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# Understanding the future of big sagebrush regeneration: challenges of projecting complex ecological processes

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**Abstract.** Regeneration is an essential demographic step that affects plant population persistence, recovery after disturbances, and potential migration to track suitable climate conditions. Challenges of restoring big sagebrush (*Artemisia tridentata*) after disturbances including fire-invasive annual grass interactions exemplify the need to understand the complex regeneration processes of this long-lived, woody species that is widespread across the semiarid western U.S. Projected 21st century climate change is expected to increase drought risks and intensify restoration challenges. A detailed understanding of regeneration will be crucial for developing management frameworks for the big sagebrush region in the 21st century. Here, we used two complementary models to explore spatial and temporal relationships in the potential of big sagebrush regeneration representing (1) range-wide big sagebrush regeneration responses in natural vegetation (process-based model) and (2) big sagebrush restoration seeding outcomes following fire in the Great Basin and the Snake River Plains (regression-based model). The process-based model suggested substantial geographic variation in long-term regeneration trajectories with central and northern areas of the big sagebrush region remaining climatically suitable, whereas marginal and southern areas are becoming less suitable. The regression-based model suggested, however, that restoration seeding may become increasingly more difficult, illustrating the particularly difficult challenge of promoting sagebrush establishment after wildfire in invaded landscapes. These results suggest that sustaining big sagebrush on the landscape throughout the 21st century may climatically be feasible for many areas and that uncertainty about the long-term sustainability of big sagebrush may be driven more by dynamics of biological invasions and wildfire than by uncertainty in climate change projections. Divergent projections of the two models under 21st century climate conditions encourage further study to evaluate potential benefits of re-creating conditions of uninvaded, unburned natural big sagebrush vegetation for post-fire restoration seeding, such as seeding in multiple years and, for at least much of the northern Great Basin and Snake River Plains, the control of the fire-invasive annual grass cycle.

**Key words:** *Artemisia tridentata*; cheatgrass-fire feedback; climate change; multi-model comparison; recruitment; reproduction; restoration seeding.

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## Introduction

Regeneration of long-lived woody plant species in dryland ecosystems is an ecological process that is limited by many variable factors. We use the term regeneration here for plant reproductive processes that include seed germination, emergence, and seedling establishment to refer to recruitment at a community perspective (Fenner 2002). Regeneration is an essential demographic step that affects plant population persistence, recovery after disturbances such as fires, land development, and die-off events, and potential migration to track suitable climate conditions (Fenner 2002). Understanding regeneration of long-lived woody species is often challenging because observational and experimental studies are often too short to capture a sufficient number of lifecycles and regeneration outcomes that represent the range of environmental conditions, particularly when these are not stationary or have a long periodicity (e.g., conditions influenced by the Pacific Decadal Oscillation PDO). While infrequent regeneration may suffice to maintain undisturbed, reproductive populations in stationary environments, it creates major challenges in the context of climate change and for current and future resource management and restoration planning (Shriver et al. 2019).

The big sagebrush region, that is, dryland ecosystems dominated by big sagebrush and perennial bunchgrasses, historically covered more than half a million square kilometers but has been reduced by approximately 50% in recent decades (Young et al. 1979, Davies et al. 2011, Finch et al. 2016, Rigge et al. 2020). Multiple factors have contributed to decreasing and fragmenting big sagebrush ecosystems, including infrastructure, resource extraction, agriculture, conifer expansion, and most prevalent in the western part of the region, positive feedbacks between invasive annual grasses (mostly *Bromus tectorum*, cheatgrass, and *Taeniatherum caput-medusae*, medusahead) and fire (Davies et al. 2011, Finch et al. 2016). Additionally, recent warming associated with climate change has been impacting the big sagebrush region by reducing snowpack and snow season (Mote et al. 2018, Zeng et al. 2018), increasing burned area and fire season length (Dennison et al. 2014, Abatzoglou and Williams 2016), and exacerbating regional droughts, particularly in the Southwestern U.S. (Williams et al. 2020). Projected 21st century climate change (U.S. Global Change Research Program 2017) is expected to intensify these trends (Coates et al. 2016) and increase drought risk (Cook et al. 2015), particularly in warm and southern areas of the big sagebrush region, whereas projected increases in growing season duration and cold-season precipitation may promote big sagebrush in cool and northern regions (Schlaepfer et al. 2012*a*, Palmquist et al. 2016*a*, Renwick et al. 2018, Bradford et al. 2019, 2020, Flerchinger et al. 2020).

The challenge of restoring big sagebrush (*Artemisia tridentata*) is a prominent example in western North America of the need to understand the complex regeneration processes of a long-lived, woody species in a variable environment (Davies et al. 2011, 2018, Schlaepfer et al. 2014*b*, Brabec et al. 2015, Germino et al. 2018, Shriver et al. 2018). Restoration of big sagebrush is slow, and outcomes, particularly of seeding efforts, are often unpredictable and mixed (Knutson et al. 2014, Rottler et al. 2018, Shriver et al. 2019, Davies et al. 2020). Because of the importance of the big sagebrush region (Davies et al. 2011, Finch et al. 2016), detailed management frameworks have been developed (Finch et al. 2016, Chambers et al. 2017, Crist et al. 2019), and the temporal, spatial, and financial extent of restoration activities in the big sagebrush region are among the largest in North America (Young et al. 1979, Pilliod et al. 2017, Copeland et al. 2018). Despite such large-scale, long-term efforts, successful restoration of big sagebrush remains rare because of the highly variable, but prevailing dry conditions in dryland environments and because of several specific characteristics of big sagebrush plants, which cannot resprout after fire, have short-lived seeds with limited dispersal, and seedlings that can be outcompeted, particularly by invasive plant species (reviewed by Schlaepfer et al. 2014*b*). Current frameworks for the management of the big sagebrush region often rely on static metrics which do not account for climate change or directly incorporate regeneration (Bradford et al. 2019, 2020). Detailed understanding of regeneration controls, particularly quantitative models of regeneration response to environmental fluctuations, would be an essential step toward developing accurate short-term regeneration forecasts (O'Connor et al. 2020) and long-term projections of plant population demographics and viability under climate change (Shriver et al. 2021).

Models are our main tool to understand complex processes such as regeneration of big sagebrush. These models can be used to develop projections under climate change scenarios that inform long-term management and restoration strategies (Clark et al. 2001, Oreskes 2003, Seidl 2017, Dietze et al. 2018). Even though validating models against observations at a future time is impossible, many modeling considerations contribute to credible long-term projections (Mouquet et al. 2015, Grimm and Berger 2016*a*) including model type (Pennekamp et al. 2017), model complexity (Coelho et al. 2019), understandability (Rastetter 2017, Gramelsberger et al. 2020), transferability (Yates et al. 2018), and robust estimates of model uncertainties (Dietze 2017). For instance, models can be validated against available observations, and model's ability to project under novel geographic or environmental conditions (transferability) can be estimated from strategically holding out groups of observations (Yates et al. 2018). Based on theoretical considerations, process-based models should transfer better to novel situations than regression-based models (Grimm and Berger 2016*b*, Radchuk et al. 2019), although the performance of process-based models is often constrained by high requirements of data and incomplete process understanding for model building (Pennekamp et al. 2017, Yates et al. 2018, Bouchet et al. 2019). An alternative approach to increase our confidence in model outcomes in the absence of future observations is to compare multiple, ideally independent models and assess robustness of outcomes as, for instance, the climate science (e.g., Knutti 2018), hydrological (e.g., Schellekens et al. 2017), and ecological niche (e.g., Hao et al. 2019) modeling communities are practicing with multi-model ensemble experiments. While making skillful predictions is difficult, rare, and generally only feasible for short time periods (Oreskes 2003, Dietze et al. 2018), models can be useful to generate hypotheses and understanding of complex processes, and to explore outcomes under what-if scenarios (Oreskes 2003).

Here, we investigate how two complementary models can contribute to our understanding of contemporary and future big sagebrush regeneration across the historical and potential future sagebrush region. One model is process-based and was designed to represent, in general, all relevant big sagebrush regeneration processes in undisturbed natural vegetation (Schlaepfer et al. 2014*a*, *b*). The other model is regression-based and was developed parsimoniously to identify and quantify the most relevant factors affecting recent big sagebrush restoration seeding outcomes following fire across the central and northern areas of the Great Basin and the Snake River Plain (Fig. 1 and Appendix S1: Fig. S1), areas with high impacts of cheatgrass and fire (Shriver et al. 2018). Both models represent major environmental controls on big sagebrush regeneration including meteorological and ecohydrological (e.g., soil moisture) factors (Fig. 2). These models provide two different perspectives on big sagebrush regeneration and, in combination, may represent the best available insights about future big sagebrush regeneration dynamics. We apply both models to address three specific objectives: (1) examine the geographic patterns of big sagebrush regeneration probabilities that the two different models project under historical conditions and future climate scenarios; (2) quantify the robustness of model projections, for example, the consistency among climate models in projected changes in regeneration for future time periods; and (3) identify how model predictions for regeneration potential relate to environmental site characteristics like climate, soil moisture, and soils.

## Methods

### *Description of simulation experiment*

We modeled big sagebrush regeneration based on daily meteorological and ecohydrological variables across the historical and potential future geographic range of big sagebrush distribution in the western United States. We simulated daily ecohydrological variables with the SOILWAT2 ecosystem water balance model in a full-factorial simulation experiment that is described in detail

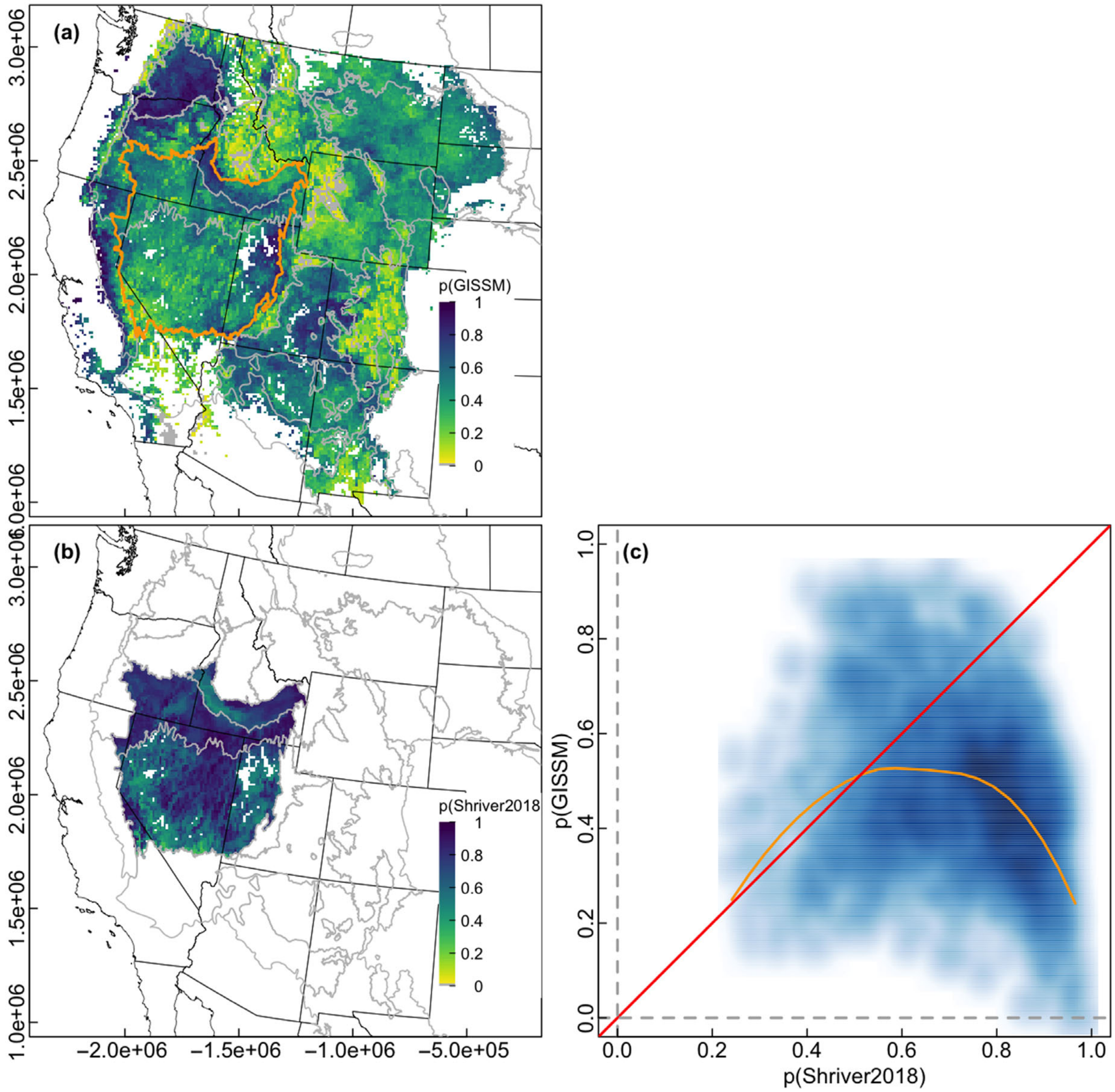



Fig. 1. Historical model outcomes: Maps and scatterplot between predictions of the potential regeneration probability of big sagebrush, *p*(GISSM), (a) and of the probability that big sagebrush restoration succeeds following fire and seeding, *p*(Shriver2018), (b) under historical conditions. The dark orange polygon in panel a indicates the applicable extent of the Shriver2018 model (including the Great Basin and Snake River Plain). Gray represents EPA level III ecoregions (EPA 2011), see Appendix S2: Fig. S1 and Appendix S1: Table S3. Dark blues in scatterplot between model outcomes for the joint extent (c) indicate a higher density of gridcells, red line represents a 1:1 relationship, and orange line is a locally fitted polynomial regression line (loess).

by Bradford et al. (2019). SOILWAT2 is a process-based daily simulation model that represents the soil profile with multiple soil layers and vegetation cover as composed of multiple co-occurring plant types responsive to atmospheric $CO_2$ concentrations. The code is available as an R package (Schlaepfer and Andrews 2019, Schlaepfer and Murphy 2019). Successful model applications cover global dryland ecosystems (e.g., Bradford et al. 2017, Schlaepfer et al. 2017,

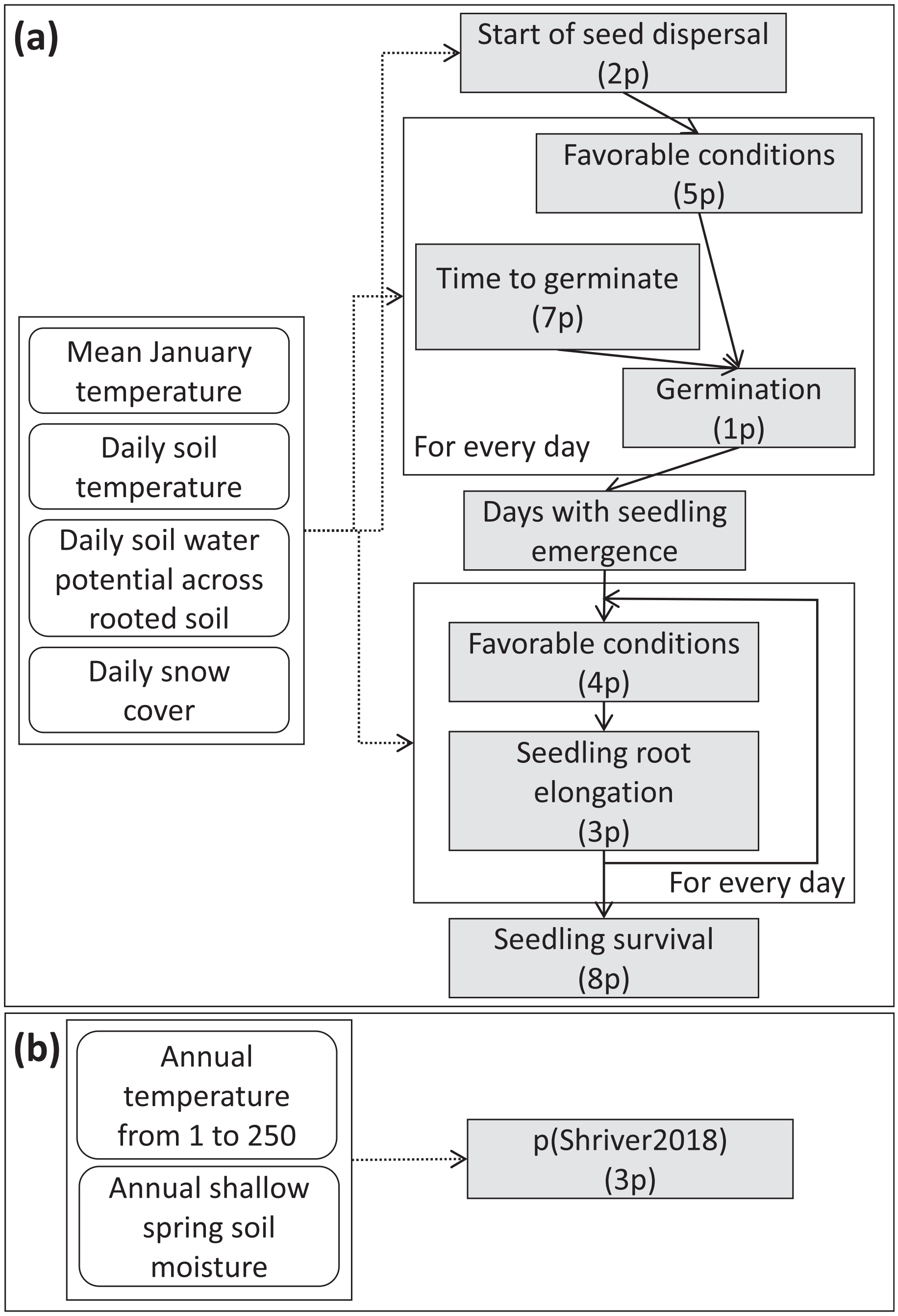



Fig. 2. Conceptual diagrams for GISSM (a) and Shriver2018 (b) models. Forcing variables (a) and predictor variables (b), in white boxes, are connected to processes (gray boxes; number of parameters in parentheses) with dotted arrows. See original publications for full details of the two models: GISSM which predicts the potential regeneration probability of big sagebrush *p*(GISSM) (Schlaepfer et al. 2014*a*) and the Shriver2018 model which predicts the probability that big sagebrush restoration succeeds following fire and seeding *p*(Shriver2018) (Shriver et al. 2018).

Tietjen et al. 2017) and North American dry grasslands (e.g., Bradford et al. 2014*b*, Lauenroth et al. 2014), dry forests (Bradford et al. 2014*a*), and shrublands (e.g., Schlaepfer et al. 2012*b*, Palmquist et al. 2016*b*, Renne et al. 2019) including simulations under climate change projections (Schlaepfer et al. 2012*a*, *c*, 2015, Palmquist et al. 2016*a*, Bradford et al. 2019).

Here, we used SOILWAT2 simulations for 23,202 gridcells at a 10-km resolution from the full simulation experiment (Bradford et al. 2019) that cover the geographic range of big sagebrush ecosystems. We determined the potential historical and future distribution of big sagebrush ecosystems based on the Gap Analysis Program (U.S. Geological Survey Gap Analysis Program 2016) and information from the Landfire Biophysical Settings (LANDFIRE 2014) and removed biologically unrealistic cells (i.e., cells that fall in the upper 2.5% of mean annual precipitation or in the upper 1% of mean annual temperature; PRISM Climate Group 2020). The simulation experimental factors included five soil textures, three 31-year time periods, and 144 climate conditions that were applied to each gridcell. One soil texture treatment extracted sand %, clay %, volume of gravel, and bulk density from 1-km gridded NRCS STATSGO (Miller and White 1998) and aggregated values for each gridcell; the remaining four soil texture treatments kept soil texture values constant across gridcells, that is, we used clay loam (27% sand, 35% clay), sandy loam (66% sand, 9% clay), silt loam (16% sand, 9% clay), and a second silt loam (30% sand, 18% clay) to represent the range of soil textures occurring across big sagebrush ecosystems. We used three time periods 1980–2010 (historical), 2020–2050 (near-future), and 2070–2100 (end 21st century future). We used daily 1/8-degree gridded meteorological data from Maurer et al. (2002) for the historical time period. We extracted monthly precipitation and temperature time series from the 1/8-degree spatially downscaled CMIP5 climate projections from the "Downscaled CMIP3 and CMIP5 Climate and Hydrology Projections" archive (http://gdo-dcp.ucllnl.org/downscaled_cmip_projections/, Maurer et al. 2007) from all participating general circulation models (GCMs) for two representative concentration pathways, that is, 37 GCMs under the medium mitigation and stabilization scenario, representative concentration pathway (RCP) 4.5; 35 GCMs under the high baseline, no-policy scenario RCP8.5 (Appendix S1: Table S1; van Vuuren et al. 2011). We generated daily meteorological forcing time series with the hybrid-delta quantile mapping approach (Hamlet et al. 2010, Tohver et al. 2014) to combine monthly GCM projections for historical and future time periods with historical daily data.

### *Description of published big sagebrush regeneration models*

We used the daily simulation output of SOILWAT2 to drive two previously published big sagebrush regeneration models (Fig. 1): GISSM and the Shriver2018 model. The two models represent related, yet distinct aspects of big sagebrush regeneration; however, both models assume that seeds are not a limiting factor and thus represent potential regeneration.

The GISSM model predicts the probability (frequency) of years when big sagebrush seedlings survive in undisturbed natural vegetation (Schlaepfer et al. 2014*a*), here in short "p(GISSM)". The model development goal was to represent key processes in a simulation model of big sagebrush regeneration that accounted for important environmental factors (Schlaepfer et al. 2014*b*) while biotic processes such as facilitation and competition are implicitly represented to the extent as they correlate with environmental factors at the sites used to estimate parameters. It requires daily forcing variables for soil water potential of each soil layer with roots, snowpack, minimum and maximum air temperature, and minimum and maximum shallow soil temperature (Fig. 1a). The 30 model parameters were estimated based on observed data from sites with natural vegetation in the absence of cheatgrass, heavy grazing, and physical or chemical sagebrush removal and our evaluation found that 74% of variation in annual outcomes of seedling survival was explained (Schlaepfer et al. 2014*a*). The code is available as part of a R package (Schlaepfer 2020). The GISSM model has been applied to historical conditions across the western US (Schlaepfer et al. 2014*a*) and to historical and future climate conditions for leading and trailing edges of the suitable big sagebrush habitat (Schlaepfer et al. 2015). Additionally, GISSM predictions and sensitivities agreed well with three independent models in a multi-model big sagebrush comparison effort that, besides GISSM, included a dynamic vegetation model, a random forest spatial correlation model, and a mixed-effects temporal correlation model (Renwick et al. 2018).

The Shriver2018 model represents the probability of big sagebrush establishment following fire and seeding as active management (Shriver et al. 2018), here in short "p(Shriver2018)." The model development goals included the inference of the impact of environmental conditions following seeding on regeneration probabilities for study sites in the central and northern Great Basin and the Snake River Plain. Effects of fire and cheatgrass are implicitly represented by the model to the extent as they correlate with the environmental factors at the sites used to estimate model parameters as well as by the selection criteria that were used to decide if restoration seeding was applied at a site following a fire. We limited our application of the Shriver2018 model to the original study extent (Fig. 1) to avoid geographic extrapolation into areas where we know that big sagebrush regeneration responds to different sets of factors, for example, the annual grass-fire cycle is not a dominant influence (e.g., Davies and Bates 2019, Hak and Comer 2020). The model is a logistic regression with two input variables, mean soil moisture from day 70 to 100 in the 0–5 cm soil layer (VWCspring), and mean air temperature from day 1 to 250 (meanT250; Fig. 2b):

$$\begin{aligned}\mathrm{logit}(p) &= 3.306 + 2.499 \times \mathrm{VWCspring} - 0.289 \\ &\quad \times \mathrm{meanT250}\end{aligned}$$

The best model structure and the resulting three model parameters were estimated using a Bayesian framework (Shriver et al. 2018); however, we considered here only the deterministic part of the model.

### *Objective 1: Geographic patterns of big sagebrush regeneration*

We mapped predictions of both models for big sagebrush regeneration during the historical time period under gridcell-specific soil textures to explore geographic patterns across the full geographic range of big sagebrush ecosystems for GISSM and across the subset covering the central and northern Great Basin and the Snake River Plain for Shriver2018. We mapped changes in modeled big sagebrush regeneration between a future and the historical time period as the median values across GCMs for each RCP and time period combination. We summarized spatial patterns by relevant EPA Level III Ecoregions (EPA 2011), see Appendix S2: Fig. S1.

We measured the strength of dependence between predictions of the two models with the unbiased distance correlation statistic (Szekely and Rizzo 2009) using function "dcor2d" of the R package "energy" version 1.7.5 (Rizzo and Szekely 2019). (Brownian) distance correlation quantifies both linear and non-linear associations in arbitrary dimensions and is zero only for independence (Szekely and Rizzo 2009).

### *Objective 2: Robustness of projections*

We measured three metrics to quantify the robustness of model projections to variation in forcing variables under future time periods: (1) agreement across GCMs for each RCP and time period combination, (2) contributions of the treatments to the factorial simulation experiment, and (3) degree of extrapolation. First, we calculated the agreement for each gridcell as the percentage of GCMs under which the direction of change between future and historical regeneration model responses was the same as the direction of the median response among runs for each RCP and time period combination. We considered both regeneration models as deterministic and did not quantify uncertainty in the regeneration model parameters themselves. Second, we quantified the contributions of the experimental treatment factors, that is, soil types, time periods, RCPs, and GCMs, and of their combined effects with a variance partitioning approach using the function "Anova" of the R package "car" version 3.0.5 (see Appendix S3 for details; Fox and Weisberg 2019). Third, we quantified the degree of model extrapolation beyond the environmental space that was available during model development using the univariate (NT1) and multivariate (NT2) distance metrics introduced by Mesgaran et al. (2014).

### *Objective 3: Interpretation of model outcomes*

To evaluate how well can we summarize, simplify, and interpret the regeneration models, we quantified statistical relationships between model outcomes and (1) two sets of predefined predictor variables and (2) sets of best-performing predictor variables. We calculated Root-Mean-Square Deviations (RMSD) and the coefficient of variation (CV) of RMSD as well as pseudo-$R^2$ values to quantify how well the statistical relationships summarized GISSM and Shriver2018 model outcomes. We used function "r2beta" of the R package "r2glmm" version 20200305 (Jaeger 2020) for binomial GLMs according to Jaeger et al. (2017) and function "r.squaredGLMM" of the R package "MuMIn" version 1.43.15 (Bartoń 2019) to calculate conditional pseudo-$R^2$ for linear mixed-effects models (LMM) according to Nakagawa et al. (2017).

We fit binomial GLMs between model outcomes for the historical time period and gridcell-specific soils for predictors and model structure used by the Shriver2018 model. For GISSM, this approach quantifies how different the two models are; for Shriver2018, this estimates how well the relationship of the model can be recovered by our model application.

To isolate and estimate the explanatory power of soil texture variables, we used the part of the simulation experiment with the four fixed soil types for the historical time period. For each gridcell, we calculated the pairwise differences between the fixed soil types for both model outcomes and soil texture (sand, clay). We used LMMs with the function "lmer" of the R package "lme4" version 1.121 (Bates et al. 2015) to fit differences in outcomes against sand and clay differences, their interactions, and squared values where an indicator of the pairs of soil types served as random error of the intercepts.

We carried out a variable selection procedure for the two following statistical model fits: We fit binomial GLMs between model outcomes for the historical time period and gridcell-specific soils for the selected predictors, their interactions, and squared values. Additionally, for each RCP, GCM, time period, and gridcell, we calculated the differences between the future and the historical time period under gridcell-specific soils. For each RCP and time period, we fit LMMs between differences in model outcome differences and selected predictors, their interactions, and squared values where GCM served as random error of the intercepts.

The variable selection procedure for each of these two statistical fitting exercises based on the strongest predictors from an ascending hierarchical variable clustering to avoid selecting strongly related variables. Specifically, we started with the 21 predictor variables that were considered relevant in previous work on big sagebrush regeneration (Appendix S1: Table S2, Schlaepfer et al. 2014*a*, 2015, Shriver et al. 2018). We transformed several of these variables to increase the symmetry of their distributions (Appendix S1: Table S2). The application for fitting differences between future and historical time period considered the historical values of these 21 predictor variables in addition to the differences of these 21 variables between the future and historical time periods; we used future median values across GCMs for each RCP and time period. We then calculated bivariate unbiased distance correlations (see objective 1) between each predictor and each model outcome as an indicator of the strength of a predictor. We determined the hierarchical clustering of the predictors using function "hclustvar" of the R package "ClustOfVar" version 1.1 (Chavent et al. 2019). We determined the stability of the clustering with the "stability" function of the same package which resulted in two stable clusters for the historical application and four clusters for the application of future change. For each cluster, we selected the predictor with the highest distance correlation value and removed any predictor if they had a higher distance correlation than 0.5 with any previously selected predictors from different clusters.

We carried out all analyses in R version 3.6.1 (R Core Team 2019). Data generated during this study are available from the USGS ScienceBase-Catalog (Schlaepfer and Bradford 2021) and code from github/zenodo (Schlaepfer 2021).

## Results

### *Objective 1: Geographic patterns of big sagebrush regeneration*

Under 1980–2010 conditions, the process-based GISSM predicted a mean potential regeneration probability of $p = 0.44 \pm 0.20$ (mean $\pm$ 1 SD) for big sagebrush with values ranging between 0 and 1 across the geographic range of big sagebrush ecosystems (Fig. 1, Appendix S1: Table S3). GISSM predicted the highest values for the Columbia Plateau, parts of the Colorado Plateau, Sierra Nevada, and Snake River Plain;

the lowest values were predicted for southern, warm areas such as the Mojave range and the Chihuahuan Desert and for mountainous areas such as the Southern and Middle Rockies and the Idaho Batholith ecoregion. GISSM projected areas of increases in potential regeneration probability (71–78% of extent) and decreases (13–16%) for future time periods and climate change scenarios compared to 1980–2010 climate conditions (Fig. 3, Table 1). Projected increases were, on average, largest for areas at high elevation and in the north (Fig. 3, Appendix S2: Fig. S2, Appendix S1: Table S3). The most extensive decreases were projected for mid-century RCP 4.5 and end-century RCP 8.5; these areas were located predominantly in the southern portions of the study area (particularly under end-century RCP 8.5) and low elevation portions of several ecoregions including the Columbia Plateau, Colorado Plateau, Great Basin, and Snake River Plain; however, they also included northeastern parts in Montana and the Bighorn Basin in Wyoming (Appendix S2: Fig. S2, Appendix S1: Table S3).

The regression-based Shriver2018 model predicted a regeneration probability of $p = 0.71 \pm 0.14$, with values between 0.24 and 0.99, for big sagebrush restoration seeding following fire across the central and northern Great Basin and the Snake River Plain for 1980–2010 climate conditions (Fig. 1, Appendix S1: Table S3). Shriver2018 predicted the highest values at high elevation areas and the lowest values in low elevation areas such as the western portion of the Snake River Plain. Shriver2018 projected, consistently and geographically relatively uniformly, decreases for future time periods and climate change scenarios compared to 1980–2010 climate conditions (Fig. 3, Table 1). Under RCP 4.5 projections, they ranged from $\Delta p = -0.09 \pm 0.02$ for mid-century to $\Delta p = -0.18 \pm 0.04$ for end-century; under RCP 8.5 projections, they ranged from $\Delta p = -0.11 \pm 0.03$ for mid-century to $\Delta p = -0.32 \pm 0.05$ for end-century (Appendix S2: Fig. S2, Appendix S1: Table S3).

### *Objective 2: Robustness of projections*

Future GISSM projections agreed across the study area on average by 83 ± 22% in the direction of the outcome across GCM climate projections under RCP 8.5, that is, GISSM runs forced by at least 29 out of the 35 GCM climate projections were consistent in projecting increases and decreases, respectively, in the outcome (Table 1, Fig. 4, Appendix S2: Fig. S3, Appendix S1: Table S3). The proportion of areas with a high (>90%) agreement among GCMs in that GISSM projections increased, rose from 35% mid-century to 53% end-century under RCP 4.5, and from 43% to 67% under RCP 8.5 (Table 1, Fig. 4). While the same pattern was true for areas with projected decreases, areas with a high agreement in decreases represented an overall smaller proportion with 6% to 8% under RCP 4.5 and 7% to 19% under RCP 8.5 (Table 1, Fig. 4).

Future Shriver2018 projections agreed to 100% across the entire area in the direction of the response; there was no variation in direction of outcomes among GCM climate projections for any simulated gridcell (Table 1, Fig. 4, Appendix S2: Fig. S3, Appendix S1: Table S3).

Across the entire simulation experiment, 66% of the GISSM outcome variation was determined by time period and its interactions with GCMs and RCPs with considerable geographic variation; in comparison, soil types explained 5% (Fig. 5; Appendix S2: Fig. S4; Appendix S1: Table S4). GCMs and the GCM x RCP interaction dominated the explanatory power within mid-century (81%) and end-century (74%) time periods while soil types determined 15% and 12%, respectively.

Similarly, 69% of the Shriver2018 model outcome was explained by time period alone with little geographic variation. Within the mid-century time period, however, GCMs and soil types were equally important with 43% and 48%, respectively, whereas the GCM × RCP interaction was not explaining much variation. Within the end-century time period, soil type lost most of the explanatory power (12%) while RCPs became relevant (47%; Fig. 5; Appendix S1: Table S4).

### *Objective 3: Regeneration patterns in relation to climate and soils*

Historical GISSM model outcomes were best summarized by the two variables mean annual temperature and spring frost exposure (Fig. 6, Table 2, Appendix S1: Table S6). GISSM outcomes showed a unimodal pattern along mean annual temperatures with a peak around 10°C; spring frost exposure affected outcomes

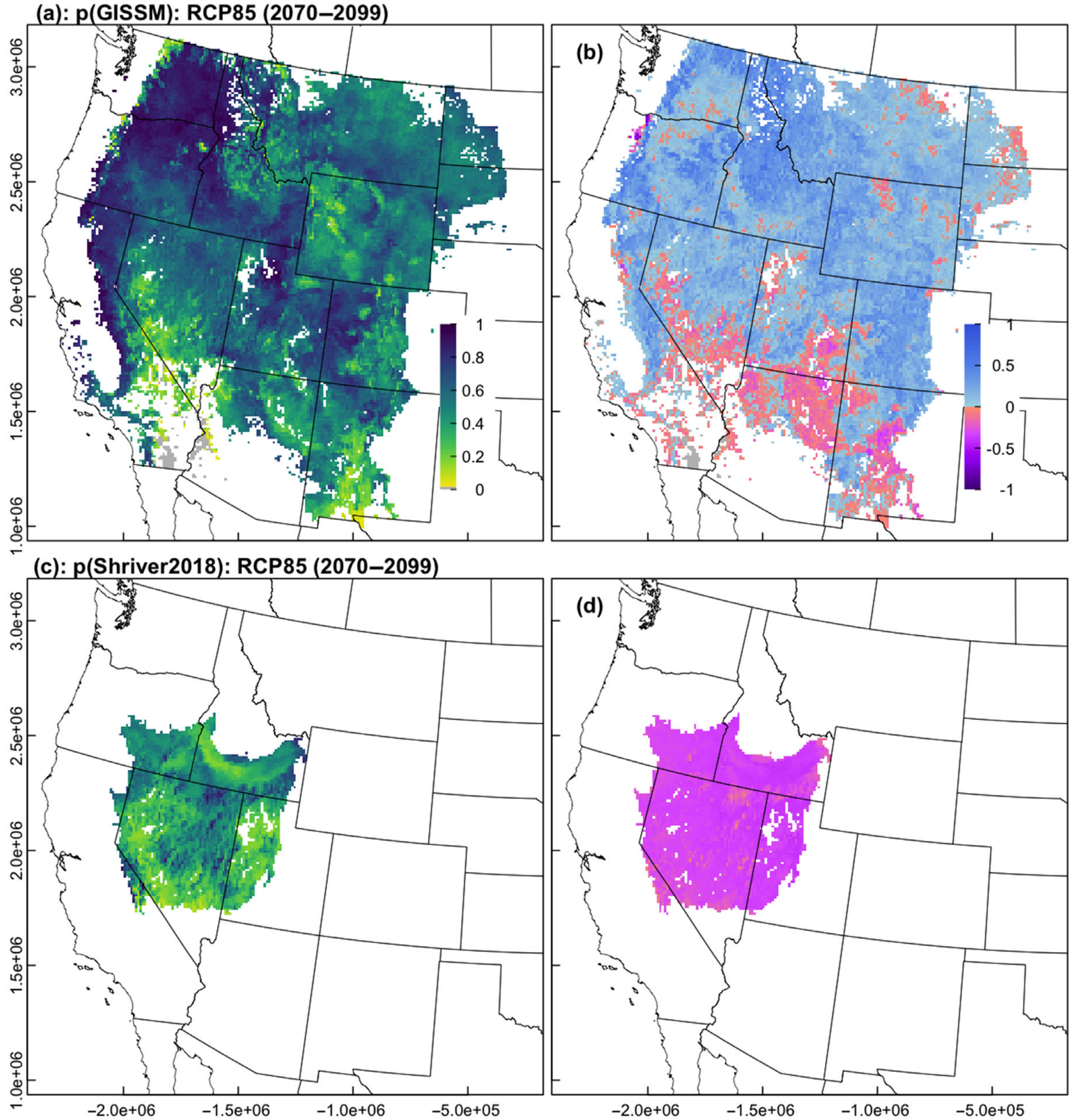



Fig. 3. Future projections: Maps of sagebrush regeneration projections by GISSM (a, b) and by Shriver2018 (c, d) under RCP 8.5 end-of-century (2070–2100) time period. Median projections across GCM-driven runs in panels a and c (color legend in panel a) and median change from historical (1980–2010) time period (see Fig. 2) in panels b and d (color legend in panel b). Results for all RCPs and time periods in Appendix S2: Fig. S1.

negatively, mostly at intermediate and warm locations. Pseudo-$R^2$ suggested that this summary explained 62% of the variation in the GISSM outcome with average deviations of the summary from mean model outcomes by 30% (Table 2). This is a better summary than one using the same predictors as in the Shriver2018 model, that is, mean temperatures in the first 250 d of a year and spring VWC at 0–5 cm depth (Table 2; Appendix S2: Fig. S9).

Table 1. Percentage of area for which decreases or increases in sagebrush regeneration probabilities are projected for mid- and end-century time periods.

| Response | Agreement | RCP 4.5 2020–2050 | RCP 4.5 2070–2100 | RCP 8.5 2020–2050 | RCP 8.5 2070–2100 |
|---|---|---|---|---|---|
| GISSM | | | | | |
| Decrease | Median | 16 | 13 | 14 | 16 |
| | >75% | 5 | 4 | 4 | 7 |
| | >90% | 1 | 1 | 1 | 3 |
| Increase | Median | 71 | 78 | 74 | 78 |
| | >75% | 48 | 61 | 52 | 64 |
| | >90% | 25 | 41 | 32 | 52 |
| Shriver2018 | | | | | |
| Decrease | Median | 100 | 100 | 100 | 100 |
| | >75% | 100 | 100 | 100 | 100 |
| | >90% | 100 | 100 | 100 | 100 |
| Increase | Median | 0 | 0 | 0 | 0 |
| | >75% | 0 | 0 | 0 | 0 |
| | >90% | 0 | 0 | 0 | 0 |

*Note:* Agreement in response direction across GCM-forced runs ($n$ = 37 under RCP 4.5 and $n$ = 35 under RCP 8.5) refers to the sign of the median value and to areas where >75% as well as >90% of runs agree in direction of response.

We recovered the predictors of the Shriver2018 model with the variable selection algorithm (Fig. 6, Appendix S1: Table S6). Pseudo-$R^2$ confirmed that these predictors explained >99% of the Shriver2018 outcome with average deviations by almost 0% (Table 2).

Differences in soil textures among the fixed experimental soil types poorly summarized the associated differences in outcomes of GISSM among these soil types with a low pseudo-$R^2$ value and average deviations larger than seven times the mean model outcome (Table 2, Appendix S2: Fig. S10). These soil texture differences captured, however, most of the variation in the Shriver2018 outcome, even though average deviations of the summary were nearly of the same size as the mean model outcome.

The four predictors that summarize GISSM model outcome differences between one of the future time period × RCP combinations and the historical time period included growing degree days under historical conditions, two variables quantifying change in snow, and change in precipitation (Fig. 7; Appendix S2: Figs S11-S13). There was an important interaction between

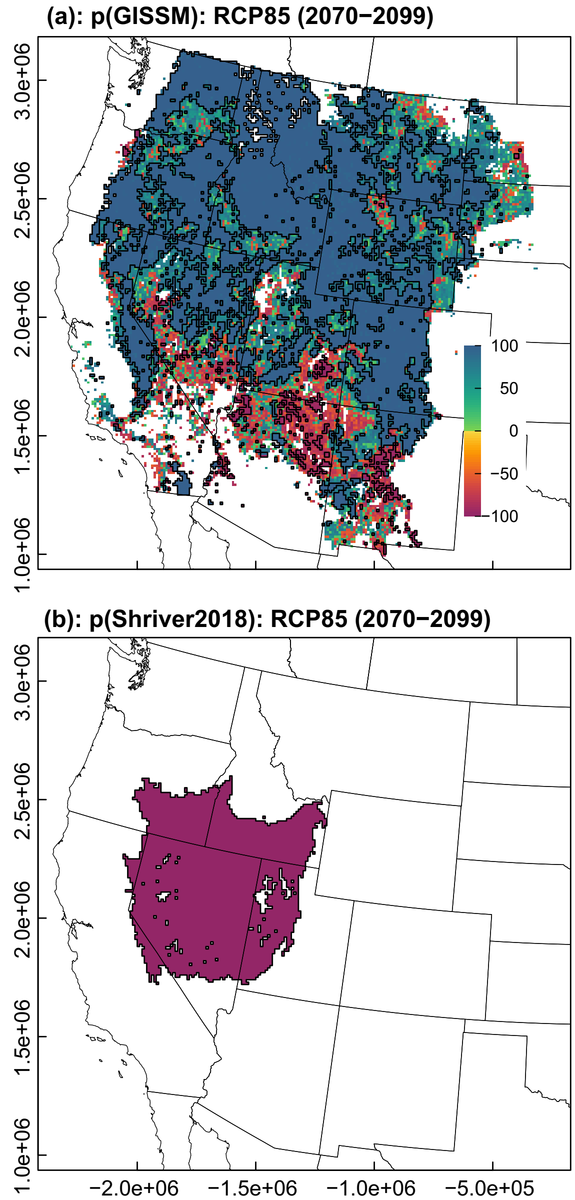



Fig. 4. Agreement in future projections: Percentage of GCM-driven runs under RCP 8.5 end-of-century (2070–2100) time period ($n$ = 35) that agree on direction of the response in the probability of regeneration compared to historical time period. Positive values indicate agreement in a median increase or no change; negative values indicate agreement in a median decrease. Black polygons mark areas with at least 90% agreement. Results for all RCPs and time periods in Appendix S2: Fig. S2.

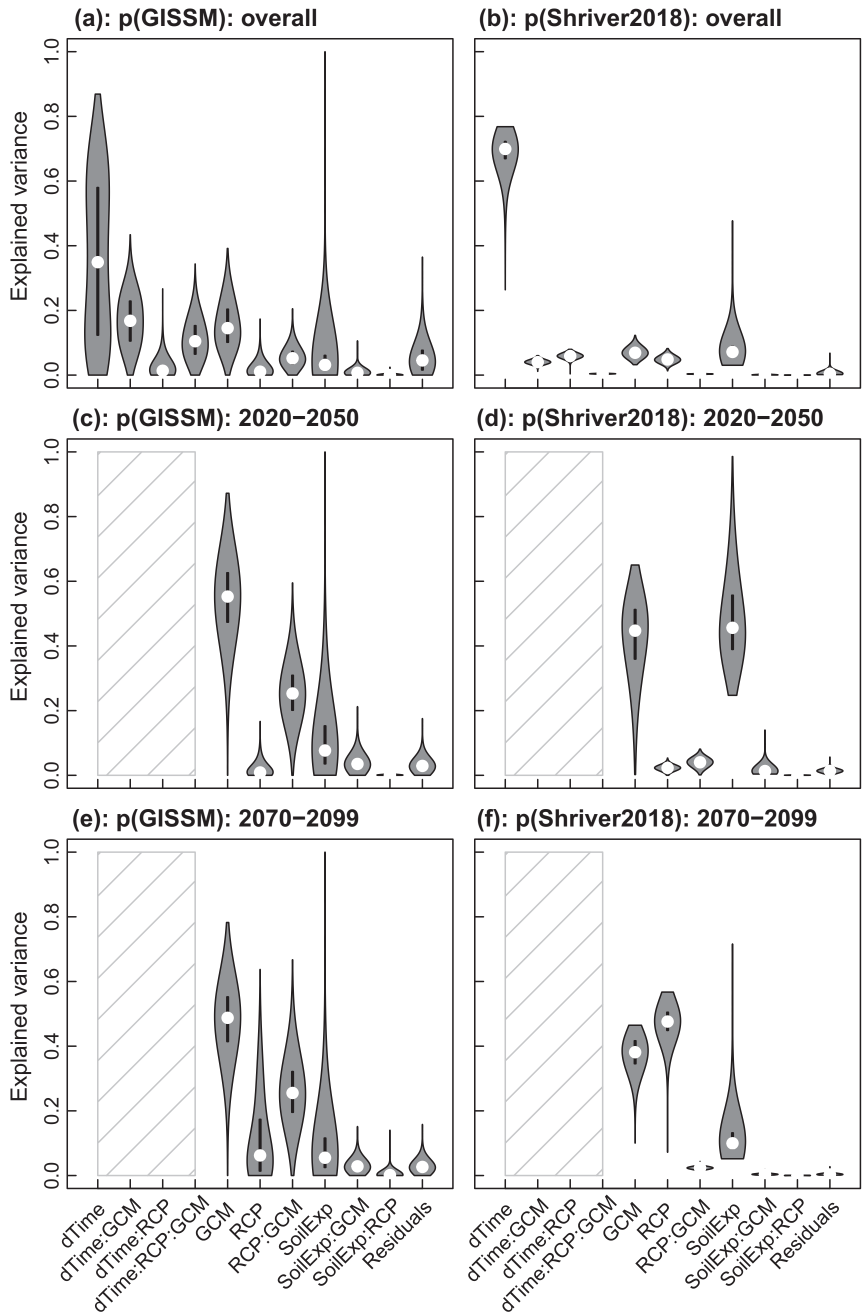



Fig. 5. Relative importance of factors: Percentage of explained variance for sagebrush regeneration projections by GISSM (a, c, e) and by Shriver2018 (b, d, f) by simulation experimental factors: time periods (3×), GCMs (35×), RCPs (2×), soil types (5×), two-way interactions, the three-way interaction time × RCP × GCM, and all remaining higher-order interactions pooled (residuals) for the full experiment (a, b; 1050 response values per gridcell), and for two future time periods 2020–2050 (c, d) and 2070–2100 (e, f; 350 response values per gridcell each). Violins represent the density distribution of values across gridcells where the white dot represents the median and the vertical bar spans the interquartile range. Gray hashed rectangles indicate a fixed time period. See Appendix S3 for full method details. Note: the two models were applied across different geographic extents (see Fig. 1).

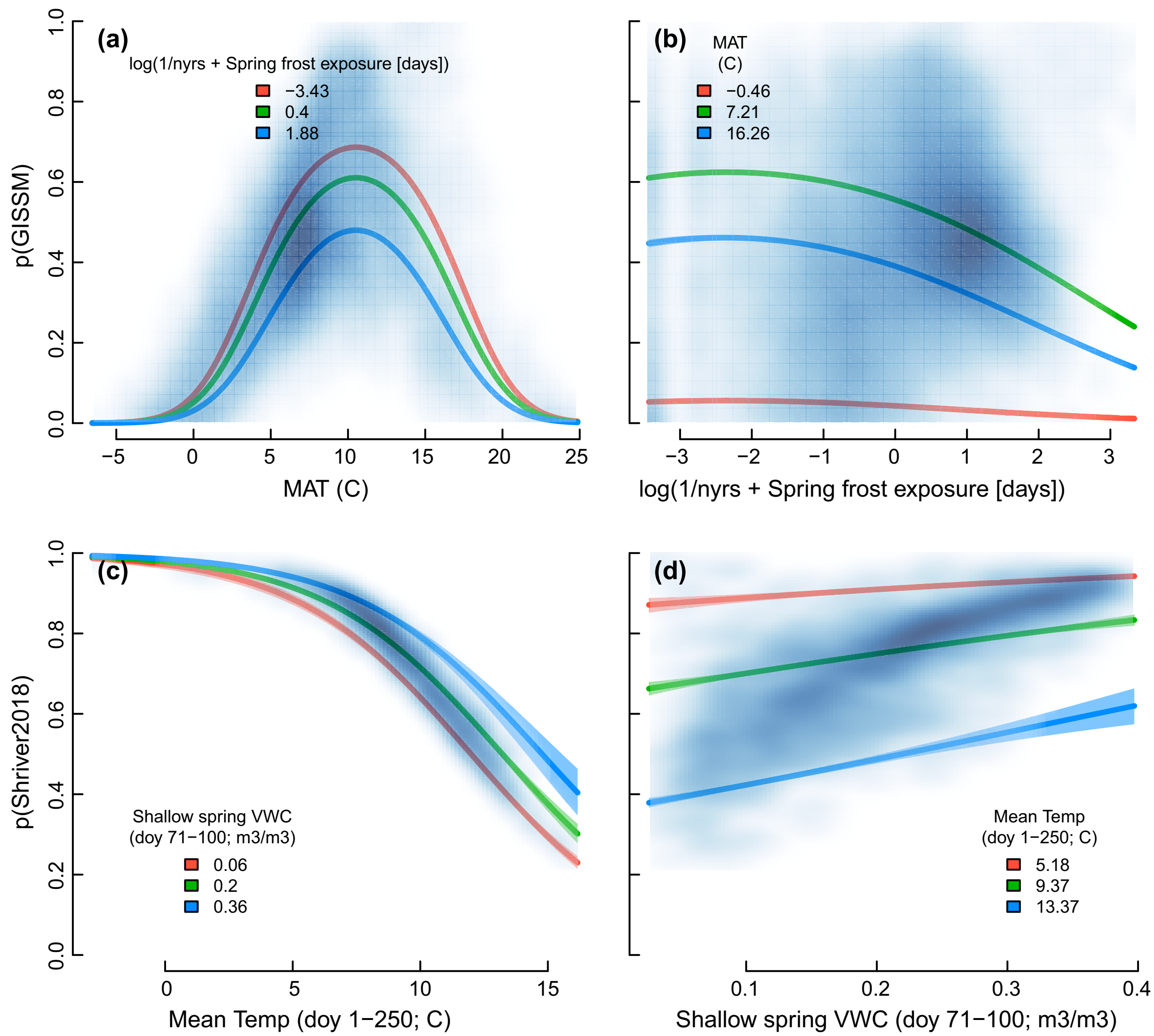



Fig. 6. Interpretation of historical model outcomes: Ability of the selected best-performing predictor variables, mean annual temperature (MAT), spring frost exposure, and volumetric water content (VWC) in 0–5 cm soils during the spring, to summarize outcomes of GISSM (a, b) and the Shriver2018 models (c, d) under historical conditions for gridcell-specific soils. Dark blue hues indicate a higher density of gridcell values; the three colored lines represent conditional relationships between $x$ and $y$ where the other predictor variable (inset legend) was held constant at its 2.5% (red), 50% (green), and 97.5% quantiles (blue). Note: the two models were applied across different geographic extents (see Fig. 1).

growing degree days and change in the proportion of precipitation that falls as snow: GISSM projected the largest increases in potential regeneration probabilities for locations with low historical growing degree days and the largest projected future decreases in the ratio of snow to precipitation; conversely, the largest decreases in potential regeneration probabilities were projected for locations with medium to high historical growing degree days and the largest projected future decreases in the ratio of snow to precipitation (Fig. 7a,b).

For the Shriver2018 model, the four selected predictors included only variables measuring change between a future and the historical time period; they were change in growing degree

Table 2. Ability of sets of predictor variables to summarize GISSM and Shriver2018 model outcomes $p(.)$ as quantified by (1) pseudo-$R^2$ and (2) root mean square deviation (RMSD) and coefficient of variation (CV) of the RMSD.

| | | Pseudo-$R^2$ | | RMSD and CV (%) | |
|---|---|---|---|---|---|
| Response to summarize | Predictor set | GISSM | Shriver2018 | GISSM | Shriver2018 |
| $p$(historical) | Selected predictors | 0.62 | 0.99 | 0.13/30% | 0.00/0% |
| $p$(historical) | Predictors of Shriver2018 | 0.24 | 0.99 | 0.18/40% | 0.00/0% |
| $p$(soil type i) – $p$(soil type j) | Soil texture differences among soil types | 0.17 | 0.99 | 0.04/746% | 0.01/−83% |
| $p$(mid-century RCP 4.5) – $p$(historical) | Selected predictors | 0.22 | 0.94 | 0.10/160% | 0.02/−16% |
| $p$(end-century RCP 4.5) – $p$(historical) | | 0.28 | 0.96 | 0.11/110% | 0.02/−13% |
| $p$(mid-century RCP 8.5) – $p$(historical) | | 0.26 | 0.93 | 0.10/136% | 0.02/−15% |
| $p$(end-century RCP 8.5) – $p$(historical) | | 0.54 | 0.87 | 0.13/92% | 0.04/−12% |

days, change in precipitation, and two variables quantifying change in recharge. Most of the Shriver2018 model outcome was explained by change in growing degree days with large increases related to large projected future decreases in model outcomes (Fig. 7e).

Projections of both models, GISSM and Shriver2018, were better summarized for the end-century than mid-century time period and under RCP 8.5 than RCP 4.5 conditions (Table 2). However, the Shriver2018 model was easier to summarize than GISSM: Under end-century time period and under RCP 8.5 conditions, the summary of GISSM explained 54% variation with mean deviations of 92% of mean model outcome, whereas the summary explained 87% of the Shriver2018 model with mean deviations of 12% (Table 2).

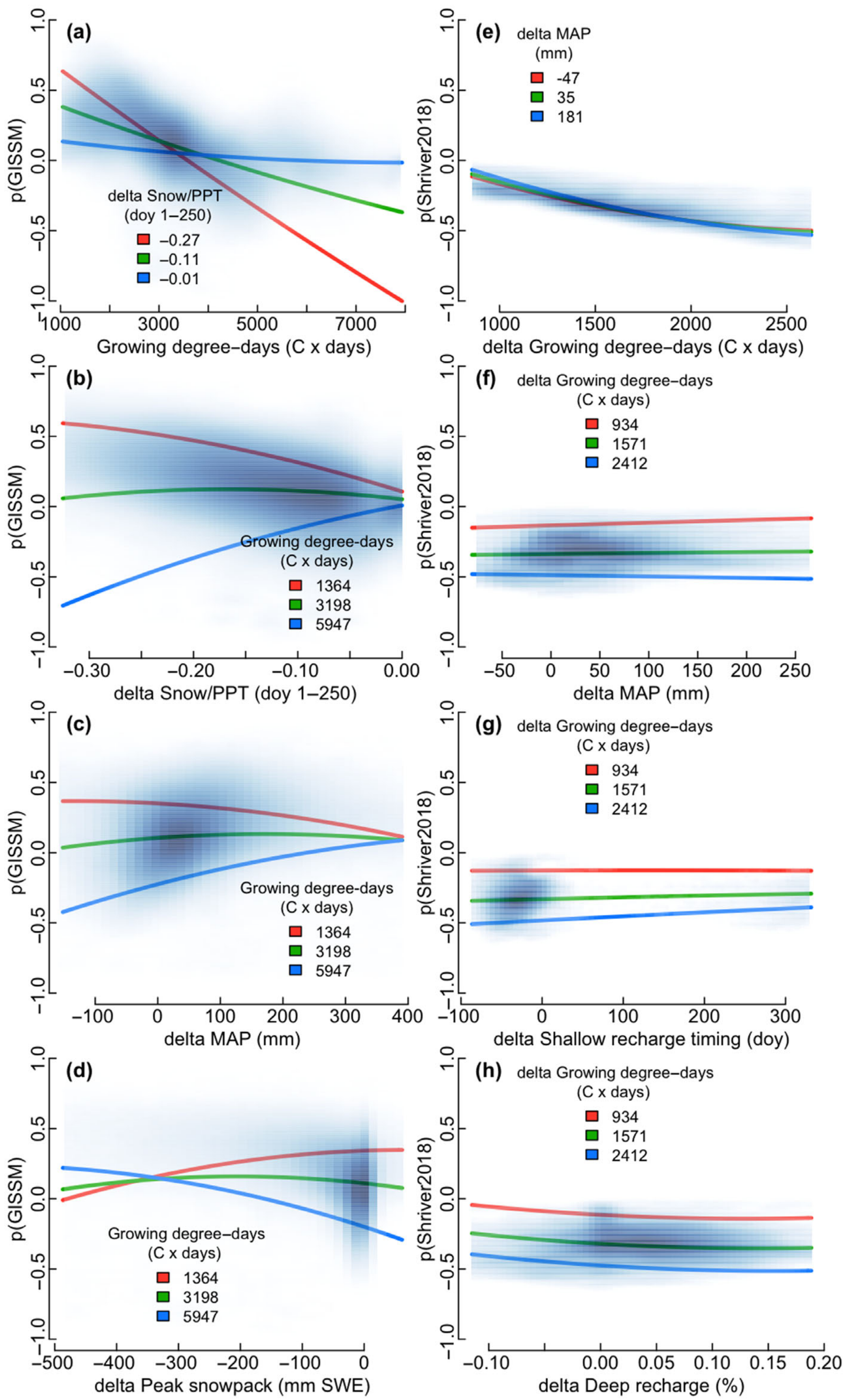
## Discussion

Quantitative, predictive understanding of regeneration for long-lived woody plants in drylands is difficult to develop but will be essential for projecting the future of these species. Regeneration is a foundational demographic process that, in some regions, can restrict the persistence and recovery of long-lived plant populations. Population and species-level constraints imposed by failed regeneration may grow as temperatures and drought risks rise under climate change (Jackson et al. 2009) and as wildfires and human land use prevalence increase (Davies et al. 2011, Shriver et al. 2018). Big sagebrush is a prime example of a long-lived dryland plant whose distribution, abundance, and potential future viability may be constrained by regeneration. The contemporary relevance of the big sagebrush regeneration challenge is highlighted by the unpredictable and often mixed outcomes from big sagebrush restoration efforts (Knutson et al. 2014, Rottler et al. 2018, Shriver et al. 2019, Davies et al. 2020).

Here, we integrated insights from two quantitative models of big sagebrush regeneration to provide the best available insights into contemporary and future regeneration probabilities under natural conditions and for post-fire restoration seeding. Both regeneration models have been successfully evaluated against field observations: The process-based GISSM was evaluated at sites under natural conditions without anthropogenic disturbances (Schlaepfer et al. 2014*a*), and the regression-based Shriver2018 was evaluated at locations with post-fire big sagebrush restoration seeding (Shriver et al. 2018). Thus, differences in model outcomes are not necessarily model disagreements (Fig. 1c). Instead, these differences reflect that the two models represent related and complementary aspects of big sagebrush regeneration associated with different drivers. Divergent drivers and resulting model outcomes are apparent, for instance, in the lower Snake River Plain (Fig. 1) where big sagebrush was historically widespread and has become less abundant due to land use, fire, and invasive annual grasses (Knick and Rotenberry 1997, Boyte et al. 2019). In this area, Shriver2018 estimated low probabilities of restoration seeding success, a result that reflects current patterns modified by agriculture, fire, and cheatgrass invasion, whereas GISSM predicted high potential regeneration that reflect the area's historical climatic suitability for big sagebrush. In general, the process-based GISSM represents the influence of climate fluctuations on potential regeneration in the absence of competition from introduced species and anthropogenic disturbances. By contrast, the regression-based Shriver2018 model implicitly incorporates the consequences of interactions among wildfire and invasive annual grasses to the extent that these are correlated with moisture availability and temperature at the original training sites. Furthermore, the Shriver2018 model also implicitly incorporates additional disturbances such as a history of livestock grazing, physical soil disturbance, and possibly failed past attempts at restoration because these factors are often linked to invasive annual grasses (e.g., Hak and Comer 2020). Results from these models, in combination, enhance our perspective on big sagebrush regeneration probability and post-fire restoration seeding outcomes under a wide range of climate and soil conditions and suggests several insights about the potential challenges of sustaining big sagebrush regeneration that were not evident from either model alone.

First, contrasting regeneration potential between the models implies insights about the contemporary challenge of promoting big sagebrush regeneration. Specifically, differences in contemporary outcomes between the two regeneration models reflect the differences in the importance of drivers in the context of natural vegetation vs. big sagebrush restoration seeding following a fire. The process-based GISSM represents regeneration processes in undisturbed natural vegetation which included reduced regeneration due to too much snow, too low or too high temperatures, and acute or chronic too low or too much soil moisture (Fig. 2; Schlaepfer et al. 2014*a*, *b*). The regression-based Shriver2018 model quantifies the most relevant environmental factors affecting recent big sagebrush post-fire restoration seeding outcomes (Shriver et al. 2018). Summarizing the Shriver2018 model indicated reduced restoration seeding success following fire in areas with high temperatures or low spring soil moisture (Fig. 3). For instance, the model does not represent a limit of regeneration at cold temperatures likely because of an absence of high elevation, cold conditions in the original set of training sites (Shriver et al. 2018). Furthermore, the Shriver2018 model may also be weighted toward sites that are both particularly prone to wildfire (e.g., hotter and drier than the sagebrush region as a whole) and considered amenable to subsequent seeding, which they received. Summarizing GISSM indicated that both high and low temperatures as well as spring frost exposure, but not at cold sites, reduced regeneration predictions. This interaction between temperature and frost may represent a high seed dormancy and slow germination rate at cold sites (Meyer and Monsen 1992) that may contribute to low damage levels due to early spring frost at these cold sites. Overall, the more limited regeneration outcomes predicted by GISSM compared to Shriver2018 across most of the study area likely reflected the positive effects that restoration seeding can have in some situations (e.g., Germino et al. 2018, Davies and Bates 2019), but see others (e.g., Davies et al. 2013, 2020), the threshold of one big sagebrush plant to define restoration success (Shriver et al. 2018), and the complexity of regeneration processes under the large variety of environmental conditions affecting big sagebrush regeneration under natural conditions (Schlaepfer et al. 2014*b*) which can more directly be represented by a process-based model (Yates et al. 2018).

Second, our results have information about the future of big sagebrush regeneration in the context of interacting climate change, enhanced wildfire frequency, and human land use. The process-based GISSM model suggested increased potential regeneration under future climate projections across part of the big sagebrush range and decreases for the warmest regions. Future GISSM projections were, across large areas, robust and in high agreement among participating GCMs; however, our assessment of robustness accounted for variation in forcing inputs and did not include model uncertainty. Degree of agreement correlated positively with magnitude of projected change reflecting that variation among GCMs was the most important experimental factor (Fig. 5). GISSM projected changes were not well summarized by simple



(a)
delta Snow/PPT (doy 1–250)
−0.27
−0.11
−0.01
p(GISSM)
Growing degree-days (C x days)
(b)
Growing degree-days (C x days)
1364
3198
5947
delta Snow/PPT (doy 1–250)
(c)
delta MAP (mm)
(d)
delta Peak snowpack (mm SWE)
(e)
delta MAP (mm)
-47
35
181
p(Shriver2018)
delta Growing degree-days (C x days)
(f)
delta Growing degree-days (C x days)
934
1571
2412
(g)
delta Shallow recharge timing (doy)
(h)
delta Deep recharge (%)

Fig. 7. Interpretation of future model projections: Ability of the selected best-performing predictor variables to summarize differences in outcomes of GISSM (a–d) and the Shriver2018 models (e–h) between RCP8.5 end-century and historical conditions for gridcell-specific soils. Dark blue hues indicate a higher density of gridcell values; the three colored lines represent conditional relationships between *x* and *y* where another predictor variable (inset legend) was held constant at its 2.5% (red), 50% (green), and 97.5% quantiles (blue). Note: the two models were applied across different geographic extents (see Fig. 1).

explanations because of considerable residual variation. Nevertheless, overall trends emerged that suggested increased potential regeneration particularly across those parts of the big sagebrush range that have a small number of growing degree days under current conditions (i.e., areas with cool summers and/or a short growing season) and are projected to receive a larger proportion of cold-season precipitation as rain instead of snow due to warming while receiving more precipitation overall. Projections of decreased regeneration were found mostly where growing degree days are currently abundant and the contribution of snow is projected to be strongly reduced at small changes to total precipitation. These responses were generally stronger end-century than mid-century and under RCP 8.5 than RCP 4.5. Other studies support the interpretation that intermediate reductions of snow under a warming climate at cool or high elevation sites may enhance deep-rooted species such as big sagebrush as long as sufficient soil moisture is available and warm-season dry periods are not too severe which instead could favor cold-season species, including the invasive annual cheatgrass (Perfors et al. 2003, Schlaepfer et al. 2012*a*, Polley et al. 2013, Flerchinger et al. 2020).

By contrast, the regression-based Shriver2018 model suggested that active restoration management may generally become increasingly more difficult under warming for northern portions of the Great Basin and the Snake River Plains. The future projections of the Shriver2018 model were uniform as expected from model structure and model purpose. The robust outcomes under climate scenarios were mostly driven by the model response to the warming signal that reflected the high agreement in temperature projections among GCMs (Appendix S2: Fig. S4; Appendix S1: Table S4; IPCC 2014), and we did not account for uncertainty in model parameters. Our variable selection procedure to summarize model outcomes did not identify the temperature-related driving model variable itself but instead a closely related variable (Appendix S1: Table S7). This summary suggested a negative relationship between projected changes in post-fire restoration seeding outcomes and projected increases in growing degree days with larger projected decreases for end-century than mid-century and under RCP 8.5 than RCP 4.5. Climate change projections with the Shriver2018 model demonstrated apparent robustness of outcomes and ease of interpretation; however, levels of interactions between big sagebrush restoration outcomes, fire, and invasive annual grasses represented by the model are specific for recent years across the northern Great Basin and Snake River Plains. Recent findings suggest that current levels may reflect a lower estimate of successful restoration outcome under future climate projections with an intensified fire-invasive annual grasses feedback (e.g., Bradley et al. 2016, Coates et al. 2016). Nevertheless, the future Shriver2018 projections are consistent with previous findings that big sagebrush restoration seeding is, on average, more successful at high elevation, cool sites than at low elevation, warm sites (Davies et al. 2011, Germino et al. 2018). We interpret these results in comparison to GISSM which omitted effects of fire and introduced species, as a model hypothesis which suggests that the fire-invasive annual grass feedback loop, as well as associated land use legacies, may play a dominant role for future big sagebrush post-fire restoration seeding success, at least across the northern Great Basin and Snake River.

Third, evaluating these divergently structured models has lessons for how to develop long-term projections for complex ecological processes. We have employed two substantially different model types, one process-based model with many parameters and one regression-based model with few parameters (Fig. 2), to generate long-term inferences about big sagebrush potential regeneration and post-fire restoration seeding success. While we were able to adequately summarize the regression-based model and explain future projections with simple variables, the process-based model outcomes could not be summarized to a similar extent, that is, much of the model outcomes remained unexplained by the summary. This suggests that the processes and/or the daily temporal resolution represented by GISSM may be necessary to appropriately capture the complex conditions that determine big sagebrush establishment suitability. However, the richness of complex model outcomes can represent challenges for interpretation and communication (Rastetter 2017, Gramelsberger et al. 2020). Multiple approaches can be used in combination to assess suitability of model projections including evaluating model performance, identifying sources of uncertainty, estimating transferability to novel conditions, and comparing agreement in projections with other models. The performance of both GISSM and Shriver2018 models has been evaluated successfully in the primary publications (Schlaepfer et al. 2014*a*, Shriver et al. 2018). As new observations and experiments are becoming available under specific simulated climate conditions, our model projections, which currently represent hypotheses about those scenarios, should be more thoroughly evaluated to augment predictive insights (Mouquet et al. 2015). The models demonstrate the need for carefully designed and interpreted approaches when projecting complex ecological processes, such as regeneration, and associated restoration efforts.

Lastly, these two models have limitations that could be addressed to improve long-term projections of big sagebrush regeneration. An important limitation of our study is that both models assume the availability of sufficient seeds: GISSM represents potential regeneration in natural vegetation in the absence of competition from introduced species and anthropogenic disturbances and Shriver2018 represents the restoration addition of seeds following fire in areas with a generally high cheatgrass prevalence. These assumptions are “baked” into model applications, that is, results are not applicable to situations with a lack of seeds such as after large fire without restoration seeding (Germino et al. 2018) and after die-off events or in situations where big sagebrush needs to track suitable habitats that are shifting location faster and over larger distances due to climate change than big sagebrush seeds disperse (mostly <30 m; reviewed by Schlaepfer et al. 2014*b*). Additionally, models are less applicable when underlying relationships change that are only represented implicitly through fitting to observed data. For instance, a regression-based model would not represent an intensified cheatgrass-fire cycle under a warming climate.

Overall, it would be helpful if models clearly quantify which conditions they are expected to represent. GISSM currently represents, in explicit form, abiotic processes affecting regeneration in undisturbed big sagebrush vegetation while biotic factors are implicitly represented; however, it may be valuable for model applications that support land management decision making, particularly under nonstationary climate conditions, to integrate and expand GISSM into a general vegetation model that explicitly represent responses to fire, invasive annual grasses, and fire-annual grass interactions as well as relevant general biotic processes affecting big sagebrush regeneration such as competition or facilitation (DiCristina and Germino 2006, Hoelzle et al. 2012, McAdoo et al. 2013, Davidson et al. 2019) such as STEPWAT2 (Palmquist et al. 2018). Further useful model developments could be to explicitly represent variable seed availability which would allow for restoration seeding events at different seeding rates instead of assuming sufficient seeds in every year as well as to differentiate big sagebrush subspecies. Important differences in regeneration have been documented among subspecies of sagebrush, for example, reviewed by Schlaepfer et al. (2014*b*); however, a scarcity of data has prevented the representation of subspecies-level differences in regeneration models (Schlaepfer et al. 2014*a*). Separately, applicability of the Shriver2018 model could be increased by expanding the model to represent areas outside the original study area and under different climate conditions than those captured in the original training data. For instance, cheatgrass and the cheatgrass-fire cycle are currently important in some, but not all areas of big sagebrush occurrence. Applying the current regression-based model in areas without a large cheatgrass and fire influence would likely result in biased outcomes, for instance, habitat in the Wyoming Basin or at high elevation (Davies and Bates 2019, Hak and Comer 2020). Additionally, the next steps in evaluation of GISSM will be to evaluate each of the submodels representing each regeneration process to avoid good fits for wrong reasons (Lorscheid and Meyer 2016); however, this will require large amounts of additional observational and experimental data (Pennekamp et al. 2017, Yates et al. 2018, Bouchet et al. 2019).

Another limitation is that neither model has been assessed for how well it performs under novel geographic and/or climate conditions, that is, transferability (Yates et al. 2018). Due to our lack of new data to assess transferability, we instead estimated the area over which the models were not required to extrapolate from conditions contained in their respective training datasets into novel conditions. Based on univariate and multivariate metrics of extrapolation (Mesgaran et al. 2014), no univariate/multivariate extrapolation across 30/34% of the study area was required by GISSM under 1980–2010 conditions and no extrapolation across 83/95% by Shriver2018 (Appendix S2: Fig. S5-S8; Appendix S1: Table S5). As expected, areas that required extrapolation increased through time periods and from RCP 4.5 to RCP 8.5 and those projections should accordingly be interpreted with care. Nevertheless, Renwick et al. (2018) carried out a multi-model comparison that included GISSM as one of four independent big sagebrush models. Their multi-model comparison suggested that outcomes of the four models including GISSM were largely in agreement and shared similar responses to changes in temperature and precipitation (Renwick et al. 2018); this supports the credibility of the regeneration model used here. Furthermore, the future projections of the regeneration response by GISSM agree well with general insights from species distribution model (SDM) projections of adult big sagebrush (Schlaepfer et al. 2012*c*, Still and Richardson 2015, and summarized by Zimmer et al. 2021). Despite the fact the SDM by Still and Richardson (2015) represents the Wyoming big sagebrush subspecies while the ensemble SDMs by Schlaepfer et al. (2012*c*) represented big sagebrush subspecies combined, they agree with each other and with GISSM in projected decreases in southern areas across Nevada, Utah, and New Mexico as well as low elevation areas along the Snake River and Columbia River. These models also agree well in projected areas of no change or increases including southwestern Wyoming, elevated areas in central and eastern Colorado, central and northern Nevada, and others. However, the Wyoming big sagebrush SDM and the ensemble SDMs disagreed in their projections in eastern and northern Wyoming and eastern Montana where the Wyoming big sagebrush SDM projected widespread decreases while the ensemble SDM projected more frequently no change in the distribution (Schlaepfer et al. 2012*c*, Still and Richardson 2015); GISSM projected mostly small positive to small negative changes in regeneration potential for those areas mostly agreeing with the general SDMs that combined all subspecies as GISSM (Fig. 3). The Shriver2018 model projected decreases throughout in contrast to the SDM projections; however, this should not be interpreted as model disagreement because the Shriver2018 model represents restoration success while the SDM represents climatical suitability of big sagebrush distribution. While the process-based GISSM and regression-based Shriver2018 models can be improved, they both remain valuable tools to increase our understanding of contemporary and future big sagebrush regeneration outcomes. Our results, particularly the contrast of models, have lessons for how to approach developing long-term projections of a complex ecological process such as regeneration.

## Conclusions

Regeneration is one aspect among many that contribute to the continuity of big sagebrush and the vegetation types that are dominated by this species. Successful establishment from seed, the only natural regeneration mode in big sagebrush (Shultz 2006), may become particularly relevant during transient, highly variable, or nonstationary conditions (Jackson et al. 2009).

This study represents the best available estimates of projected future probabilities of regeneration potential under natural conditions and of restoration seeding outcomes following fire for big sagebrush. Our results imply general future trajectories for big sagebrush regeneration and identify the critical factors that shape those trajectories. In particular, divergent projections between the two models suggest that, for much of the region, big sagebrush regeneration will continue to be feasible, despite a warming climate, under natural conditions in unburned, intact plant communities. In the northern Great Basin and Snake River Plains, big sagebrush persistence will be influenced more by fire-invasive annual grass interactions (that itself is affected by climate change) than directly by 21st century climate conditions. Future research to confirm these results will need to include model transferability studies as well as heated common garden experiments with inclusion and exclusion of cheatgrass. Our results corroborate what others have found, that is, that sustaining big sagebrush in heavily invaded areas throughout the 21st century hinges on solving the fire-invasive annual grass problem. However, our results additionally suggest that solutions may be found by promoting conditions similar to those found in undisturbed environments.

For natural resource managers, uncertainty is a major challenge related to climate change, and our study assessed that challenge for big sagebrush regeneration. Our observation of relatively high agreement among GCMs indicates that variation among long-term future climate projections does not translate into high uncertainty about big sagebrush regeneration. However, we did observe substantial geographic variation in long-term regeneration trajectories, and these have potentially important management implications. Specifically, the central and northern areas of the big sagebrush region were projected to climatically sustain frequent regeneration in the long term, whereas marginal and mostly southern areas were projected to experience less frequent regeneration (consistent with other studies, e.g., Renwick et al. 2018).

While the big sagebrush restoration challenge is multidimensional, valuable insights for resource management may be gained by our comparison, particularly for post-fire restoration seeding in the northern Great Basin and Snake River Plain. Our results suggest that restoration practices which create conditions similar to uninvaded, unburned natural big sagebrush vegetation might be successful under 21st century climate conditions. Big sagebrush seeds are commonly available in most years (reviewed by Schlaepfer et al. 2014*b*), whereas in post-fire restoration seeds are predominantly available for one year. If this is relevant, then one question to explore further could be whether post-fire restoration seeding in multiple years in the hotter conditions expected in the future might increase big sagebrush regeneration outcomes (Shriver et al. 2018). Additional processes that are mostly absent in burned stands, including facilitation by adult shrubs, shade effects, and mycorrhizal interactions, may contribute to big sagebrush regeneration in natural vegetation (e.g., Huber-Sannwald and Pyke 2005, Hulvey et al. 2017, Hovland et al. 2019) and might be overcome by directly planting big sagebrush seedlings (Davidson et al. 2019, Davies et al. 2020). Our study suggested general patterns and did not examine exactly which conditions of natural vegetation need to be matched for big sagebrush restoration to be successful under 21st century climate; these remain to be identified by future work.

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## Data Availability

This work builds on output from a simulation experiment described in Bradford et al. (2019 2020) [https://doi.org/10.3389/fevo.2019.00358].

Code of the simulation model is available in C and R (Schlaepfer and Andrews 2019, Schlaepfer and Murphy 2019) [https://doi.org/10.5281/zenodo.3352249].

Datasets utilized for the simulation experiment include gridded soil data NRCS STATSGO by Miller and White (1998) [https://doi.org/10.1175/1087-3562(1998)002<0001:ACUSMS>2.3.CO;2]; gridded meteorological data from Maurer et al. (2002) [https://www.engr.scu.edu/~emaurer/gridded_obs/index_gridded_obs.html]; downscaled CMIP5 climate projections from the "Downscaled CMIP3 and CMIP5 Climate and Hydrology Projections" archive (Maurer et al. 2007) [http://gdo-dcp.ucllnl.org/downscaled_cmip_projections].

Additional datasets utilized for this research are as follows: Gap Analysis Program (U.S. Geological Survey Gap Analysis Program 2016) [https://doi.org/10.5066/f7zs2tm0]; Landfire Biophysical Settings (LANDFIRE 2014) [https://www.landfire.gov/bps.php]; gridded climate data (PRISM Climate Group 2020) [http://prism.oregonstate.edu; query details: 30 Year Normals (1981–2010), 800 m and annual values, Download all Normals Data]; EPA Level III Ecoregions (EPA 2011) [https://www.epa. gov/eco-research/level-iii-and-iv-ecoregions-continental-united-states; query details: GIS data, US Level III Ecoregions shapefile without state boundaries (28 mb), https://gaftp.epa.gov/EPADataCommons/ORD/Ecoregions/us/us_eco_l3.zip].

This work utilizes two sagebrush recruitment models: Shriver et al. (2018) [https://doi.org/10.1111/gcb.14374] and GISSM (Schlaepfer et al. 2014*a*) [https://doi.org/10.1016/j.ecolmodel.2014.04.021 including R code]. The code of GISSM is also available as part of an R package (Schlaepfer 2020) [https://doi.org/10.5281/zenodo.5056859; https://github.com/DrylandEcology/rSW2funs].

Raw data used to generate tables, figures, plots are available from the USGS ScienceBase-Catalog (Schlaepfer and Bradford 2021) [https://doi.org/10.5066/P9MB2QB8].

Code utilized to generate results or analyses is available from github/zenodo (Schlaepfer 2021) [http://doi.org/10.5281/zenodo.4750193].

## Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3695/full