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Climate-based seed transfer of a widespread shrub: population shifts, restoration strategies, and the trailing edge

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Abstract. Genetic resources have to be managed appropriately to mitigate the impact of climate change. For many wildland plants, conservation will require knowledge of the climatic factors affecting intraspecific genetic variation to minimize maladaptation. Knowledge of the interaction between traits and climate can focus management resources on vulnerable populations, provide guidance for seed transfer, and enhance fitness and resilience under changing climates. In this study, traits of big sagebrush (*Artemisia tridentata*) were examined among common gardens located in different climates. We focus on two subspecies, *wyomingensis* and *tridentata*, that occupy the most imperiled warm-dry spectrum of the sagebrush biome. Populations collected across the sagebrush biome were recorded for flower phenology and survival. Mixed-effects models examined each trait to evaluate genetic variation, environmental effects, and adaptive breadth of populations. Climate variables derived from population-source locations were significantly associated with these traits ($P < 0.0001$), explaining 31% and 11% of the flower phenology and survival variation, respectively. To illustrate our model and assess variability in prediction, we examine fixed and focal point seed transfer approaches to map contemporary and climate model ensemble projections in two different regions of the sagebrush biome. A comparison of seed transfer areas predicts that populations from warmer climates become more prevalent, replacing colder-adapted populations by mid-century. However, these warm-adapted populations are often located along the trailing edge, margins of the species range predicted to be lost due to a contraction of the climatic niche. Management efforts should focus on the collection and conservation of vulnerable populations and prudent seed transfer to colder regions where these populations are projected to occur by mid-century. Our models provide the foundation to develop an empirical, climate-based seed transfer system for current and future restoration of big sagebrush.

Key words: *adaptive traits;* Artemisia tridentata; *assisted migration; climate change; clinal variation; sagebrush; seed zones.*

Introduction

Climate change is increasing the impetus for managing genetic resources. Given the strong linkages between climate and plant adaptation (Woodward 1987, Shaw and Etterson 2012), one strategy for managing resources is the movement of genotypes to enhance fitness, broadly referred to as a translocation. More specific terms for translocation include seed transfer, assisted gene flow, or assisted migration, depending on the geographic scale (Weeks et al. 2011, Aitken and Whitlock 2013, Williams and Dumroese 2013). If translocation strategies can be implemented that increase fitness, then the movement of genotypes can aid in promoting ecosystem resilience and resistance to environmental change (Millar et al. 2007, Chambers et al. 2017). However, a knowledge base of climate change models, monitoring programs, species distribution models (i.e., bioclimatic niche) and genetic data is essential for providing greater confidence in developing effective management strategies (McMahon et al. 2011). There are several questions that should be addressed prior to developing seed transfer and other translocation strategies (Kilkenny 2015): which populations are most vulnerable to extirpation, what traits are important to climatic adaptation and fitness, and how far can populations be translocated before traits become maladaptive?

Species range shifts have often accompanied past climate change (i.e., glacial and inter-glacial cycles) over millennia (Jackson and Overpeck 2000, Williams et al. 2004). These shifts have shaped the distribution of intraspecific genetic variation (Hewitt 2000, Davis and Shaw 2001, Hu et al. 2009). Populations occurring in lower latitudes of a species distribution typically have a higher proportion of the genetic diversity (Richardson et al. 2002, Petit 2003, Hampe and Petit 2005) and harbor adaptive genetic variation important for plant fitness in warmer climates (St Clair et al. 2005, Rehfeldt et al. 2014a, Richardson et al. 2014). Given important characteristics of lower latitude populations and the documented occurrences of climate-implicated die-offs (Breshears et al. 2005, Worrall et al. 2013), these populations should be a focus for conservation.

Cold semiarid environments extend across a large segment of the western United States. The sagebrushes (subsection Tridentatae), particularly big sagebrush (*Artemisia tridentata*), are the foundational species across western North America, supporting diverse plant and wildlife communities (Dumroese et al. 2015). Big sagebrush has an immense geographic distribution, spanning elevations from 100 m to upward of 3,000 m above sea level. The environmental breadth can be attributed in part to diversification into three predominant subspecies that occupy different environmental niches (McArthur and Plummer 1978, Barker and McKell 1983, McArthur and

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Sanderson 1999). These subspecies include *tridentata* (basin big sagebrush) and *wyomingensis* (Wyoming big sagebrush) occupying the lower elevation basins, and *vaseyana* (mountain big sagebrush) occupying dry, montane regions (McArthur and Plummer 1978, Mahalovich and McArthur 2004).

Frequent disturbances in the sagebrush biome followed by invasions from exotic species (e.g., cheatgrass [*Bromus tectorum*]) are transforming these ecosystems into fire-prone annual grasslands. Research studies examining the climatic niche and process-based models of regeneration support a contracting niche and declining regeneration opportunities for big sagebrush (Rehfeldt et al. 2012, Schlaepfer et al. 2015, Still and Richardson 2015) and an increasing niche for cheatgrass (Bradley et al. 2016). In particular, subspecies *wyomingensis*, occupying the warmest and most arid regions of this species distribution, is likely to have the highest vulnerability to projected climate change. The bioclimatic niche of subspecies *wyomingensis* is projected to contract considerably by mid-century, especially in the Great Basin, the warmest and driest region within this species range (Still and Richardson 2015). Given the threats from climate change illustrated in niche models and declining resistance and resilience of sagebrush communities to cheatgrass (Brooks et al. 2016, Chambers et al. 2016), management strategies need to integrate these projected threats to conserve genetic resources.

FIG. 1. Locations of *Artemisia tridentata* seed collection sites (referred to as populations) used in the survival analysis. Circles designate subsp. *wyomingensis,* and triangles designate subsp. *tridentata*. The contemporary bioclimatic niche for subsp. *wyomingensis* (adapted from Still and Richardson [2015]) is shown in gray.

In this study, seed transfer strategies of big sagebrush are explored for contemporary through mid-century climates. Genetic models of two traits (flower phenology and survival) and a bioclimatic niche model are used to assess projected impacts imposed by climate change for the most imperiled sagebrush communities occupied by subspecies *wyomingensis* and *tridentata*. We address questions important to planning restoration and managing the genetic resources of big sagebrush: what climate variables are associated with adaptive traits; how are adaptive genetic variation and associated climate variables arrayed across the landscape; which populations are vulnerable to climate extirpation; do vulnerable populations exhibit genetic value in future climates; and what are the pros and cons of different seed transfer approaches?

Material and Methods

Data collection

Big sagebrush seed was collected from 55 locations (Fig. 1) in the fall of 2009 and planted in three common garden locations (Table 1). Seed source locations are hereafter referred to as populations. The three common garden locations differed in climate: a warm-dry basin site, Orchard, Idaho, USA; a cold-dry basin site with deep soils, Ephraim, Utah, USA; and a cold-mesic mountain site, Majors Flat, Utah, USA. Assignment of subspecies was completed using a combination of morphological traits (height and stature), ploidy (cytotype) via flow cytometry (Richardson et al. 2012), and volatile organic compounds (Jaeger et al. 2016). An average of eight plants represented each population in each garden, ranging between 2 and 11 individuals. Plants were arranged in a completely randomized design for each garden. To ensure establishment, plants were watered periodically during the first growing season. No data collection occurred during this period (May–October 2010). See Chaney et al. (2017) for more detail on seed collection, processing, seedling rearing, and common garden establishment.

Traits of focus in this study are flower phenology and survival. Flower phenology was measured as Julian date (i.e., day of year) in which anthesis reached 50% for each plant based on visual inspection. Flower phenology was collected over one year in 2012 on a weekly basis from early July to late November from three common gardens containing 55 populations and three subspecies. For full details on flower phenology data, see Richardson et al. (2017). Survival was measured by recording when all foliage was missing from a plant and no re-greening occurred during the growing season. Survival data were collected approximately four times a year for nearly 5 yr (58 months) and included data from two common gardens with 37 populations (24 *tridentata* and 13

TABLE 1. Geographic and climatic attributes and data collection of the *Artemisia tridentata* common gardens.

Garden	Latitude (°N)	Longitude (°E)	Elevation (m)	*N*	MCTM (°C)	MWTM (°C)	MAP (mm)	Trait measured
Ephraim, Utah	39.370	111.577	1,686	284	−9.8	21.2	248	F, S
Majors Flat, Utah	39.339	111.520	2,105	237	−4.7	20.8	414	F, S
Orchard, Idaho	43.322	115.998	974	258	−2.9	25.0	257	F

Notes: N, sample size; MCTM, mean coldest month temperature; MWTM, mean warmest month temperature; MAP, mean annual precipitation; F, flower phenology; S, survival. Climate data are based on values from 2010–2013 water years.

wyomingensis, omitting *vaseyana*; Appendix S1: Table S1). For this paper, we focused on subspecies *tridentata* and *wyomingensis* because these two subspecies occupy the bioclimatic niche (Still and Richardson 2015), subsp. *vaseyana* was found to have a significantly different linear slope the other subspecies (Chaney et al. 2017) and Wyoming big sagebrush ecosystems are of the greatest conservation concern.

Climate data

Population-source climate data were obtained for each population from 1-km^2 gridded climate surfaces developed from 30-yr (1961–1990) climatic data using ClimateNA_MAP (Wang et al. 2016; program *available online*).[4] The data included 29 climate variables describing minimum or maximum temperature sums, yearly or seasonal temperature and precipitation, frost-free periods, and other climate variables that can be important to plant adaptation. The genetic models and a bioclimatic niche model (Still and Richardson 2015) were mapped to three 30-yr time periods: contemporary (1981–2010), 2020 (2011–2040), and 2050 (2041–2070). Climate surfaces were obtained from ensemble projections comprised of eight global circulation models based on the fifth assessment (AR5) IPCC/CMIP5 (Adaptwest Project 2015). Variability in model projections for future climates was assessed by using two carbon emissions scenarios: Representative Concentration Pathways (RCP) 4.5 (Thomson et al. 2011) and RCP8.5 (Riahi et al. 2011).

Statistical analyses

A linear mixed-effects model was used for flower phenology (lmer function). A quasi-binomial error distribution (glmer function) was used for the survival model because of the binary (dead or alive) nature of this data (Chaney et al. 2017). These functions are part of the lme4 package (v. 1.1-12; Bates et al. 2015). The lmerTest package v. 2.2 (Kuznetsova et al. 2016) was used to evaluate predictors, model fit, and significance of fixed and random effects in the mixed models. The analyses were run in the R statistical framework v 3.4.4 (R Core Team, 2018); the code can be found at GitHub, and the data are archived at Dryad (see *Data Availability*).

In each model, trait predictors were segregated into either fixed or random effects. Fixed effects were assigned to climate variables derived at each population origin; these predictors transcend the experimental design and have been shown to be associated with trait variation in plants. Random effects were assigned to experimental factors: garden locations, subspecies, and populations. Garden location describes environmental differences, subspecies describes taxonomical differences, and population × subspecies × garden describes genotype-by-environment interactions (G × E). Since survival was a summary at the population level (i.e., no variation among individuals), G × E could not be measured. The experimental factors subspecies and population were a full factorial design among gardens.

Predictors were fitted to the trait data using a two-step process to cull poorly fitting variables. In the first step, correlations between trait population means and population climate variables were used to guide the selection of climate variables. This step was conducted by setting a Pearson correlation coefficient r value threshold to eliminate variables. A threshold of $|r| = 0.5$ and 0.2 was set to retain six variables for flower phenology and survival, respectively. In the second step, we use a similar approach to Rehfeldt et al. (2014b). The ANOVA function (lme4 package), a likelihood-ratio test, was used to evaluate model predictors and selected a "best" model based on AIC (Akaike information criterion). Model fit was evaluated by conditional and marginal R^2 (Johnson 2014), using the r.squaredGLMM function in MuMin (Bartoń 2015). Conditional R^2 (R^2_c) described the percent of variance explained by fixed and random effects, and marginal R^2 (R^2_m) described fixed effects alone.

The genetic functions, the intercept and fixed effect coefficients of the mixed-effects models (Table 2), were used to calculate confidence intervals. Genetic variation bounded by upper and lower confidence intervals is referred to as climatypes (Rehfeldt et al. 2014b). Confidence intervals were calculated with the predictionInterval function in the merTools package (Knowles and Frederick 2016). For flower phenology, we adopt the approach of Rehfeldt et al. (2014b) for partitioning clinal genetic variation. A confidence level of 0.8 ($\alpha = 0.2$) was used to define confidence intervals. Because of the binary nature of the survival trait, a different approach was used to define climatypes for survival. We assume a survival rate change of ±0.15 (e.g., a 15% increase in mortality) would be unacceptable outcome for restoring big sagebrush. Therefore, confidence intervals were set at 0.25 ($\alpha = 0.75$), reflecting a survival rate change of approximately 0.15 between climatypes.

Mapping

Mapping of the linear functions from flower phenology and survival was completed using the gridded cell values from the relevant climate-surface variables. The yaImpute package v 1.0-22 (Crookston and Finley 2008) was used within the R framework to map the linear functions within a geographic window of 130–100° W and 50–30° N. ArcMap (v 10.3; ESRI, Redlands, California, USA) was used to visualize the genetic models within the predicted boundaries of *A.t. wyomingensis* using a modified version of Still and Richardson (2015) bioclimatic niche model (discussed in the Climate data section). To map continuous variation in survival probabilities, the data were back-transformed using a log-link transformation of coefficients; otherwise, mapping seed transfer areas for this trait were completed in the transformed state.

Genetic models were mapped using fixed and focal point seed transfer systems. Fixed seed zones were defined by

Table 2. Mixed-effects model summaries of the genetic regression functions, conditional R^2 (R^2_c) and marginal R^2 (R^2_m) values for flower phenology and survival traits of *Artemisia tridentata*.

Trait	Regression function	R^2_c	R^2_m
Flower date	$381 + (-1.72 \times \text{LAT}) + (-0.011 \times \text{DDL18})$	0.80	0.31
Survival	$-6.30 + (0.284 \times \text{TD}) + (0.007 \times \text{PPTsm})$	0.51	0.11

Notes: TD, continentality (summer–winter temperature differential); PPTsm, summer precipitation; LAT, latitude (surrogate variable for photoperiod); DDL18, degree day <18°C. Mixed model results are shown in Appendix S1: Table S2.

[4] www.climatewna.com

combining flower phenology and survival climatypes (i.e., combine function in ArcMap). A focal point approach defines seed transfer limits for a specific restoration site (Parker 1992, Parker and van Niejenhuis 1996), typically by developing trait response functions from multiple reciprocal transplant sites. In our approach, we utilize confidence intervals from the two traits to define transfer limits for specific sites. Seed transfer areas were calculated for select populations representing wide-ranging climates. The clinal variation from each trait was reclassified in ArcMap to fit the upper and lower confidence intervals surrounding the specific population (Appendix S1: Table S2). Raster calculator was then used to combine the reclassified surfaces. We focus on focal point seed transfer areas for three populations in the Great Basin and two populations in the Wyoming Basin/Northern Plains (hereafter referred to as the Wyoming Basin).

Results

Mixed models

Mixed-effects models explained a substantial amount of the trait variation, ranging from 51% to 80% (conditional R^2 = 0.51 to 0.80, Table 2). Genetic variation, predicted by population-sourced climate variables (e.g. fixed effects), explained 31% and 11% of the variation for flower phenology and survival, respectively (Table 2). A combination of temperature and photoperiod (latitude) best explained flower phenology. Temperature and precipitation variables best explained survival (Table 2; Appendix S1: Table S3). Populations from colder climates and higher latitudes were predicted to have earlier autumn flowering (Fig. 2a). Populations from continental climates (i.e., higher continentality, TD) and higher summer precipitation were predicted to have higher

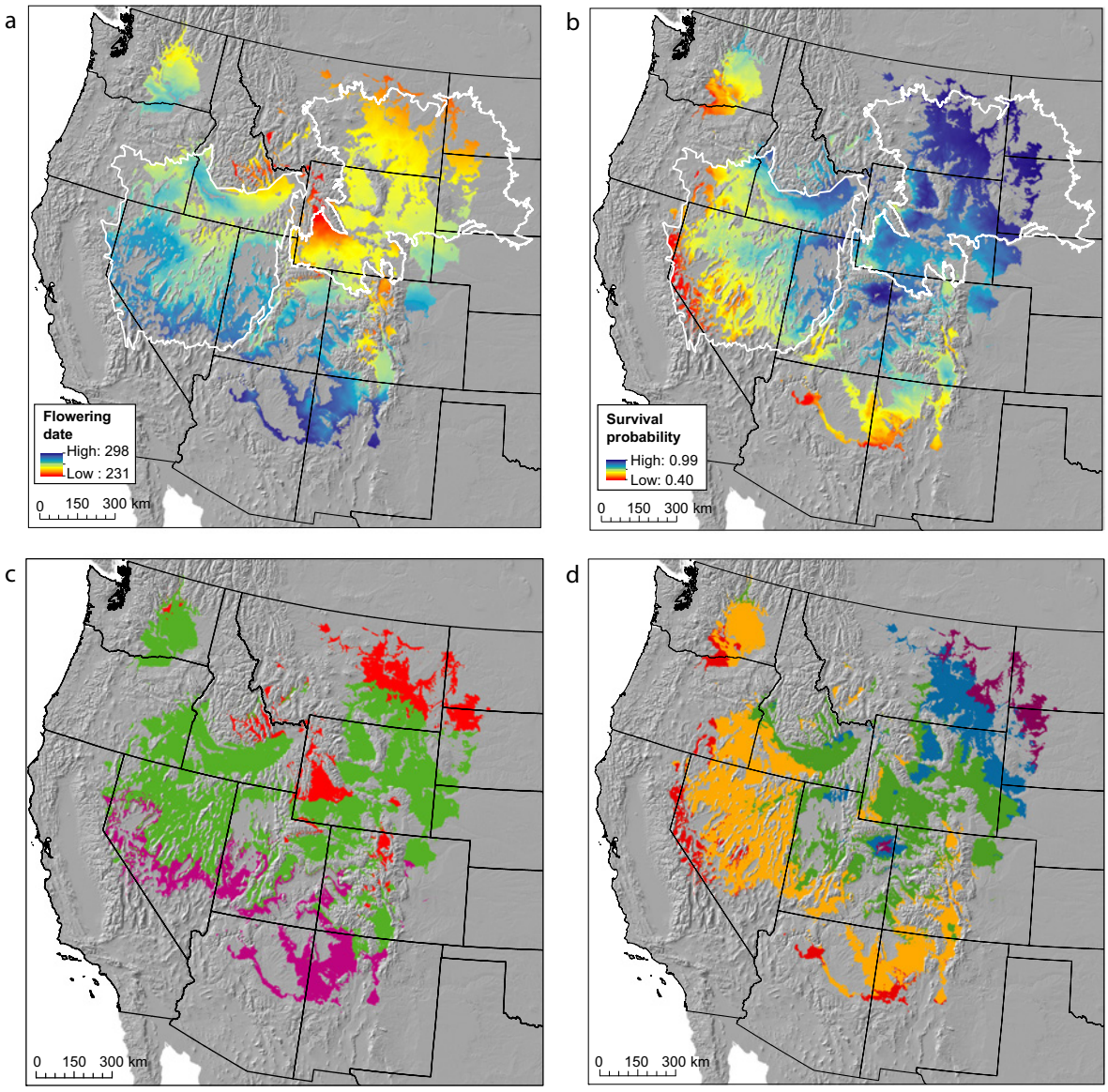

Fig. 2. Projected clinal variation of (a) flower phenology and (b) survival of *Artemisia tridentata* subsp. *tridentata* and *wyomingensis*. Climatypes (see *Material and Methods: Statistical analysis*) are mapped for (c) flower phenology and (d) survival. White outlines show the boundaries of the Great Basin and Wyoming Basin, USA. Climatypes are combined to map the fixed seed zones (Fig. 3).

proportion of survival (Fig. 2b). Across the contemporary (1981–2010) bioclimatic niche of *A.t.* subsp. *wyomingensis*, the genetic regression functions (Table 2) are predicted to vary 67 d in flowering date and 0.59 in survival probability (Fig. 2a, b). Confidence intervals supported three climatypes for flowering date across the climate niche of *A.t. wyomingensis*. Each climatype spanned 21 d (Fig. 2c). Five climatypes were supported for survival probability. Each climatype spanned an interval of approximately 0.18 (Fig. 2d).

Combined climatypes of flower phenology and survival are mapped to illustrate fixed seed transfer zones. The process of combining these different climatypes created 14 discrete zones across the range of the contemporary bioclimatic niche. However, two zones are relatively small in areal coverage (<500 km^2). Eight zones are found within the Great Basin and six within the Wyoming Basin (Fig. 3a). To evaluate how seed zones respond to projections of climate change, areal extent changes in three seed zones were calculated for contemporary, 2020s and 2050s climates, using two greenhouse gas emission scenarios (RCP4.5 and RCP8.5). Seed zone 1, occupying a warmer region of the Great Basin, is one of the few seed zones that are projected to experience expansion from ~12,000 km^2 to >40,000 km^2 by mid-century. Whereas seed zones 2 and 3 currently occupying large portions, the Great Basin and Wyoming Basin are projected to experience large reductions in areal extent. Areal extent rates of decline among zones 2 and 3 are steepened by scenarios with increased greenhouse gas emissions (RCP8.5, Fig. 3b).

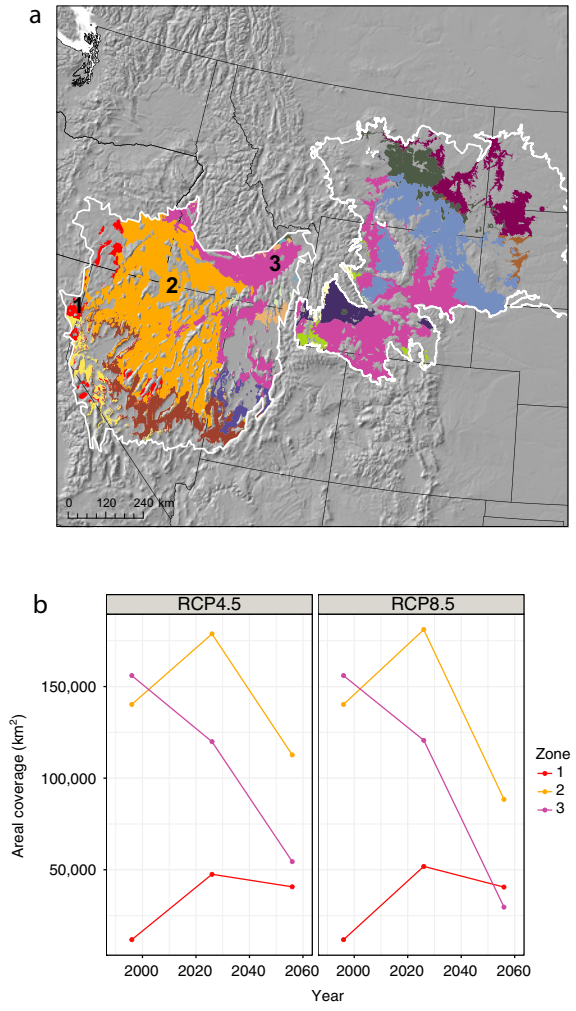

FIG. 3. (a) Fixed seed transfer zones for *Artemisia tridentata* subsp. *tridentata* and *wyomingensis* under a contemporary climate, 1981–2010. Zones are mapped within the Great Basin and the Wyoming Basin (white outlines). (b) Projected areal coverages for three zones (1, 2, and 3) are calculated with ensemble models using low (RCP4.5) and high (RCP8.5) emission scenarios for two 30-yr periods: 2020s (2011–2040) and 2050s (2041–2070).

Another means to define seed zones is by a focal point seed transfer approach. Seed transfer areas are mapped for three populations located within the Great Basin (Fig. 4) and two populations within the Wyoming Basin (Fig. 5). Focal point seed transfer limits are drawn using the genetic functions for survival and flower phenology, bounded by their confidence intervals. The selected populations represent the warm and cold spectrums of climates within each ecoregion. Transfer areas are displayed for contemporary climates, 2020s and 2050s. Future projections (2020s and 2050s) were composed of ensemble models using RCP4.5 and RCP8.5. In both regions, the warmer-adapted populations maintain or increase their relative areal coverage in relation to the mid-century climatic niche compared to colder-adapted populations. For example, while the Great Basin bioclimatic niche contracts seed transfer areal coverage, warm-adapted populations (CAT2) increase their prominence in the Great Basin, while colder populations (UTW2) decline (Table 3, Fig. 4). Similarly, in the Wyoming Basin, warmer populations (MTW3) develop a larger seed transfer area as colder populations are displaced outside of the Wyoming Basin (e.g., MTW1), losing much of the areal coverage by the 2050s (Table 3, Fig. 5).

DISCUSSION

Genetic models

Minimum winter temperatures, which contribute to continentality, have been shown to be a common factor in genetic adaptation for a number of plant species, affecting phenology, growth, and survival (St Clair et al. 2013, Richardson et al. 2014, Rehfeldt et al. 2017, Warwell and Shaw 2017, Montwé et al. 2018). For widespread desert shrubs, big sagebrush and blackbrush (*Coleogyne ramosissima*), continentality appears to be strongly associated with variation in survival (Richardson et al. 2014, Chaney et al. 2017). Populations of *A. tridentata* from more continental climates had higher survival rates, especially at the coldest garden, Ephraim (Table 1). Patterns of survival appear to highlight the adaptive differences in coping with freezing, tied to two physiological strategies: avoidance and resistance (Brabec et al. 2017). Moreover, minimum temperatures are an important factor affecting flower phenology. Populations that experience more degree days below 18°C (DDL18) flowered earlier in the year than populations from warmer climates. It is plausible that these adaptive clines are steepened by the topography: the north-to-south mountain ranges that act to buffer more western *A. tridentata* populations from cold air masses that frequent eastern populations and the interior of the continent.

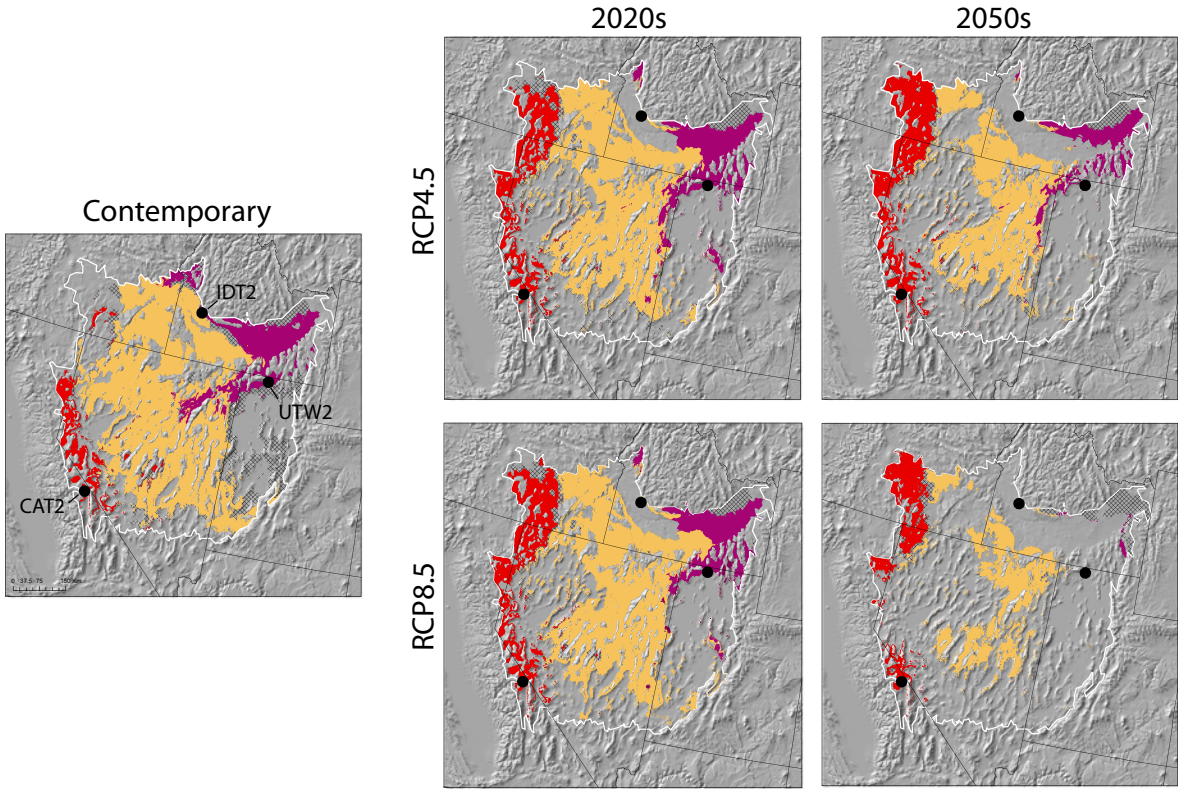

FIG. 4. Focal point seed transfer areas of three Great Basin, *Artemisia tridentata* populations depicted in color fill. Transfer areas are shown for contemporary climate (1981–2010) and 2020s (2011–2040) and 2050s (2041–2070; RCP4.5). Focal points are depicted with black dots. Areas that are outside the focal point transfer limits but within the bioclimatic niche are depicted with diagonal hatching.

Seed zone constraints

The Great Basin and Wyoming Basin are distinctly different regions of the sagebrush biome. These regions differ in climate, disturbance type, ecological interactions, and scale of restoration (Chambers et al. 2017). Since the vast majority of restoration occurs in the Great Basin and Wyoming Basin, we have constrained mapping seed transfer areas to these regions. Our results highlight the similarities and differences between the two regions in projected climate warming vulnerabilities for *A.t. wyomingensis*. A notable similarity is the substantial contraction in the projected bioclimatic niche of *A.t. wyomingensis* in both regions by mid-century (Table 3). Niche contraction is supportive of previous distribution models of biotic communities (Rehfeldt et al. 2012) and *A. tridentata* process-based models (Schlaepfer et al. 2015). However, Still and Richardson (2015) show that niche contraction in these regions could be caused by different climate factors: temperature-driven aridity in the Great Basin and shifting seasonal precipitation patterns in the Wyoming Basin. These climate factors have different levels of uncertainty associated with the prediction. Predicting precipitation changes magnify the uncertainty (Woldemeskel et al. 2016); therefore, niche loss likely caused by precipitation changes in the Wyoming Basin should be interpreted with more caution than the contraction of niche space predicted for the Great Basin.

Seed transfer

The use of sagebrush seed in restoration has been occurring for several decades. However, limits to seed transfer have only occurred more recently with the use of provisional seed zones (Bower et al. 2014). The empirical, climate-based seed zones presented in this study provide a simplified seed transfer system compared with provisional seed zones. The fixed seed zones presented here in the Great Basin (Fig. 4a) are approximately half the number of zones delimited by provisional seed zones (i.e., from ~15 provisional to 7 provisional zones). Reducing seed zones decreases the complexity for both seed collectors and land management agencies. Broader seed zones enable collectors more choices to inspect and collect the highest yielding stands and allow agencies to utilize seed collections over a broader range of restoration sites.

A number of studies have shown that the trailing edge, populations occupying the warmest margins and lower latitudes, can harbor unique genetic diversity important for adaptation and evolution of the species (Hampe and Petit 2005, Provan and Maggs 2011). Our results support that some populations of trailing edge harbor the necessary adaptive traits to expand into an increasing portion of Great Basin climatic niche by mid-century (Figs. 3 and 4). Expansion of warm-adapted populations could occur by displacement and introgression with colder-adapted populations or by colonizing new niche space. Directional seed transfer from warmer to colder climates will be warranted to

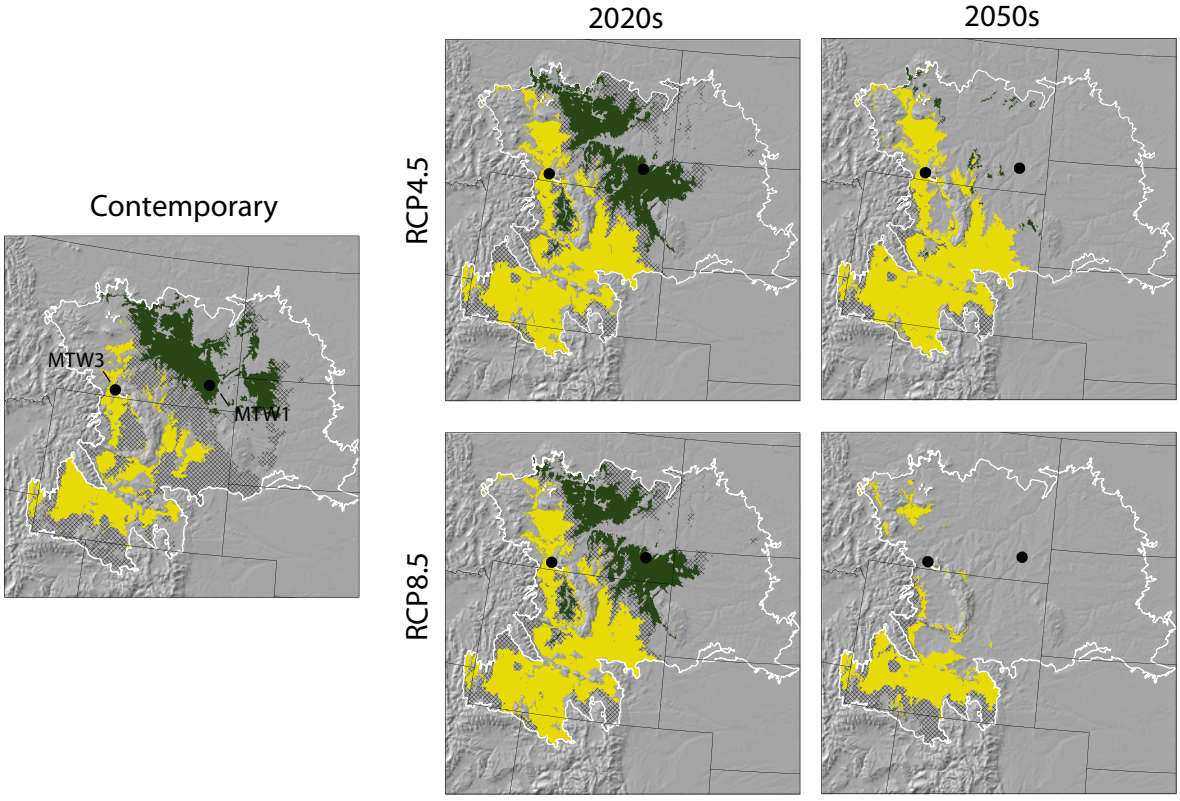

FIG. 5. Focal point seed transfer areas of two Wyoming Basin, *Artemisia tridentata* populations depicted in color fill. Transfer areas are shown for contemporary climate (1981–2010) and 2020s (2011–2040) and 2050s (2041–2070; RCP4.5). Focal points are depicted with the black dots. Areas that are outside the focal point transfer limits but within the bioclimatic niche are depicted with diagonal hatching.

TABLE 3. Predicted focal point and seed transfer areal coverages for five *Artemisia tridentata* populations in two regions.

Region/Population	MCMT (°C)	Contemporary (km^2)	2050s RCP4.5 (km^2)	Areal change (%)
Great Basin	na	(307,092)	(192,824)	−37
CAT2	−1	4.6% (14,318)	16% (32,714)	56
IDT2	−2.3	54% (165,906)	49% (95,285)	−42
UTW2	−4.5	11% (33,928)	10% (20,177)	−41
Wyoming Basin	na	(293,094)	(147,906)	−50
MTW3	−5.1	21% (60,438)	34% (95,535)	63
MTW1	−7.9	17% (50,717)	1.3% (3,698)	−93

Notes: na, not applicable. Populations are listed in descending order from warmest to coldest according to mean coldest month temperature (MCMT). Areal coverages are calculated separately for the Great Basin and Wyoming Basin. Percent coverage in the region and population areal coverages in parentheses shown in Figs. 4 and 5 is presented for the contemporary and 2050s climates. The difference between contemporary and mid-century is shown in the areal change column.

promote plant fitness and to facilitate movement over large geographic distances. In the Great Basin, the warmest seed zones (e.g., seed zone 1, Fig. 3) or populations (e.g., CAT2, Fig. 4) are projected to double-seed transfer areal coverage by mid-century, whereas colder-adapted seed zones and populations experience marked declines in areal coverage in the Great Basin (Table 3, Figs. 3 and 4). To facilitate adaptation, our model supports transferring populations from eastern California (e.g., CAT2) northward to eastern Oregon (Fig. 5a). Similarly, in the Wyoming Basin, warmer populations (e.g., MTW3) increase in areal coverage as colder populations (e.g., MTW1) decline.

There are notable limitations to our model and prediction. First, predictions are based solely on climate and do not consider other biotic and abiotic factors. Sagebrush interactions with other plants and soils can have influence on sagebrush establishment and distribution. Second, measures of genetic variation encompass possible maternal effects. Third, genetic adaptation to a changing climate will be negligible. Fourth, future predictions reflect the limitations associated with the climate models and RCPs (Riahi et al. 2011, Pachauri et al. 2014). Finally, the model assumes limitless seed/pollen dispersal to fill future niche space. The changing seed zones and niche space would require assisted migration to match these mid-century projections.

Several translocation strategies have been developed (Weeks et al. 2011, Aitken and Whitlock 2013, Williams and Dumroese 2013). Ultimately, the specific characteristics and

conservation needs of the species in question will necessitate tailored strategies. Big sagebrush in the Great Basin and Wyoming Basin face different threats due to contrastive ecology and climate (Still and Richardson 2015, Chambers et al. 2017). Our analysis of the climatic niche and seed transfer supports an approach specific to different ecological regions of *A.t. wyomingensis* and *tridentata*. Based on degree of projected range contraction and displacement by exotic annual grasses at the warmer climatic spectrum (Bradley et al. 2016), we recommend more urgency in the proactive seed transfer in the Great Basin. Seed collections in the warmest and driest areas of the region (e.g., IDT2 and CAT2, Fig. 4) could be mixed with local seed sources from cooler areas within the stable climatic niche. This would introduce warm-adapted traits into areas where they are expected to be favorable by mid-century and potentially rescue genotypes that may face extirpation in the next few decades. Seed transfer in the Wyoming Basin from warmer to cooler areas does not appear to be as urgent; however, in the future, we recommend the transfer of seed from warmer areas to cooler areas in this region (Fig. 5).

Seed transfer approaches

Our goal is to provide guidance on contemporary and future seed transfer that can improve seeding success and resiliency of restored sagebrush sites. We illustrate two seed transfer approaches, fixed and focal seed zones, for sagebrush. Ukrainetz et al. (2011) evaluated the advantages and disadvantages of these two approaches in interior spruce (*Picea glauca*). The authors concluded that while focal point seed zones are more complex to develop, this approach provided greater flexibility with changing climates. The authors use a hybrid system where focal point seed zones were constrained by fixed jurisdictions (Ukrainetz et al. 2011). We advocate for a similar approach in sagebrush where focal point seed transfer is constrained by ecoregions (Figs. 4 and 5). The disadvantage to a focal point approach is the difficulty in developing transfer limits for each restoration or collection site. The steps in calculating focal point transfer limits can be accomplished by automating these calculations through a web-based platform. To provide a user-friendly application, our plan is to integrate the sagebrush genetic models into a web-based tool (Climate Smart Restoration Tool) that is under development and modeled after the Seedlot Selection Tool (Howe et al. 2009; tools *available online*).[5,6] This web-based platform will use a focal point seed transfer method to project transfer limits around any user-defined geographic point for contemporary and projected future climates. The tool will allow land managers and seed collectors to target a seed transfer area based on the restoration site and plan seed transfer for a site's long-term climatic trajectory.

Conclusion

The demand for sagebrush seed for restoration has been increasing over the past decade. Land management agency requests for sagebrush seed have approached 500,000 pounds in years with frequent and large fires. Our research shows seed zones delimited on clinal variation are largely associated with continentality. In addition, our model predicts that warm-adapted populations, typically occurring near the trail edge, will be key to conservation and restoration of this species for decades to come. We advocate the use of empirically based seed transfer zones that can simplify current provisional zones and could aid in the improvement of big sagebrush establishment and long-term resiliency of restored sites.

[5] climaterestorationtool.org

[6] seedlotselectiontool.org

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Supporting Information

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.1804/full

Data Availability

Code can be found at GitHub (https://doi.org/10.5281/zenodo.1409268), and the data are archived at Dryad (https://datadryad.org/resource/doi:10.5061/dryad.q477f90).