

## Simulated big sagebrush regeneration supports predicted changes at the trailing and leading edges of distribution shifts

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**Abstract.** Many semi-arid plant communities in western North America are dominated by big sagebrush. These ecosystems are being reduced in extent and quality due to economic development, invasive species, and climate change. These pervasive modifications have generated concern about the long-term viability of sagebrush habitat and sagebrush-obligate wildlife species (notably Greater Sage-Grouse), highlighting the need for better understanding of the future big sagebrush distribution, particularly at the species' range margins. The leading and trailing edges of potential climate-driven distribution shifts are likely to be areas most sensitive to climate change. Although several processes contribute to distribution shifts, regeneration is a fundamental requirement, especially for species with episodic regeneration patterns, such as big sagebrush. We used a process-based regeneration model for big sagebrush to simulate potential germination and seedling survival in response to climatic and edaphic conditions. We estimated current and future regeneration under 2070–2099 CMIP5 climate conditions at trailing and leading edges that were previously identified using traditional species distribution models. Our results supported expectations of increased probability of regeneration at the leading edge and decreased probability at the trailing edge compared to current levels. Our simulations indicated that soil water dynamics at the leading edge will become more similar to the typical seasonal ecohydrological conditions observed within the current range of big sagebrush. At the trailing edge, increased winter and spring dryness represented a departure from conditions typically supportive of big sagebrush. Our results highlighted that minimum and maximum daily temperatures as well as soil water recharge and summer dry periods are important constraints for big sagebrush regeneration. We observed reliable changes in areas identified as trailing and leading edges, consistent with previous predictions. However, we also identified potential local refugia within the trailing edge, mostly at higher elevation sites. Decreasing regeneration probability at the trailing edge suggests that it will be difficult to preserve and/or restore big sagebrush in these areas. Conversely, increasing regeneration probability at the leading edge suggests a growing potential for conflicts in management goals between maintaining existing grasslands and croplands by preventing sagebrush expansion versus accepting a shift in plant community composition to sagebrush dominance.

**Key words:** *Artemisia tridentata*; climate change response; germination; Greater Sage-Grouse; reclamation; restoration; seedling survival; species distribution.

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## INTRODUCTION

Big sagebrush (*Artemisia tridentata* Nutt., a long-lived shrub [Shultz 2006]) dominates semi-arid plant communities across western North America (McArthur and Plummer 1978, West 1983). A large part of the economy of this region depends on livestock grazing, crop production, energy extraction, and recreation on lands potentially covered by big sagebrush. Additionally, sagebrush-dominated ecosystems provide important services such as wildlife habitat, nutrient and water cycling, and carbon storage (West and Young 1999). These ecosystems, however, have been reduced in distribution and quality due to economic and agricultural activity, infrastructure expansion, invasive species, and altered fire regimes (Welch 2005, Meinke et al. 2009, Davies et al. 2011, Knick et al. 2011, Manier et al. 2013).

Many sagebrush-dependent species have experienced declines following recent decreases in quality and area of big sagebrush habitat, prompting increased attention to sagebrush ecosystem management practices (Rowland et al. 2006, Hanser et al. 2011). Decisions on a number of sagebrush-relevant management actions are currently expected from land managers and conservationists (Davies et al. 2011, Manier et al. 2013, US Fish and Wildlife Service 2013). These include managing cheatgrass (*Bromus tectorum*) invasions, addressing conifer encroachment, and promoting habitat for at-risk species, such as Greater Sage-Grouse (*Centrocercus urophasianus*, Manier et al. 2013). The most prominent is the pending final listing decision in 2015 by the U.S. Fish and Wildlife Service on the potential inclusion of Greater Sage-Grouse (Aldridge et al. 2008, Manier et al. 2013) on the Endangered Species List (US Fish and Wildlife Service 2013). Previous studies have found strong potential responses of big sagebrush to future climate scenarios (Shafer et al. 2001, Schlaepfer et al. 2012c), potentially compounding the impacts of current threats (Neilson et al. 2005, Bradley 2010). Important conservation planning decisions in sagebrush ecosystems, and the Greater Sage-Grouse listing decision, in particular, require an understanding of climate change impacts and information on the future distribution and habitat suitability of

target species (Glick et al. 2011, Stein et al. 2014).

Species distribution models (SDMs) are widely-used to estimate climate change impacts on the suitability of climate or habitat space for a particular species (e.g., Wiens et al. 2009, Franklin et al. 2013). SDM results are useful because large-scale spatial patterns of species distributions are dominated by climatic factors (Walther et al. 2002) and potentially certain types of biotic interactions (Araújo and Rozenfeld 2014). Traditionally, SDMs rely on climatic variables to derive a species' suitability distribution (Franklin and Miller 2009), although measures that are directly related to the physiological requirements of plants can be better predictors of species distributions (e.g., soil water availability, Rickebusch et al. 2008, Schlaepfer et al. 2012c, Piedallu et al. 2013). Both range expansions as well as contractions have been observed under recent climate change (Thomas et al. 2006, Bell et al. 2014) and most SDMs tend to predict large geographic shifts in suitable areas under future climate scenarios (e.g., Shafer et al. 2001, Walther et al. 2002).

Despite their utility, SDMs have several limitations that decouple results from expected distributions and restrict their ability to appropriately inform management decisions. Some of these limitations include failure to represent key biological processes, notably migration, biotic interactions, and physiological sensitivity of different life-stages and incorporation of systematic biases by selection of spatial data, statistical modeling techniques, and assumption of equilibrium conditions (Guisan and Thuiller 2005, Wiens et al. 2009). For example, some studies have not observed recent large-scale range shifts forecasted by SDMs (Zhu et al. 2012) and highlight the need to scrutinize SDM predictions with independent approaches (Dawson et al. 2011). Thus, a combination of approaches and data are suggested to confirm SDM predictions: if multiple independent lines of study come to the same conclusion about species responses to climate change scenarios, then we can be more confident in the importance of those findings (Dawson et al. 2011).

Of particular importance for understanding climate change impacts are geographic shifts near the margins of a current species' range

(Thuiller et al. 2008). Populations persisting near these range margins are expected to be particularly sensitive to changing conditions (Anderson et al. 2009) and will represent the initial locations of altered species distributions. Leading edges are current unoccupied areas where a species may expand its distribution in the future; while trailing edges are areas of contraction in a species' distribution that are currently occupied but may not be in the future (Hampe and Petit 2005, Anderson et al. 2009). Because of the transient nature of range shifts, leading and trailing edges may be strongly influenced by non-climate controls such as recruitment or mortality due to climate fluctuations and other events, which are not captured by SDMs relying on assumptions of species distributions existing in equilibrium with mean climatic conditions (Jackson et al. 2009).

Successful plant population expansion at a leading edge will necessarily involve successful regeneration. Population contraction at a trailing edge will very likely include regeneration failure in addition to increased mortality. Regenerative stages often have a narrower environmental tolerance than adult stages, particularly of long-lived species (Grubb 1977) such as big sagebrush (Schlaepfer et al. 2014b) as demonstrated by the episodic nature of recruitment in big sagebrush stands (Perryman et al. 2001). Consequently, understanding regeneration is crucial for population dynamics (Harper 1977, Fenner 2002) and responses to climate change (Jackson et al. 2009, Russell et al. 2011, Mok et al. 2012). Checking expectations about regeneration responses will thus also assess the delineation of trailing and leading edges based on SDMs.

Our overall goal was to characterize the effects of climate change on the regeneration success of big sagebrush at the trailing and leading edges that were previously predicted using SDMs (Schlaepfer et al. 2012c). Using an established process-based model that represents sagebrush germination and first-year survival, we quantified the probability of conditions suitable for sagebrush regeneration under current and future climates at the leading and trailing edges. These results allowed us to compare the correspondence between the SDM predictions and those of a process-based regeneration model (Schlaepfer et al. 2014b). This work provides insight into the

impact of climate change on a key life stage for big sagebrush in areas likely to experience changes in sagebrush suitability.

## METHODS

### *Study area and site selection*

We based our study on a framework of big sagebrush SDMs that compared predictions of habitat suitability based on either climatic or ecohydrological explanatory variables for reference (1971–2000) and ensemble future (2070–2099) conditions under SRES A2 for the western United States of America (Schlaepfer et al. 2012c). We sampled 100 random sites from the trailing and leading edge of future big sagebrush habitat suitability (Fig. 1). A site here represents a 10 km × 10 km cell as defined by Schlaepfer et al. (2012c). Our point model simulation defines the entire cell by summarizing conditions for the extent of that cell. We defined the trailing/leading edges as those areas where climatic and ecohydrological SDMs agreed that habitat suitability will change from either suitable to unsuitable or from unsuitable to suitable in the future (cf. Fig. 3 in Schlaepfer et al. 2012c). To simplify presentation of the results, we excluded suitability changes based along elevational gradients even though these are also potentially important changes. The latter criterion further narrowed the geographic extent of our sample population: (1) trailing edge sites were drawn from E of  $-117^\circ$  longitude to exclude the White Mountains and the Sierra Nevada, from S of  $40^\circ$  latitude and from elevations lower than 2137 m to exclude mountain ranges in northern Utah and southern Rocky Mountains; (2) leading edge sites were drawn from E of  $-110^\circ$  longitude to exclude the central Rocky Mountains and from N of  $45^\circ$  latitude to exclude the southern Rocky Mountains (Fig. 1). We acknowledge that our study area definition implies a more homogenous leading edge, whereas sites from the trailing edge are expected to show a larger spread due to a larger geographic extent and a higher topographic richness.

### *Process-based regeneration model*

To assess regeneration probabilities at each of the 200 sites we used a process-based model of sagebrush regeneration, which simulates suitable

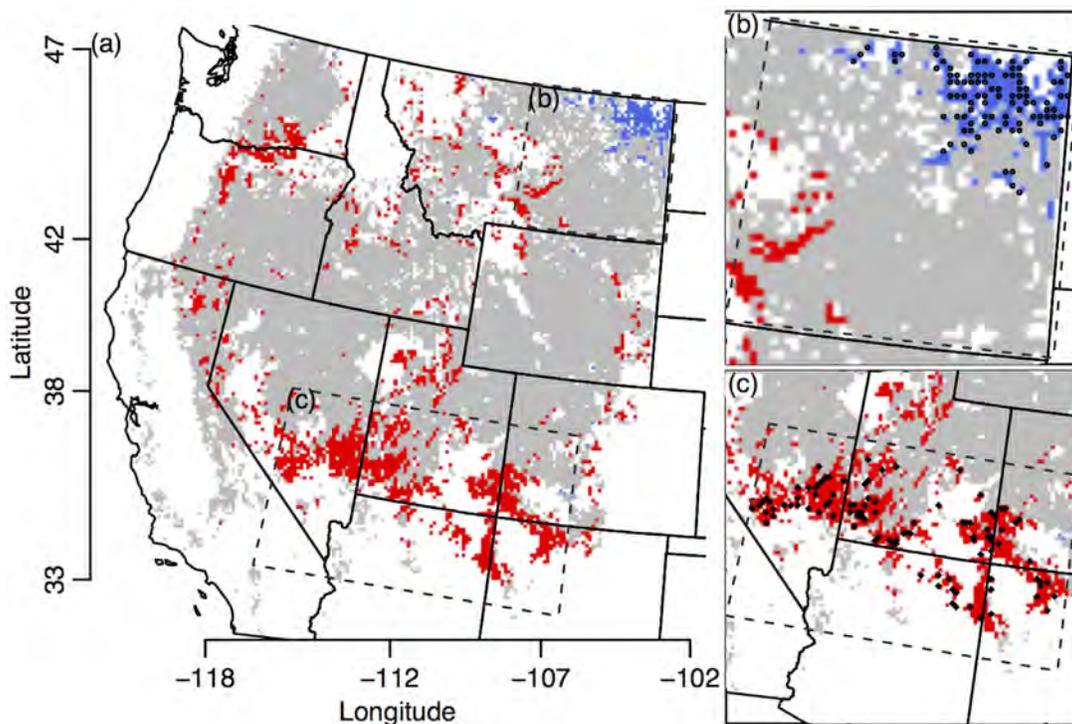


Fig. 1. Geographic map of sample sites at the leading (b, black dots) and trailing edge (c, black dots) based on published SDMs of big sagebrush (gray, current predicted suitability, red, decrease in suitability under SRES A2 for 2070–2099, blue, increase in suitability, Schlaepfer et al. 2012c). The combined area of no change (gray) and trailing edge (red) indicate the extent of suitable habitat for current (1970–1999) conditions. Black lines indicate U.S. state boundaries; dashed boxes indicate study area (a; see *Methods* for details). Map is Albers equal area projection.

conditions for germination and seedling survival in response to soil conditions and weather (Schlaepfer et al. 2014a). The model was trained and tested for big sagebrush with a total of 1435 site-years of observations and explained 74% of variability of numbers of years with successful regeneration and achieved 60% overall accuracy predicting yearly regeneration success/failure (Schlaepfer et al. 2014a). The model uses daily forcing data of air and top-soil temperature, water potential in soil layers, and snow cover to simulate favorable periods for germination, time to germination, and germination success. Based on germination success, the model simulates days with seedling emergence, favorable and lethal periods for seedling growth, root elongation of seedlings, and first-season seedling mortality or survival.

Daily forcing data were provided by SOILWAT, a daily-time step, multiple soil layer,

ecosystem water balance simulation model (Parton 1978, Sala et al. 1992), which has been adapted and tested for sagebrush ecosystems (Schlaepfer et al. 2012a, b, Bradford et al. 2014a, b). The first year of each 32-year simulation period was excluded to limit effects of initial conditions. We used cell-specific daily historical weather data for 1979–2010 (a 1/8-degree gridded product, Maurer et al. 2002), soil information (Miller and White 1998), and estimates of vegetation composition, biomass, rooting distribution, and seasonal phenology (details in Bradford et al. 2014b) to run SOILWAT. Details of data preparation for the 10-km grid are provided in Schlaepfer et al. (2012c). There were no obvious relationships between soil texture (sand and clay content) and climate among the sampled sites (Appendix: Fig. A2).

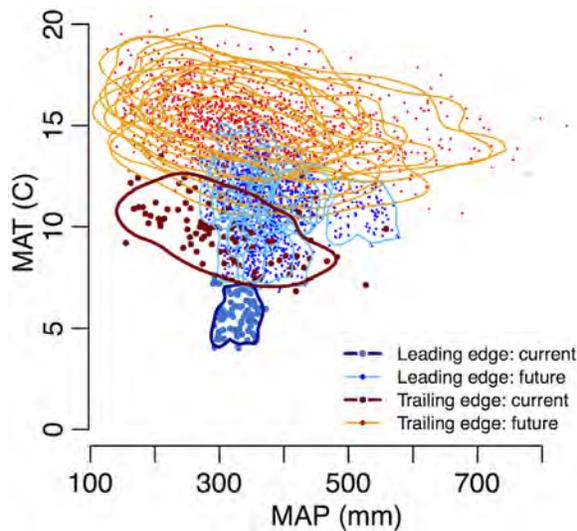


Fig. 2. Climate space of mean annual precipitation (MAP) and mean annual temperature (MAT) of sample sites (dots) and 90% data cloud (lines) at the trailing (red hues) and leading edge (blue hues) under current climate 1980–2010 (fat dots, bold lines) and future climate conditions (small dots, thin lines) of 16 GCMs with RCP8.5 for 2070–2099. See Appendix: Fig. A3 for RCP4.5 data.

### Climate scenarios

We extracted monthly time-series for 2069–2099 of 1/8-degree downscaled and bias-corrected products of the fifth phase of the climate model intercomparison project (CMIP5; Taylor et al. 2012) of 16 global circulation models (GCMs) for two representative concentration pathways (RCPs; Moss et al. 2010), RCP4.5 and RCP8.5, from the “Downscaled CMIP3 and CMIP5 Climate and Hydrology Projections” archive at [http://gdo-dcp.ucllnl.org/downscaled\\_cmip\\_projections/](http://gdo-dcp.ucllnl.org/downscaled_cmip_projections/) (data accessed on February 3, 2014, Maurer et al. 2007). We applied a hybrid-delta downscaling approach to combine historic daily data with monthly future predictions to obtain future daily forcing (Hamlet et al. 2010, Dickerson-Lange and Mitchell 2014). Because we did not include all GCMs that participated in CMIP5, we selected 16 GCMs based on a family tree of GCMs and their evaluation against observed data (Knutti et al. 2013). Specifically, we chose the best performing GCM (based on Fig. 3 in Knutti et al. 2013) from each group from the family tree that we cut into

16 branches (Fig. 1b in Knutti et al. 2013). This approach selected the most independent and best performing subset of GCMs (Appendix: Table A1).

### Analysis of simulation output

Regeneration probabilities were calculated as the fraction of years in each 31-year simulation period with germination and seedling success. Because the regeneration model is deterministic, we performed an evaluation of model results, but no hypothesis testing (Simpson et al. 1997, White et al. 2014). We examined relationships between explanatory variables (Appendix: Table A2), regeneration probabilities, and changes of regeneration probabilities between future and current climate scenarios. We summarized relationships with locally weighted polynomial regression smoothers (R function ‘lowess’) and the (non-linear) Brownian distance correlation (Szekely and Rizzo 2009) using 2000 bootstrap replicates as implemented in the *energy* R package (Rizzo and Szekely 2014) with Bonferroni adjustment.

We selected 21 variables to explain patterns in regeneration responses based on their importance in our previous work on big sagebrush (Appendix: Table A2; Schlaepfer et al. 2012a, b, c, Schlaepfer et al. 2014a, b). To reduce the number of variables for further analysis, we performed a principal component analysis by singular value decomposition (R function ‘prcomp’ with rotation, scaling, and centering) of the 21 variables under current climate conditions for all 200 simulated sites. We first selected those variables that are more proximate to big sagebrush biology than overall climate and soil variables. Then we chose the least correlated variables, i.e., those with the strongest and most unambiguous loadings on the first five principal components (Appendix: Table A2 and Fig. A1). We used R version 3.1.0 (R Development Core Team 2014) for all simulations and analyses.

## RESULTS

### Climate and soil water

Mean annual precipitation (MAP) and mean annual temperature (MAT) climate spaces did not overlap between trailing and leading edges under current climate (Fig. 2). Because of the

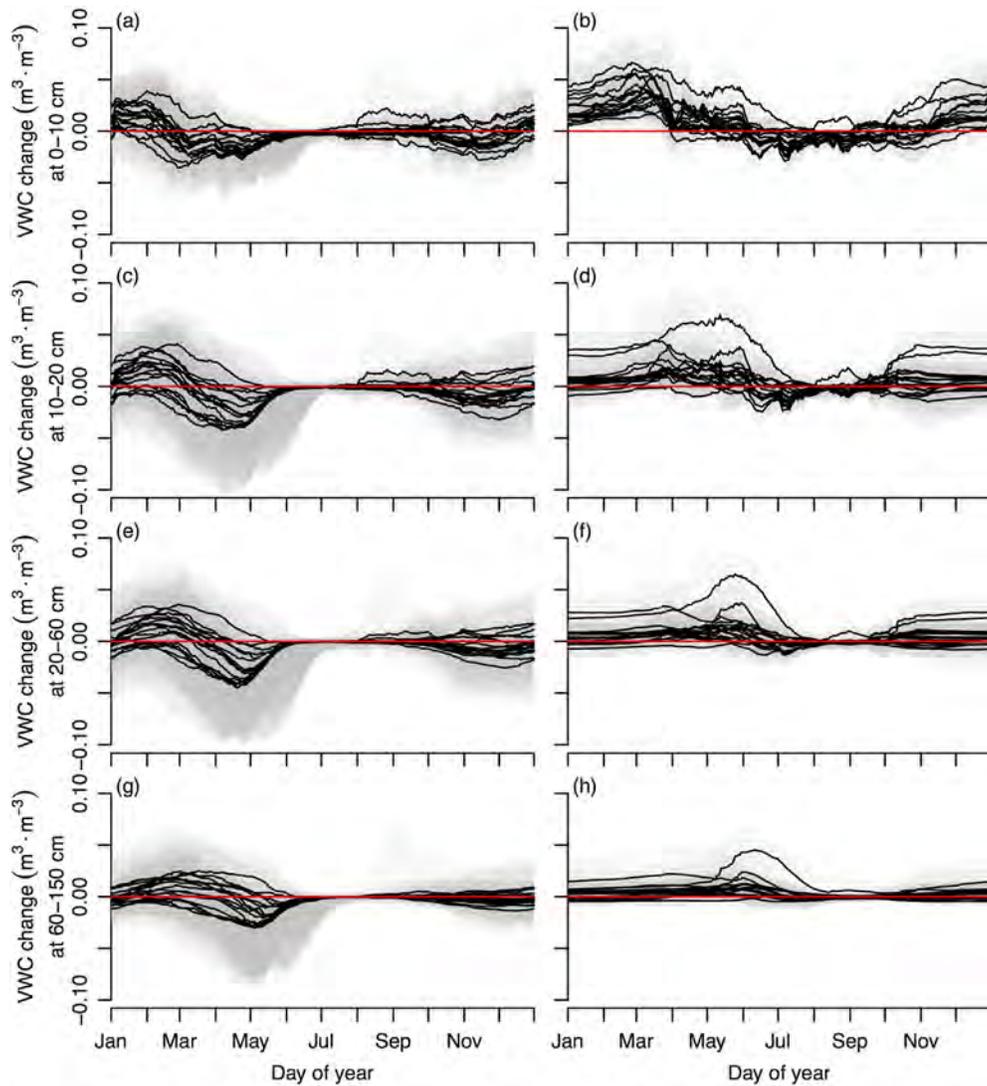


Fig. 3. Changes of mean daily volumetric water content (WVC) in four aggregated soil layers between future climate conditions of 16 GCMs with RCP8.5 for 2070–2099 (black, median among sites; gray, range of all sites) and current 1980–2010 climate (red) for the trailing (a, c, e, g) and leading edge (b, d, f, h). Positive/negative values indicate an increase/decrease in WVC under future scenarios compared to current climate. See Appendix: Fig. A6 for RCP4.5 data.

similar overall pattern and direction of trends among the simulations driven by RCP4.5 and RCP8.5, we focus here on RCP8.5 (all results based on RCP4.5 are available in the appendices). On average, the current climate of the trailing edge was 20 mm/yr drier and 4.2°C warmer than at the leading edge. The spread among sites in MAP at the trailing edge encompassed the range at the leading edge, whereas sites at the trailing edge were consistently warmer than at the

leading edge (Table 1). With future scenario RCP8.5, leading and trailing edges both became 13% wetter while the spread among sites increased by 23% and 16%, respectively. For the leading and trailing edges, MAT increased by 5.4°C and 5.2°C and the spread decreased by 2% and 3%, respectively (Table 1 and Fig. 2). Seasonal patterns in changes at both edges included greater warming trends during winter and late summer than for the rest of the year. At

Table 1. Climatic conditions of sample sites at the trailing and leading edges for current 1980–2010 and future conditions of 16 GCMs with RCP4.5 and RCP8.5 for 2070–2099. Percentiles are means among scenarios for 5% and 95% of values.

Edge	Condition	Mean annual precipitation (mm)					Mean annual temperature (C)				
		Mean	5%	95%	Ratio of means <sup>†</sup>	Ratio of 90% <sup>‡</sup>	Mean	5%	95%	Difference of means <sup>§</sup>	Ratio of 90% <sup>‡</sup>
Trailing edge	Current	309	181	442	1.00	1.00	9.84	7.75	12.15	0.00	1.00
	RCP4.5	340	203	498	1.10	1.13	12.73	10.72	15.04	2.89	0.98
	RCP8.5	348	208	511	1.13	1.16	15.06	13.07	17.35	5.22	0.97
Leading edge	Current	329	295	356	1.00	1.00	5.67	4.40	7.10	0.00	1.00
	RCP4.5	357	322	390	1.09	1.13	8.71	7.47	10.12	3.05	0.98
	RCP8.5	372	333	407	1.13	1.23	11.10	9.86	12.50	5.44	0.98

<sup>†</sup> Ratio of means = mean(future)/mean(current).

<sup>‡</sup> Ratio of 90% = spread among sites = [95% – 5% of future]/[95% – 5% of current].

<sup>§</sup> Difference of means = mean(future) – mean(current).

the trailing edge, increased precipitation was predicted by most GCMs during winter and late summer and a drying during spring/early summer. At the leading edge, increased precipitation was predicted during late winter/early spring and a drying during summer (Appendix: Fig. A4).

Seasonal dynamics of soil water in current habitats of big sagebrush at the trailing edge are characterized by winter to late spring recharge of the soil profile followed by a dry summer period (Appendix: Fig. A5; Schlaepfer et al. 2012b). At the leading edge, winters are dry and recharge is incomplete for deep soils under current conditions (Appendix: Fig. A5). Future climate conditions of most GCMs at the trailing edge increased volumetric water content (VWC) during winter and decreased during early to late spring with some delay at deeper soils; VWC was unchanged during summer periods (Fig. 3). Soil water dynamics kept the typical seasonal pattern albeit with an earlier onset of the dry warm period. At the leading edge, VWC increased in soils between 0–60 cm depth for most GCMs during fall to late spring while VWC of surface soils increased during winter/spring and decreased during summer (Fig. 3). At greater depths, the leading edge experienced only modest change with the exception of increased VWC during late spring to early summer.

#### Regeneration potential of big sagebrush

Under current conditions, germination probability at both the leading and trailing edges was high, with a median and adjusted median absolute deviation (MAD) of  $1.00 \pm 0.00$  among

sites (Fig. 4). By contrast, the probability of seedling success was  $0.39 \pm 0.19$  at the trailing edge and  $0.26 \pm 0.10$  at the leading edge. Future climatic conditions at the trailing edge decreased median probabilities of germination by  $-0.13 \pm 0.08$  among GCMs (all but two GCMs agreed on the direction) and seedling success by  $-0.10 \pm 0.10$  (all but four GCMs agreed). Future climatic conditions at the leading edge did not impact germination probability ( $0.00 \pm 0.00$ ) but increased median probabilities of seedling success by  $0.10 \pm 0.10$  (all but one GCM agreed; Fig. 4).

We found strong relationships between explanatory variables and germination or seedling success at both the leading and trailing edges (Fig. 5). Snowfree days with minimum temperatures of less than  $-9^{\circ}\text{C}$ , while generally not related to germination, correlated negatively with probabilities of seedling success at both edges (Fig. 5c). For future scenarios, sites with a high number of such cold days also showed an increase in seedling success, whereas sites with a smaller number showed a decrease (Fig. 5d). Hot days with maximum temperatures of  $>34^{\circ}\text{C}$  were negatively related to germination probabilities at the trailing edge (Fig. 5e). This variable was also negatively related to seedling success at the trailing edge, but positively at the leading edge albeit with overall fewer hot days (Fig. 5g). For future scenarios, sites with a high number of hot days also displayed a decrease in seedling success, whereas sites with a smaller number displayed an increase (Fig. 5h). Relative maximum soil water recharge showed a strong positive relationship with all responses both

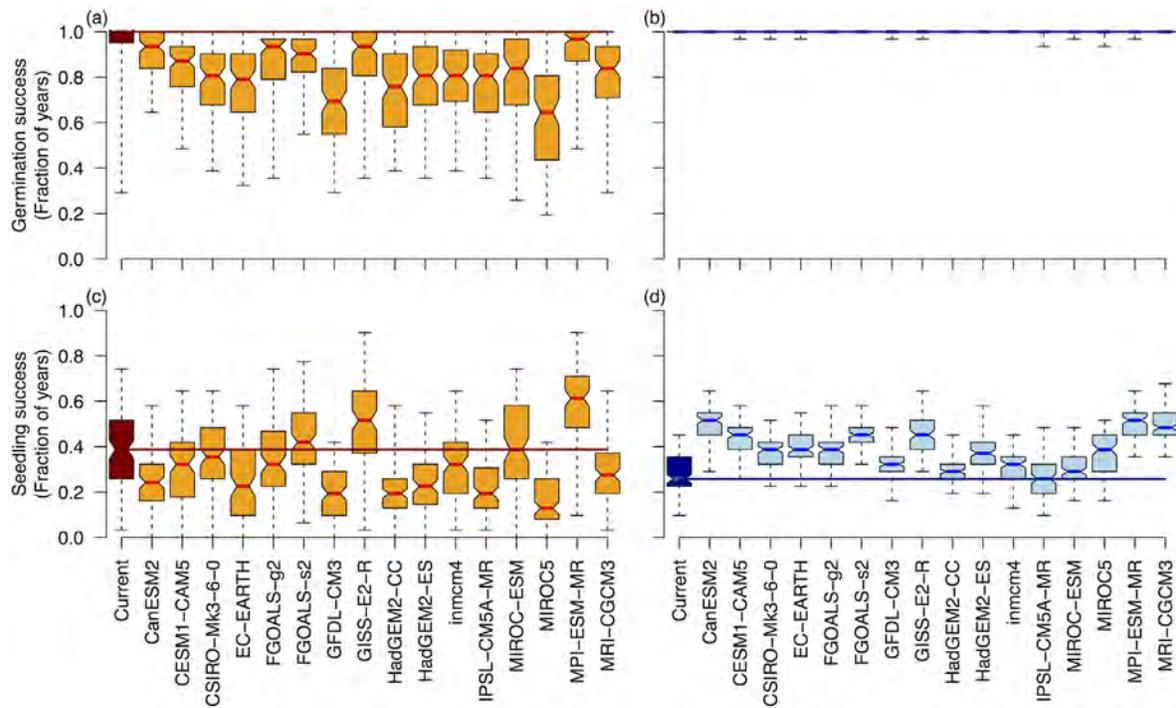


Fig. 4. Potential regeneration probabilities (median, interquartile range, whiskers include all data) of germination and seedling success under current 1980–2010 climate and future climate conditions of 16 GCMs with RCP8.5 for 2070–2099 for the trailing (a, c; red hues) and leading edge (b, d; blue hues). Horizontal lines indicate the median of current conditions. See Appendix: Fig. A7 for RCP4.5 data.

under current and future scenarios at the trailing edge, but few at the leading edge (Fig. 5i–l). The timing of maximum recharge mostly related to increased probabilities at the trailing edge; relationships at the leading edge were less clear (Fig. 5m–p). Duration of the longest drought period during the growing season negatively correlated to germination probabilities for durations of >100–150 d depending on soil depth (Fig. 5q, r, u, v). However, seedling success was primarily negatively related with drought duration with a clear decrease after 50–75 d (Fig. 5s, w). Future conditions increased seedling success at the trailing edge for sites with the shortest drought periods at 0–20 cm soil depth, but not for sites with longer drought periods (Fig. 5t). At the leading edge, future climates influenced seedling success via drought periods primarily at greater depths (20–150 cm) with increases for sites with drought periods of <100 d (Fig. 5x).

## DISCUSSION

### *Regeneration at trailing and leading edges*

Big sagebrush is a long-lived species (Ferguson 1964) that, under recent climate conditions, has persisted regionally with episodic recruitment (reviewed in Schlaepfer et al. 2014b). For instance, recruitment probability in Wyoming, an area with abundant big sagebrush, has been reported to be between  $0.4\text{--}0.6\text{ yr}^{-1}$  (Perryman et al. 2001). Our results of seedling success under current conditions at the trailing edge were comparable ( $\sim 0.4\text{ yr}^{-1}$ ), whereas they were one-third lower at the leading edge, where currently no big sagebrush occurs. Our simulations under future conditions reversed this pattern: in the future at the leading edge, probability of seedling success was close to the values found in Wyoming, whereas at the trailing edge, they decreased to a level similar to what we found under current conditions at the leading edge. These values suggest that regeneration of big

sagebrush will be able to expand populations at the leading edge in the future; conversely, probability of regeneration will decrease at the trailing edge below what is currently observed, presumably limiting the ability of sagebrush to recover from disturbances. Our results suggest that regeneration may play an important role in defining the trailing and leading edge for big sagebrush.

We found strong relationships between regeneration success and temperature and availability of soil water. We described relationships in our results using a set of variables based on previous research that attempted to describe physiological constraints on big sagebrush regeneration such as temperature or drought periods leading to direct mortality of embryos or seedlings (Appendix: Table A1). Therefore, we argue that the patterns in our results support (multi-) causal relationships. For instance, we found support that minimum and maximum daily temperatures as well as soil water recharge and summer dry periods are important constraints for big sagebrush regeneration. Seasonal dynamics of soil water in habitats that support big sagebrush are characterized by winter to late spring recharge of the soil profile followed by a dry summer period (Schlaepfer et al. 2012b). Soil water dynamics at the leading edge in our future simulations became more similar to typical current seasonal patterns for big sagebrush ecosystems; at the trailing edge, the increased winter/spring dryness represented a departure from conditions typically supportive of big sagebrush (Appendix: Fig. A5). These changes in seasonal soil water dynamics correspond with expectations of increased and/or decreased suitability of big sagebrush habitat as well as regeneration patterns.

Even though we selected variables describing physiological constraints of big sagebrush, our results represented aggregation across years, which demonstrated only a portion of the reasons for annual success/failure because annual probabilities are the product of day-to-day survival/mortality dynamics by the model. For instance, the number of very hot days at the trailing edge was negatively related to regeneration probability (as expected), but positively at the leading edge, possibly, because hot days are related to greater growing season length. Never-

theless, our results also correlate strongly with surrogate climate and topographic variables (Appendix: Fig. A8; Franklin and Miller 2009). For instance, more available water increased regeneration success, be it measured as recharge, MAP, or aridity. Such climate and topographic variables can provide a summary of our insights into the expected regeneration patterns within the leading or trailing edges. For instance, elevation, which is related negatively to temperature and positively to precipitation, provides an integrative example (Appendix: Fig. A8c, d): elevation correlates positively with regeneration at the trailing edge (where cooler, wetter high-elevation sites may become refugia), while elevation correlates negatively with regeneration at the leading edge (where the growing season is reduced by snow and colder/wetter temperatures at high elevation sites; Appendix: Fig. A8aa; Schlaepfer et al. 2012a).

#### *Regeneration modeling supports changes in habitat suitability from SDMs*

Our results confirm previous SDM predictions by showing consistent changes in areas identified as trailing and leading edges by previous SDMs. Several recent studies have reported differences in climate responses among life stages supporting the expected higher sensitivity of regeneration vs. adults to climate change (Jackson et al. 2009, Russell et al. 2011). For instance, seedlings of tree species in forests of the western United States demonstrated mostly more severe range contractions than adults under recent climate change (Bell et al. 2014). In southern Spain, seedlings of cork oaks may profit from warmer and wetter winters whereas adults may only do so in sandy soils (Ibáñez et al. 2014). Low forests on subantarctic Campbell Island (New Zealand) experienced decreased adult growth under warm and wet winters in the last 50 years, whereas regeneration is increased in warm and dry winters (Harsch et al. 2014). Similarly, regeneration processes of five eucalypt species in southeastern Australia were linked to SDMs and this combined simulation resulted in divergent responses among species and wet vs. dry ecosystems (Mok et al. 2012). These studies suggest that sensitivity of juvenile life stages to climate change are not easily generalized across species and ecosystems; they can, however, be markedly

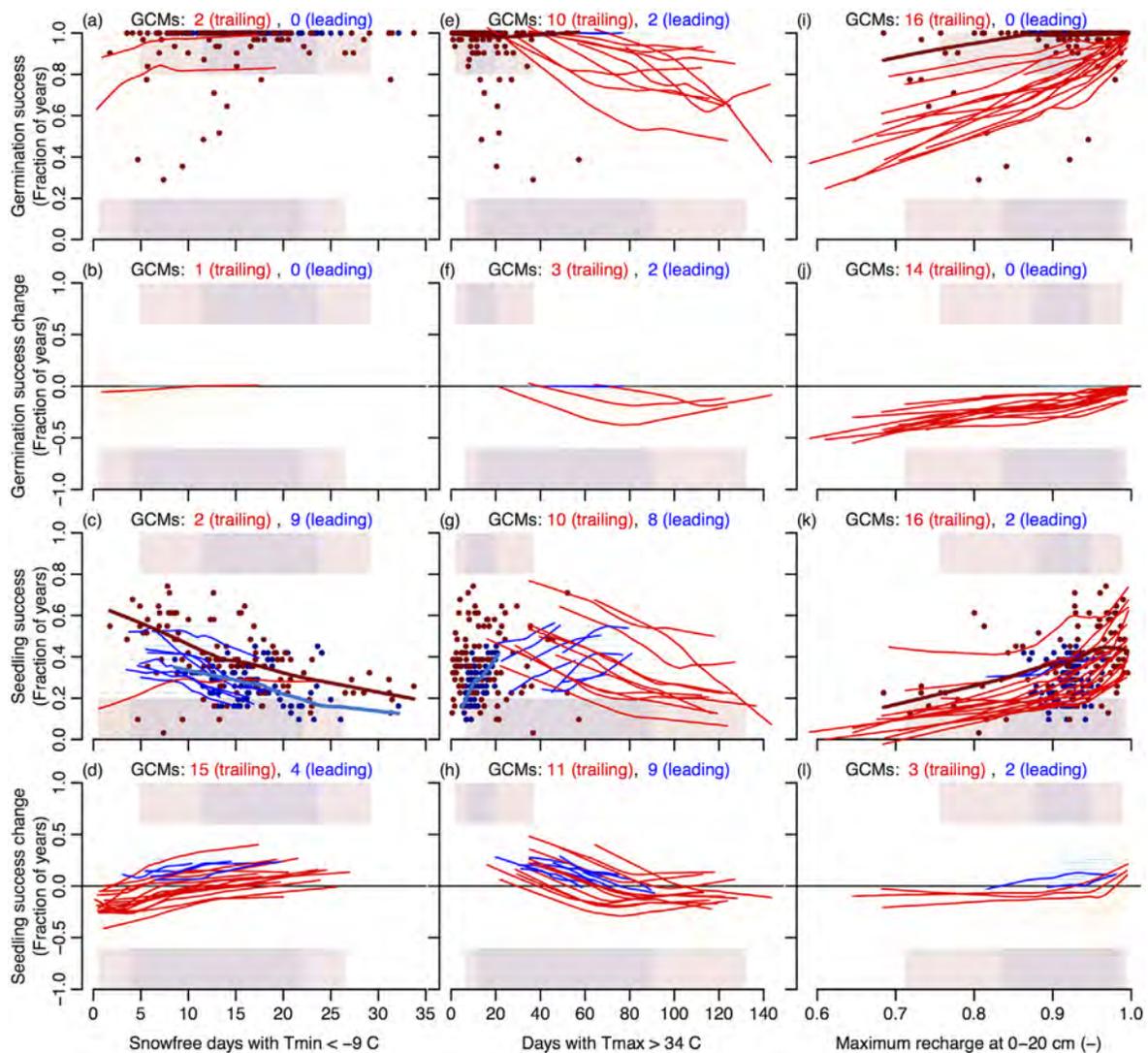


Fig. 5. Relationships between potential regeneration probabilities of germination and seedling success and change and selected explanatory variables (Appendix: Fig. A1 and Table A2) under current 1980–2010 climate (bold lines/dots) and future climate conditions of 16 GCMs with RCP8.5 for 2070–2099 (simple lines/small dots) for the trailing (red) and leading edge (blue). Locally-weighted polynomial regression (lowess) lines indicate that the Brownian distance correlation was significant after Bonferroni adjustment (counts displayed in panel header). Bars at top of each panel indicate range of current conditions; bars at bottom indicate range of minimum/maximum among 5–95% of each GCM. See Appendix: Fig. A9 for RCP4.5 data.

different from adult life stages. While SDMs relate climate variables to a prediction of adult presence/absence of a species, our regeneration model relates weather and soil variables to a particular life history stage of recognized importance for big sagebrush. Therefore, our study contributes to the notion that the predicted shifts

in habitat suitability of big sagebrush may indeed indicate geographic range shifts.

Studying the causes of range limits allows us to better understand a variety of important ecological topics including ecological niches, evolutionary processes, (meta-) population dynamics, biodiversity patterns, and conservation

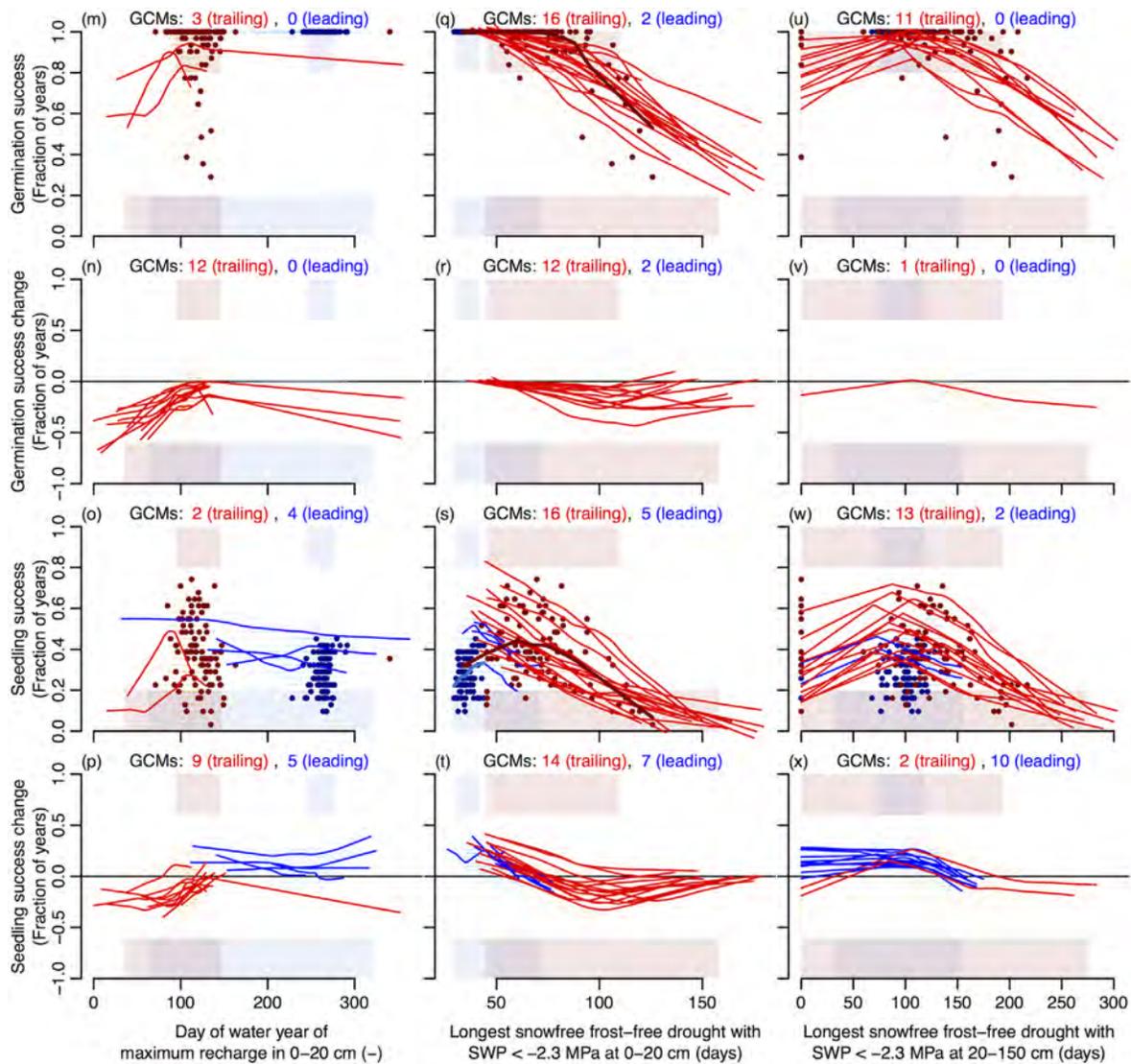


Fig. 5. Continued.

and management issues (e.g., Anderson et al. 2009, Angert 2009). Cahill et al. (2014) reviewed the causes of range limits at low elevations and latitudes and found much stronger support for abiotic factors such as temperature and moisture than for biotic factors such as competition. While our study did not compare the relative importance of biotic vs. abiotic factors, our simulation confirmed that temperature extremes and a lack of soil moisture are strongly related to regeneration at the trailing edge. Similarly, D'Odorico et al. (2012) synthesized that shrubland replacing grassland (e.g., what we simulated as the leading

edge; often also called 'shrub encroachment') is driven by conditions favoring shrub dominance such as overgrazing and climate changes (e.g., reduced limitation of shrubs by increasing lower temperatures). Once those changes in plant functional types have occurred, they can be sustained by the absence of positive fire-grass and negative erosion-grass feedbacks and by the presence of positive microclimate-shrub and small-mammal-shrub feedbacks (D'Odorico et al. 2012). Because the trailing and leading edges are likely limited primarily by abiotic factors that are directly and immediately impacted by chang-

es in climate, regeneration and big sagebrush distribution at the trailing edge may be especially sensitive to climate change.

#### *Limitation on interference*

Our study focused on a comparison between responses of simulations of physiological processes constraining germination and seedling survival to climate change with responses of correlative models of habitat suitability. However, our models have important limitations and regeneration is only one process, albeit a necessary one, contributing to species distributions, which are emerging patterns from the entire suite of population dynamic, ecological, and evolutionary processes in combination with land use and management actions (Wiens et al. 1985, Caughley et al. 1988, Holt 2003, Angert 2009, Sexton et al. 2009). Because big sagebrush is a long-lived species with episodic recruitment, field-based experiments and observations may not address our objectives, which simulation models can attempt to answer.

Our study examined the impacts of climate change on regeneration as a fundamental process contributing to distributional shifts. In the future, not only climate will be different, but CO<sub>2</sub> concentration is increasing, disturbance regimes are altered, management actions and land use will be adjusted, and other species will respond to global change as well leading to altered competitive interactions in addition to interactions among such factors (Shugart and Woodward 2011, Moran and Alexander 2014, Piontek et al. 2014). Global change acts both on adult as well as on regenerative stages. However, a plant population may only expand in distribution and can only survive over the long term if regeneration success is large enough.

Our study did not account for effects of disturbances and adult mortality. Big sagebrush mortality has been observed following insect outbreaks (Haws et al. 1990), fungal pathogens (Nelson and Krebill 1981), freezing damage associated with the absence of snow cover (Hanson et al. 1982), and other causes (Cárdenas et al. 1997). Such causes of mortality will likely become more important with climate change (Wheeler et al. 2014) and mortality due to fire in the sagebrush region will increase as well (Westerling et al. 2006, Westerling et al. 2011). Our

study also did not account for seed production. Generally, seed production rates are high in big sagebrush, but they can vary drastically from year to year and with climate (reviewed in Schlaepfer et al. 2014b). Observed migration distances of big sagebrush are short because seed dispersal is limited from a few meters up to about 30 m (reviewed in Schlaepfer et al. 2014b). Slow recovery rates in large burn areas or restoration efforts have been attributed to slow migration rates in combination with episodic recruitment (e.g., Ziegenhagen and Miller 2009, Nelson et al. 2014). Slow migration will inhibit a fast tracking of changing climate by big sagebrush, particularly over the very large spatial scales over which habitat suitability is predicted to change (Shafer et al. 2001, Schlaepfer et al. 2012c). Our study also did not incorporate effects of biotic interactions such as competition. Big sagebrush can be outcompeted by the exotic annual grass cheatgrass partially because cheatgrass increases fire frequency (Knapp 1996, Bradford and Lauenroth 2006, Balch et al. 2013). Pinyon-juniper woodland may also encroach on sagebrush dominated areas in the future, particularly at lower elevations (Bradley 2010). Furthermore, this study focused on latitudinal and not elevational distribution shifts, this is why we sampled sites from a 10-km grid; consequently, this study cannot draw conclusions about short-distance and upslope movement of vegetation. These and others factors may help to explain why our regeneration model was not able to explain 26% of variation among year-to-year regeneration success during model testing (Schlaepfer et al. 2014a). This error could also have propagated to the results of this study; however, the results and conclusions should be robust against such variation. Consequently, by not including biotic interactions and other factors discussed above in our study, it is possible that we overestimated the future distribution of big sagebrush. This will need to be addressed by future research.

#### *Management-relevant conclusions for big sagebrush-dominated ecosystems*

Our simulation results support previous SDM predictions about the distribution of future big sagebrush habitat suitability; furthermore, they provide insights into the contribution of regen-

eration to range shifts. Current literature related to the management of big sagebrush ecosystems generally does not incorporate climate change. This is at least partially due to the previous degree of uncertainty and the long-term nature of climate change impact studies (Manier et al. 2013). While many management recommendations concern vegetation treatments and are designed for short-term success (Meinke et al. 2009, Davies et al. 2011, Madsen et al. 2013), many management strategies require long-term investments, which can have enormous financial consequences. Such strategies include controlling landscapes against anthropogenic development (Davies et al. 2011) and identifying management zones for Greater Sage-Grouse conservation (US Fish and Wildlife Service 2013). In the past, priority areas for big sagebrush restoration have been identified based on criteria including favorable conditions for revegetation, wildlife habitat connectivity, important Greater Sage-Grouse areas, and cheatgrass invasions (Meinke et al. 2009). For instance, Meinke et al. (2009) identified much of Wyoming big sagebrush in Nevada and Utah as high priority areas for restoration. Our results indicate, however, that much of that area, which lies in what we identified as the trailing edge, may be unsuitable for longer-term goals of maintaining it as sagebrush habitat. This finding is supported by the establishment failure after seeding in drier and low-elevation burns in the Great Basin (Knutson et al. 2014). Therefore, long-term management actions need to include a climate change vulnerability assessment (Glick et al. 2011, Stein et al. 2014). Otherwise, potentially large, investments may be made in areas where big sagebrush will no longer be present in the future.

At the trailing edge, our results suggest a decrease in habitat suitability and a decrease in regeneration probability under most future scenarios. A management plan that relies upon long-term maintenance of big sagebrush dominated ecosystems in the trailing edge is more likely to fail than a plan built upon maintenance of sites with stable climatic suitability. However, we also identified several variables that can account for variation in current and future regeneration within the trailing edge. These variables (for which elevation provides a reason-

able surrogate) may be useful for identifying small local areas that will remain suitable for big sagebrush. These potential refugia are areas with high soil water recharge, short drought periods during the growing season, and few hot days (Fig. 5), i.e., mostly sites at higher elevations. This finding is supported by higher chances of successful seeding at higher elevations, whereas low elevations experience establishment failure, after fire in the Great Basin (Knutson et al. 2014). However, a scenario where low-elevations are invaded by exotic grasses that promote fire spread also into higher elevations could hamper big sagebrush at these potential refugia. Such areas may benefit from management actions that promote seedling survival, including prevention of fires, conifer encroachment, and exotic annual grass invasion. Maintaining sagebrush-dominated ecosystems within the trailing edge may also benefit from targeting restoration at areas that are expected to be climatically suitable, although restoration of areas invaded by exotic annual grasses remains a challenge even under current climatic conditions (Davies et al. 2011). An alternative may be management to encourage native non-fire promoting shrubs and perennial grasses that will experience a distributional shift and will find their leading edges where big sagebrush's trailing edge is.

At the leading edge, our results suggest an increase in habitat suitability and an increase in regeneration probability under most future scenarios. Action plans at the leading edge may need to resolve potential conflicts between management goals to maintain existing grasslands and croplands and prevent sagebrush expansion and those to accept and promote new areas with big sagebrush dominated plant communities (cf. D'Odorico et al. 2012). Removal of big sagebrush has been practiced extensively and much practical knowledge has been accumulated (e.g., Torell et al. 2005, Bastian et al. 2012, D'Odorico et al. 2012). Promoting regeneration and restoring big sagebrush is currently difficult (Lambert 2005, Shaw et al. 2005, Davies et al. 2013, McAdoo et al. 2013, Knutson et al. 2014). Future climate conditions may not only promote big sagebrush in areas at the leading edge, but also potential competitive species (e.g., conifers) and agricultural practices. Conifer encroachment in these new sagebrush areas

may become a concern, but studies indicate that sagebrush can be managed at moister sites with prescribed burning and seeding (Davies et al. 2011, Davies et al. 2014, Nelson et al. 2014). Even though accepting sagebrush advancement in the future may not seem to require management actions in our present time, delineating land at the leading edge as future big sagebrush habitat to support sagebrush-dependent species may eventually warrant more detailed consideration.

## CONCLUSIONS

Our study successfully applied a process-based regeneration model to evaluate future scenarios of big sagebrush germination and seedling survival. We used a set of 16 global circulation models with two representative concentration pathways to simulate changes in regeneration probabilities at the end of this century. Results among individual global circulation models agreed, but with some important variation depending on the region. Our results generally confirmed expectations that regeneration at the trailing edge would decrease and increase at the leading edge. Furthermore, our results supported earlier predictions of changes in habitat suitability based on correlative species distribution models. Shifts in the distribution of big sagebrush likely will involve changes in plant functional dominance between shrubs and grasses, which can have important ecohydrological consequences, mostly in dry areas and where disturbances reduce biomass (Bradford et al., 2014b). Our study yielded important implications for long-term management of big sagebrush habitats, including identification of processes contributing to leading and trailing edges and recognition of potential refugia within the overall trailing edge.

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## SUPPLEMENTAL MATERIAL

## APPENDIX

Table A1. CMIP5 GCM available from the “Downscaled CMIP3 and CMIP5 Climate and Hydrology Projections” archive at [http://gdo-dcp.ucllnl.org/downscaled\\_cmip\\_projections/](http://gdo-dcp.ucllnl.org/downscaled_cmip_projections/), their node number in Knutti et al.’s family tree (Fig. 1B, Knutti et al. 2013) after cutting at level 16, and performance against temperature and precipitation observations, i.e., normalized distance from observations (smaller is better) (Fig. 3, Knutti et al. 2013). We selected the best performing GCM from each node with available information.

CMIP5 GCM	Selection in our study	Node in family tree	Performance
ACCESS1.0		1	0.76
ACCESS1.3		1	0.91
BCC-CSM1.1		2	1.11
BCC-CSM1.1(m)		NA	NA
BNU-ESM		NA	NA
CanESM2	10	10	0.91
CCSM4		11	0.67
CESM1(BGC)		11	0.66
CESM1(CAM5)	11	11	0.60
CMCC-CM		4	0.72
CNRM-CM5		2	0.73
CSIRO-Mk3.6.0	14	14	1.19
EC-EARTH	2	2	0.70
FGOALS-g2	15	15	0.97
FGOALS-s2	12	12	0.96
FIO-ESM		11	0.98
GFDL-CM3	5	5	0.76
GFDL-ESM2G		5	NA
GFDL-ESM2M		NA	0.92
GISS-E2-H-CC		NA	NA
GISS-E2-R	7	7	0.92
GISS-E2-R-CC		NA	NA
HadCM3		NA	NA
HadGEM2-AO		NA	NA
HadGEM2-CC	1	1	0.74
HadGEM2-ES	9	9	0.71
INM-CM4	8	8	1.32
IPSL-CM5A-LR		13	1.01
IPSL-CM5A-MR	13	13	0.96
IPSL-CM5B-LR		NA	1.28
MIROC-ESM	16	16	1.26
MIROC-ESM-CHEM		16	1.27
MIROC4h		NA	0.87
MIROC5	3	3	0.78
MPI-ESM-LR		4	0.71
MPI-ESM-MR	4	4	0.67
MRI-CGCM3	6	6	0.99
NorESM1-M		3	0.87
NorESM1-ME		NA	0.88

Table A2. Potential explanatory variables, justification for inclusion, selection, and principal components loadings. Selection based on strongest and most unambiguous loadings.

No.	Variable	Justification	Selection	Loadings				
				PC1	PC2	PC3	PC4	PC5
1	Sand 0–20 cm (–)	(Schlaepfer et al. 2012b): Overall soil	Fig. A8: PC1, 4	–0.56	–0.05	0.35	–0.56	0.37
2	Clay 0–20 cm (–)	(Schlaepfer et al. 2012b): Overall soil	Fig. A8: PC4	0.42	0.06	–0.32	0.70	–0.39
3	MAT (C)	(Schlaepfer et al. 2012b): Overall climate	Fig. A8: PC1	–0.91	–0.33	0.03	0.00	–0.20
4	MAP (mm)	(Schlaepfer et al. 2012b): Overall climate	Fig. A8: PC2	0.05	0.95	–0.03	–0.07	–0.03
5	PET (mm)	(Schlaepfer et al. 2012b): Overall climate		–0.90	–0.37	0.04	0.14	–0.08
6	Seasonality = cor(monthlyT, monthly PPT)	(Schlaepfer et al. 2012b): Overall climate		0.95	0.10	–0.07	–0.20	–0.03
7	Aridity index = MAP/PET	(Schlaepfer et al. 2012b): Overall climate	Fig. A8: PC2, 1	0.51	0.83	–0.03	–0.13	0.00
8	Snowfall/PPT (–)	(Schlaepfer et al. 2012a): Overall climate	Fig. A8, PC4, 1–5	–0.37	0.46	0.20	0.54	0.40
9	Mean January Temperature (C)	(Schlaepfer et al. 2014a): maternal effects influences seed dispersal timing and germination rates		–0.95	–0.20	0.04	0.15	–0.04
10	Snowfree days with Tmin < –9 C	(Schlaepfer et al. 2014a): survival temperature may limit distribution at higher elevations and latitudes	Fig. 5: PC5	0.32	–0.36	–0.11	0.14	0.46
11	Days with Tmax > 34 C	(Schlaepfer et al. 2014a): maximum survival temperature may limit at southern latitudes	Fig. 5: PC2, 4, 5	–0.25	–0.58	–0.05	–0.49	–0.48
12	Maximum recharge at 0–20 cm (–)	(Schlaepfer et al. 2012c): Winter recharge is important	Fig. 5: PC2	–0.14	0.86	0.19	0.08	–0.25
13	Day of water year of maximum recharge in 0–20 cm (–)	(Schlaepfer et al. 2012c): Timing of recharge is important	Fig. 5: PC1	0.91	0.19	–0.07	–0.19	–0.06
14	Longest snowfree frost-free drought with SWP < –2.3 MPa at 0–20 cm (days)	(Schlaepfer et al. 2014a): growing season dry periods (defined here below chronic minimum SWP)	Fig. 5: PC1, 2	–0.76	–0.56	0.18	0.20	–0.03
15	Longest snowfree frost-free drought with SWP < –2.3 MPa at 20–150 cm (days)	(Schlaepfer et al. 2014a): growing season dry periods (defined here below chronic minimum SWP)	Fig. 5: PC3	–0.13	–0.46	–0.77	0.04	0.15
16	Soil water with SWP > 2.3 MPa during snowfree frost-free periods at 0–20 cm (mm)	(Schlaepfer et al. 2014a): growing season dry periods (defined here below chronic minimum SWP)		–0.58	0.66	–0.06	–0.09	–0.14
17	Soil water with SWP > 2.3 MPa during snowfree frost-free periods at 20–150 cm (mm)	(Schlaepfer et al. 2012c): Available soil water during growing season		–0.56	0.41	–0.45	–0.16	0.11
18	Median suitable period with SWP > 2.3 MPa during snowfree frost-free periods at 0–20 cm (days)	(Schlaepfer et al. 2012c): Available soil water during growing season		–0.81	0.44	–0.14	–0.19	–0.08
19	Median suitable period with SWP > 2.3 MPa during snowfree frost-free periods at 20–150 cm (days)	(Schlaepfer et al. 2012c): Duration of suitable growing conditions		–0.60	0.31	–0.65	–0.15	0.12
20	Longest saturated period with SWP > 0.1 MPa at 0–20 cm (days)	(Schlaepfer et al. 2014a): big sagebrush is sensitive to saturated conditions		–0.74	0.54	0.23	0.15	–0.06
21	Longest saturated period with SWP > 0.1 MPa at 20–150 cm (days)	(Schlaepfer et al. 2014a): big sagebrush is sensitive to saturated conditions		–0.65	0.43	–0.17	–0.04	0.06

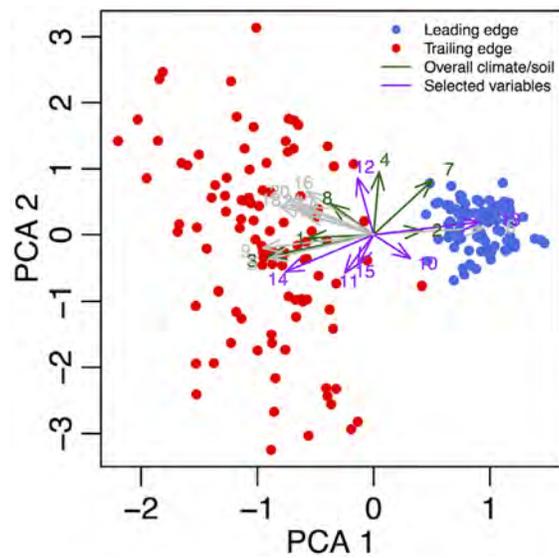


Fig. A1. Correlation biplot of principal component analysis of explanatory variables for trailing and leading edge sample sites under current climate conditions 1980–2010. Variable selection and numbers based on Table A2.

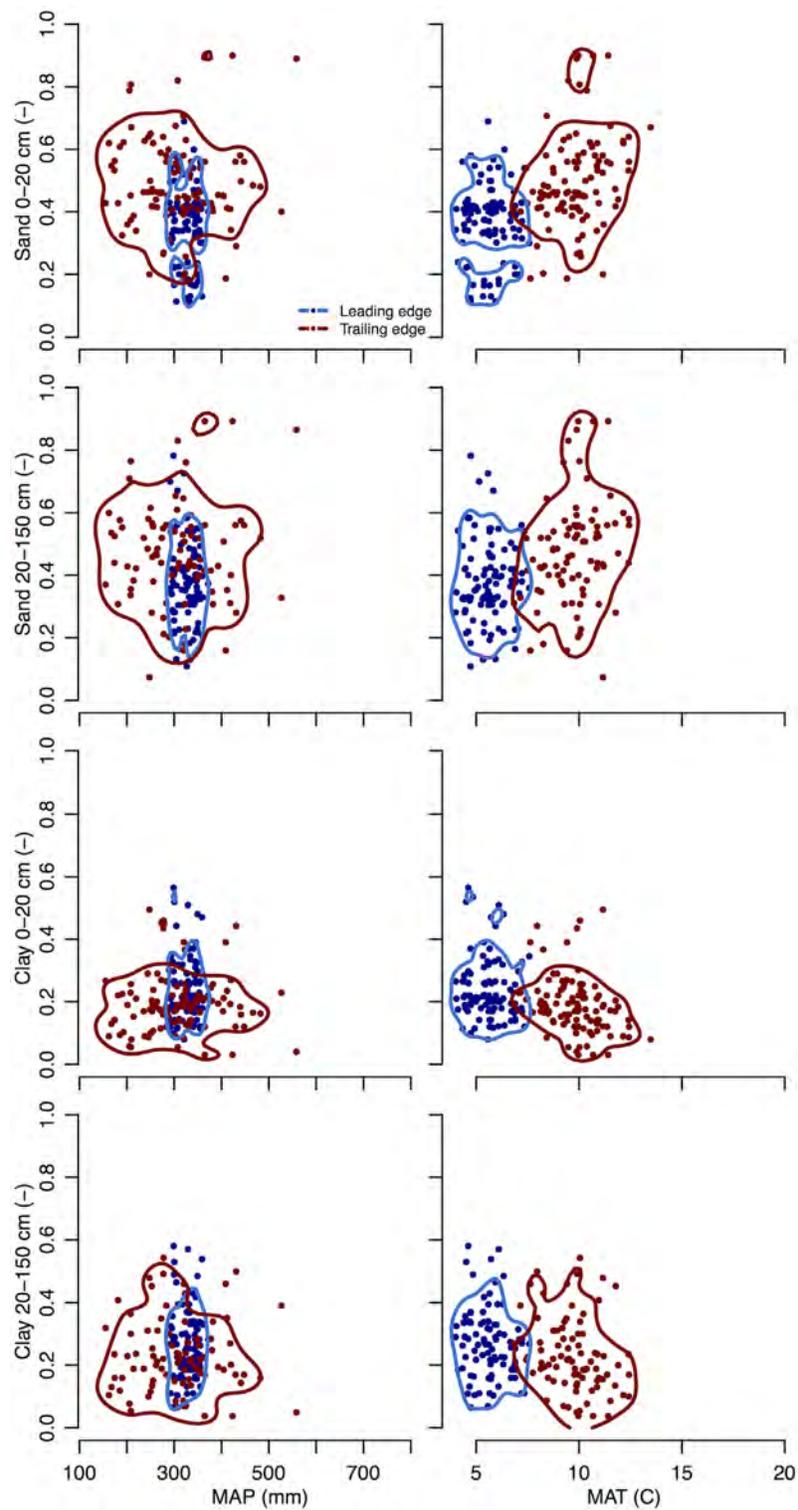


Fig. A2. Relationship between soil texture (sand and clay content at 0–20 cm and 20–150 cm depth) at the trailing (red) and leading edge (blue) under current climate 1980–2010 (fat dots). Lines indicate the 90% data cloud.

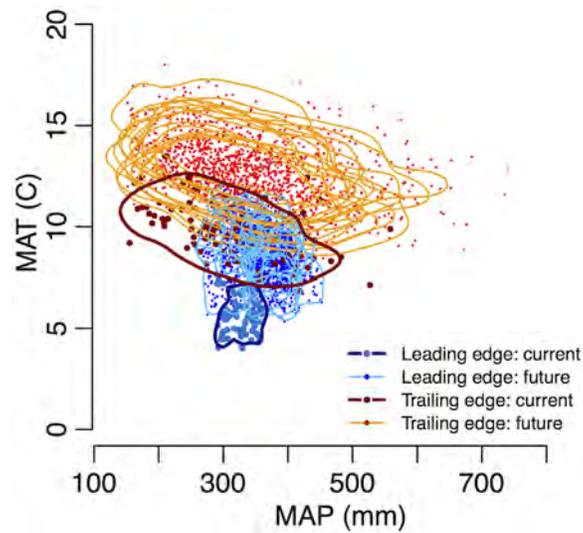


Fig. A3. Climate space of sample sites (dots) and 90% data cloud (lines) at the trailing (red hues) and leading edge (blue hues) under current climate 1980–2010 (fat dots, bold lines) and future climate conditions (small dots, thin lines) of 16 GCMs with RCP4.5 for 2070–2099.

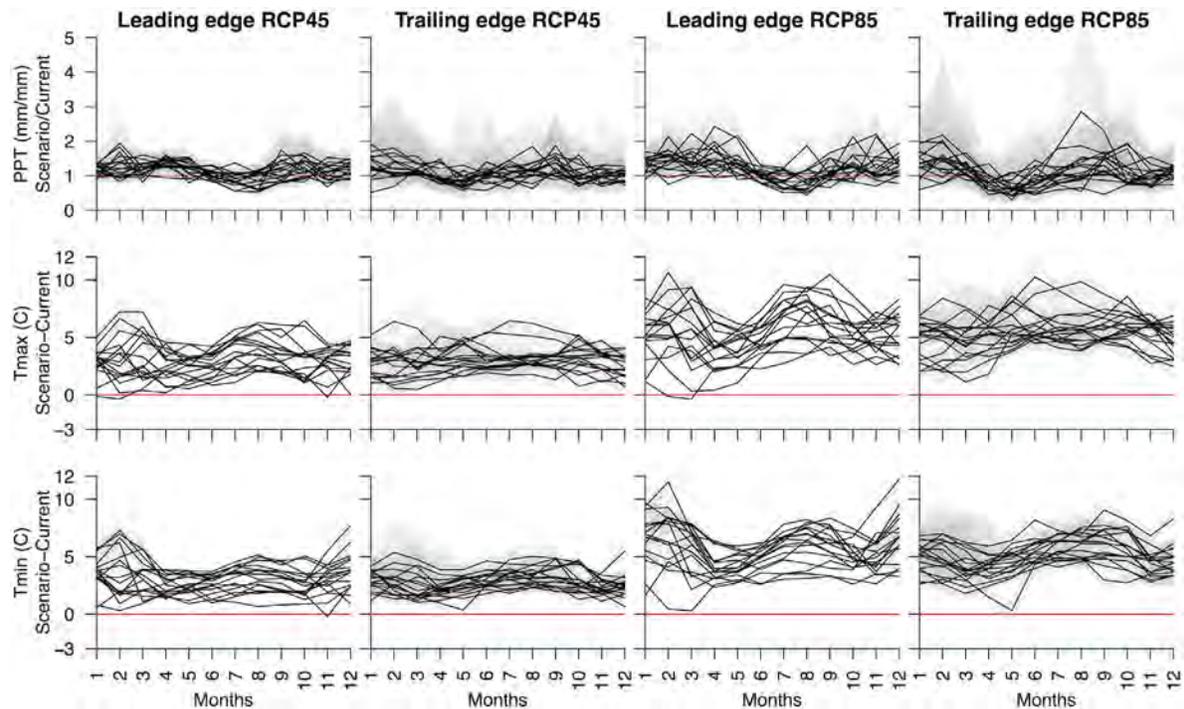


Fig. A4. Mean monthly climate perturbations from the current climate 1980–2010 (red) for future climate conditions of 16 GCMs with RCP4.5 and RCP8.5 for 2070–2099 (mean and range of sites) at the trailing and leading edge. Note, actual simulations used the hybrid-delta downscaling method, which is a time-series approach (see *Methods*).

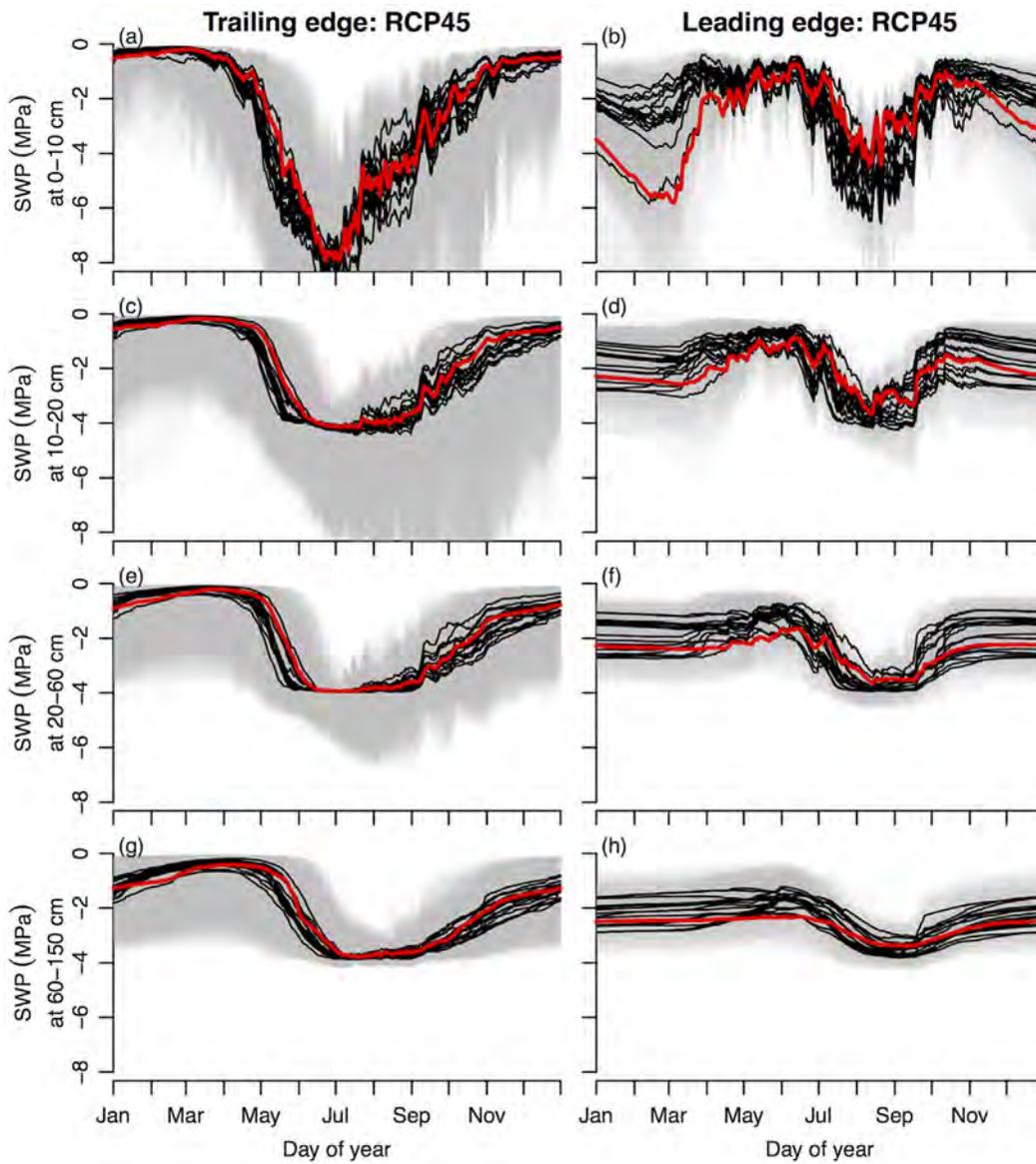


Fig. A5. Seasonal soil water potential (SWP) in four aggregated soil layers under current 1980–2010 climate (red, median among sites) and future climate conditions of 16 GCMs with RCP4.5 and RCP8.5 for 2070–2099 (black, median among sites; orange resp. blue, range of all sites) for the trailing and leading edge.

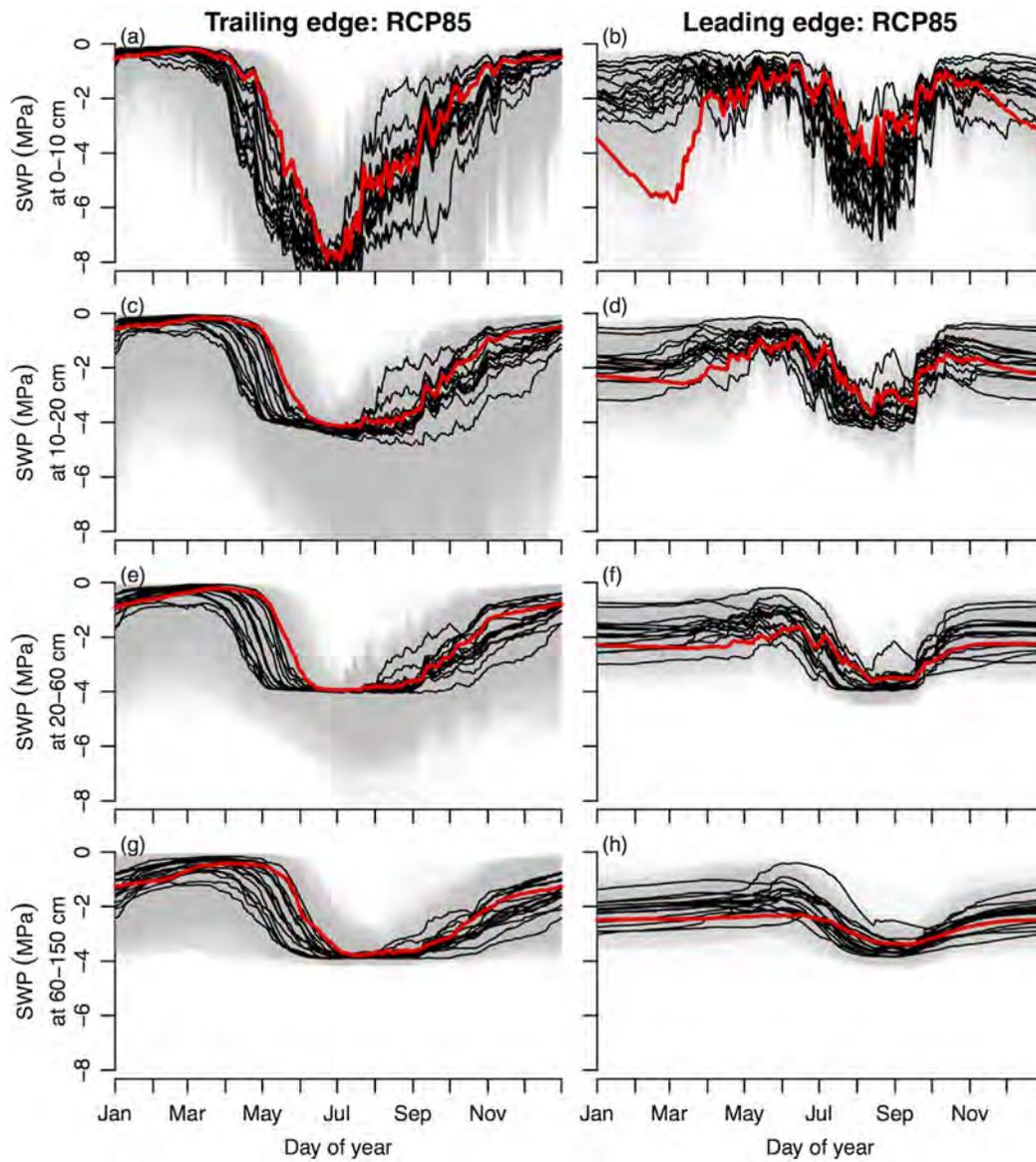


Fig. A5. Continued.

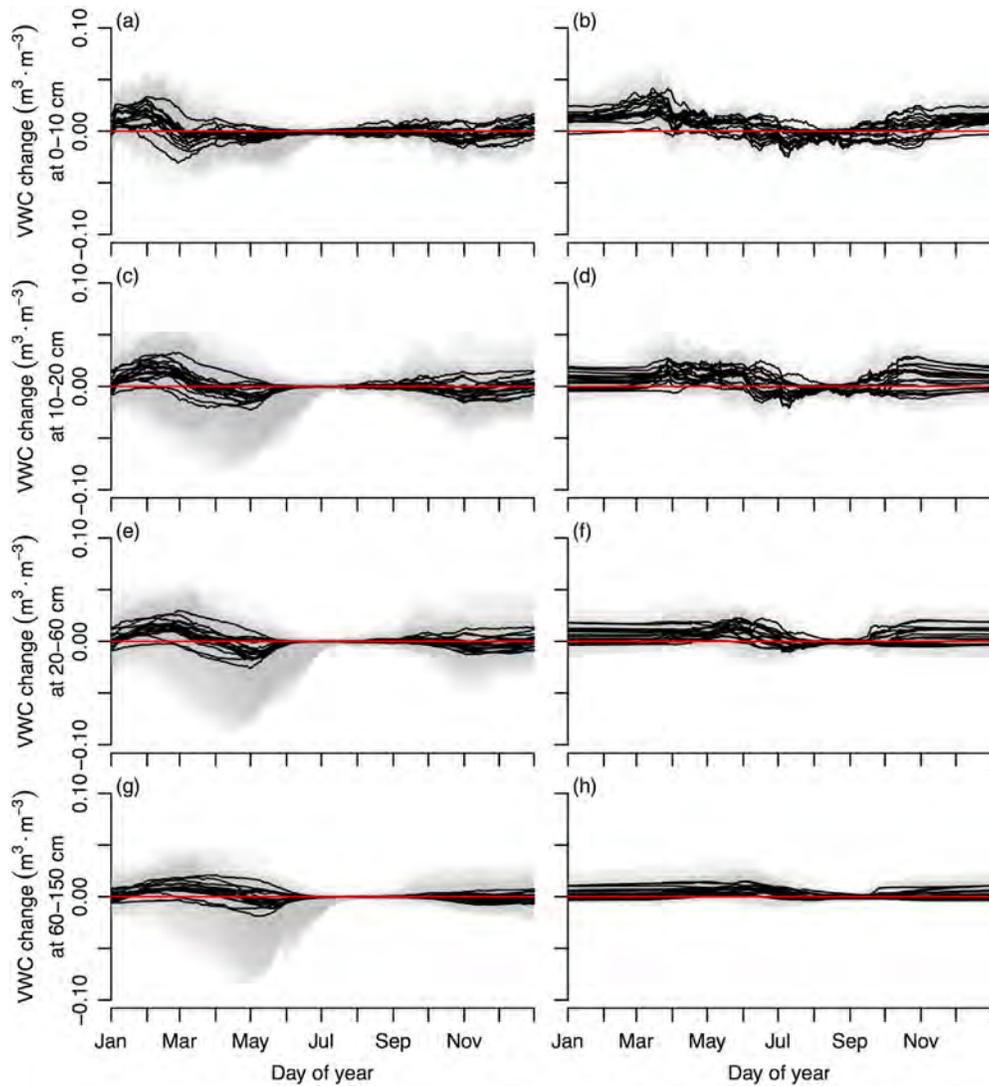


Fig. A6. Changes of seasonal volumetric water content (VWC) in four aggregated soil layers between future climate conditions of 16 GCMs with RCP4.5 for 2070–2099 (black, median among sites; gray, range of all sites) and current 1980–2010 climate (red) for the trailing (a, c, e, g) and leading edge (b, d, f, h).

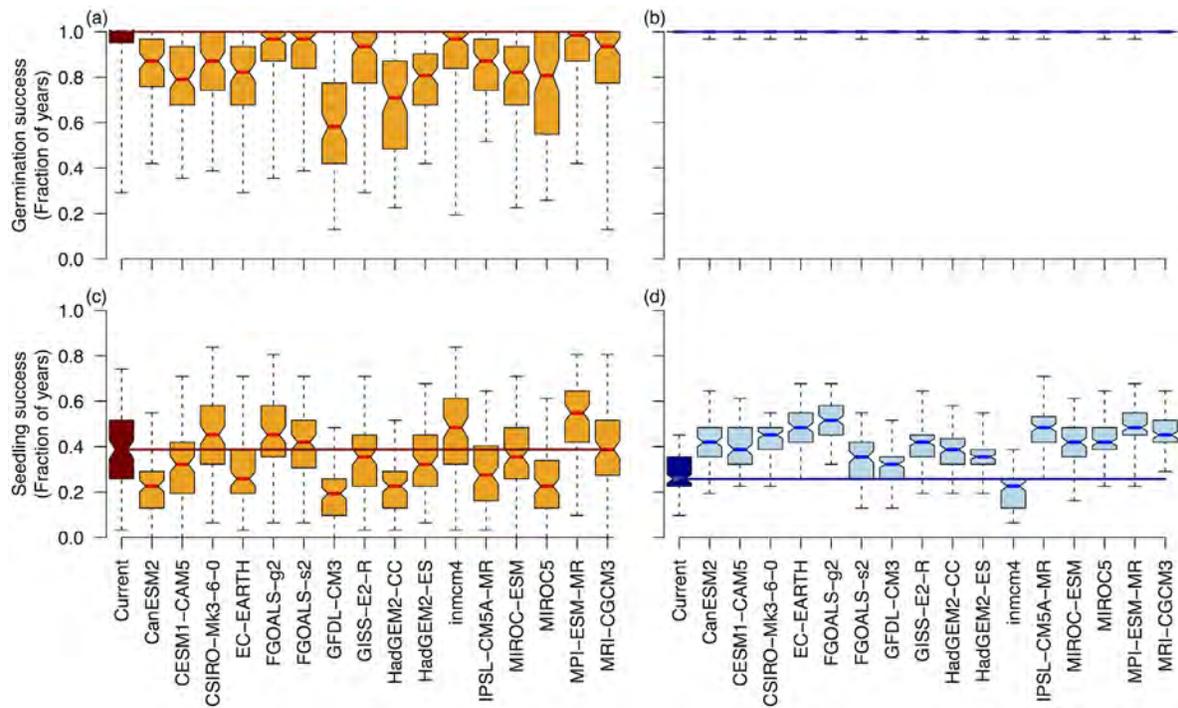


Fig. A7. Potential regeneration probabilities (median, interquartile range, whiskers include all data) of germination and seedling success under current 1980–2010 climate and future climate conditions of 16 GCMs with RCP4.5 for 2070–2099 for the trailing (a, c; red hues) and leading edge (b, d; blue hues). Horizontal lines indicate the median of current conditions.

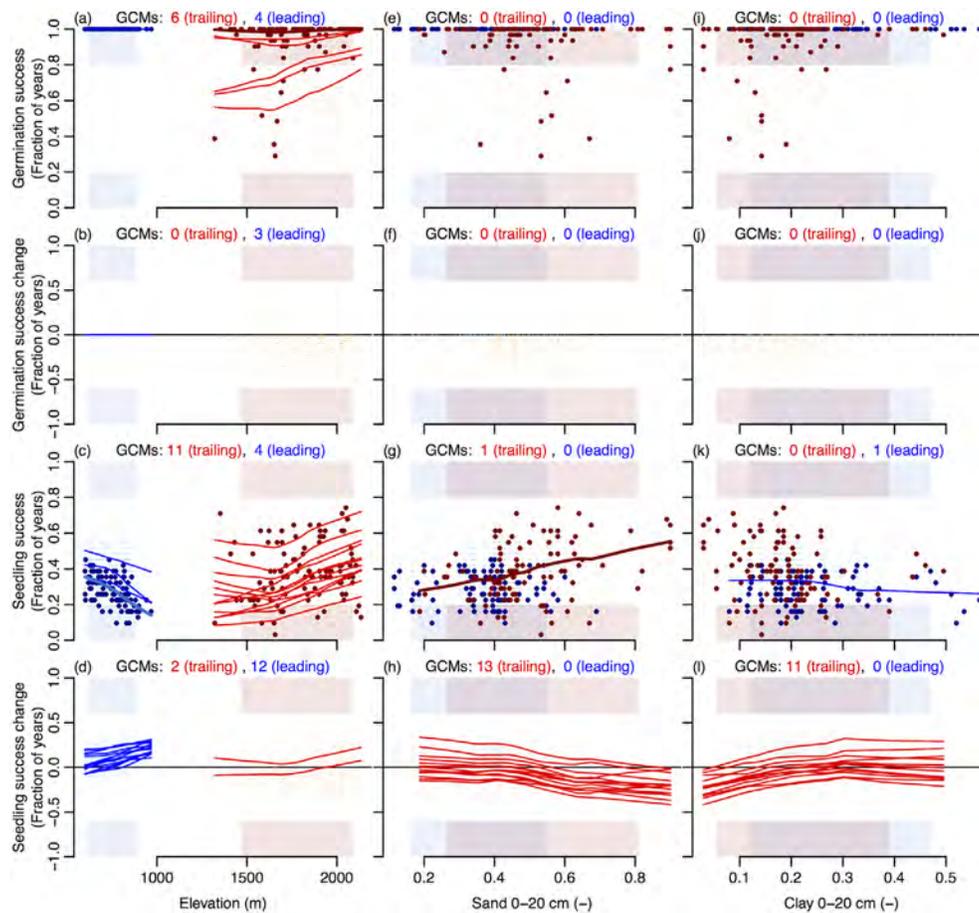


Fig. A8. Relationships between potential regeneration probabilities of germination and of seedling success and elevation and overall soil and climate variables (Fig. A1 and Table A1) under current 1980–2010 climate (bold lines/dots) and future climate conditions of 16 GCMs with RCP8.5 for 2070–2099 (simple lines/small dots) for the trailing (red) and leading edge (blue). Locally-weighted polynomial regression (lowess) lines indicate that the Brownian distance correlation was significant after Bonferroni adjustment (counts displayed in panel header). Bars at top of each panel indicate range of current conditions; bars at bottom indicate range of minimum/maximum among 5–95% of each GCM.

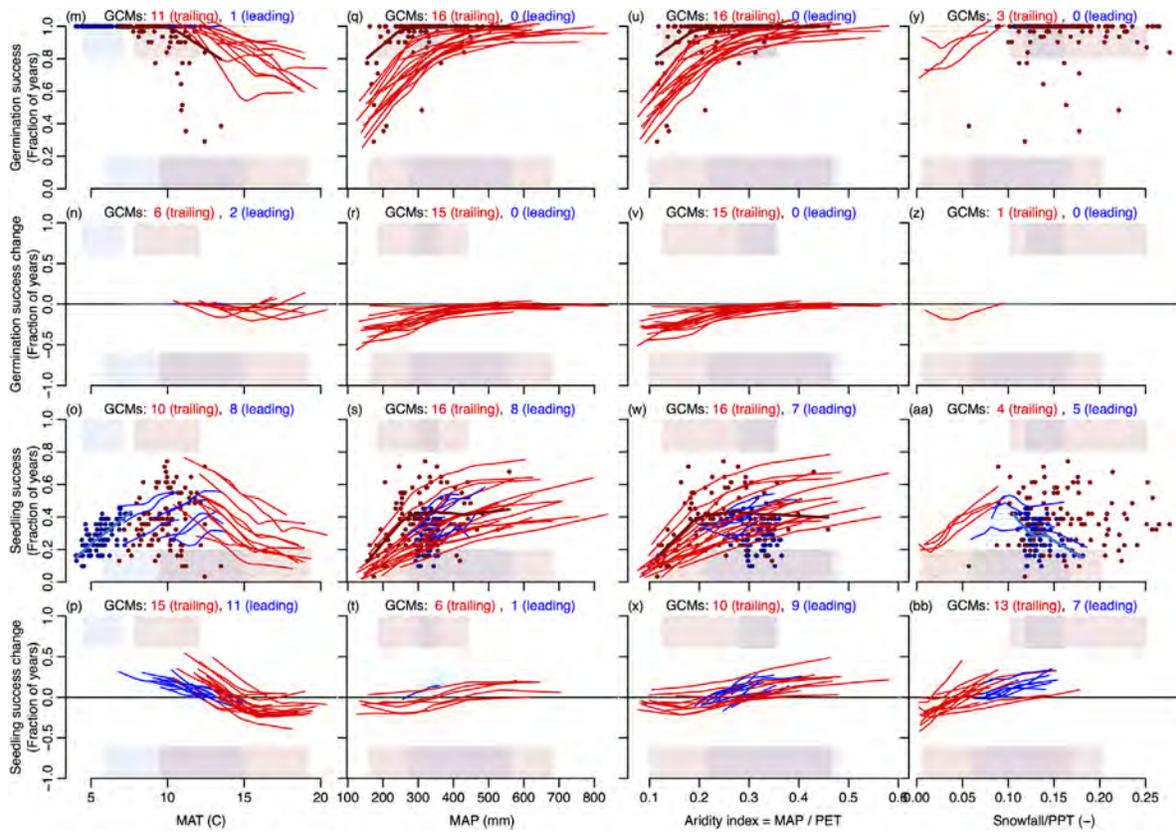


Fig. A8. Continued.

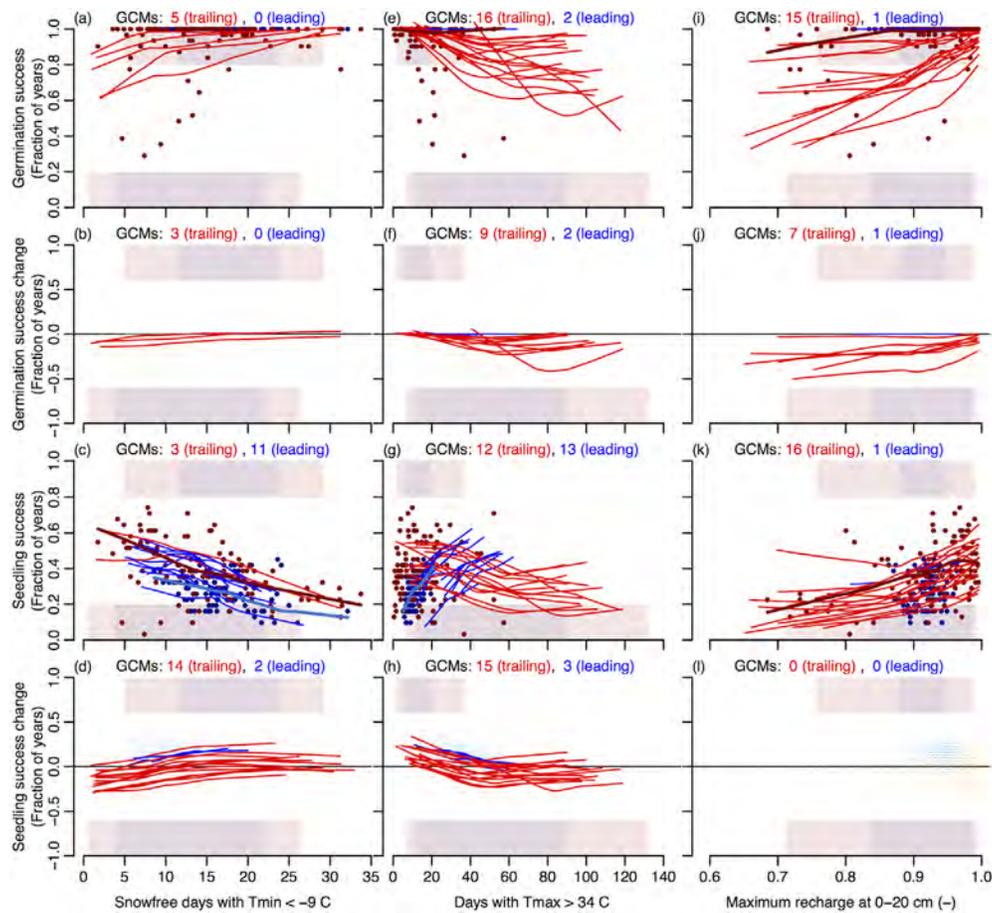


Fig. A9. Relationships between potential regeneration probabilities of germination and seedling success and change and selected explanatory variables (Fig. A1 and Table A1) under current 1980–2010 climate (bold lines/dots) and future climate conditions of 16 GCMs with RCP4.5 for 2070–2099 (simple lines/small dots) for the trailing (red) and leading edge (blue). Locally-weighted polynomial regression (lowess) smoothers indicate that the Brownian distance correlation was significant after Bonferroni adjustment (counts displayed in panel header). Bars at top of each panel indicate range of current conditions; bars at bottom indicate range of minimum/maximum among 5–95% of each GCM.

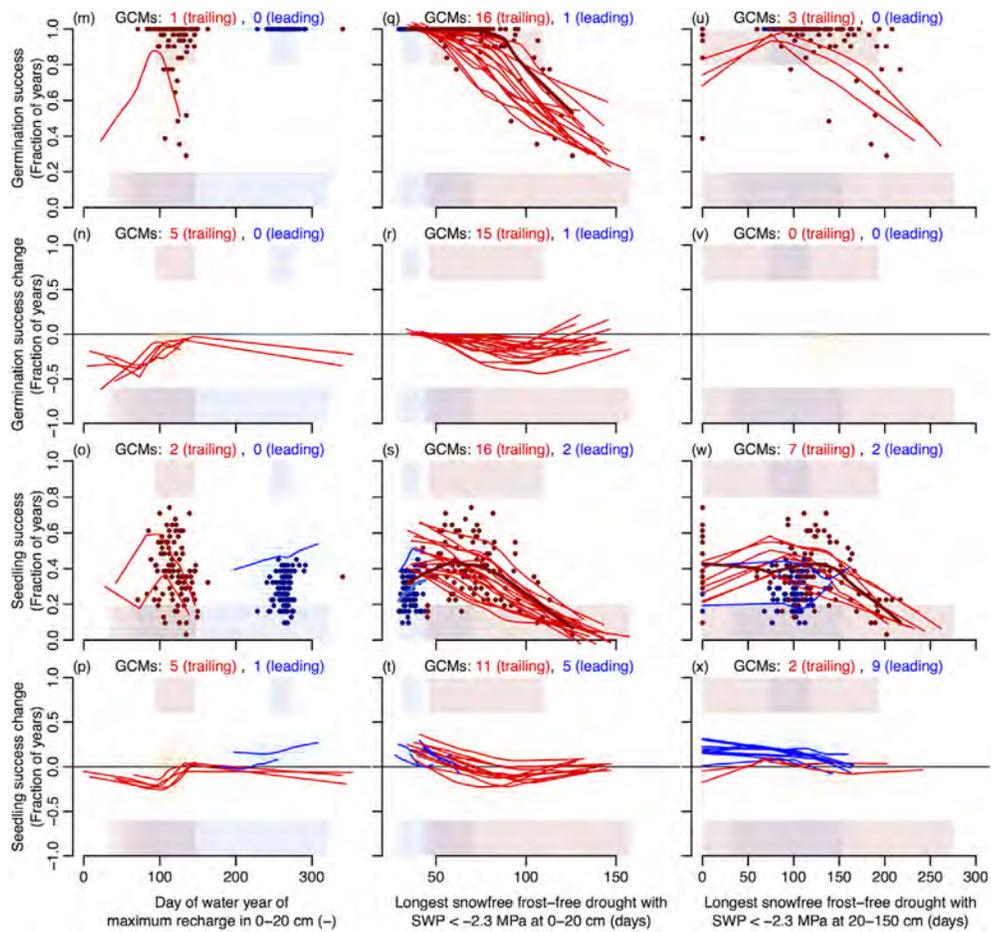


Fig. A9. Continued.

## SUPPLEMENT

R script and data to reproduce analyses of big sagebrush regeneration at leading and trailing edges of distribution shifts (*Ecological Archives*, <http://dx.doi.org/10.1890/ES14-00208.1.sm>).