

PRIMARY RESEARCH ARTICLE

Multi-model comparison highlights consistency in predicted effect of warming on a semi-arid shrub

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Abstract

A number of modeling approaches have been developed to predict the impacts of climate change on species distributions, performance, and abundance. The stronger the agreement from models that represent different processes and are based on distinct and independent sources of information, the greater the confidence we can have in their predictions. Evaluating the level of confidence is particularly important when predictions are used to guide conservation or restoration decisions. We used a multi-model approach to predict climate change impacts on big sagebrush (*Artemisia tridentata*), the dominant plant species on roughly 43 million hectares in the western United States and a key resource for many endemic wildlife species. To evaluate the climate sensitivity of *A. tridentata*, we developed four predictive models, two based on empirically derived spatial and temporal relationships, and two that applied mechanistic approaches to simulate sagebrush recruitment and growth. This approach enabled us to produce an aggregate index of climate change vulnerability and uncertainty based on the level of agreement between models. Despite large differences in model structure, predictions of sagebrush response to climate change were largely consistent. Performance, as measured by change in cover, growth, or recruitment, was predicted to decrease at the warmest sites, but increase throughout the cooler portions of sagebrush's range. A sensitivity analysis indicated that sagebrush performance responds more strongly to changes in temperature than precipitation. Most of the uncertainty in model predictions reflected variation among the ecological models, raising questions about the reliability of forecasts based on a single modeling approach. Our results highlight the value of a multi-model approach in forecasting climate change impacts and uncertainties and should help land managers to maximize the value of conservation investments.

KEYWORDS

Artemisia, climate change, correlative models, model comparison, process-based models, sagebrush, vegetation change

1 | INTRODUCTION

Researchers have developed a rich array of models designed to predict the ecological impacts of climate change and inform environmental policy (Clark et al., 2001). Ideally, decision-makers would focus on projections from the models that make the most skillful predictions. However, with the exception of paleoecological studies (e.g., Blois, Williams, Fitzpatrick, Jackson, & Ferrier, 2013), we cannot observe the impacts of climate change at regional spatial scales and decadal time scales in real time, making it virtually impossible to quantify and compare the predictive skill of competing models. In the absence of rigorous validation, we can use the diversity of predictive models to help assess uncertainty. Where multiple models based on independent approaches agree, we can gain confidence in predictions, whereas conflicting predictions from independent models would emphasize uncertainty. This multi-model, comparative approach is already used in climate research (Knutti, 2008), though many climate models do share similarities in their representation of key processes. Ecologists studying species distributions have begun to embrace multi-model comparisons (e.g., Case & Lawler, 2017; Cheaib et al., 2012; Estes et al., 2013; Gritti, Gaucherel, Crespo-Perez, & Chuine, 2013), but our discipline has yet to take full advantage of the breadth of modeling approaches available.

Consistency in predictions from multiple models can only build confidence to the extent that the models are independent; we expect models based on similar approaches and datasets to make similar predictions. Models used to predict the ecological impacts of climate change can draw from three very different sources of information. *Spatial correlations* capture landscape or regional-scale relationships between climate and an ecological response. In the case of species distribution models (Elith & Leathwick, 2009), the ecological response is usually the occurrence of a focal species. However, spatial correlations can also be used to model species abundance (e.g., Estes et al., 2013; Huntley, Altwegg, Barnard, Collingham, & Hole, 2012). Advantages of models based on spatial correlations include their broad spatial scale and availability of training data. Disadvantages include the lack of understanding of dynamics, which means predictions have no associated time scale (Pearson et al., 2006) and rely on space-for-time substitution. This can lead to poor predictions if the current spatial patterns of the ecological response are not in equilibrium with climate drivers (Guisan & Thuiller, 2005; Pearson & Dawson, 2003) or if climate-response correlations reflect biotic interactions or disturbance regimes which may themselves be altered by climate change (Franklin, Serra-Diaz, Syphard, & Regan, 2016; Gilman, Urban, Tewksbury, Gilchrist, & Holt, 2010).

Temporal correlations between species abundances and climate drivers represent an alternative source of data for predicting response to climate change. While such time series have most often been used to fit plant and animal population models to data from just one site (e.g., Adler, Dalglish, & Ellner, 2012; Aldridge & Boyce, 2007; Tredennick et al., 2016), it is possible to use long-term data sets from multiple sites (Gedir, Cain, Harris, Turnbull, & Peters, 2015; Kleinhesselink, 2017; Piepho & Ogutu, 2002) to gain

inferences about population responses. Models based on temporal correlations have the advantage of a strong causal link between climate drivers and ecological responses and make explicit predictions about the time scales over which ecological changes occur. Disadvantages of this approach are the requirement for long time series (Teller, Adler, Edwards, Hooker, & Ellner, 2016), and the assumptions that responses to short-term weather fluctuations can be extrapolated over longer time scales.

Mechanistic representations of key processes, rather than empirical correlations, are the basis for a third approach, exemplified by dynamic global vegetation models (Prentice et al., 2007) and bioenergetics models (Buckley, 2008). The chief advantage of mechanistic models is that predictions are based on processes and thus do not depend on statistical extrapolation and so are assumed to be more robust to novel conditions. However, mechanistic models typically require information on many parameters, which can increase uncertainty in predictions (Wramneby, Smith, Zaehle, & Sykes, 2008).

Software for ensemble modeling (e.g., BIOMOD R package, Thuiller, Lafourcade, Engler, & Araújo, 2009) facilitates the use of multiple niche-based distribution models, but these models are not independent because they are fit using the same training data. Recent work has compared predictions generated by models based on spatial correlations to predictions made by one or more mechanistic models (e.g., Hijmans & Graham, 2006; Keenan, Maria Serra, Lloret, Ninyerola, & Sabate, 2011; Morin & Thuiller, 2009; Rickebusch et al., 2008; Serra-Diaz et al., 2013), yet none have also included a model based on temporal correlations. We lack a robust understanding of how model choice contributes to uncertainty in ecological forecasts, particularly given the breadth of different modeling approaches that could potentially be used. Combining spatial, temporal, and mechanistic approaches for a single focal species will help us to identify locations and conditions with consistent predictions while exploring how model choice contributes to uncertainty.

Big sagebrush (*Artemisia tridentata*, hereafter sagebrush) is a habitat-defining species that is actively managed throughout much of the western United States (Davies et al., 2011). Sagebrush provides a prime example of a species for which ecological forecasts could help prioritize conservation and restoration investments. Sagebrush ecosystems provide critical habitat and forage for over 350 vertebrate species (Hanser, Leu, Knick, & Aldridge, 2011; Wisdom, Rowland, Suring, Dobkin, & Abbey, 2005), but are threatened by cultivation (Leonard, Reese, & Connelly, 2000), energy development (Walston, Cantwell, & Krummel, 2009), urbanization (Welch, 2005), wildfire (Miller et al., 2011), and invasive species (Bradley, 2010; Welch, 2005). Since 2010, targeted conservation efforts have aimed to maintain millions of acres of viable habitat for the greater sage-grouse and associated sagebrush species. Two major initiatives include the identification of Priority Areas for Conservation (U.S. Fish and Wildlife Service 2013, 2015) and the Sage-Grouse Initiative, both targeting conservation easements to benefit both wildlife conservation and sustainable ranching on private lands (NRCS, 2015). However, information about climate change impacts on future habitat quality is necessary to inform ongoing conservation and restoration efforts.

Previous research on potential range-wide impacts of climate change has focused on the distribution of big sagebrush (e.g., Schlaepfer et al., 2015; Shafer, Bartlein, & Thompson, 2001; Still & Richardson, 2015), using models to predict areas suitable for sagebrush occurrence under current and future climate conditions. These studies suggest that climate change could reduce the range currently occupied by big sagebrush. However, spatial correlations derived from occurrences alone cannot assess how sagebrush abundance might change within its current range. In contrast to these large-scale projections of range contraction, several local field studies have found that climate change could improve sagebrush performance and increase abundance. For example, Debinski, Wickham, Kind-scher, Caruthers, and Germino (2010) found that percent cover of sagebrush increased in response to drought, and Harte, Saleska, and Levy (2015) found that sagebrush biomass increased in response to both ambient and experimental warming. These conflicting results highlight the need for more research using different approaches to fully understand potential range-wide variability in sagebrush response to climate change.

Here, we examine three related questions: (1) How vulnerable is sagebrush to the direct effects of climate change? (2) How does that vulnerability vary across its current range? (3) What are the greatest sources of uncertainty in the direction of future change? We compared predicted climate change impacts from four independent models: a model based on spatial correlations between sagebrush cover and mean climate, a model based on temporal correlations between sagebrush cover and interannual variation in weather, and two mechanistic models, one focused on seedling germination and establishment, and one incorporating processes that affect recruitment, growth, and mortality. We focus on cross-model agreement about where the effects of projected climate change will be positive or negative for sagebrush across its current geographic range.

2 | MATERIALS AND METHODS

2.1 | Study system

Big sagebrush is a long-lived evergreen shrub that is widely distributed across the western United States (McArthur & Plummer, 1978). It is the dominant plant species in many arid and semiarid ecosystems across a broad range of elevations (West, 1983). Sagebrush develops a deep root system (Reynolds & Fraley, 1989; Sturges, 1977) that provides a competitive advantage over shallow-rooted grasses and forbs when precipitation is limited (Debinski et al., 2010). Recruitment is sensitive to soil moisture, and seedlings do poorly when conditions are too wet or too dry (Schlaepfer, 2014). Sagebrush is sensitive to fire and can take several decades to recover following burning (Lesica, Cooper, & Kudray, 2007; Miller & Heyerdahl, 2008; Miller et al., 2011).

There are several subspecies of big sagebrush, the most common of which are subspp. *wyomingensis*, subspp. *tridentata*, and subspp. *vaseyana* (Shultz, 2009). These tend to occupy different environments, with *wyomingensis* and *tridentata* primarily occurring on drier

sites at lower elevations while *vaseyana* is more common at higher elevations where there is more moisture (McArthur, 1994). Despite these differences in habitat preference, the three common subspecies are functionally similar and known to hybridize (Wang, McArthur, & Freeman, 1999). They are also morphologically similar and difficult to distinguish in the field (Dean, Burkhardt, & Meeuwig, 1981), which complicates efforts to obtain distribution or parameter data at the subspecies level. For these reasons, we model big sagebrush at the species level.

2.2 | Modeling approaches

The long-term viability of sagebrush at any given location will depend on a number of different factors, including recruitment success, growth, and survival. Each of the four models that we used reflects a different subset of the processes that affect sagebrush persistence and abundance, thus providing complementary sources of information. Each model was parameterized using different observations or driven by different climatic inputs, ensuring that they represent independent sources of information about sagebrush "performance," a term that we use to describe the different measures of abundance or recruitment success being modeled. Predictions from all models were, however, obtained for the same set of sites, time frames, and climate scenarios.

The spatial correlations model predicts the maximum potential percent cover of sagebrush at any given site as a function of eight bioclimatic variables, listed here in order of importance: temperature seasonality, precipitation of the coldest quarter, isothermality (mean diurnal range/temperature annual range), minimum temperature of the coldest month, mean temperature of the driest quarter, precipitation of the warmest quarter, temperature annual range, and precipitation seasonality (coefficient of variation). These climatic predictor variables were created from Daymet climate data (Thornton, Running, & White, 1997) based on average conditions from 1980 to 2014. To fit the model we compiled estimates of sagebrush percent cover from five sources (Table S1). The cover data were spatially aggregated to 1-km resolution, which was consistent with the resolution of the climate predictor layers. We assumed the maximum reported percent cover value within each 1-km pixel represented the maximum percent cover that sagebrush could achieve given that pixel's climate conditions. We modeled maximum percent cover because the field measurement at any given location could be lower than what is climatically possible due to disturbance or other anthropogenic activities, which would bias estimates of the mean.

We fit the spatial model using Random Forests, which creates a series of decision trees to classify given climate conditions into a percent cover category. For each tree, a training data set is created from bootstrap sampling of two-thirds of the data. Likewise, a subset of the predictor variables is randomly selected for use in each node and the best split is obtained based that subset. The one-third of the data not used for training (i.e., the out-of-bag (OOB) data) is used to calculate fit statistics including classification error and variance explained. The final classification is found by vote counting

over all trees (Liaw & Wiener, 2002). This analysis is very effective for estimating continuous cover (Cutler et al., 2007), but, because the prediction relies on decision trees, does not directly output a relationship between climate and percent cover. The subset of important predictor variables used in our model was selected from an initial set of 19 bioclimatic variables (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005) using the Random Forest Cross-Validation for Feature Selection function within the RandomForest package for R (Liaw & Wiener, 2002).

The temporal correlations model (Kleinhesselink, 2017) predicts annual changes in percent cover of sagebrush at a given site based on annual climate experienced at that site. This approach used a discrete time log Gompertz population model,

$$y_t = a + by_{t-1} + X'_{t-1} \times \theta, \quad (1)$$

where y_t is log cover of a transect or plot in year t , which is related to log cover in the previous year (y_{t-1}), a constant growth rate (a), a measure of density dependence (b), a set of annual climate anomalies in year $t-1$ (x_{t-1}), and a vector of coefficients describing the effect of each climate covariate on change in sagebrush cover (θ) (see Ives, Dennis, Cottingham, & Carpenter, 2003). We included two temperature variables and two precipitation variables in this model: average spring temperature of year t , average spring through fall temperature for years $t-1$ to $t-3$, cumulative precipitation of November to May of year t , and cumulative precipitation of years $t-1$, $t-2$, and $t-3$. These short-term climate variables were chosen a priori as predictors for this model based on previous research that has shown the importance of cool season moisture and spring through summer temperatures for sagebrush growth (Adler et al., 2012; Germino & Reinhardt, 2014; Tredennick et al., 2016). Each climate variable was expressed as an anomaly from the long-term average at each site. We included interaction terms for each temperature or precipitation variable with long-term average temperature or precipitation at each site. These interaction terms allowed the effect of climate anomalies to vary across the range of sagebrush. We also allowed the intercept and slope of the population model to vary with the sagebrush subspecies type in each plot, reflecting differences in the average abundance and growth rates of each subspecies. A summary of the model coefficients is given in Table S2.

Model fit was tested using the MuMIn package (Barton, 2014), which calculates a marginal R^2 to describe the effect of fixed effects, as well as a conditional R^2 that incorporates the effects of fixed and random effects. Output from this model was percent cover of sagebrush. Additional details on the model and data sources can be found in Kleinhesselink (2017).

The seedling survival model is a mechanistic model that simulates responses to soil conditions and weather of two critical, demographic stages, sagebrush germination, and establishment (Schlaepfer, Lauenroth, & Bradford, 2014). Model inputs include data on soil depth and texture (1-km regrided STATSGO dataset; Miller & White, 1998) as well as daily temperature and precipitation (1-km Daymet). We scaled daily weather data to match the yearly

conditions extracted from the 1/8-degree gridded product (Maurer, Wood, Adam, Lettenmaier, & Nijssen, 2002) that was used during model fitting (Schlaepfer et al., 2014). Model tests suggest a 60% overall accuracy for yearly regeneration success/failure (Schlaepfer et al., 2014). The model obtains daily air and top-soil temperature, water potential in soil layers, and snow cover from SOILWAT2, a daily time step, multiple soil layer, ecosystem water balance simulation model (Bradford, Schlaepfer, Lauenroth, & Burke, 2014; Palmquist, Schlaepfer, Bradford, & Lauenroth, 2016; Schlaepfer, Lauenroth, & Bradford, 2012a). The model determines favorable periods for germination, time to germination, and daily germination success and seedling emergence. Seedlings are tracked as daily cohorts throughout each water year, grow roots to access available moisture from different soil depths, and experience favorable, stagnant, or lethal periods. The output from this model was summarized as the percentage of years with regeneration success (first-year seedling survival) over a 30-year simulation period. Additional details on the model can be found in Schlaepfer et al. (2014).

Lastly, we used the LPJ-GUESS dynamic global vegetation model (DGVM) (Smith, Prentice, & Sykes, 2001), which uses data on soil texture, annual CO_2 concentrations, and daily temperature, precipitation, and solar radiation to simulate establishment, growth, and mortality for cohorts of plants within different patches of vegetation. LPJ-GUESS is the only model we used to explicitly consider the effects of competition. Vegetation in LPJ-GUESS is represented by any number of generalized plant functional types (PFTs) that are defined by different physiological parameters. We used four functional types to represent sagebrush and competing species: a generic C_3 grass/forb, a generic C_4 grass, sagebrush, and juniper (*Juniperus* spp.). The parameters for the two grass PFTs were taken from the global functional types (Smith et al., 2001). New parameters for sagebrush and juniper are given in Table S3. We evaluated the ability of the model to reproduce temporal trends in sagebrush performance at two sites where long-term shifts in sagebrush performance have been linked to climate change: a cold site at the Rocky Mountain Biological Laboratory (RMBL) near Crested Butte, CO (Harte et al., 2015), and a warm site in southwestern Wyoming (Xian, Homer, & Aldridge, 2012).

For each model simulation, LPJ-GUESS was first run for a 1,000-year spin-up to allow vegetation and carbon pools to reach equilibrium before altering the climate or CO_2 concentration. We ran the model with 100 replicate patches in each 1-km grid cell. Individual patches were subject to generic disturbance events occurring randomly with a probability of .01 in any given year. Fire was also enabled, and patches could burn whenever they accumulated sufficient fuel and climatic conditions were dry enough.

For all simulations, the spin-up period used detrended Daymet climate data (Thornton et al., 1997) and the preindustrial CO_2 concentration (287 ppm), while the "current" period (1980–2014) used historic Daymet data and atmospheric CO_2 concentration data developed for use with the TRENDY project (<http://dgvm.ceh.ac.uk/node/9/index.html>). For future climate scenarios, we used projected CO_2 concentrations associated with the corresponding

representative concentration pathway (4.5 or 8.5). This differs from the climate perturbation runs (see below), where CO₂ was held constant at the current concentration so that we could isolate the effects of temperature and precipitation change. Soil data for all model runs consisted of sand, silt, and clay fractions for each of two soil layers taken from the 1-km resolution Harmonized World Soil Database v.1 (Fischer et al., 2008). Output from the DGVM was summarized as the average percent cover of sagebrush within each 1-km pixel over a 30-year simulation period.

2.3 | Focal sites

Our selection of sites was designed to capture the full range of climate conditions found in the current range of sagebrush. To do this, we first compiled a comprehensive dataset of 15,590 records of sagebrush presence from various databases (Table S1) along with 467 sites with long-term (multiyear) records (Kleinhesselink, 2017). These locations were used to extract climatological data from WorldClim (Hijmans et al., 2005) for 19 bioclimatic variables representing annual, seasonal, and extreme values of temperature and precipitation. To reduce dimensionality in the climate data set, we conducted a principal components analysis and retained the first two principal components, which together explained 62% of the variance in climate space. The first principal component represents a temperature gradient, while the second represents a gradient in precipitation seasonality (Figure 1a).

Because the two mechanistic models are computationally intensive, we selected a subset of the total presence records to use in our analysis. All 469 sites with long-term data were included. To ensure that all climates where sagebrush is currently found were represented, we plotted all additional presence records on the first two principal components and overlaid a grid that was used to select one point in each grid cell (Figure 1a). This generated 245 points evenly distributed across climate space. The addition of these points brought our total number of "focal sites" to 714 (Figure 1).

2.4 | Sensitivity analysis

To examine the sensitivity of sagebrush to specific climate drivers, we predicted changes in performance of each model resulting from simple perturbations of temperature or precipitation. For these simple climate perturbations, each model generated predictions for the baseline period (1980–2014) using Daymet climate data (Thornton et al., 1997), then for six scenarios where the baseline climate was altered by a fixed amount. We used three levels of temperature increase (+0.2°C, +2°C, and +4°C), and three levels of precipitation change (−10%, +10%, and +20%). The climate perturbations were applied uniformly to all model input variables ('delta' approach; Hay, Wilby, & Leavesley, 2000). For instance, if a model included terms for winter and summer precipitation, both of these seasonal variables would be altered by the same proportion. Change in sagebrush performance ("sensitivity") for each of the six perturbations was calculated by subtracting predictions for the baseline period from predictions for the climate manipulation.

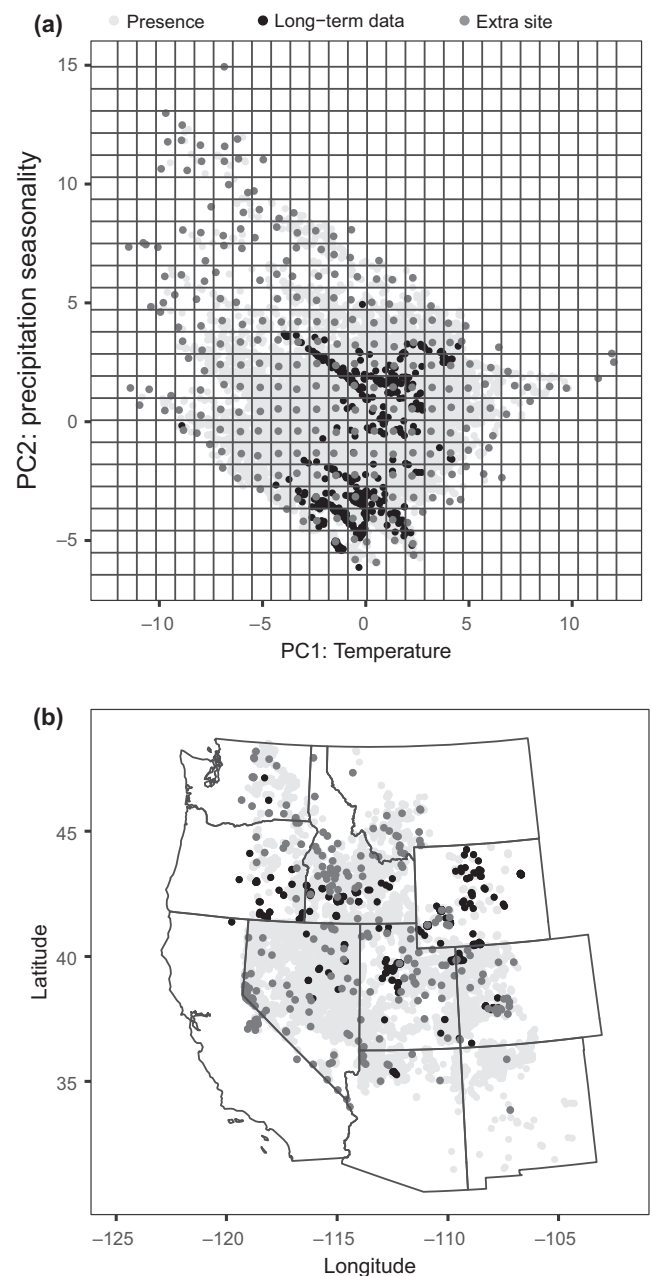


FIGURE 1 Location of focal sites in climate space (a) and geographic space (b). Light gray represents all presence record, black are sites with long-term data, and dark gray are extra sites chosen to characterize the full range of climates occupied by sagebrush

The perturbation levels were chosen to facilitate analysis of model sensitivity to temperature and precipitation, and do not necessarily correspond to predicted changes. Compared to climate model predictions, which suggest that the climate in western North America may warm as much as 5°C by 2100 (median of General Circulation Model [GCM] predictions for RCP8.5, Christensen et al., 2013), these temperature perturbations are somewhat modest. The precipitation perturbations, on the other hand, are larger than the 6% increase expected under RCP8.5 (median of GCM predictions, Christensen et al., 2013).

2.5 | Climate change scenarios

We examined potential climate change effects under two emissions scenarios, or Representative Concentration Pathways (RCPs), from the Intergovernmental Panel on Climate Change Fifth Assessment Report (IPCC, 2013). Climate data for each emissions scenario (RCP4.5 and RCP8.5) were taken from five different general circulation models (GCMs), for a total of 10 climate change scenarios. The GCMs were selected based on several criteria outlined in McSweeney, Jones, Lee, and Rowell (2014). First, we excluded models that did not perform well for our region based on their ability to reproduce twentieth century climate observations (Rupp, Abatzoglou, Hegewisch, & Mote, 2013). For the remaining set of 26 models, we examined the spread in both annual and seasonal temperature and precipitation by looking at the predicted change for the 2090s compared to the baseline historic climatology (1961–1990). Based on a principal components analysis, we selected five models that bracket the range of uncertainty in future climate projections. For RCP8.5, the models predict an increase in temperature ranging from 3.1°C to 7.1°C (mean 5.1°C) and an increase in precipitation ranging from 2% to 18% (mean 8%). Data from the five GCMs were statistically downscaled to 1-km resolution using the downscaling and bias-correction method described in Babst et al. (2013). We used Daymet data (Thornton et al., 1997) for the period 1980–1999 for bias correction.

For the 10 climate change scenarios, we generated predictions with each model for each focal site for two time periods: the baseline (1980–2014) and future (1970–2099). Both of the correlative models (spatial correlations & temporal correlations) used the 30-year mean of each climate variable to drive predictions. In contrast, the mechanistic models used monthly climate data disaggregated to a daily time step to drive predictions, then summarized predictions as average performance in each time period. Changes in sagebrush performance were calculated for all four models by subtracting predictions for the baseline period from predictions for the future period.

2.6 | Model comparison

Because the response variable differed among models (i.e., cover, seedling survival, or growth), for comparison reasons we standardized the vulnerability analysis by assessing effects by the direction (increase vs. decrease) and magnitude of change (Gelman & Carlin, 2014). To evaluate consistency in the direction of predicted change for the various climate change scenarios, we created an aggregate measure of both vulnerability and uncertainty: for each site, we tallied the number of model $\times$ GCM combinations where sagebrush performance was expected to increase vs. decrease. This was done separately for each of the two emissions scenarios. We then subtracted the number of predicted decreases from the number of predicted increases, resulting in a “vulnerability index” that ranged from –20 (all 20 model combinations agree on a decrease) to +20 (all agree on an increase).

We also examined pairwise agreement among models using Cohen's Kappa (Cohen, 1960) for direction and Spearman's rank correlations for magnitude. Cohen's Kappa is used to evaluate pairwise agreement in predictions of a categorical variable and is frequently used to evaluate the accuracy of species distribution models (Manel, Williams, & Ormerod, 2001). We also used Fleiss' Kappa (Fleiss, 1971), a similar measure of agreement across multiple models, to compare levels of agreement between all GCMs and all ecological models simultaneously. Both Kappa values range from 0 (agreement between models is no better than random) to 1 (perfect agreement between models). Values for Spearman's rank correlations range from –1 to 1, with higher values indicating higher levels of correlation.

3 | RESULTS

3.1 | Model performance

The spatial correlations model explained 25% of the variance in maximum percent cover values. The temporal correlations model achieved a conditional R^2 of 0.91, while the marginal R^2 (variance explained by the fixed effects alone, Johnson (2014)) was 0.22. The seedling survival yielded an in-sample R^2 of 0.74 and an out-of-sample R^2 of 0.60 (Schlaepfer et al., 2014). The DGVM was able to replicate the increasing trend in sagebrush biomass at the cold site, and also mimicked the observed decline in C_3 forbs (Harte et al., 2015). At the warm site, the DGVM reproduced the small decline in average cover observed using remote sensing data from 1988 to 2006 (Xian et al., 2012).

3.2 | Sensitivity to temperature and precipitation

The sensitivity analysis suggests that sagebrush performance is more strongly linked to changes in temperature than precipitation, particularly given that our precipitation perturbations were larger than the changes that are expected. All four models showed the largest response to the 4°C temperature perturbation, though the difference in response to temperature vs. precipitation perturbations was less dramatic for the spatial correlations model (Figure 2). All four models also agreed that sagebrush populations are resilient to small changes in temperature, with relatively small changes in performance predicted with a 0.2°C temperature increase.

The models tended to agree more frequently on the direction of change in response to temperature perturbations compared with precipitation perturbations. Models were in full agreement on the direction of change for 24% of sites with a 4°C temperature increase, compared to just 3% of sites with a 20% precipitation increase. Levels of consensus (three out of four models) were also somewhat higher for the three temperature perturbations, averaging 80% of sites compared to 74% of sites for the precipitation perturbations. Within the temperature perturbations, full model agreement was lower (9% of sites) for the smaller (0.2°C) temperature increase compared to the larger (4°C) temperature increase, though the

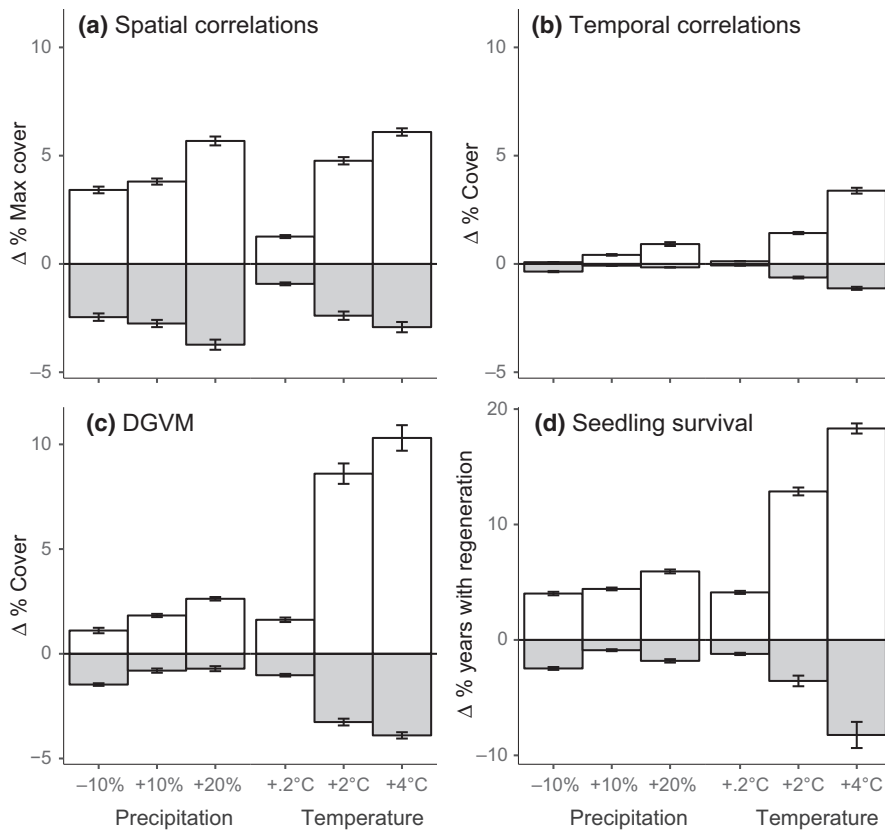


FIGURE 2 Average change ($\pm$ SE) in modeled sagebrush responses across all sites where sagebrush performance was predicted to increase (positive bars, white) vs. decrease (negative bars, gray) for each of the temperature and precipitation perturbations. Averages were calculated separately for sites where sagebrush performance is expected to increase vs. decrease to highlight the absolute magnitude of change, which would be obscured by averaging positive and negative values together. Panels represent output from (a) the spatial correlations model, (b) the temporal correlations model, (c) the DGVM, and (d) the seedling survival model. The y-axis for panel (d) differs because the seedling survival model predicts a fundamentally different measure of sagebrush performance

percentage of sites where at least three models agreed was similar across all of the temperature perturbations (79%–81% of sites).

For several of the models, the impact of temperature and precipitation perturbations varied predictably along underlying temperature and precipitation gradients. All of the models showed a more positive response to increasing temperatures at the coolest sites (Fig. S1), though this pattern was less distinct with the spatial correlations model. The response to precipitation perturbations was more mixed (Fig. S2). The temporal correlations model responded more positively to increased precipitation at the wettest sites, whereas the seedling survival and spatial correlations models responded more positively at the driest sites. The DGVM did not show a distinct trend in response across the underlying precipitation gradient.

3.3 | Vulnerability to predicted climate change

The multi-model consensus on direction of change was mostly positive. At 90% of the focal sites, a majority of model $\times$ climate change scenarios predicted an increase in sagebrush performance. The number of sites where at least three out of the four ecological models predicted an increase in performance varied minimally across the two emissions scenarios and five GCMs, ranging from 89% to 94% of focal sites. The DGVM was the most optimistic model, suggesting that sagebrush performance will increase at 88% of sites, while the other three models predicted increases in performance at 75%–80% of sites.

The magnitude of predicted change in performances was more variable (Figure 3), reflecting both differences in the model

structures as well as the response variables. The seedling survival model, which predicts the proportion of years with successful seedling recruitment, predicted larger changes compared to the other three models, which all predict a measure of percent cover. The magnitude of increases was higher and more variable than the magnitude of decreases across all four models. This partly reflects low values in the baseline period, which limited potential for large declines. The magnitude of change was sensitive to the choice GCM and RCP, and different models responded differently to the various climate change scenarios (Figure 3).

3.4 | Spatial patterns of vulnerability

Across all climate change scenarios, the ecological models identified some sites where performance is likely to decline in the future, as well as some sites where the direct effects of climate change may prove beneficial to sagebrush. All models agreed that declines in performance are more likely at hotter sites, whereas cooler sites may prove less vulnerable, or even experience increased performance with warming (Figure 4). Models tended to disagree more on the direction of change at sites where the mean annual temperature is more moderate. As with the sensitivity analysis, the temporal correlations, and seedling survival models predicted greater increases in performance at wetter sites (Fig. S3). The spatial correlations model and DGVM did not show a consistent trend with respect to the underlying precipitation gradient.

The spatial pattern of vulnerability becomes clearer when looking at the aggregate response. Plotting the vulnerability index (the

number of ecological models $\times$ GCM scenarios for which our models agree that sagebrush performance will increase [positive model agreement] or decrease [negative model agreement] along the two principal component axes used in site selection shows that most of the sites where sagebrush is expected to decline occur in the warmest portion of sagebrush's range (Figure 5a). These sites are primarily located in Nevada and Arizona, along sagebrush's southern range margin, though several vulnerable sites do occur in relatively low-elevation sites in the Snake River Plain and Columbia Basin (Figure 5b).

Vulnerability class could not be distinguished based on mean annual temperature alone, but it is likely that climate change will have a negative impact on sites with a mean annual temperature above 16°C and a positive impact on sites with a mean annual temperature below 2°C (Figure 6a). For sites in the center of this temperature range, the outcome will likely depend on other variables (Figure 6b).

3.5 | Sources of uncertainty

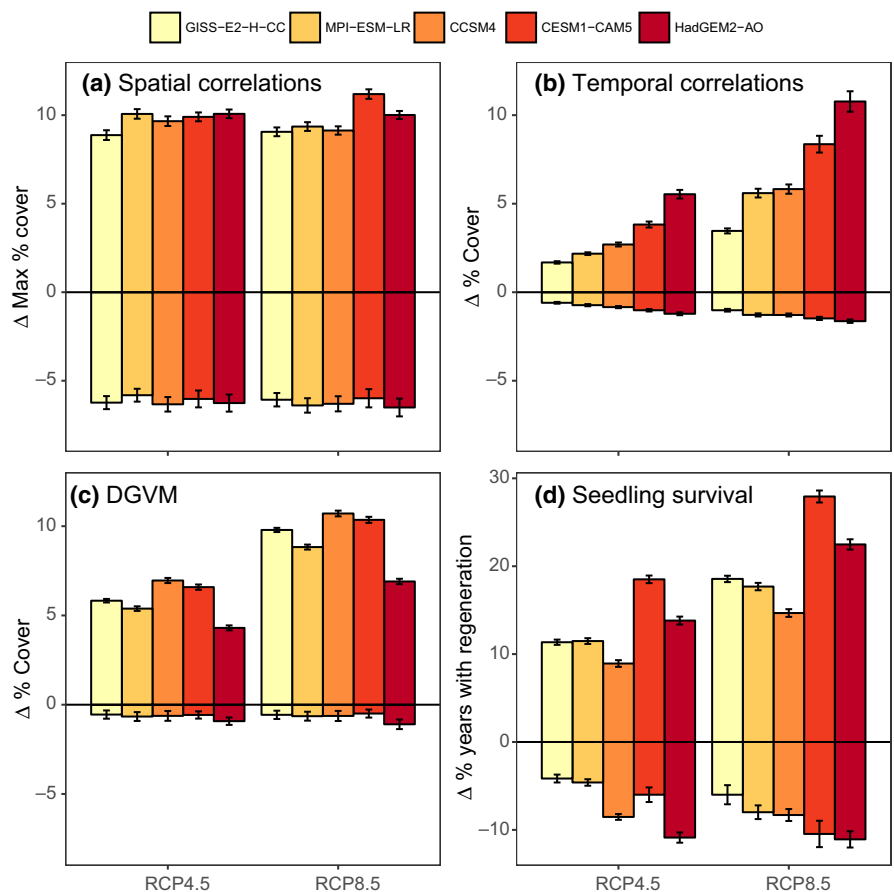
We found a relatively high level of agreement on the direction of change across emissions scenarios, GCMs, and the four ecological models. The choice of emissions scenario had little impact on the direction of change. Within models and GCMs, we predicted the same direction of change under the two emissions scenarios at 93%

of the sites. The Cohen's Kappa value for comparing emissions scenarios was 0.79, which indicates substantial agreement in the predicted direction of change. The seedling survival model was much more sensitive to the choice of RCP compared to the other three ecological models: for 19% of sites, the predicted direction of response in seedling survival differed between the two emissions scenarios.

The choice of GCM also had a minimal effect on direction of change. Within emissions scenarios and models, predictions driven by the five GCMs were consistent in direction of change for 82% of the sites. Cohen's Kappa values for the pairwise comparisons between predictions driven by different GCMs ranged from 0.67 to 0.78 and averaged 0.73. The Fleiss' Kappa value for agreement across all five GCMs was 0.74, which suggests a high level of agreement. The seedling survival model again proved to be more sensitive to choice of GCM compared to the other ecological models. Across all GCMs, the seedling survival model predictions were consistent at 56% of the sites. For the other three models, predictions were consistent across GCMs for at least 81% of sites. Predictions driven by different GCMs were more consistent under the higher emissions scenario (agreement at 88% of sites compared to 77%).

The choice of ecological model was the greatest source of uncertainty in direction of change. All models were in perfect agreement on the direction of change for 48% of the site $\times$ GCM combinations, and they reached consensus (at least three out of four models)

FIGURE 3 Average change ($\pm$ SE) in modeled sagebrush responses across all sites where sagebrush performance was predicted to increase (positive bars) vs. decrease (negative bars) for each RCP and GCM combination. Averages were calculated separately for sites where sagebrush performance is expected to increase vs. decrease to highlight the absolute magnitude of change, which would be obscured by averaging positive and negative values together. GCMs are ordered from smallest predicted temperature increase (light) to largest predicted temperature increase (dark). Panels represent change predicted by (a) the spatial correlations model, (b) the temporal correlations model, (c) the DGVM, and (d) the seedling survival model. The y-axis for panel d differs because the seedling survival model predicts a fundamentally different measure of sagebrush performance [Colour figure can be viewed at wileyonlinelibrary.com]



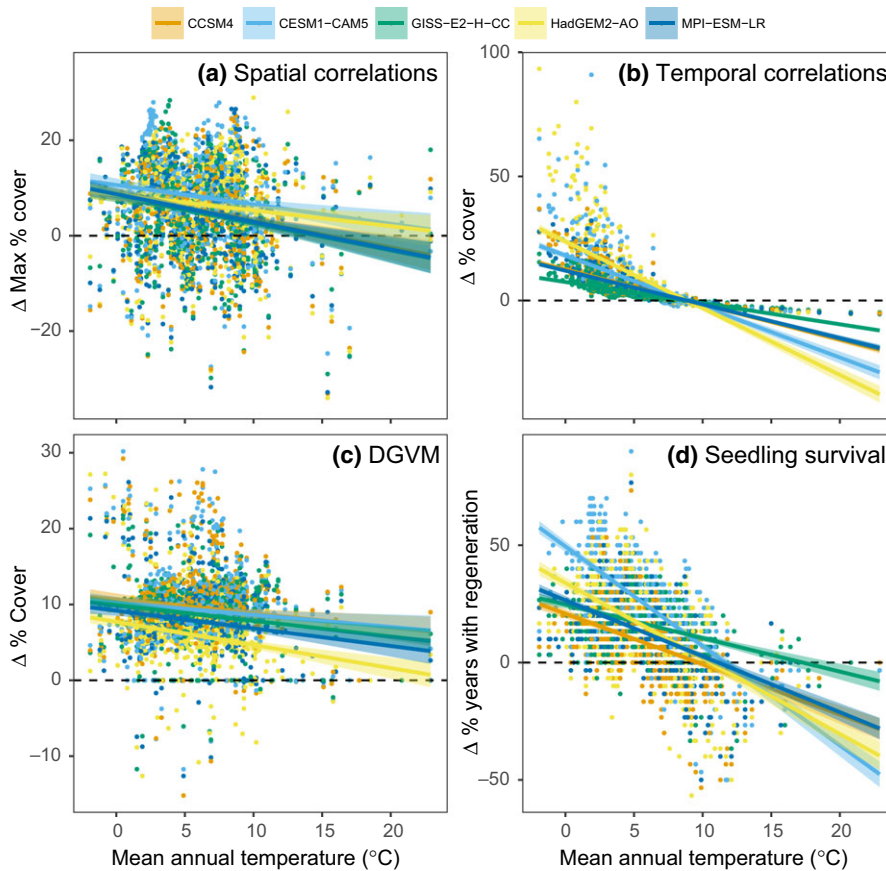


FIGURE 4 Predicted change in sagebrush performance under RCP8.5 for the five GCMs suggests that cooler regions will experience an increase in sagebrush. Panels represent the change predicted by (a) the spatial correlations model, (b) the temporal correlations model, (c) the DGVM, and (d) the seedling survival model. The y-axis differs among panels to highlight qualitative trends rather than the magnitude of predicted change. Lines represent a linear fit to the change predicted using climate data from each GCM; shaded areas are the 95% confidence interval

for 85% of these combinations. As with the GCMs, the models agreed more frequently under the higher emissions scenario (53% with RCP8.5 compared to 43% with RCP4.5). Cohen's Kappa values for pairwise comparisons between the ecological models ranged from 0.01 to 0.26 (Table S4), while Fleiss' Kappa for agreement across all four models was 0.12.

For magnitude of change, predictions from the two emissions scenarios were highly correlated (Spearman correlation coefficient = .67), but models driven by RCP8.5 as opposed to RCP4.5 predicted larger shifts in performance (absolute value for vulnerability score of 10.3 vs. 7.0). The magnitude of predicted changes driven by different GCMs was also correlated (mean 0.74, range 0.64–0.82). For the four ecological models, pairwise correlation coefficients ranged from 0.02 to 0.46 and averaged 0.16.

4 | DISCUSSION

Our analysis yielded three important findings: (1) sagebrush vulnerability to projected climate change is low in many locations, (2) sagebrush populations at warmer sites are more vulnerable, and (3) the choice of ecological model is the largest source of uncertainty in future predictions. This final point is particularly important given that many climate change impact analyses are based on the results of a single model. Overall, we demonstrate how using multiple independent modeling approaches can increase confidence in ecological

forecasts, identify areas of uncertainty, and yield new insights into expected patterns of change.

4.1 | Vulnerability to climate change

Our results indicate less vulnerability than previous studies forecasting climate change impacts on big sagebrush, many of which predicted more dramatic declines in the area climatically suitable for sagebrush (Bradley, 2010; Schlaepfer, Lauenroth, & Bradford, 2012b; Still & Richardson, 2015). At the more pessimistic end of the spectrum, Still and Richardson (2015) predicted the loss of subspecies *wyomingensis* across 67% of its current range. In contrast, our multi-model consensus predicted declines in performance under RCP8.5 at just 9% of the focal sites, which represent a relatively small proportion of sagebrush's range. If we ignore the consensus and instead consider all instances where at least one of our twenty model $\times$ GCM combinations predicted a decline, our results are still somewhat more optimistic, suggesting that sagebrush could decline at 53% of the focal sites. This estimate is probably overly conservative, however, because it weights outlier predictions that may be due to an idiosyncrasy of one specific model more heavily than predictions from the other three models.

The broad geographic coverage of our focal sites allowed us to consider climate change impacts at sites with widely varying climates, including many cool, high-elevation sites. This may help to explain why our results seem more positive than those from several

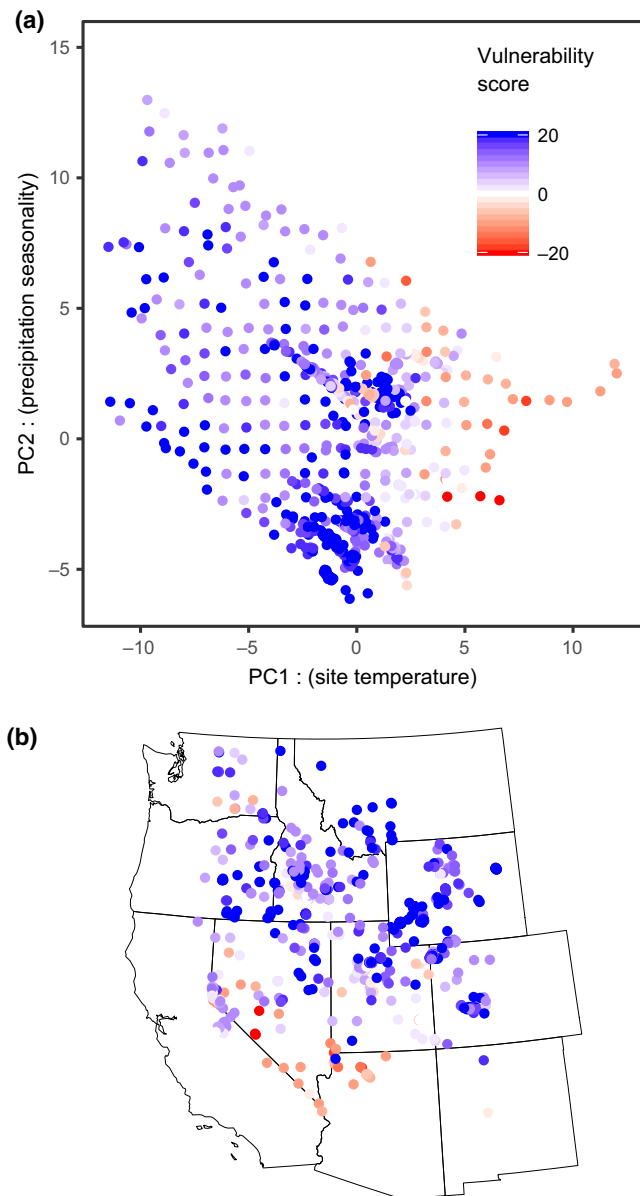


FIGURE 5 Vulnerability score under RCP8.5 for each focal site, plotted (a) on principal component axes and (b) in geographic space. Red indicates high confidence that performance will decrease, blue indicates high confidence that performance will increase

local-scale ring width studies that found a negative correlation between sagebrush performance and higher temperatures (Apodaca, 2013; Poore, Lamanna, Ebersole, & Enquist, 2009). We also predicted different outcomes (increase vs. decrease in performance) at a number of sites that are relatively close in geographic space but differ in elevation and climate, suggesting that the results of small-scale field studies may not be generalizable to other nearby sites if the underlying climate or soil conditions differ.

The sensitivity analysis indicated that sagebrush is more sensitive to changes in mean annual temperature than mean annual precipitation, but that small shifts in temperature (e.g., 0.2°C) have little impact on performance. The low sensitivity to precipitation perturbations can perhaps be explained by the fact that sagebrush develops

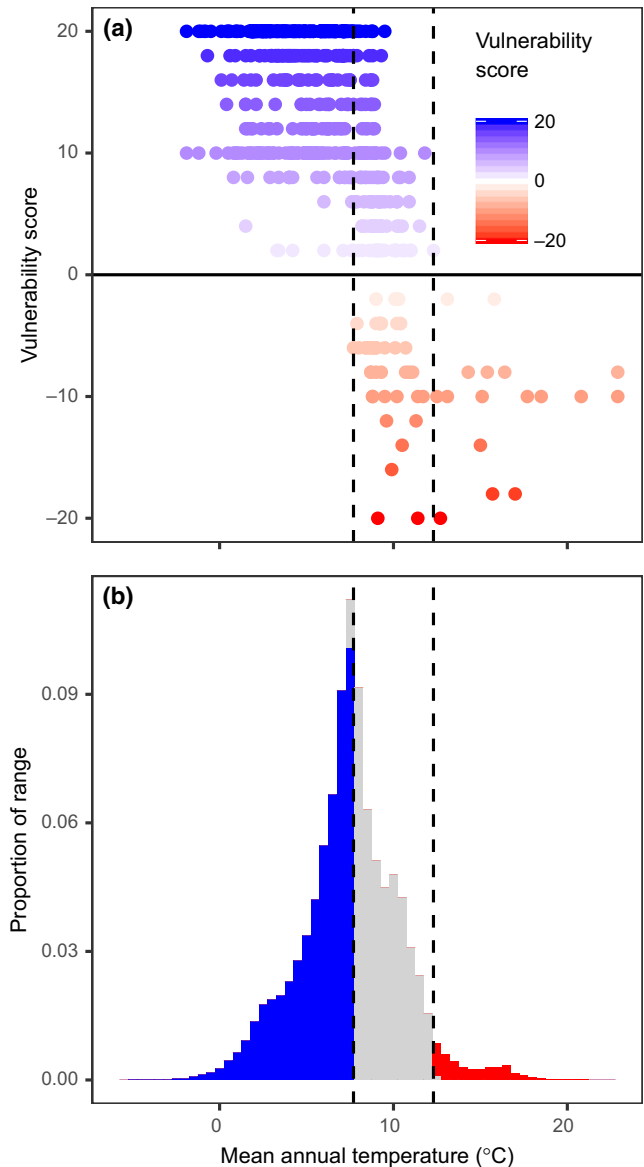


FIGURE 6 Relationship between mean annual temperature and (a) vulnerability scores under RCP8.5, and (b) area occupied by sagebrush. Dashed lines represent the temperature below which no declines were predicted and above which no increases were predicted. Area occupied data from LANDFIRE program (LANDFIRE, 2016)

a two-layer root system with deep and shallow roots (Bates, Svejcar, Miller, & Angell, 2006; Sturges, 1977) and is able to access water from lower soil layers (Leffler, Ivans, Ryel, & Caldwell, 2004; Ryel, Leffler, Peek, Ivans, & Caldwell, 2004) that are less sensitive to small fluctuations in precipitation. The low sensitivity to precipitation at the aggregate level may also mask significant sensitivity at finer spatial scales or in response to particular seasonal changes in precipitation: Germino and Reinhardt (2014) found that increases in precipitation did lead to increases in sagebrush cover in some situations, but the effect depended on both the seasonality of precipitation additions and soil depth. Only the seedling survival model included variable soil depth, and our precipitation perturbations were

applied uniformly across all months or seasons represented in each model.

Several landscape-scale studies have also found an association between sagebrush cover and precipitation in southwestern Wyoming. Increases in bare ground and decreases in sagebrush cover were correlated with observed changes in precipitation (Xian et al., 2012). Homer et al. (2015) further evaluated the impacts of climate change through 2050 in this area and found that cover of sagebrush and other vegetation components were predicted to decrease; this change was most closely correlated with reductions in predicted precipitation. Together these studies suggest that how sagebrush responds to precipitation may vary locally, depending on the current climatic conditions.

4.2 | Spatial patterns of vulnerability

Based on earlier work, we hypothesized that sagebrush vulnerability to climate change would vary across its geographic range, and our results indicate that this is likely the case. All of the models agree that sagebrush performance will increase as a consequence of climate change throughout the cooler portion of its range, while warmer sites are more vulnerable to declines. The positive response to increasing temperatures at cooler sites is in keeping with prior research suggesting that high-elevation sagebrush populations will benefit from warming as a result of earlier snowmelt dates (Harte et al., 2015; Perfors, Harte, & Alter, 2003; Schlaepfer, Lauenroth, & Bradford, 2012c). At warmer sites where growing season length is not limiting, the greater evaporative demand associated with increasing temperature may contribute to the declines in sagebrush performance that our models predict (Homer et al., 2015; Xian et al., 2012).

4.3 | Sources of uncertainty

The high levels of agreement on the direction of change predicted using different emissions scenarios and GCMs suggest that considering several types of ecological models may be even more important than using different climate change scenarios to drive predictions. Several previous model comparison studies have similarly found that different ecological models can differ in their predictions of future range shifts (e.g., Case & Lawler, 2017; Cheaib et al., 2012; Gritti, Duputié, Massol, & Chuine, 2013; Keenan et al., 2011), though none of these explicitly compared the degree to which model formulation and choice of GCM or emissions scenario contributes to uncertainty. Despite the relatively small effect of different climate scenarios on our model output, it remains important to account for this source of uncertainty. The seedling survival model did demonstrate a wider range of responses to the different GCMs, perhaps due to its emphasis on daily precipitation, which is less consistent than temperature across different GCMs.

In addition to providing more robust estimates of uncertainty, multi-model comparisons can use areas of disagreement among different ecological models to inform future research and model

development. Our results suggest that additional research on the physiological and demographic processes that most limit sagebrush under different climatic conditions might improve our understanding of potential climate change impacts. All four ecological models predicted increases in sagebrush performance at the coldest sites, which complements evidence from field studies suggesting that sagebrush is cold limited in some areas (Harte et al., 2015; Perfors et al., 2003). Our models tended to disagree more on the how performance might change at sites near the center of sagebrush's current temperature range, however. The seedling survival model was more pessimistic than others at cool sites, particularly under the lower emissions scenario, suggesting that the temperature threshold for successful recruitment is higher than that related to growth or cover. The DGVM often projected a more negative response than other models at wetter sites, potentially reflecting the effect of competing species that benefit more from warming when conditions are less arid. In contrast, the DGVM tended to predict increases in performance at warmer sites than to the other three models, due mostly to its inclusion of a CO₂ fertilization effect on water-use efficiency and productivity. Additional research is needed to fully understand how recruitment and competition affect sagebrush under different climatic conditions, as well as the degree to which CO₂ enrichment may buffer sagebrush populations at hotter sites against the effects of climate change.

The sensitivity analysis is an important complement to the GCM predictions and can help to identify additional research priorities. For example, the sensitivity analysis yielded lower levels of agreement on the impacts of our chosen precipitation perturbations compared to temperature. This suggests that the effect of precipitation change (Homer et al., 2015; Xian et al., 2012) is an area where more research and subsequent model development may be necessary. We also found lower levels of agreement on the effects of smaller changes, as evidenced by both the sensitivity analysis and comparison of the two emissions scenarios. This may complicate efforts to forecast changes expected over the next several decades, during which climatic changes will be more modest.

Our study focused on identifying areas where the direct effects of climate change may prove detrimental to sagebrush. The indirect effects of climate change, however, may have a larger impact than climate change alone. Invasive species such as cheatgrass may expand into new areas or gain a competitive advantage as a consequence of climate change (Bradley, 2009). Feedbacks between climate, cheatgrass, and the fire cycle could prove detrimental to sagebrush (Chambers et al., 2014; Coates et al., 2016), even in areas where our analysis indicates that the direct effects of climate change will be minimal. Additional research is needed to link the direct and indirect effects of climate change in a cohesive modeling framework.

4.4 | Multi-model approach increases confidence

While the magnitude of expected changes differed among modeling scenarios, consistency in the direction of change suggests a reasonable level of confidence in determining where sagebrush populations

are vulnerable to future declines. This confidence would not have been possible with fewer models. Individual pairs of models provided contradictory predictions at many sites, which is not surprising given the differences in model structure, the data sources used, the response they are modeling, and inherent assumptions of the different modeling techniques. The multi-model approach allowed us to achieve a consensus (at least three out of four models agree) on the direction of change for most sites. Utilizing multiple types of ecological models can minimize the impact of idiosyncrasies and problematic assumptions associated with any one model, enhancing our confidence in ecological forecasts and providing better estimates of uncertainty.

While the models that we used were notably distinct, studies with fewer or more closely related models (e.g., multiple correlative SDMs) may still yield some of the benefits of a multi-model approach (Araujo & New, 2007) when the component models have been carefully chosen and evaluated (Elith, Kearney, & Phillips, 2010). Estimates of climate change response may be more robust compared to forecasts derived from a single model but should be interpreted with caution given that they may underestimate model-based uncertainty. Such cases might warrant a different approach to interpretation: the vulnerability index that we developed emphasizes model consensus, whereas a more cautious approach might emphasize areas where at least one model predicted a decline.

Multi-model forecasts are relatively rare (but see Cheaib et al., 2012; Gritti et al., 2013; Iverson et al., 2016), due in part to the difficulty of assembling the necessary data and modeling expertise. This approach will become increasingly feasible, however, as broad-scale data collection and data sharing programs gain traction. Searchable data archives such as DataOne (dataone.org), VegBank (vegbank.org), and the TRY plant trait database (try-db.org) are already proving to be valuable resources for modelers, and regional programs such as national forest inventories also provide a wealth of high-quality data that is publicly available. Our hope is that the multi-model approach demonstrated here could be used to forecast the climate change response and associated uncertainty for an ever-increasing number of species.

Quantifying uncertainty through the use of multiple models is particularly important when forecasts are used to guide conservation and land management decisions (Guisan et al., 2013; Meller et al., 2014; Pearson et al., 2006). Our results provide valuable information by categorizing not only where sagebrush is most vulnerable to climate change, and possible mechanisms for that vulnerability, but also where more information may be needed to understand potential climate change impacts. This can help managers to identify sites where investments in conservation or restoration have the highest likelihood of success under a range of potential future climate conditions.

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AUTHOR CONTRIBUTIONS

PA, CA, BB, and BP conceived the study; CC, AK, KR, and DS developed and ran models; PA, AK, BP, and KR designed the analysis; and KR led writing with comments from all co-authors. CC, AK, and DS contributed equally.

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