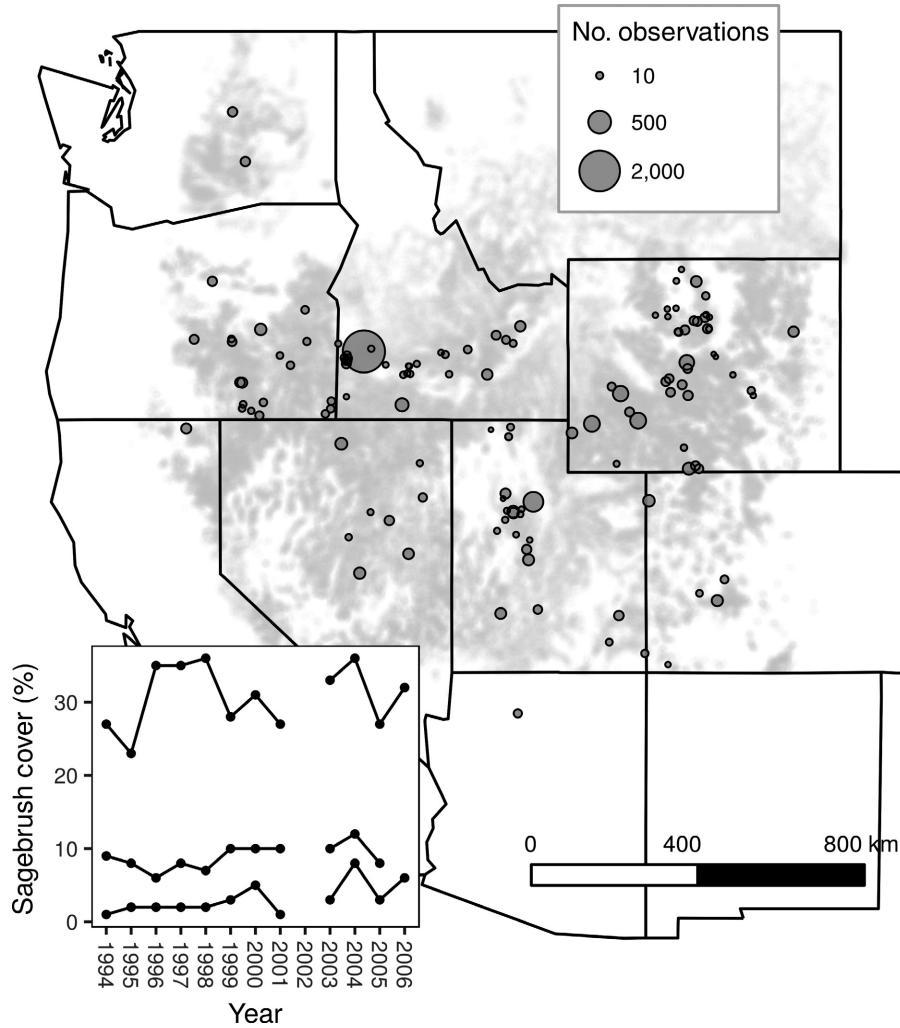


FIG. 2. Map of sites with multi-year sagebrush cover data in the western United States. Point size corresponds to number of observations at each site. Gray areas show the distribution of sagebrush based on the USGS SAGEMAP data set (<http://sagemap.wr.usgs.gov/>). Inset shows an example of multi-year sagebrush cover data from three monitoring plots at Camp Williams, Utah.

dependence on previous year's population abundance. Log transforming the abundance values results in a simple linear model

$$y_t = a + by_{t-1} \quad (2)$$

where  $y_t = \log n_t$ . Importantly, this model predicts a stable long-term equilibrium abundance  $\hat{y}$  for the population at

$$\hat{y} = a/(1 - b). \quad (3)$$

Annual climate covariates can be incorporated in this model as simple additive effects on the log-transformed abundance,  $y_t$ , during the transition from year  $t - 1$  to year  $t$

$$y_t = a + by_{t-1} + \mathbf{x}'_{t-1} \boldsymbol{\theta} \quad (4)$$

where  $\mathbf{x}'_{t-1}$  is a vector of annual weather variables in year  $t-1$  and  $\boldsymbol{\theta}$  is a vector of coefficients describing the effects of each variable on the population growth rate.

#### Climate covariates

For each study site, we extracted monthly historical weather data from the PRISM data set (Daly et al. 2008; data available online).<sup>3</sup> We focused on growing season temperature at two different time windows:  $t_{\max}$ , the average daily maximum temperature of the spring of year  $t$ , and  $t_{\max, \text{lag}}$ , the average daily maximum temperature for the spring through fall season for years  $t - 1$  to  $t - 3$ , where  $t$  is the year of the current observation of sagebrush cover (Appendix S1: Fig. S3a). In most of its distribution, this represents the seasonal window when sagebrush is actively growing. Although sagebrush may be influenced by winter temperatures (Brabec et al. 2017), this effect may depend on snow cover (Hanson et al. 1982). We avoided this complication of winter temperature by focusing instead on spring through fall temperatures. Likewise we considered  $t_{\max}$  rather than the average daily minimum temperature because  $t_{\max}$  is associated with daytime highs that control spring snowmelt and sagebrush

<sup>3</sup> <http://www.prism.oregonstate.edu>



growth in cold climates and, in warm climates, could be associated with mid-day water stress. Moreover, there is some evidence that  $t_{\max}$  is a better predictor of sagebrush growth than  $t_{\min}$  (Apodaca et al. 2017). We included cumulative precipitation at two different time windows:  $ppt$ , November to May in year  $t$ , and  $ppt_{\text{lag}}$  cumulative precipitation of the previous three years starting in November, (year  $t - 3$  to year  $t - 1$ ) (Appendix S1: Fig. S3b). Our choice to include two time windows for the temperature and precipitation variables was motivated by the observation that growth of big sagebrush, and closely related *Artemisia* species, can show lag responses to climate: i.e. the effect of climate variation experienced in the past 12 months may not match the effect of climate variation experienced in the years before that (Adler et al. 2012, Apodaca et al. 2017).

We chose these seasonal windows and lags a priori based on the rationale above and previous research on sagebrush demographic response to climate (Tredennick et al. 2016, Apodaca et al. 2017). We focused on this limited number of climate variables rather than undertaking a variable selection process to avoid evaluating all possible combinations between seasonal windows and annual lags for each of the four climate variables. This allowed us to more rigorously test our main hypotheses within a small set of defensible and interpretable climate effects (Fig. 1). After completing our main analysis, we tested whether our main conclusions were sensitive to the number of years included in the  $ppt_{\text{lag}}$  and  $t_{\max_{\text{lag}}}$  variables (Appendix S1: Table S7).

For analysis, the seasonal temperature and precipitation measures were centered on their long-term averages at each site for the period 1901–2000. We also calculated standardized precipitation evapotranspiration index (SPEI) for each time window. SPEI takes into account temperature and precipitation and accounts for the fact the two can interact to influence water availability for plants. We calculated SPEI in the SPEI package in R (Begueria and Vicente-Serrano 2013). We fit four candidate models expressing the short-term precipitation anomalies either as a raw deviation from the average, the raw deviation divided by the standard deviation, the deviation as a proportion of the average, or as SPEI. We compared these models using Akaike Information Criteria (AIC), and if these scores were appreciably different, we chose the precipitation transformation with the lowest AIC score for further analysis.

We also calculated site-specific long-term averages for spring through fall monthly maximum temperature ( $t_{\max_{\text{avg}}}$ ) and winter through spring precipitation ( $ppt_{\text{avg}}$ ). To allow for the effect of temperature anomalies to vary across sites with different average temperature, we included the interaction of each of the short-term temperature anomalies with the site-specific long-term temperature averages ( $t_{\max} : t_{\max_{\text{avg}}}$  and  $t_{\max_{\text{lag}}} : t_{\max_{\text{avg}}}$ ). Likewise, we included interactions between the short-term precipitation anomalies and the long-term average of cumulative winter through spring precipitation ( $ppt : ppt_{\text{avg}}$  and  $ppt_{\text{lag}} : ppt_{\text{avg}}$ ). These four interaction effects are key to testing our hypothesis that annual climate effects should change systematically across gradients in average climate (Fig. 1). If sagebrush distribution is limited by temperature or precipitation at the extremes of its climate distribution, then we expect to find negative interaction effects.

### Statistical model

To fit the autoregressive population model, we used a general linear mixed effects model in the lme4 package in R (Bates et al. 2015, R Core Team 2015). Our model included random effects to reflect spatial and temporal grouping factors in the data: each unique plot or transect, plot location, and year. Location groups were designated as in the original studies, but generally grouped plots at the scale of 1–5 km. Year effects were unique to each location so that only plots near one another and exposed to similar conditions experienced the same year effects. We allowed the intercept of the Gompertz model to vary with each of these grouping factors. Likewise, we allowed the relationship between the previous year's abundance ( $y_{t-1}$ ) and the current year's abundance ( $y_t$ ) to vary by plot, reflecting variation between plots in the strength of density dependence.

We also allowed the intercept and slope of the Gompertz model to vary with the sagebrush subspecies type in each plot, reflecting differences in the average abundance and growth rates of each subspecies. The data set is mainly comprised of absolute percent cover estimates ( $N = 7,976$ ), but there were also some data sets that reported annual production estimates for sagebrush in grams per square meter per year ( $N = 199$ ; Appendix S1: Table S1). We fit a separate intercept and slope for each data type as indicated by the variable *dtype*.

Finally, we added the four annual weather variables ( $t_{\max}$ ,  $t_{\max_{\text{lag}}}$ ,  $ppt$ ,  $ppt_{\text{lag}}$ ) and their interaction with long-term average climate variables ( $t_{\max_{\text{lag}}}$ ,  $ppt_{\text{avg}}$ ) as fixed effects in order to model the effects of weather and climate. The full model written in lmer notation is given in Appendix S1: Eq. S1.

We judged interaction effects between average climate and annual deviation in climate as significant by comparing models with and without the interaction effect using a likelihood ratio test ( $P(\chi^2) < 0.05$ ). We calculated an  $R^2$  for our model using the MuMIn package in R (Johnson 2014, Bartoń 2016).

After fitting models to the full data set, we explored whether sagebrush subspecies responded differently to annual variation in climate by fitting data from each subspecies to a separate model with the same structure as the overall model above but without the separate term for subspecies.

### Climate change sensitivity

We used the fitted model to examine how perturbations in temperature or precipitation could affect sagebrush abundance across the sites observed in the data set. For each site, we predicted the proportional change in sagebrush cover that would occur with a one standard deviation increase in temperature or precipitation across all locations in the data set. These perturbations changed the values of  $t_{\max}$ ,  $t_{\max_{\text{lag}}}$ ,  $ppt$ , and  $ppt_{\text{lag}}$  but do not affect the values of  $t_{\max_{\text{avg}}}$  and  $ppt_{\text{avg}}$ . As a baseline, we set sagebrush abundance at each site to its hypothetical equilibrium abundance determined by Eq. 3. At this abundance, sagebrush population growth rate is predicted to be zero in the absence of annual weather fluctuations (Ives et al. 2003). Setting the abundances to this equilibrium and then imposing an

increase in temperature or precipitation is a way to isolate the change in abundance caused only by the weather anomalies rather than the effects of density dependence. We generated predictions and bootstrapped 95% confidence intervals around predictions using the `bootMer` function in `lme4` (Bates et al. 2015). Predictions were generated without incorporating the uncertainty from the plot, location and year-specific random effects.

## RESULTS

We found that all four transformations of the precipitation anomalies (raw, standardized, proportion of average, and SPEI) produced models with nearly equal AIC scores (within 1). In our subsequent analyses, we used the model with precipitation anomalies (`ppt` and `pptlag`) scaled by their standard deviations and report these results in Table 1. The marginal  $R^2$ , meaning the variance explained only by fixed

TABLE 1. Coefficients from a linear mixed effects model fit to sagebrush data ( $n = 8,175$ ).

Fixed effect	Estimate	SE	<i>t</i> Value	LRT	$P(\chi^2)$
<i>a</i>	1.26	0.58	2.16		
<i>b</i>	0.50	0.02	22.91		
<code>ssp_basin</code>	-0.41	0.25	-1.61		
<code>ssp_mountain</code>	0.70	0.20	3.54		
<code>ssp_Wyoming</code>	0.37	0.14	2.59		
<code>dtype_production</code>	1.27	0.30	4.31		
<code>ppt<sub>avg</sub></code>	0.98	0.73	1.34		
<code>ppt</code>	-0.01	0.03	-0.17		
<code>ppt<sub>lag</sub></code>	-0.03	0.05	-0.73		
<code>tmax<sub>avg</sub></code>	-0.03	0.03	-0.96		
<code>tmax</code>	-0.21	0.14	-1.54		
<code>tmax<sub>lag</sub></code>	0.38	0.14	2.65		
<code>ssp_basin:b</code>	-0.05	0.08	-0.65		
<code>ssp_mountain:b</code>	-0.40	0.05	-7.72		
<code>ssp_Wyoming:b</code>	-0.23	0.04	-6.30		
<code>dtype_production:b</code>	-0.32	0.08	-3.86		
<code>ppt:ppt<sub>avg</sub></code>	0.14	0.14	1.02	1.059	0.303
<code>ppt<sub>lag</sub>:ppt<sub>avg</sub></code>	0.17	0.20	0.87	0.765	0.382
<code>tmax:tmax<sub>avg</sub></code>	0.01	0.01	1.34	1.829	0.176
<code>tmax<sub>lag</sub>:tmax<sub>avg</sub></code>	-0.02	0.01	-2.49	6.194	0.013*
Random effect	no.	SD	cor		
<code>loc</code>	131	0.44			
<code>loc/year</code>	844	0.38			
<code>plot</code>	1,066	0.80			
<code>plot:y<sub>t-1</sub></code>	1,066	0.30	-0.584		
Residual		0.32			

Notes: Estimates for the model intercept (*a*) and the effect of last year's abundance (*b*) correspond to the variables in the Gompertz population model described in Eq. 1. The effects `ssp_basin`, `ssp_mountain` and `ssp_wyoming` give the intercepts of each for subspecies with unidentified sagebrush as the reference level. The effect `dtype_production` gives the intercept for plots in which sagebrush production ( $\text{g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ ) was measured rather than cover. LRT and  $P(\chi^2)$  report a likelihood ratio test on the climate interaction effects (an "\*" indicates significance at the  $P < 0.05$  level). Weather and climate effects are defined in the "climate covariates" section of the methods. Random effects are for location (`loc`), location by year (`loc/year`), plot (`plot`), and a plot-dependent effect of last year's sagebrush abundance (`plot:yt-1`). `cor` reports the correlation between the plot-level effects.

factors, for this model was 0.19 while the conditional  $R^2$ , which includes variance explained by the random effects, was 0.92 (Bartoń 2016).

Using the estimates of the model intercept (*a*), the effect of last year's abundance (*b*), and the fixed effects for subspecies (Table 1) allowed us to calculate equilibrium abundances from Eq. 3 of 6.6%, 2.6%, 7.2%, and 6% for cover of unidentified, basin, mountain, and Wyoming sagebrush subspecies. These equilibrium values were close to the observed log-average cover for each subspecies: 8.4%, 3.6%, 5.1%, and 8% for cover of unidentified, basin, mountain, and Wyoming sagebrush, respectively.

The strongest of the four climate interaction effects was the interaction between the lag growing season temperature and long-term average growing season temperature at that site (`tmaxlag` by `tmaxavg` interaction; Table 1). The effect of `tmaxlag` was negative at the hottest sites but positive at coldest sites; sagebrush cover increased after periods with warm growing seasons at cold sites, but decreased after periods with warm growing seasons at hot sites (Fig. 3d). A likelihood ratio test showed that including this interaction effect significantly improved model fit compared to a model without this effect (Table 1).

The effect of spring average maximum temperature (`tmax`) was in the opposite direction of the lag growing season temperature (`tmaxlag`), although this effect was not significant based on the likelihood ratio test (Table 1). The direction of this effect means that warmer spring temperatures had a negative effect at colder sites but a positive effect at warmer sites (Fig. 3B). Neither of the precipitation effects showed a significant interaction with long-term average precipitation (Table 1; Fig. 3A,C).

A model fit only to the Wyoming sagebrush data showed a positive interaction between `pptlag` and `pptavg` and a significant positive interaction between `tmax` and `tmaxavg` (Appendix S1: Table S4). This meant that wetter than average years preceding sagebrush measurement had a negative effect at drier sites but a positive effect at wetter sites (Appendix S1: Fig. S4c). Likewise, warmer than average spring temperatures had a positive effect at warmer sites but a negative effect at colder sites (Appendix S1: Fig. S4b).

A model fit just to mountain sagebrush did not show significant interactions between the short-term climate variables and their long-term averages (Appendix S1: Table S5). However, mountain sagebrush showed a positive response to above average precipitation throughout its distribution (Appendix S1: Fig. S5a,c). Likewise it responded positively to warmer lag temperatures throughout its range (Appendix S1: Fig. S5d). None of the climate interaction effects were significant for basin big sagebrush, although there were many fewer observations of this species in the data set (Appendix S1: Table S6; Fig. S6).

The predicted effect of a one standard deviation increase in `ppt` and `pptlag` across all sites was an increase in sagebrush cover in the wettest sites and no change in the driest sites (Fig. 4). The predicted response to a one standard deviation increase in `tmax` and `tmaxlag` was a slight increase in sagebrush at the coldest sites and a slight decrease at the warmest sites. For both scenarios, bootstrapped 95% confidence intervals around the predictions widely overlapped zero (Fig. 4).

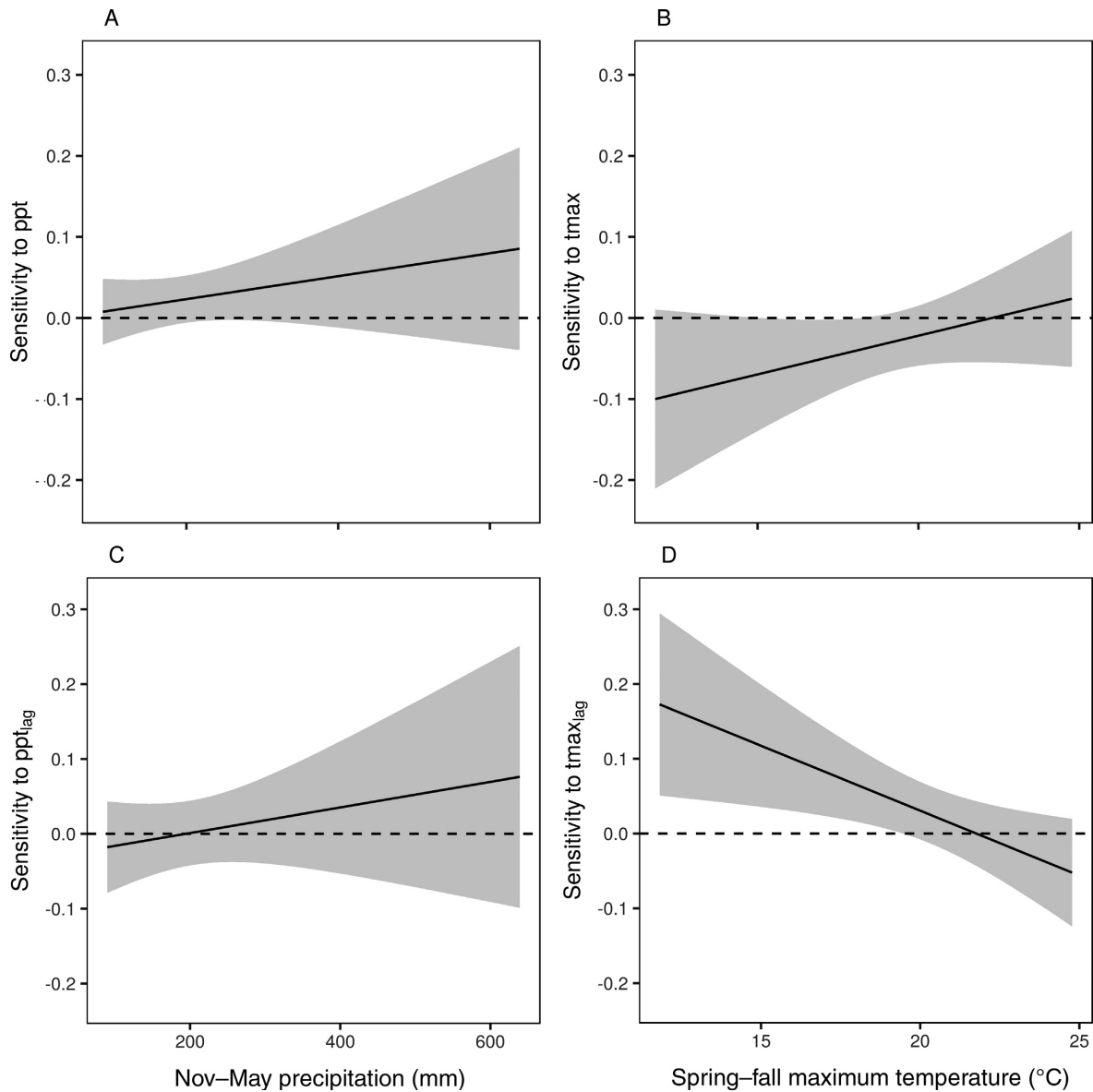


FIG. 3. Sensitivity of sagebrush abundance to annual climate plotted against average site climate. Sensitivity is defined as the log change in sagebrush abundance produced by a one standard deviation increase in ppt (A), ppt<sub>lag</sub> (C), tmax (B) or tmax<sub>lag</sub> (D). Effects below zero indicate where above average temperature or precipitation would decrease population growth rate, while effects above zero indicate where above average annual temperature or precipitation would increase population growth rate. Gray areas show 95% confidence intervals.

To evaluate whether our choice of the time window for the ppt<sub>lag</sub> and tmax<sub>lag</sub> variables affected our results, we re-fit our basic model using a set of alternative definitions for the ppt<sub>lag</sub> and tmax<sub>lag</sub> variables and ranked these models using AIC (Appendix S1: Table S7). The top ranked models included lag growing season temperature averaged over the previous 1–4 or 1–3 years and all showed a negative interaction between this variable and site-level average growing season temperature (tmax<sub>lag</sub>:tmax<sub>avg</sub> interaction).

#### DISCUSSION

We found mixed support for our conceptual model that the response of sagebrush populations to annual climate would vary systematically across its climatic range.

Sagebrush response to the growing season temperature anomaly of the previous three years (tmax<sub>lag</sub>) matched our hypothesis well, but sagebrush response to spring temperature anomalies and precipitation anomalies did not (Fig. 3). A significant negative interaction between average growing season temperature and annual temperature deviation (Table 1) shows that sagebrush cover decreased in response to warmer than average years in hot sites but increased in response to warmer than average years in cold sites. This supports the idea that average growing season temperatures may broadly limit where sagebrush can grow. Thus, growing season temperature may be a key variable for predicting the future of sagebrush distribution and local abundances.

Our analysis shows the potential utility of analyzing population sensitivity to climate at the scale of an entire species'



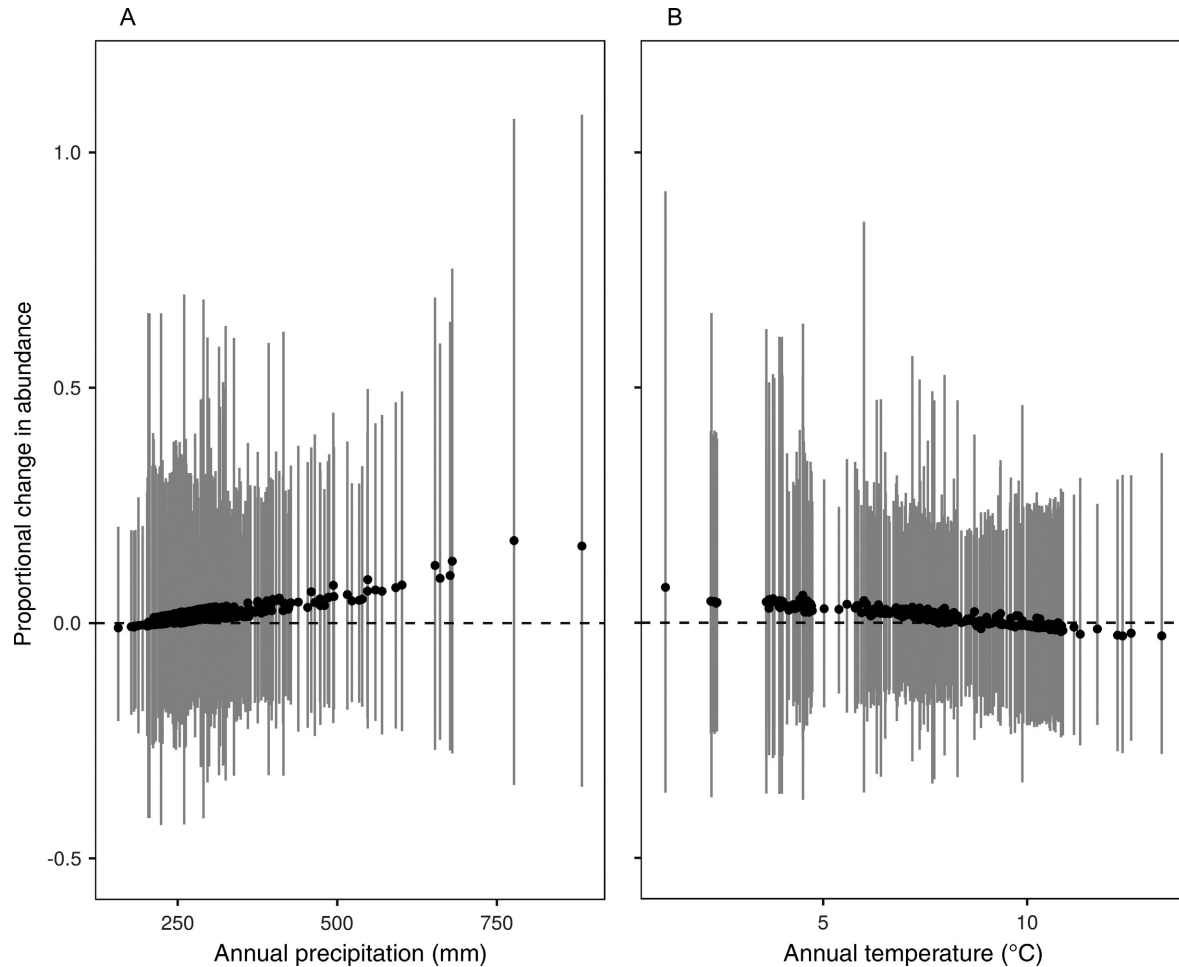


FIG. 4. Predicted change in sagebrush cover in response to a one standard deviation increase in either (A) precipitation or (B) temperature. In panel A, the effect of an increase in both ppt and ppt<sub>lag</sub> is plotted against mean annual precipitation. In panel B, the effect of an increase in tmax and tmax<sub>lag</sub> is plotted against mean annual temperature. Gray bars show 95% confidence intervals.

distribution (Ehrlén and Morris 2015). Our results can be compared with those recently published by Amburgey et al. (2018) for a widespread species of amphibian. As in our analysis, they found that populations at the warmer edge of the range showed a negative response to periods of above average temperatures, whereas populations located at the colder edge showed a positive response. They also found that population sensitivity to other climate drivers, such as precipitation, were not as expected. These studies show the potential for using demographic analyses to determine which of the many aspects of climate are most important for determining species' ranges and abundance. In the context of climate change, the models presented in Amburgey et al. (2018) and in our current study, generate testable predictions about how species will respond to climate variation. Importantly, these predictions are at the scale of short-term changes in local abundance, thus they can be generated and validated annually, which will allow for a continuous process of model improvement. This contrasts with SDMs, which are often used to predict species' distributions many decades in the future, making them difficult to validate empirically.

Our results suggest that future studies should focus on the effects of above average temperatures on sagebrush in the warmest parts of its range. We found that sagebrush

population growth rates decline in response to warming in locations where average growing season temperatures are above 22°C (corresponding to about 10°C mean annual temperature; Figs. 3D and 4A). This point can be compared to the climate pivot points observed for desert vegetation in the American southwest (Munson et al. 2013). The negative effects of temperature may be due to direct effects on the growth and respiration of sagebrush (Hansen et al. 2008), or to temperature driven changes in soil moisture and plant water status (Schlaepfer et al. 2012c). Physiological data suggest that growth and photosynthesis of sagebrush leaves may be optimum at about 20°C and decline at higher temperatures (DePuit and Caldwell 1973, Hansen et al. 2008). Likewise, Apodaca et al. (2017) and Poore et al. (2009) found that sagebrush growth rings were reduced in response to above average spring through summer temperatures in Nevada and Colorado, indicating that warm temperatures, either directly or indirectly, inhibit sagebrush growth.

In colder climates, however, both experimental evidence and some observational data show that warmer than average temperatures can enhance sagebrush growth (Perfors et al. 2003, Harte et al. 2015, Tredennick et al. 2016). In cold regions, below average temperatures may be especially detrimental for sagebrush if they lengthen the duration of snow

cover and shorten the growing season (Harte et al. 2015). Importantly, the benefit of warmer temperatures to sagebrush in cold sites appeared to be greater than the negative effect of warmth at hot sites (Fig. 3D). We also found that the lag effects of temperature ( $t_{\max, \text{lag}}$ ) and the immediate effects of spring temperature ( $t_{\max}$ ) were nearly opposite (Fig. 3B,D; but note that the effect of  $t_{\max}$  was not significant). The opposing spring and lag growing season effects counter one another over the longer-term: warm years at cold sites for instance tend to reduce sagebrush growth in the first year, but the legacy of this effect is a strong increase in growth over the next few years. This counterbalancing effect may explain why we predict only a limited change in cover in response to a simultaneous increase in both temperature anomalies (Fig. 4B).

The effects of precipitation were not significant and their direction was opposite to that we expected. The interaction between lag precipitation and average precipitation was positive (Table 1), meaning that the effect of precipitation either does not change from the dry to wet locations or has a positive effect only at the wettest edge of sagebrush distribution. Our result indicates that low annual precipitation may not be the limiting factor for sagebrush populations at the dry edges of its distribution. Indeed some SDMs show that precipitation is only a weak predictor of sagebrush occurrence (Still and Richardson 2015).

Our model predicts that a hypothetical increase in precipitation will be most beneficial to sagebrush populations already growing in the wetter parts of its range (Fig. 4A). There is evidence that sagebrush growth can be water limited even in relatively moist climates (Loik 2007, Poore et al. 2009, Reed and Loik 2016). Over longer time periods however, precipitation may still play a role in limiting sagebrush if it promotes competition with other species such as trees (Leffler and Caldwell 2005).

Our result that sagebrush did not respond strongly to wet years at dry sites seems strange. For instance, sagebrush growth rings at relatively dry sites in Nevada (mean annual precipitation 250–300 mm) showed a positive response to years with above average precipitation (Apodaca et al. 2017). The response of sagebrush to precipitation may be complicated by an interaction with local soil depth: at a dry site in Idaho (mean annual precipitation 220 mm), winter irrigation increased sagebrush growth in deeper soils but decreased growth in shallow soils (Germino and Reinhardt 2014). A possible explanation for this phenomenon is that sagebrush root growth is very sensitive to low oxygen (Lunt et al. 1973) and may die off rapidly in response to flooding or rapid spring snow melt (Ganskopp 1986).

We saw important differences between two dominant ecotypes of sagebrush, Wyoming sagebrush and mountain sagebrush. Above average temperatures and above average precipitation had weak positive effects on mountain sagebrush throughout its range (Appendix S1: Fig. S5c,d). This finding agrees with the surprising fact that mountain sagebrush is more sensitive to freezing temperatures than Wyoming sagebrush (Brabec et al. 2017). Wyoming sagebrush, which is generally found in drier and warmer conditions than mountain sagebrush, responded positively to  $t_{\max}$  in warmer locations and negatively in colder locations (Appendix S1: Fig. S4b). One potential explanation for this

counterintuitive result is if warm temperatures in colder parts of this species range induce earlier snowmelt or earlier leaf out; either could expose plants to more freezing damage in the spring as growth begins (Brabec et al. 2017, Chaney et al. 2017). Wyoming sagebrush also responded negatively to above average precipitation in the driest part of its range but benefited from precipitation in the wettest parts of its range (Appendix S1: Fig. S4c). We speculate that this may reflect sensitivity of Wyoming sagebrush to saturated soils (Lunt et al. 1973), or to increased competition from perennial grasses. In drier locations, periods of above average precipitation may stimulate the growth of grass at the expense of sagebrush. This kind of negative indirect effect has been reported for three-tip sagebrush *Artemisia tripartita*, a close relative of *A. tridentata* (Adler et al. 2012).

Basin big sagebrush showed no significant response to the weather variables. This lack of sensitivity may reflect the small sample size, but also could be due to where this subspecies occurs, often growing along seasonal drainages and in coarser textured soils (Barker and McKell 1983). This access to a more consistent supply of moisture may dampen the effects of weather on this species.

#### *Implications for the future of sagebrush*

Climate models consistently project a region-wide increase in temperatures across western North America, accompanied by more complex and less certain changes in precipitation (Garfin et al. 2014). Species distribution models for sagebrush predict that regional warming will result in large areas of current sagebrush habitat becoming unsuitable for sagebrush in the future (Neilson et al. 2005, Bradley 2010, Schlaepfer et al. 2012a, Still and Richardson 2015). Moreover, physiological, demographic and species distribution models appear to agree on the general direction of sagebrush sensitivity to climate (Renwick et al. 2018). All these models project that sagebrush populations in warmer regions are most at risk of decline, but that warming could bring cold regions currently without sagebrush within the climate niche of sagebrush. The results of our analysis lend some, albeit weak, support to this projected pattern (Fig. 4).

While our model cannot predict population extinction or colonization it does at least suggest that population growth rates will change at the warm and cold edges of sagebrush distribution in ways that would promote extinction and colonization. Moreover, changes in the abundance of sagebrush where it already exists could have important consequences for other species and ecosystem function. For instance, the threatened Greater Sage-grouse requires 10–30% cover of sagebrush for winter habitat (Connelly et al. 2000). Our model predicts that before large-scale shifts in sagebrush distribution become apparent, several years of anomalously warm weather could lower sagebrush cover and decrease habitat quality for this species in warmer areas and increase habitat quality in colder areas (Fig. 4).

Our model leaves out many factors that could influence the future of sagebrush including the effects of fire. The probability of fires in sagebrush ecosystems is closely tied to cheatgrass (*Bromus tectorum*) invasion, which may increase with climate change (Bradley 2009). Recovery of sagebrush

populations following fire requires germination and seedling survival in burned areas, demographic processes that are controlled partly by annual climate (Maier et al. 2001, Chaney et al. 2017). Reduced seedling survival in warmer years in hot sites could exacerbate the population-level effects of reduced sagebrush cover we predict for those sites (Schlaepfer et al. 2014); while in colder sites, increases in mountain sagebrush recruitment in warmer years (Maier et al. 2001) may reinforce the increases in sagebrush abundance we predict at these sites (Fig. 4). Unfortunately, our data are likely to miss the effects of climate on these processes because the growth and survival of tiny seedlings are unlikely to have much influence on sagebrush cover at the scale of plots and transects. We also confined our analysis to effects of temperature during the growing season, but winter temperatures either directly, or through their effects on snow pack, could also have importance consequences for sagebrush (Schlaepfer et al. 2012b, Brabec et al. 2017, Chaney et al. 2017).

At longer time scales, changes in the distribution of sagebrush subspecies, hybridization between subspecies and evolutionary adaptation within populations may give sagebrush some potential to adapt to warmer temperatures. Our results indicate different sagebrush subspecies respond differently to the effects of annual climate variation (Appendix S1: Table S4–S6), a finding which agrees with many physiological and demographic differences between subspecies (Meyer et al. 1990, Kolb and Sperry 1999, Brabec et al. 2017, Chaney et al. 2017). Hybridization between subspecies or populations could allow the flow of genes conferring local adaptation between populations (Chaney et al. 2017).

#### CONCLUSION

The challenges of understanding the effects of climate change on local population abundance and large scale spatial distributions should not be tackled separately. Understanding the full ecological effects of climate change will require drawing inference from multiple data sources that span a range of temporal and spatial scales. Towards this goal, our work presents a new approach that could be used for many species to connect the short-term effects of annual climate variability with the long-term impacts of climate change on species' abundances and distributions.

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