

# Adaptive responses reveal contemporary and future ecotypes in a desert shrub

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**Abstract.** Interacting threats to ecosystem function, including climate change, wildfire, and invasive species necessitate native plant restoration in desert ecosystems. However, native plant restoration efforts often remain unguided by ecological genetic information. Given that many ecosystems are in flux from climate change, restoration plans need to account for both contemporary and future climates when choosing seed sources. In this study we analyze vegetative responses, including mortality, growth, and carbon isotope ratios in two blackbrush (*Coleogyne ramosissima*) common gardens that included 26 populations from a range-wide collection. This shrub occupies ecotones between the warm and cold deserts of Mojave and Colorado Plateau ecoregions in western North America. The variation observed in the vegetative responses of blackbrush populations was principally explained by grouping populations by ecoregions and by regression with site-specific climate variables. Aridity weighted by winter minimum temperatures best explained vegetative responses; Colorado Plateau sites were usually colder and drier than Mojave sites. The relationship between climate and vegetative response was mapped within the boundaries of the species–climate space projected for the contemporary climate and for the decade surrounding 2060. The mapped ecological genetic pattern showed that genetic variation could be classified into cool-adapted and warm-adapted ecotypes, with populations often separated by steep clines. These transitions are predicted to occur in both the Mojave Desert and Colorado Plateau ecoregions. While under contemporary conditions the warm-adapted ecotype occupies the majority of climate space, climate projections predict that the cool-adapted ecotype could prevail as the dominant ecotype as the climate space of blackbrush expands into higher elevations and latitudes. This study provides the framework for delineating climate change-responsive seed transfer guidelines, which are needed to inform restoration and management planning. We propose four transfer zones in blackbrush that correspond to areas currently dominated by cool-adapted and warm-adapted ecotypes in each of the two ecoregions.

**Key words:** assisted migration; blackbrush; climate change; *Coleogyne ramosissima*; ecological restoration; seed transfer zones.

## INTRODUCTION

Being sessile organisms, plant species are attuned to their local or regional climate. Therefore, climatic variation across a species distribution can have a profound effect on the degree and spatial patterns of adaptive population divergence (Turesson 1925, Davis et al. 2005, Shaw and Etterson 2012). Climate adaptation can exhibit a clinal or continuous gradient of adaptive genetic variation across the landscape, or it can exhibit ecotypic differentiation, where the shift in genetic variation is relatively abrupt (Turesson 1925, Ledig et al. 2013). In either case, an understanding of how genetic variation is arrayed across the landscape can greatly

enhance the success of restoration and conservation. Movement of seed populations to areas outside of their zone of optimal adaptation can have a negative impact on fitness, and may result in restoration failure. Even if successful, the introduction of marginally adapted populations could potentially result in reduced fitness of adjacent natural populations through introgression with the transferred plants (Hufford and Mazer 2003, McKay et al. 2005). This has prompted researchers and managers to define seed transfer zones to provide a foundation for collecting and distributing seed populations for conservation and restoration projects.

There is now considerable support for climate change impacts across different terrestrial ecosystems (Walther et al. 2002). Studies employing different approaches have shown an association between plant range shifts and climate change. These studies have found close relationships between climate patterns and contempo-

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rary plant die-offs (Breshears et al. 2005, Rehfeldt et al. 2009), plant physiology (Jeltsch et al. 2008, Anderegg 2012) and plant distributions (Hamann and Wang 2006, Rehfeldt et al. 2006, Iverson et al. 2008). Much of this research has focused on understanding the associations at larger ecological scales, including species and biological community-level interactions. However, populations, the manifestation of spatial patterns of intraspecific genetic variation, are the fundamental units for conservation and restoration (Moritz 1994), and have been one of the principal issues of contention in assisted migration debates (Hoegh-Guldberg et al. 2008, Ricciardi and Simberloff 2009). While populations defined by adaptive genetic patterns have been studied in many plant species, especially trees, rarely have these patterns been examined under future climate scenarios (e.g., Etterson 2004, Rehfeldt and Jaquish 2010, Gray et al. 2011). Delineating seed transfer zones that consider both contemporary and future climate will help resolve unanswered questions in assisted migration, a critical need in restoration planning and seed banking for resource management (Friggens et al. 2012, Richardson et al. 2012).

Deserts currently occupy approximately one-third of the global, terrestrial landmass, and this figure is expected to increase substantially for warm deserts in the near future (Zeng and Yoon 2009). It is predicted that two of the desert biomes in western North America, the Mojave and the Great Basin Deserts, including the Colorado Plateau ecoregion, are expected to increase 40% and 45% by 2060, respectively, due to predicted climate change (Rehfeldt et al. 2012). However, while the climate that supports these biomes will likely increase in area, there is uncertainty in whether the current native plant species or communities will occupy these expanded regions. Ecological modeling, monitoring, and vulnerability assessments have shown that these shrub-dominated biomes are threatened by the interactions between climate and invasive annual grasses, which can influence fire regimes by accelerating fire frequency (Balch et al. 2012, Comer et al. 2012). Moreover, ecological theory suggests greater climate variability will likely favor plant invasion (Bradley et al. 2010). For western North American deserts, lower mean rainfall and greater variability in precipitation can result in reduced resiliency of native vegetation following disturbance (e.g., wildfire), making these areas more susceptible to invasive weeds (Brooks and Matchett 2003, Brooks and Chambers 2011, Diez et al. 2012). Decreased precipitation and increased variability are likely outcomes of climate change in this region (Dominguez et al. 2010, Seager et al. 2012). Under the circumstances outlined above, blackbrush and other desert shrub ecosystems have a high risk of failure without restoration guided by ecological genetic information.

Successful restoration and maintenance of desert shrubland communities is contingent upon developing an understanding of climate-adapted patterns and their

potential movement with a changing climate for key shrub species. Shrubs are a predominant cover type in the cold and warm desert biomes of western North America and are of critical importance to ecosystem stability, supporting numerous plant and wildlife species. Three shrub species are considered widespread landscape dominants across the Mojave Desert and Colorado Plateau ecoregions, hereafter referred to as Mojave and Plateau, respectively. Creosote bush (*Larrea tridentata*) occupies the Mojave (warm desert), big sagebrush (*Artemisia tridentata*) occupies much of the higher elevations of the Plateau (cold desert), and blackbrush (*Coleogyne ramosissima*), which occupies both ecoregions, is distributed along the ecotone between plant communities dominated by cold and warm desert species (Beatley 1975, Bowns and West 1976).

Our study focuses on the distribution of adaptive genetic variation in blackbrush. A monotypic member of the Rosaceae, blackbrush owes its taxonomic distinction to unusual features for a rosaceous shrub, including opposite branching, obligate wind pollination, and an unusual chromosome number (Pendleton and Pendleton 1998). This monotypic classification has also been confirmed by phylogenetic analyses (Potter et al. 2007). Because of its unique morphology and life history traits, Stebbins and Major (1965) considered blackbrush to be a paleoendemic, suggesting that it could be genetically depauperate. However, a recent population genetic study of blackbrush has shown that it possesses considerable genetic diversity, and that a moderate proportion of this genetic diversity is structured between the Mojave and Plateau ecoregions (Richardson and Meyer 2012). These data, along with the Early Holocene and Late Pleistocene fossil record, suggest that this species has long been segregated into two metapopulations, and that high plateaus between the Mojave and Plateau maintain the geographic isolation to the present (Richardson and Meyer 2012).

In the current study, we assess adaptive genetic variation in blackbrush by: (1) quantifying different vegetative responses among populations and ecoregions in two common gardens, (2) evaluating the associations among mortality, growth, carbon isotope ratios, and population-specific climate variables, (3) developing a genecological model from which vegetative responses are predicted from climate, (4) mapping this genecological model within the distribution of a blackbrush bioclimate model for contemporary and future climates, and (5) using the resulting insights to develop seed transfer zones and guidelines.

## MATERIAL AND METHODS

### *Samples and data collection*

Blackbrush seeds were collected from 26 sites, hereafter referred to as populations. Seedlings were derived from different plants in each population. Eleven populations were located within the Plateau and 15

TABLE 1. Geographic descriptions and common-garden sample sizes of blackbrush (*Coleogyne ramosissima*) populations.

Population	Ecoregion	Longitude (N)	Latitude (W)	Elevation (m)	Planting Year	DER <i>N</i>	LUNA <i>N</i>
ARCH	CP	38.761	109.600	1494	2009	16	12
BRD2	CP	37.752	110.280	1429	2009	16	12
GBTO	CP	38.651	109.677	1407	2009	13	13
HITE	CP	37.879	110.354	1278	2009	15	12
ISKY	CP	38.582	109.801	1799	2009	15	11
MHAT	CP	37.159	109.855	1293	2009	16	12
SOBL†	CP	37.281	109.694	1442	2009	16	12
LROK	CP	37.761	110.651	1684	2010	16	13
NEED	CP	38.168	109.760	1494	2010	15	9
SOBL†	CP	37.281	109.694	1442	2010	16	0
WMES	CP	37.435	109.473	1607	2010	16	11
BDAM	M	37.100	113.823	1482	2009	15	12
BRWS	M	37.660	110.183	1610	2009	16	12
HMES	M	37.226	113.257	1117	2009	16	12
LEGR	M	37.175	113.338	985	2009	16	12
RROV	M	36.116	115.444	1173	2009	11	12
RRCT	M	37.275	113.646	1439	2009	16	12
SNOW	M	37.225	113.636	1235	2009	16	11
TOQP	M	37.276	113.299	1133	2009	14	12
WHIL	M	37.212	113.629	1187	2009	16	12
LEEC	M	36.421	115.541	1485	2010	16	12
LPIN	M	36.640	118.088	1134	2010	16	11
LHMR	M	33.952	116.153	1467	2010	16	12
SMRD	M	36.698	115.068	1559	2010	16	12
TOQO	M	37.264	113.327	1132	2010	16	0
WTHP	M	35.515	115.105	1393	2010	16	12

Notes: Key to abbreviations: CP, Colorado Plateau; M, Mojave; *N*, number of plants at the Desert Experimental Range (DER) and Los Lunas (LUNA). For a complete list of the population responses and climate data see Appendix A.

† The SOBL population was replicated for both the 2009 and 2010 planting years.

within the Mojave. In November 2009 and 2010 common gardens were established from containerized seedlings at the Desert Experimental Range (DER), Utah, and at the Los Lunas Agricultural Science Center (LUNA), New Mexico (see Table 1 for collection site locations and numbers of plants outplanted). Both garden locations are outside the blackbrush natural range and were chosen based upon differences in the climate, availability of onsite weather stations, and logistics. LUNA has temperatures similar to those experienced by this species on the Plateau, and is generally colder than normal for Mojave blackbrush. Because of its position near the bottom of a small, closed valley, the DER site is subject to extended periods of intense cold due to midwinter atmospheric inversions. Consequently, DER temperatures are colder than Plateau blackbrush sites and much colder than Mojave sites (Fig. 1).

The experimental designs for these gardens included a randomized complete block design at the DER and a completely randomized design at LUNA. Blocking at the DER garden was established for future treatments; however, no treatments were imposed during this study. All seedlings were greenhouse grown in 15-cm (six-inch) cone-tainers for 6–8 months. The plants were then hardened off prior to planting by placing them outside for two weeks to reduce transplant shock. Seedlings of 16 of the 26 populations were outplanted in November 2009, and the remaining 10 populations were planted in November 2010. For the first two growing seasons after

planting, supplemental water was added at both common gardens to ensure establishment. Plants were watered individually to deliver similar amounts of water to each plant.

Data collection was initiated one year after the planting date. Mortality was measured twice a year in early spring and fall, and crown area was measured once a year in fall. Mortality was confirmed in the spring when living plants flush out new leaves. Crown area was calculated using an overhead digital photo of each plant. For digital processing, a white background was placed under each plant to add contrast, and a visual scale was added to calibrate each photo's pixel size. These photos were then analyzed using ImageJ ver. 1.46 (Schneider et al. 2012), and crown areas were reported in square centimeters. Crown areas were recorded one year after the planting dates, 2010 for the 2009 planting and 2011 for the 2010 planting. Due to the substantial mortality that occurred after the 2010–2011 winter at the DER, crown area for the 2010 plantings at this common garden was not measured. Population means for crown areas, mortality, and carbon isotope ratios at each garden were used in the subsequent data analyses (Appendix A).

Carbon isotope ratio ( $^{12}\text{C}:^{13}\text{C}$ ) is an indicator of the concentration gradient of  $\text{CO}_2$  between air and leaves during photosynthesis, and can be used to compare intrinsic water-use efficiency, the amount of  $\text{CO}_2$  assimilated per unit water diffusing through stomata, given similar environmental conditions (e.g., common

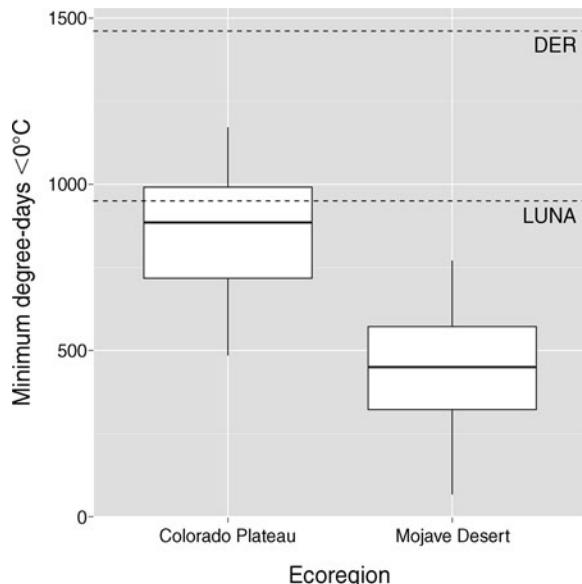


FIG. 1. Boxplot of minimum degree-days  $<0^{\circ}\text{C}$  at blackbrush (*Coleogyne ramosissima*) sites segregated between the Colorado Plateau ( $n = 60$ ) and Mojave ( $n = 52$ ) ecoregions. These minimum degree-days are estimated from a spline model (Rehfeldt 2006) during a period from 1961 to 1990. Higher values indicate colder winters. The ecoregion means are significantly different ( $P < 0.0001$ ). The dashed lines show the 1961–1990 minimum degree-days  $<0^{\circ}\text{C}$  predicted for the two common gardens: Desert Experimental Range (DER), latitude  $38.596^{\circ}\text{N}$ , longitude  $113.748^{\circ}\text{W}$ , elevation 1599 m; and Los Lunas (LUNA), latitude  $34.769^{\circ}\text{N}$ , longitude  $106.762^{\circ}\text{W}$ , elevation 1477 m. The top and bottom of the boxes indicate the upper and lower quartiles, respectively. The bold line within the box represents the median. The whiskers define the variability outside of the quartiles.

gardens [Farquhar and Richards 1984, Farquhar et al. 1989]). Samples were collected in September of 2011 from both living and recently dead plants ( $<6$  months) in the common gardens at both locations, and carbon isotope ratios were obtained from shoot tips. Shoot tips (leaves and stem) were dried, ground for one minute using cleaned metal beads in a TissueLyser (Qiagen, Valencia, California, USA), and the carbon isotope composition was determined using a Picarro 2020 CRDS laser spectrometer (Picarro, Santa Clara, California, USA) with Costech 3140 flash combustion gas chromatograph (Costech, Valencia, California, USA) to deliver samples. Analytical precision, calculated from analysis of standards distributed throughout each run, was  $\pm 0.2\%$  or less. Isotopic values are reported in the conventional  $\delta$ -notation ( $\delta = ([R_{\text{sample}}/R_{\text{standard}}] - 1) \times 1000$ , where  $R = {}^{13}\text{C}/{}^{12}\text{C}$ ) relative to the international standard Vienna Pee Dee Belemnite (VPDB) and expressed as parts per thousand (‰).

#### Climate estimates

Climate estimates were obtained from Crookston and Rehfeldt (2008) by providing geographic coordinates and elevations for each of the original population

locations. These estimates were obtained from thin plate splines using ANUSPLIN v4.1 (Hutchinson 2000) to obtain normalized monthly means from the period between 1961 and 1990 (Rehfeldt 2006). Eighteen variables were derived directly from the monthly means (see Rehfeldt et al. 2006) that described annual and seasonal precipitation and temperatures, freezing dates, and heat sums; and an additional 16 variables considered precipitation–temperature interactions (see Rehfeldt et al. 2006). Climate estimates relevant to the genetic analyses are listed in Appendix A.

#### Genetic analysis and modeling

Prior to genecological model development, analysis of variance (ANOVA) was conducted to assess the differentiation among population means at two spatial scales: populations and ecoregions (i.e., groups of populations). Separate ANOVAs were performed for each garden and planting year for mortality, crown area, and carbon isotope data. A Bonferroni test was used to detect outliers in the ecoregional means. Three factors were included at the DER (i.e., populations, ecoregions, and blocks), and two factors were included at LUNA (i.e., populations and ecoregions) due to the completely randomized design.

Development of the genecological model focused on mortality as a response variable. Percent mortality was chosen because of the strong differentiation observed between ecoregions at the DER garden in each planting year, and the high correlation with climate variables (Appendix B). This analysis began with the regression of the 2012 population mean percent mortalities from both 2009 and 2010 planting years at the DER with each of the 34 climate predictors. Based on the Pearson's correlation coefficient ( $r$ ), nine climate variables showed a superior fit ( $r > 0.8$ ) to population mean mortality (Appendix B). All nine climate predictors were highly collinear ( $r > 0.7$ ); therefore the best-fitting single predictor, aridity weighted by winter cold, was used in a linear regression model. Aridity weighted by winter cold, hereafter referred to as the climate predictor, can be defined as: (the sum of warm days  $>5^{\circ}\text{C} \div$  mean annual precipitation)  $\times$  the sum of minimum degree-days  $<0^{\circ}\text{C}$ . For cross validation, the climate predictor was regressed with the other vegetative responses showing significant differences between ecoregions detected from ANOVA.

#### Bioclimate model

The Random Forests classification tree of Breiman (2001) was used to develop a bioclimate model suited to predicting presence or absence of blackbrush from our array of 34 climate variables. The statistical procedures parallel Rehfeldt et al. (2006), use the algorithm in R (R Development Core Team 2006), and produce a model suited to predicting blackbrush occurrence, that is, the realized climate niche. The analysis used the 112 data points of the genecological modeling, and, as absence data points, a sample of the 1.75 million observations

used in analyses of North American biomes (Rehfeldt et al. 2012). This sample was obtained by discarding all observations far beyond the geographic scope of this study, that is, retaining those observations between 25° and 50° latitude that were west of 96° W longitude. We further discarded all observations that by chance could have been proximal to presence observations, that is, all observations in the Mojave Desert, Great Basin Desertscrub, and Great Basin Shrub–Grassland biomes within the geographic distribution of blackbrush. These deletions made available for our modeling 54 872 observations for which blackbrush assuredly was absent.

Assembling presence–absence data for analysis requires satisfying Breiman’s recommendation that absence data be in reasonable balance with presence data. In following the protocol of Rehfeldt et al. (2006), we prepared 25 data sets within which presence and absence data points represented 40% and 60% of the total, respectively. Each data set contained all 112 presence observations, weighted by a factor of two. Weighting assures that the resulting model is most robust for climates in which blackbrush actually occurs (Rehfeldt et al. 2006, Ledig et al. 2010, Worrall et al. 2013) and allows the number of absence data points in each data set to be doubled.

In sampling the observations lacking blackbrush, the 112 presence locations of blackbrush were used to create a climatic hypervolume from the 18 derived variables. This hypervolume was then expanded by  $\pm 1.25$  standard deviations, and absence points were obtained by a random sample within and outside the hypervolume such that those sampled within the hypervolume amounted to 40% of the total number of observations in the data set and those sampled outside the hypervolume represent  $\sim 20\%$  of the total. This procedure forced a preponderance of the observations to be in climates that would be most difficult to separate from presence. The 25 data sets compiled by these procedures thus contained about 560 observations.

Model development was initiated by using each data set to construct a set of 100 classification trees in 25 forests, using 34 climate variables as predictors. The predictors then were eliminated in a stepwise process using the mean decrease in accuracy to judge variable importance until only one variable remained. The best-fitting model was selected according to out-of-bag errors, calculated from a subsample of the presence–absence data set. Although intercorrelations among the original 34 variables tended to be strong, collinearity and over-parameterization are inconsequential in the Random Forests algorithm because the generalization error converges to a limit as the number of trees in a forest becomes large (Breiman 2001).

#### *Mapping*

The selected bioclimate model from Random Forest analysis was mapped within a geographic window (30°–51° N latitude and 100°–122° W longitude) using the

climate grids of Crookston and Rehfeldt (2008). Each of the contemporary climate grid cells (0.0083° resolution or  $\sim 1 \text{ km}^2$ ) was evaluated for climate suitability for blackbrush by the number of votes cast averaged for the 100 trees in the 25 forests. A grid cell was considered to have suitable climate for blackbrush when the majority of the total of 2500 votes (one each from 100 trees in 25 forests) were cast in favor of the climate being suitable for blackbrush.

Climate surfaces for the decade 2060 (2056–2065 [Crookston and Rehfeldt 2008]) were used to project a blackbrush bioclimate for this decade. To provide a consensus of 2060 climates, we used methods similar to Ledig et al. (2012) and Wang et al. (2012) where the outputs from three General Circulation Models (GCMs) and two carbon emission scenarios (SRES) are combined into an agreement map. GCMs included the Canadian Center for Climate Modeling and Analysis (CCCMA) [A2 and B1 scenarios]; Met Office, Hadley Centre (UKMO) [A2 and B2 scenarios]; and the Geophysical Fluid Dynamics Laboratory (GFDL) [A2 and B1 scenarios]. Information on the GCMs and scenarios can be found elsewhere (IPCC 2007). Agreement mapping of the six GCM–scenarios combinations was performed in ArcMap v10.0 (ESRI, Redlands, California, USA). Predicted presence of blackbrush-suitable climate is mapped only where more than three of the six GCM/scenarios combinations showed agreement.

The genealogical model was mapped within the same geographic window as above, where the climate predictor was obtained from each of the gridded cells in the climate surface window. The model values for each grid cell ( $\sim 1 \text{ km}^2$ ) were written into an ASCII file using the R statistics package *yaImpute* (Crookston and Finley 2008). Mapping was performed using the bioclimate model to locate grid cells of suitable climate. Model values were mapped as continuous variation. Because the climate space extends to climate conditions that exceed the mortality observations (values from 0% to 100%), the modeled range of mortality included negative or  $>100\%$  values. Ecotypes were also mapped based upon the steep clines predicted in the continuous variation. We set an ecotype division using climate predictor values of the HITE and BRD2 populations (Appendix A) that occupy the ends of the steep clinal transition in the Colorado Plateau. This climate predictor value was 188, equal to a mortality value of 37.8%. This value serves as the division between cool-adapted and warm-adapted ecotypes.

## RESULTS

### *Common-garden responses*

Differences in mortality, carbon isotope ratios, and crown area means were principally observed at the DER. For example, DER mortality averaged across planting years was 15.8% and 74.9% for Plateau and Mojave ecoregions, respectively. In contrast, at LUNA,

TABLE 2. Comparisons of Colorado Plateau and Mojave mean plant responses: mortality, crown area, and carbon isotopes.

Garden and planting year	Mortality (%)		Crown area (cm <sup>2</sup> )		Isotope ratio (δ <sup>13</sup> C)	
	Plateau	Mojave	Plateau	Mojave	Plateau	Mojave
DER						
2009	19.6	<b>80.7***</b>	135	<b>92</b>	-25.61	<b>-27.36***</b>
2010	4.8	<b>65.6***</b>	na	na	-26.55	<b>-27.99</b>
LUNA						
2009	16.7	9.1	121	111	-25.42	<b>-25.95</b>
2010	15.6	33.9	183	145	-26.92	-26.77

*Notes:* These data were collected at two gardens, Desert Experimental Range (DER), Utah, and Los Lunas (LUNA), New Mexico, and two planting years, 2009 and 2010. Significant differences were determined by ANOVA performed with two levels: among populations and between ecoregions. Population comparisons are not shown. Values in boldface type indicate  $P < 0.05$ . The letters "na" mean not available.

\*\*\*  $P < 0.001$  between Colorado Plateau and Mojave ecoregions.

ecoregion mortality was 16.6% and 17.7% for Plateau and Mojave, respectively. To evaluate these data ANOVA was performed using two levels, population and ecoregion means, for each garden and planting year. However, due to the significant differences observed between ecoregions, we focus on presenting the data that compare ecoregions. A Bonferroni test determined that mortality and carbon isotope means of the HITE population were outliers ( $P < 0.001$ ) when comparing ecoregions, supporting HITE as a member of the Mojave rather than the Plateau. Hereafter, we consider HITE as a member of the Mojave. At the DER, ecoregional effects were significant for mortality, carbon isotope, and crown area responses in the 2009 planting and for mortality and isotope means in the 2010 planting. No block effects were observed (data not shown). The LUNA garden showed no significant differences between ecoregion with the exception of carbon isotope ratios in the 2009 planting (Table 2). We use significant vegetative response differences between ecoregions to assess climate associations.

To deduce potential climatic influences on these vegetative responses at the DER and LUNA gardens, we examined records from the weather stations adjacent to each garden. The significantly increased mortality of Mojave populations at the DER coincided with low monthly mean minimum temperatures for January of 2011. From September 2010 to June 2011, mortality of the 2009 planting of Mojave populations (including HITE) increased substantially from 2.4% to 89.2%. The corresponding mortality in Plateau populations was much smaller, increasing only from 2% to 6.6% across the same periods. Mean monthly minimum temperature in January 2011 at the DER was  $-17^{\circ}\text{C}$ , approximately  $8^{\circ}$  colder than that of the same year at LUNA.

Because accumulating winter temperatures, mean minimum degree-days  $<0^{\circ}\text{C}$ , are an integral part of the climate predictor, a comparison of among ecoregions and garden locations is essential to understand blackbrush adaptive responses. Mean minimum degree-days  $<0^{\circ}\text{C}$  for the 2010/2011 winter summed to 862 and

1237 degree-days for the LUNA and the DER gardens, respectively (data not shown). These values were slightly warmer than the 29-year average based on the spline climate model, 950 and 1461 degree-days for the LUNA and DER gardens, respectively (Fig. 1). Boxplots illustrate the significant winter temperature differences between Mojave and Plateau blackbrush and differences relative to the garden locations.

#### Genecological model

Mortality data collected in 2012 at the DER from the 2009 and 2010 plantings served as the response variable for developing a genecological model using the climate predictor (Table 3) estimated from each population's site of origin (Appendix A). We use a linear regression model (Fig. 2A)

$$\text{mortality \%} = 120.76 + \text{climate predictor} \times (-0.44).$$

TABLE 3. Relevant climate variables in the bioclimate and genecological models.

Bioclimate model	
1)	Mean annual precipitation $\times$ mean temperature in coldest month
2)	Ratio of summer to total precipitation
3)	Summer dryness index (SDI; degree-days $>5^{\circ}\text{C}$ accumulating within the frost-free period $\div$ growing season precipitation, April to September)
4)	SDI $\times$ minimum degree-days $<0^{\circ}\text{C}$
5)	Mean temperature of the warmest month
6)	Degree-days $>5^{\circ}\text{C}$ accumulating within the frost-free period
7)	Growing season precipitation, April to September $\times$ degree-days $>5^{\circ}\text{C}$
8)	Degree-days $>5^{\circ}\text{C}$
Genecological model	
Climate predictor = (degree-days $>5^{\circ}\text{C} \div$ mean annual precipitation) $\times$ accumulating mean minimum degree-days $<0^{\circ}\text{C}$	

*Notes:* Bioclimate model variables are listed in order of importance. For a full list of climate variables used in the analysis see Rehfeldt (2006).

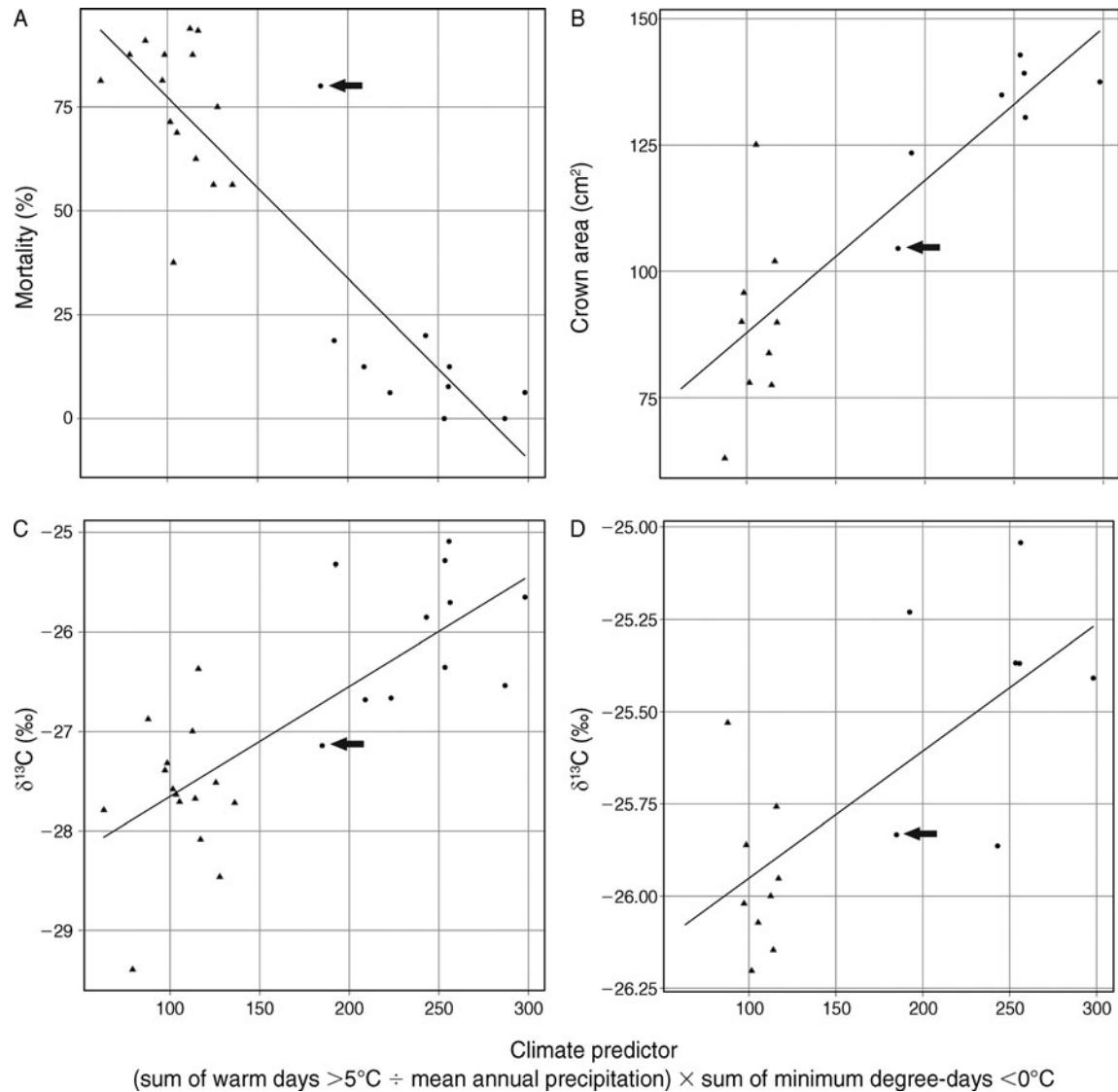


FIG. 2. Blackbrush (*Coleogyne ramosissima*) average population responses regressed on the climate predictor at each population's site of origin. Lower values of the climate predictor equate to warmer and wetter climates. Panels show (A) mean population mortality (%) from 2009 and 2010 plantings, (B) crown area ( $\text{cm}^2$ ) from the 2010 planting, and (C) carbon isotope ratio ( $\delta^{13}\text{C}$ ) from the 2009 and 2010 plantings from the Desert Experimental Range garden. Panel (D) shows the carbon isotope ratio ( $\delta^{13}\text{C}$ ) of the 2009 planting shown from the Los Lunas garden. Triangles and circles represent populations originating from the Mojave Desert and Colorado Plateau ecoregions, respectively. The arrow denotes the outlier population in the Colorado Plateau, Hite, discussed in *Results: Common-garden responses*. The diagonal line represents the linear model for each plot. Correlation coefficients can be found in Appendix B.

This linear model supports a negative relationship between the response variable and the predictor ( $r = -0.89$ ,  $P < 0.0001$ ), whereby populations from warmer and wetter sites are more likely to have higher mortality at the DER (Fig. 2A).

Carbon isotope and crown area population means that showed ecoregion effects in the ANOVA (Table 2) were also used to evaluate the climate predictor. These variables included crown area at the DER and carbon isotope values from both gardens. Small crown areas were positively associated with lower climate predictor

values and warmer and wetter climates (Fig. 2B,  $r = 0.86$ ,  $P < 0.0001$ ). Similarly, more negative values of  $\delta^{13}\text{C}$  were associated with lower climate predictor values (Fig. 2C,  $r = 0.77$ ,  $P < 0.0001$ ) and at LUNA (Fig. 2D,  $r = 0.72$ ,  $P < 0.0001$ ).

#### *Bioclimate model*

The step-down procedure employed by Random Forests produced 34 potential models. Model error rates remained relatively constant during the step-down procedure until reaching a seven-variable model where

the error began to increase. To balance commission, omission, and out-of-bag error rate, we chose an eight-variable model (Table 3) with an out-of-bag error of 3.04%, which only differed slightly from the lowest out-of-bag error of 2.9%, a 33-variable model. Commission and omission rates for this model were 5.1% and 0%, respectively. The most important variable in this model was the interaction between mean temperatures in the coldest month and mean annual precipitation. The mapped prediction of contemporary distribution of blackbrush climate space served to overlay values from the geneecological model (Fig. 3A).

#### *Geneecological model mapping*

The mapped predictions from the geneecological model were obtained by running the climate predictor values of each grid cell through the linear regression model. Areas predicted to have suitable climate for blackbrush on the Plateau are predominately cooler, depicted by cooler colors, than the Mojave ecoregion, depicted by warmer colors (Fig. 3A). One exception in the Plateau ecoregion is the Colorado River valley where significantly warmer winter temperatures are found. To illustrate the cline in temperatures, we chose to simplify the climate predictor interaction into one of its components, accumulating mean minimum degree days  $<0^{\circ}\text{C}$ . These warmer winter minimum temperatures associated with the Colorado River are depicted in the climate surface (Fig. 3B). The climate along the Colorado River in the Plateau more closely resembles a Mojave climate. Likewise, the HITE population, adjacent to the Colorado River, has the warmest winter minimum temperatures in the Plateau ecoregion. HITE plant mortality was similar to Mojave populations at 80% (Appendix A), and displayed intermediate values between Mojave and Plateau populations for crown area and carbon isotope ratios (Fig. 2B–D).

#### *Future climates*

The blackbrush climate space was projected for 2060 climate space by mapping a consensus of six projections, that is, three GCMs and two carbon emission scenarios. Models with overlapping projections of four or more of the six GCM/scenarios were mapped as suitable climate space (Fig. 4). Using the four-model agreement projection (Fig. 4), a comparison between contemporary and future projections show that the climate space increases 52% by decade 2060 from 94 000 km<sup>2</sup> at present to 179 000 km<sup>2</sup> in 2060. Much of this expansion is predicted to occur in the lower basins of the Great Basin (i.e., Lahontan and lower Snake River Plain) and the Columbia Basin, where there is agreement across all six GCM/scenarios. Moreover, suitable climate space expansion occurs into the higher elevations of the Plateau; however, most of this region is supported by four of six GCM/scenarios. Loss of climate space occurs predominantly in the lower latitudes of Mojave (Fig. 4).

#### *Ecotypic differentiation*

Results of ANOVA suggested that the populations could be segregated into high- and low-mortality groups, supporting warm- and cool-adapted ecotypes. The threshold set for separating these groups was a mortality of 37.8%, or a climate predictor value of 188. These ecotypes were plotted within the boundaries of the contemporary and future bioclimate space (Fig. 5A, B). Under a contemporary climate, cool-adapted and warm-adapted ecotypes are largely distributed between ecoregions with the exception of the Colorado River drainage in the Plateau and the northern periphery of the Mojave. The cool-adapted ecotype potentially occupies 40 000 km<sup>2</sup> of the contemporary climate space and the warm-adapted ecotype occupies 54 000 km<sup>2</sup>. The expansion of climate space by 2060 (Fig. 4) supports a considerably different potential climate space distribution for warm-adapted and cool-adapted ecotypes (Fig. 5B). The climate space for the cool-adapted ecotype would expand to an estimated 141 000 km<sup>2</sup>, a 71% increase. However, the climate space for the warm-adapted ecotype would contract to 39 000 km<sup>2</sup>, a 28% reduction.

#### DISCUSSION

##### *Adaptive genetic responses to climate*

Minimum temperatures have been shown to be an important factor in the adaptive genetic variation of other grass, shrub, and tree species (St Clair et al. 2005, Horning et al. 2010, Johnson et al. 2012). Our data suggest that the accumulation of minimum degree-days  $<0^{\circ}\text{C}$  is a principal factor in blackbrush adaptive genetic variation. First, minimum degree-days  $<0^{\circ}\text{C}$  derived from the contemporary climate surface indicate Plateau blackbrush sites have significantly colder winters than Mojave blackbrush sites ( $P < 0.0001$ ; Fig. 1). Second, the vegetative responses at the DER, an extremely cold site for Mojave blackbrush (Fig. 1), show considerable differentiation between Mojave and Plateau populations, which support mainly warm-adapted and cool-adapted ecotypes, respectively. This is in contrast to the milder LUNA garden climate where no differentiation was detected in crown or mortality measurements (Table 2). And third, the mortality observed among Mojave populations at the DER followed a colder than normal winter with a monthly minimum temperature of  $-17^{\circ}\text{C}$ . This period was associated with a temperature inversion that occurred in early January of 2011 (data not shown). Similar conditions occur on the Plateau where episodic cold air inversions are common in the winter (Whiteman et al. 1999a). For example, during this same period at Hanksville, Utah near the northern periphery of blackbrush on the Plateau, the mean minimum temperature was  $-10^{\circ}\text{C}$ . However, inversions within the Grand Canyon and areas upstream along the Colorado River are rare due to several weather factors that are influenced by Grand Canyon topography (Whiteman

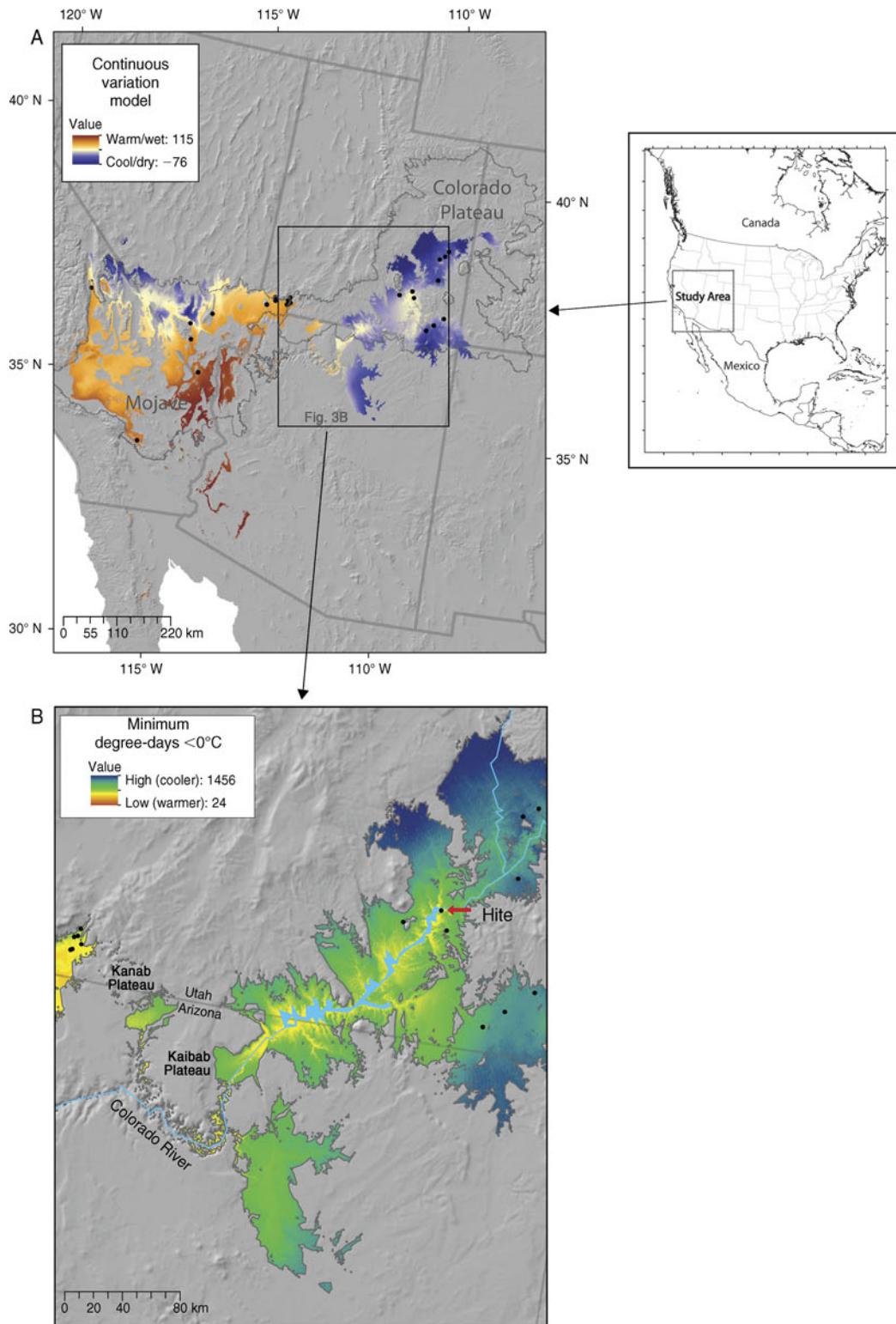


FIG. 3. (A) Mapped genecological model within the bounds of the bioclimate model of blackbrush (*Coleogyne ramosissima*). The points represent population locations. The gray line circumscribes the ecoregions. (B) This map illustrates the climate surface for accumulating minimum degree days  $<0^{\circ}\text{C}$  projected within the bioclimate model of blackbrush in the Colorado Plateau based on monthly means from the years 1961–1990. Colors from red to dark blue indicate areas of warmer and cooler winter temperatures, respectively.

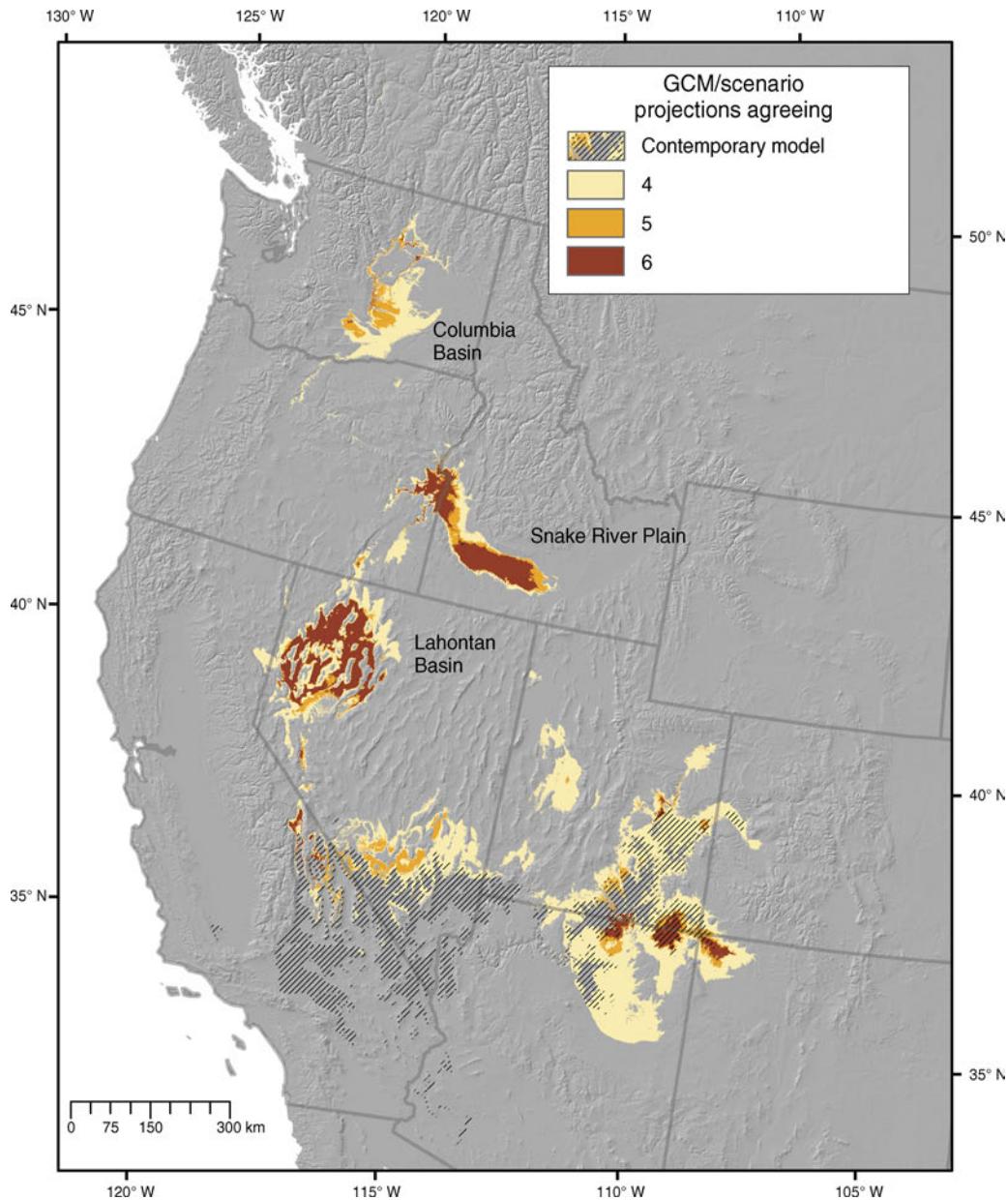


FIG. 4. A consensus bioclimate profile for blackbrush (*Coleogyne ramosissima*) based on decade 2060 projections using three General Circulation Models (GCM) (CCMA, Canadian Center for Climate Modeling; GFDL, Geophysical Fluid Dynamics Laboratory; UKMO, Met Office, Hadley Centre), and two carbon emission scenarios (SRES) each. GCM/SRES agreements of 4 or greater are shown according to color (see key). The contemporary bioclimate profile is illustrated by the diagonal pattern.

et al. 1999b). Along with temperature inversions, increasing minimum degree-days  $<0^{\circ}\text{C}$  associated with increasing elevation may explain the sharp cline in the genealogical model between HITE, located near the Colorado River, and surrounding Plateau populations (Fig. 3), supporting a warm-adapted ecotype in this area (Fig. 5A).

The warmer LUNA garden showed no significant differences in vegetative responses between warm-adapted and cool-adapted populations, with the excep-

tion of carbon isotope ratios. In this case, the variation in carbon isotopes at the LUNA garden was significantly correlated with DER carbon isotopes in the 2009 plantings ( $r = 0.84$ ,  $P < 0.0001$ ); however, carbon isotope values were typically more negative at the DER garden. While the LUNA garden is warmer than the DER, it remains a relatively cold site for Mojave populations (Fig. 1). More negative  $\delta^{13}\text{C}$  can result from either increased diffusive supply of  $\text{CO}_2$  into leaves as a result of greater stomatal opening, or can result

from decreased biochemical demand for CO<sub>2</sub> in leaves. Chilling during photosynthesis in the gardens would promote the more negative  $\delta^{13}\text{C}$  values that we observed with smaller plants and less survival by either relaxing constraints to stomatal conductance by lessening the leaf-to-air vapor gradient, or by reducing carboxylation. Winter chilling could have a legacy effect in spring, when appreciable carbon gain occurs, or cooler spring conditions may occur where minimum temperatures are lower. Regardless of the mechanism and interpretation, the carbon isotopes are likely symptomatic of the genetic variation between warm and cooler ecotypes.

This study focuses on genetic and physiological adaptations to climate for blackbrush populations in the vegetative state. We have found in earlier studies that ecotypic differentiation associated with the Mojave and Plateau ecoregions also occurs in traits associated with the regeneration niche of this species. In studies of seed germination response to chilling based on most of the same populations included in the current study, seeds of Mojave populations had shorter chilling requirements and a higher optimum chilling temperature for dormancy removal than seeds of Plateau populations (Pendleton and Meyer 2004). In a reciprocal seeding study at Mojave and Plateau sites, the existence of local adaptation in seedling establishment traits also was demonstrated. Each local population showed significantly improved establishment success relative to the nonlocal population when planted at its site of origin (Meyer and Pendleton 2005). These earlier studies combined with the common-garden studies reported here indicate that the cool-adapted and warm-adapted ecotypes of blackbrush are each characterized by an integrated suite of coevolved adaptive traits.

#### *Mojave and Colorado Plateau climates*

Previous literature suggested that the Plateau receives greater precipitation, especially in summer, compared to the Mojave (West 1983a, Comstock and Ehleringer 1992). On the Plateau, blackbrush took up more water from simulated summer monsoon events than did other dominant shrub species of the region, and exhibited a correspondingly greater increase in water status (Lin et al. 1996). However, use or uptake of a water resource does not necessarily establish a physiological dependency on the resource. Lin et al. (1996) also noted that the distribution of blackbrush occupies a transition zone between monsoonal and nonmonsoonal ecosystems, and is not squarely in one or the other regime. In contrast to the previous reports, we found that mean annual precipitation is significantly higher on the Mojave compared to Plateau sites (261 mm/yr compared to 203 mm/yr, respectively; 1961–1990;  $P < 0.0001$ ), but there are no differences in mean summer precipitation (~98 mm in each ecoregion from April to September, data not shown) for our 112 broadly distributed blackbrush sites. Springtime water availability is a key factor for growth of desert plants (Comstock and

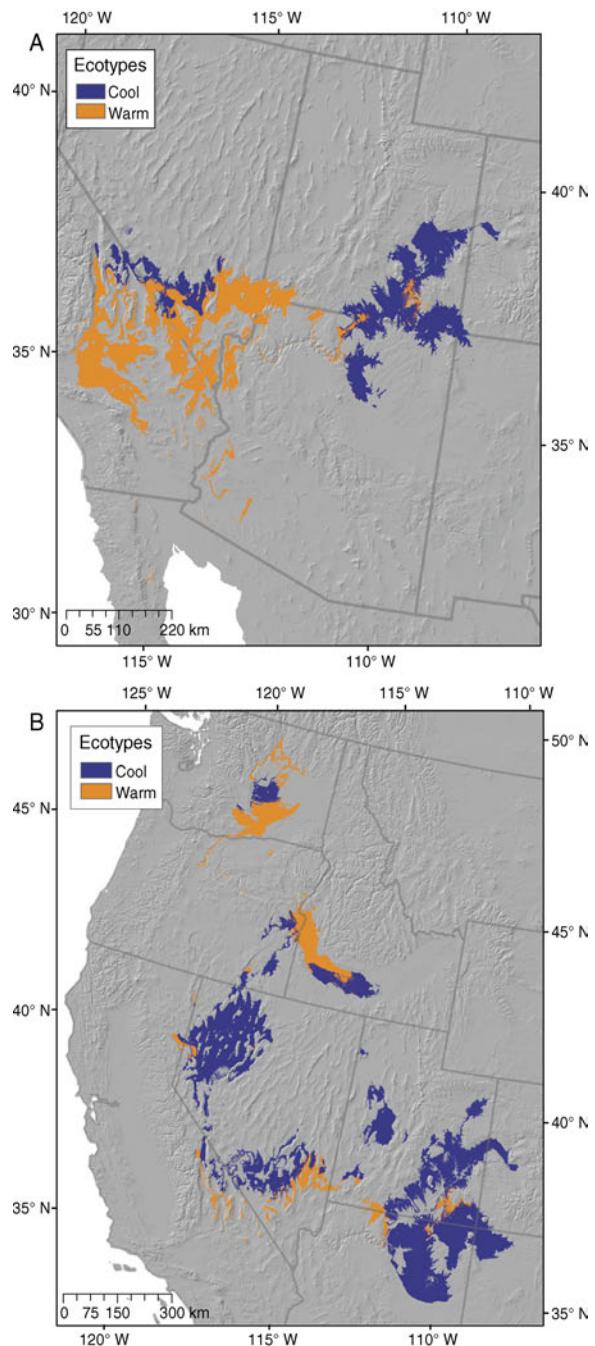


FIG. 5. (A) Mapped cool and warm ecotypes of blackbrush (*Coleogyne ramosissima*) within the bounds of the bioclimate profile for a contemporary climate and (B) a decade 2060 consensus using the agreement of four GCM/SRES combinations (see Fig. 4). Ecotypes are delineated based upon a mortality threshold of 37.8% (<37.8% = cool ecotype).

Ehleringer 1992), and the relatively longer period of lower temperature that prevails during spring on the Plateau may contribute to blackbrush's ability to persist there, and furthermore may be reflected in the Plateau ecotype's innately greater survivorship in response to

low temperatures and its greater photosynthetic water-use efficiency ( $\delta^{13}\text{C}$ ). These data support a hypothesis that Plateau populations have greater tolerance to colder and drier conditions found on the Plateau. Greater growth was observed in Plateau populations at the DER prior to the 2011 mortality; however, similar trends are not seen at the LUNA garden. Therefore, slow growth in the Mojave populations is more likely attributable to the 2009/2010 winter stress than an adaptive growth response.

#### *Genecology and bioclimate maps*

The blackbrush bioclimate model provides a means for projecting the contemporary realized niche into climates expected in the future. While there is limited research on blackbrush biogeography, our model has similarities to a previously circumscribed distribution of this species (Bowns and West 1976). However, our model has two major differences relative to that of Bowns and West (1976). (1) It indicates a greater area of suitable climate in the western Mojave, and (2) suggests that the Kaibab and Kanab Plateaus in southern Utah and northern Arizona (Fig. 3B) essentially separate the Mojave and Plateau blackbrush ecoregions (Fig. 4B). This biogeographic separation is supported by previous population genetic analyses using AFLPs (amplified fragment length polymorphisms) that showed significant genetic structure between Mojave and Plateau populations (Richardson and Meyer 2012). Our model does depict that a narrow corridor of blackbrush climate space occurs along the benches in the Grand Canyon (Fig. 3A, B). Blackbrush has been part of the Grand Canyon plant assemblages dating back to 45 000 yr BP based upon packrat midden fossils, but was absent at midden sites at higher latitudes and elevations on the Plateau until the Holocene (Hunter and McAuliffe 1994, Coats and Cole 2008). Populations of blackbrush within the Grand Canyon may have served as a refugia during the late Pleistocene that later colonized the Plateau as the climate warmed (Richardson and Meyer 2012).

The projection of the cool-adapted and warm-adapted blackbrush ecotypes within the boundaries of the bioclimate model provides a means of assessing adaptive variation throughout the climate space. Mapping the ecotypes within the contemporary bioclimate model shows that the majority of cool-adapted ecotypes should be distributed within the Plateau and warm-adapted ecotypes within the Mojave. There are two exceptions, however. A warm-adapted ecotype is predicted in the Colorado River drainage of the Plateau, and the cool-adapted ecotype is predicted to occur in the northwestern Mojave (Fig. 4A). Vegetative responses of the HITE population support the existence of this warm-adapted ecotype along the Colorado River drainages. HITE was the only Plateau population that had mortality, growth, and carbon isotope responses similar to Mojave populations. However, we have no empirical data supporting a cool-adapted northwestern Mojave eco-

type. The existence of this ecotype is based entirely on the model prediction. Two possible scenarios may explain the predicted existence of a cool-adapted Mojave ecotype. (1) Such an ecotype may have developed *de novo* in the northwestern Mojave or may have become disjunct from the cool-adapted ecotype emerging from Grand Canyon refugia during the early Holocene. (2) It is also possible that, as the model does not have any presence points for this area in the Mojave, this prediction could be a result of commission error, a prediction of presence when absence is the case. In this case, commission error could occur because the cool-adapted ecotype that allows blackbrush to occur in this climate space on the Plateau is assumed to be present on the Mojave, but in fact it is not. In other words, the bioclimate model alone assumes genetic composition is homogeneous (O'Neill et al. 2008, Jay et al. 2012). For blackbrush, the first scenario is more likely, as there are accounts of the occurrences of blackbrush populations in the northwestern region of the Mojave that most likely represent a cool-adapted ecotype (Beatley 1975). Other assumptions leading to possible commission error in the bioclimate model are discussed later.

#### *The future for blackbrush*

Blackbrush climate space for the decade surrounding 2060 is expected to expand by an estimated 52% when compared to the contemporary climate space. This is consistent with predicted climate space of the Mojave and Great Basin Desertscrub biomes during this decade (Rehfeldt et al. 2012). However, a number of ecological factors deserve consideration when interpreting this climate space. Edaphic conditions play an important role in plant biogeography, especially in deserts where soil texture can strongly affect availability of limited water (McAuliffe 1994, Sperry and Hacke 2002). In the context of blackbrush, soil type and temperature appear to influence its occurrence (West 1983b, Bai et al. 2013). Moreover, blackbrush is absent in salt deserts, which could be due to intolerance to soil salinity or to competition (Beatley 1975). Our bioclimate profile predicts a considerable area of suitable climate space in the Lahontan Basin (Fig. 4) by 2060. However, our model does not consider that the lower basins in this region are principally salt desert with considerably different soil textures, chemistry, and hydrology. In contrast, agriculture and urban development will exclude blackbrush over much of the Snake River Plain and Columbia Basin. Another consideration is seed dispersal. Our bioclimate model assumes limitless seed dispersal; however, movement from the northern Mojave to the nearest basin (i.e., Lahontan Basin) is >100 km, a distance too great for its principal dispersal agent, heteromyid rodents (Beatley 1976, Meyer and Pendleton 2005). Human-mediated dispersal will be required for blackbrush to occupy areas of suitable future climate in the Lahontan and Columbia Basins and the Snake River Plain. Finally, since blackbrush is believed to take

several decades to centuries to establish, altered fire regimes and interactions with nonnative grasses will likely have a major negative impact on the occurrence of blackbrush under future climates compared to historic conditions (Brooks et al. 2007). These ecological interactions are not modeled, and all could limit blackbrush distribution and abundance in the landscape.

An intuitive expectation under climate change is that natural selection will favor plant populations adapted to warmer conditions. Bioclimate and geneecological modeling in blackbrush suggest that this may not be the case for all plants. In this case, blackbrush is expected to occupy regions in the Great Basin. This region is considerably different from the current physiography of the Mojave. Some of the differences include higher elevation, topographically closed valleys, and a more continental climate (Comstock and Ehleringer 1992). These features will likely result in climates with colder minimum temperatures that would be more likely to support a cool-adapted ecotype over the majority of the predicted future climate space.

#### *Management recommendations*

To understand the components of plant adaptation fundamental to ecological restoration and conservation, we use vegetative responses from common-garden experiments to assess adaptive genetic variation in blackbrush. This genetic variation is associated with population-specific climate variables that can be estimated or predicted throughout the climate space of this species. Based on these results and those from AFLP analysis (Richardson and Meyer 2012), we recommend that seed transfer guidelines for blackbrush be based on a minimum of four seed zones. These four seed zones include the concept that blackbrush populations are likely to belong either to the cool-adapted or the warm-adapted ecotype, but they also include the concept that populations of both ecotypes are genetically distinct between ecoregions (Richardson and Meyer 2012). While it is true that most Plateau populations belong to the cool-adapted ecotype and most Mojave populations belong to the warm-adapted ecotype, our model does support the existence of both ecotypes in both ecoregions (Fig. 5A), although populations from cool-adapted Mojave populations have not been tested in this study.

Blackbrush climate space predictions for 2060, based on the agreement of four of the six GCM and carbon emission scenarios, suggest that climate space for this species will expand northward mainly into the lower basins of the Great Basin, Columbia Basin, and Snake River Plain, a prediction consistent with an expected increase in climate space for the Mojave and Great Basin Scrub biomes (Rehfeldt et al. 2012). Due to dispersal limitations, assisted migration would be necessary for blackbrush to occupy this predicted climate space. These geographic regions of predicted expansion, especially the Lahontan Basin, will be suited

predominantly for the cool-adapted ecotype. However, ecological factors such as soils and competition primarily from nonnative annual grasses will likely affect habitat suitability and therefore presence of blackbrush at local spatial scales. Blackbrush in the southern latitudes of the Mojave will likely face an increasing risk of extirpation due to climate change (Fig. 4). To capture the genetic diversity of these populations, seed banking or assisted migration are possible options. Since these areas are currently occupied by the warm ecotype, managers may consider relocating these warm-adapted populations to areas in the northeastern Mojave where the climate may support warm-adapted blackbrush in coming decades.

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## SUPPLEMENTAL MATERIAL

### Appendix A

Blackbrush population climate estimates ([Ecological Archives A024-024-A1](#)).

### Appendix B

Climate variables with significant correlation to blackbrush plant responses ([Ecological Archives A024-024-A2](#)).