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RESEARCH ARTICLE

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Projections of Contemporary and Future Climate Niche for Wyoming Big Sagebrush (*Artemisia tridentata* subsp. *wyomingensis*): A Guide for Restoration

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ABSTRACT: Big sagebrush (*Artemisia tridentata*) is one of the most widespread and abundant plant species in the intermountain regions of western North America. This species occupies an extremely wide ecological niche ranging from the semi-arid basins to the subalpine. Within this large niche, three widespread subspecies are recognized. Montane ecoregions are occupied by subspecies *vaseyana*, while subspecies *wyomingensis* and *tridentata* occupy basin ecoregions. In cases of wide-ranging species with multiple subspecies, it can be more practical from the scientific and management perspective to assess the climate profiles at the subspecies level. We focus bioclimatic model efforts on subspecies *wyomingensis*, which is the most widespread and abundant of the subspecies and critical habitat to wildlife including sage-grouse and pygmy rabbits. Using absence points from species with allopatric ranges to Wyoming big sagebrush (i.e., targeted groups absences) and randomly sampled points from specific ecoregions, we modeled the climatic envelope for subspecies *wyomingensis* using Random Forests multiple-regression tree for contemporary and future climates (decade 2050). Overall model error was low, at 4.5%, with the vast majority accounted for by errors in commission (>99.9%). Comparison of the contemporary and decade 2050 models shows a predicted 39% loss of suitable climate. Much of this loss will occur in the Great Basin where impacts from increasing fire frequency and encroaching weeds have been eroding the *A. tridentata* landscape dominance and ecological functions. Our goal of the *A. tridentata* subsp. *wyomingensis* bioclimatic model is to provide a management tool to promote successful restoration by predicting the geographic areas where climate is suitable for this subspecies. This model can also be used as a restoration-planning tool to assess vulnerability of climatic extirpation over the next few decades.

Index terms: bioclimatic model, climate change, ecological restoration, Random Forests, sagebrush

INTRODUCTION

Wide-ranging plant species can be composed of distinct groups, such as subspecies or races, which are often differentiated by climate or other environmental factors. A challenge for bioclimatic modeling is to discern when it may be more conducive and practical to develop these models below the species level. Bioclimatic analysis of taxa below the species level requires more in-depth biological knowledge, such as phylogenetic or population genetic information, but may improve modeling performance by reducing over parameterization (Pöyry et al. 2008; Warren and Seifert 2011) and aid in interpreting climate change impacts (Rehfeldt 2004; O'Neill et al. 2008). Another challenge in bioclimatic model development is determining whether spatial scale of the plant niche is representative of the spatial scale of environmental variables derived from a climate surface (Elith and Leathwick 2009). This can be problematic in deserts where limited resources like water can be highly influenced by topography and soils and, therefore, affect presence or absence of plants. These features can often vary at spatial scales well below the 1 km to 800 m gridded climate surfaces.

The challenges discussed above are factors for consideration in developing a bioclimatic model for big sagebrush (*Artemisia tridentata* Nutt.). Different climates define the three most widespread subspecies of big sagebrush (Mahalovich and McArthur 2004): *Artemisia tridentata* Nutt. subsp. *tridentata* (Beetle & Young) Welsh, *Artemisia tridentata* Nutt. subsp. *vaseyana* (Rydb.) Beetle, and *Artemisia tridentata* Nutt. subsp. *wyomingensis* Beetle & Young. Subspecies *tridentata* occurs in basins and lower mountain valleys where deep, well-drained soils support its large stature and rapid growth (McArthur and Welch 1982); shorter statured *vaseyana* and *wyomingensis* occur in the mountains and in dry basins, respectively. While *tridentata* and *wyomingensis* distributions can often be sympatric, an important distinction is that *tridentata* presence is usually controlled by local topographic features that affect soil properties (e.g., soil depth) and provide the additional moisture (Barker 1983; McArthur et al. 1988). For example, *tridentata* can become established in *wyomingensis* habitat along roadside ditches and fence lines where rainwater from roadways or snowdrifts adds the needed water to support *tridentata*. The same can be true for natural features like dry washes where additional rainwater and soil depth accumulate to support *tridentata* (McArthur and Sanderson 1999). Because of the spatial

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context of these features (<100 m^2), distinguishing the environmental components that support *tridentata* is beyond the scope of bioclimatic modeling. Hybridization among subspecies is another concern that could affect bioclimatic modeling results. Big sagebrush subspecies are known to form hybrid swarms along ecotones at the foot of mountains (McArthur et al. 1988; Wang et al. 1997) and also between *wyomingensis* and *vaseyana* of the same ploidy (McArthur and Sanderson 1999; Richardson et al. 2012). In such cases, presence or absence data that does not assess hybrid characters could confound a subspecies bioclimatic model.

Another consideration in bioclimatic model development of big sagebrush is the utility for ecological restoration. Successful restoration requires deploying the appropriately adapted seed into a suitable environment. A primary step in this process for big sagebrush is identifying subspecies climate niche, and whether it will migrate in a changing climate. Among the subspecies, *wyomingensis* warrants the most attention for ecological restoration. This subspecies occupies the warmest and driest areas of the species range—areas that are more susceptible to wildfire and cheatgrass (*Bromus tectorum* L.) invasion (Chambers et al. 2007; Bradley 2010; Chambers et al. 2013). The degradation of these sagebrush ecosystems to weeds is a key factor in the loss of sage-grouse habitat (Crawford et al. 2004). A contemporary and future bioclimatic model of *wyomingensis* would provide, at a broad scale, a means to assess areas where this subspecies would be the most suitable for restoration.

Previous bioclimatic models of big sagebrush have utilized a broader group of taxa. Bradley (2010) used land surface data (GAP analysis) of two subspecies of big sagebrush, *tridentata* and *wyomingensis,* and other sagebrush species that inhabit intermountain basin communities of the western United States (e.g., low sagebrush, *A. arbuscula* Nutt.; and black sagebrush, *A. nova* A. Nelson) in developing a bioclimatic model and risk mapping of cheatgrass invasion for the state of Nevada. Schlaepher et al. (2012) used a similar approach with the addition of subspecies *vaseyana* in developing a bioclimatic model, and its comparison to a mechanistic model developed from ecohydrological data. Here, our bioclimatic modeling efforts are focused on defining the climate niche of a single subspecies, Wyoming big sagebrush, by developing a data set of occurrences, as well as a data set of absence points from species that occupy adjacent plant communities. Our goal is to develop a bioclimatic model for Wyoming big sagebrush that would provide a broad-scale reference for ecological restoration, including a management tool to promote successful restoration by predicting geographic areas suitable for this subspecies, and a planning tool to assess vulnerability of climatic extirpation over the next few decades.

MATERIALS AND METHODS

Samples and Data Collection

The climate model was developed from presence and absence points. Presence data, consisting of 131 occurrence points (Appendix 1), were derived principally from previous studies: McArthur and Sanderson (1999), Richardson et al. (2012), and Wilt et al. (1992). Techniques used to determine subspecies are described within each publication, but in nearly all cases flow cytometry or chromosome counts were used to confirm ploidy. The exception is Wilt et al. (1992), who use morphology and an assessment of phenolic compounds. Absence data was derived through several sources and contained 4464 points consisting of both target-group absences (TGA) and randomly selected background points. TGA, localities for other taxa that do not co-occur with the target species, have been used successfully in species distribution modeling (Mateo et al. 2010). A total of 3964 TGA were derived from previous studies (Richardson and Meyer 2012; Esque et al. unpubl. data), the USDA Forest Service, Forest Inventory and Analysis Program (FIA) (Bechtold and Patterson 2005), and the Consortium of California Herbaria (CCH) (data provided by the participants of the Consortium of California Herbaria [ucjeps.berkeley.edu/consortium]). The taxa used in TGA are listed in Appendix 2, along with their respective sources. A total of 500 background points were randomly selected from a group of three Level III Ecoregions (Omernick 1987). These ecoregions, Nebraska Sandhills, Northwestern Glaciated Plains, and Southwest Tablelands were chosen to provide additional absence points in areas lacking TGA to fill out the range of climatic variation.

Climatic Data

The geographic extent for both models and projections was set from 30° N to 55° N latitude and from 130° W to 100° W longitude to incorporate the entire range of possible sagebrush habitat. The baseline climatic data set was acquired from WorldClim (Hijmans et al. 2005), comprising 19 bioclimatic (BIOCLIM) variables (Appendix 3) for present conditions (mean 1950–mean 2000) at 30 arc-second resolution, which is roughly 1 km^2 at the equator. The BIOCLIM variables have been widely used in modeling work as variables that are biologically important for various species (Hijmans et al. 2005).

Bioclimatic Model

To model the climate-defined area of Wyoming big sagebrush, we estimated the likelihood that the climate was suitable across a large section of western North America. The estimate was derived from a climate profile, which is a multivariate description of the climatic niche. The climate profile was developed from bioclimatic models, that is, regressions of the presence and absence of a species on climate variables. The modeling techniques used here closely follow those of Rehfeldt et al. (2006) as explained in detail in Rehfeldt et al. (2009) and Crookston et al. (2010).

The Random Forests classification tree of Breiman (2001), implemented in R 3.02 (R Core Team 2013) by Liaw and Wiener (2012) in the package "RandomForest," was used to predict the presence or absence of species from the climate variables. The Random Forests algorithm constructs a set of classification trees from an input data set and outputs statistics that reflect the likelihood that the climate at a location is suitable for the species (Rehfeldt et al. 2009). The trees in aggregate are called a forest. The climate profile was built on 12 forests, each with 100 trees (i.e., decision trees).

To create the trees, a majority of the data, usually around 64%, were used to create the model, and the remaining portion of the data set, the out-of-bag occurrence points, were used to test the model. The best-fitting model for each tree was built by comparing the out-of-bag error. Out-of-bag errors are comprised of rates of errors in commission (where the model predicts an occurrence when no plant is present), and errors in omission (where the model predicts an absence when a species is actually present). To make predictions about presence of a species, each tree in the forest provides one vote to the classification of an observation. Because classification errors approach a limit as the number of trees in the forest increase, collinearity and over-parameterization are inconsequential (Breiman 2001). The approach has been shown to be robust and has worked for widely distributed species (Ledig et al. 2010).

Assembling the presence-absence data for analysis requires satisfying Breiman's recommendation that presence data be in reasonable balance with absence data (Breiman 2001). Each forest would need one data set, and each data set was prepared within which presence and absence points represented 40% and 60% of the total, respectively. For each of the data sets, the amount of presences was fixed at 40% to limit the amount of out-of-bag errors, which increase when the number of presence points is less than 40% of total points used in the model (Rehfeldt et al. 2006).

All data sets contained all 131 presence points, each of which was weighted by a factor of two (each was included twice). This weighting assures that the resulting model is most robust for climates in which *A. tridentata* subsp. *wyomingensis* actually occurs (Rehfeldt et al. 2006; Ledig et al. 2010), and allows the number of absence points in the data set to be doubled, allowing for more complete sampling of the climatic variation. Each data set, therefore, included about 655 observations, with 262 observations with sagebrush, and about 393 observations without sagebrush.

Absence points for the data sets were chosen in two steps. First, following the protocol of Rehfeldt et al. (2006), we defined an expanded climatic envelope as a 19-variable hypervolume corresponding to the climatic limits of distribution expanded by ±1 SD. Then, for each data set we randomly selected 40% of the points as absences from points that are within, and 20% of points were chosen randomly as absences from points outside, the climatic hypervolume detailed above. The number of forests was chosen by dividing the total number of absence points within the climate hypervolume described above by the number of presence points multiplied by two. Therefore, using 12 forests would assure that the probability would be high that all observations within the hypervolume would be used in at least one forest.

The final predictor variables used were culled from the 19 BIOCLIM variables through a variable reduction process following Rehfeldt et al. (2006) and Rehfeldt et al. (2009). Based upon the out-of-bag error, the predictors were eliminated using the mean decrease in accuracy to judge variable importance until only one variable remained. Then the top seven variables were chosen to use as predictive variables to create the climate profile.

Mapping

The climate profile from Random Forests analysis was mapped to the WorldClim climate grids. Each of the contemporary grid cells was evaluated for climatic suitability for sagebrush by the number of votes cast for the 100 trees in the 12 forests. A grid cell was considered to have suitable climate for sagebrush when the majority of the 1200 votes were cast in favor of the climate being suitable for sagebrush. This creates the bioclimatic model. Models were evaluated using the Area Under the Curve of Receiver-Operating Characteristic (AUC), a common measure for evaluating model fitness (Elith and Leathwick 2009).

The climatic data sets for the 2050s were acquired from WorldClim (Hijmans et al. 2005) and comprise the same bioclimatic variables as the contemporary data set. Climate surfaces for the 2050s (2040–2069) (Hijmans et al. 2005), derived from the IPCC (Intergovernmental Panel on Climate Change) 4th Assessment (IPCC 2007), were used to project the sagebrush bioclimate for this decade. To provide a consensus of 2050s projections, we used methods similar to Ledig et al. (2012) and Wang et al. (2012), where the outputs from five General Circulation Models (GCMs) are combined into an agreement map. GCMs included the A1b emission scenarios for the following five models: Canadian Center for Climate Modeling and Analysis (CCCMA CGCM3.1); Bjerkes Centre for Climate Research Norway (BCCR BCM2.0); Institute for Numerical Mathematics, Russia (INM-CM3.0); Commonwealth Scientific and Industrial Research Organization (CSIRO MK3.0); and the Center for Climate System Research (University of Tokyo), National Institute for Environmental Studies, and Frontier Research Center for Global Change (JAMSTEC), Japan (MIROC3.2 medres). Information on the GCMs and emission scenarios can be found elsewhere (IPCC 2007). Agreement mapping of the five GCM–scenario combinations were performed in R using the RandomForest package as above. The threshold used to calculate suitable area for the contemporary and each of the future models was 0.5. For the 2050s, the predicted presence of sagebrush-suitable climate is mapped only where more than two of the five GCMs showed agreement.

Ecoregional Assessment of Climate Niche Loss

For both contemporary and future (2050s) projections of the bioclimatic model, the total area (km^2) predicted to have suitable climate was calculated. We also calculated the area where both contemporary and future models overlapped (stable), the area that is suitable in the contemporary model but not suitable in the future model (contracting), and the area that is not suitable in the contemporary model but is suitable in the future model (expanding).

Climate comparisons were made between two geographic regions that are predicted to have the greatest losses in climate niche: the Great Basin and the Great Plains. We defined the regions by a combination of Omernik's (1987) Level III Ecoregions. The Great Basin region is defined here by three of the ecoregions: Northern Basin and Range, Central Basin and Range, and Snake River Plain. The Great Plains region is here defined by several of the ecoregions: Middle Rockies, Southern Rockies, Northwestern Great Plains, Nebraska Sand Hills, High Plains, and Southwest Table Lands. The contemporary climate niche of Wyoming big sagebrush was split by whether the area is predicted to contract or remain stable by mid century. For these geographic areas, we compared Annual Dryness Index (ADI; mean annual precipitation / degree-days >5 ºC), as calculated in Rehfeldt et al. (2006), and summer-winter precipitation ratio (SWP; warmest quarter precipitation [PWQ, BIO18] / coldest quarter precipitation [PCQ, BIO19]). These values were extracted in each raster grid cell for the Great Basin and Great Plains. Two-way ANOVA and Tukey's HSD was used to test post-hoc mean differences between ecoregions and stable and contracting areas within each region.

RESULTS

Bioclimatic Model

The average model AUC was excellent at 0.979. To balance commission, omission, and out-of-bag error, we chose a seven-variable model with an out-of-bag error of 2.65%. Commission and omission rates for this model were 4.51% and 0.03%, respectively (Table 1). The climatic data set comprised seven bioclimatic variables (Table 2). The seven-variable model was chosen as being reasonably parsimonious while providing a buffer against reliance on single variables. The most important variable for this model was the mean temperature for the warmest quarter. The second most important variable was the annual mean temperature, and the third most important variable was temperature annual range. Of the seven variables used in the model, six were related to temperature. Mean annual precipitation was the only precipitation related variable and was the sixth most important.

Table 1. Confusion matrix of Wyoming big sagebrush (*Artemisia tridentata* subsp. *wyomingensis*) bioclimatic model showing the class error and number of observations classified by the Random Forests algorithm. Mean of the 12 Random Forests.

Observed occurrence	Predicted occurrence		Class error (%)
	absent	present	
Absent (commission)	362.08	17.08	4.51
Present (omission)	0.08	261.92	0.03

Mapped Projections

The contemporary climate niche predicts an area of nearly 108 million hectares (1,086,697 km^2, Figure 1A) for Wyoming big sagebrush. By midcentury, a 39% reduction is predicted in this climate niche, totaling 66 million hectares (Figure 1B). Only 32% of the contemporary climate niche is stable by the middle of the century, while 67% of the contemporary climate niche is predicted to be lost and 28% will be gained. Regions predicted to be most vulnerable to climate change extirpation include the trailing edge (i.e., the southern periphery of the subspecies), the western Great Plains, and lower elevations of the Columbia and Great Basin. Regions that retain or gain climate niche include western Wyoming and eastern Idaho, higher elevations in the Great Basin and the northern Great Plains.

Ecoregional Assessment of Climate Niche Loss

The range of climatic conditions affecting the predicted loss of Wyoming big sagebrush differed among spatial and temporal scales (Appendix 4). The SWP and ADI were significantly different between ecoregions (Great Basin versus Great Plains; $P < 0.0001$) and within ecoregions between predicted stable and contracting areas. For both ecoregions, the stable areas of the climate niche had a lower ADI than the contracting areas ($P < 0.0001$). ADI values and differences between stable and contracting areas were much greater in the Great Basin than Great Plains ($P < 0.0001$) (Figure 2A and C). While small, the difference between stable and contracting

Table 2. Climate variables used to predict the climate niche of Wyoming big sagebrush (*Artemisia tridentata* subsp. *wyomingensis*) bioclimatic model. Bioclimatic model variables are listed in order of importance.

	Variable	Variable explanation
1	BIO10	Mean Temperature of Warmest Quarter
2	BIO1	Annual Mean Temperature
3	BIO7	Temperature Annual Range (max. T warmest month - min. T coldest month)
4	BIO4	Temperature Seasonality (T sd * 100)
5	BIO8	Mean Temperature of Wettest Quarter
6	BIO12	Annual Precipitation
7	BIO2	Mean Diurnal Range (mean of monthly [max. T - min. T])

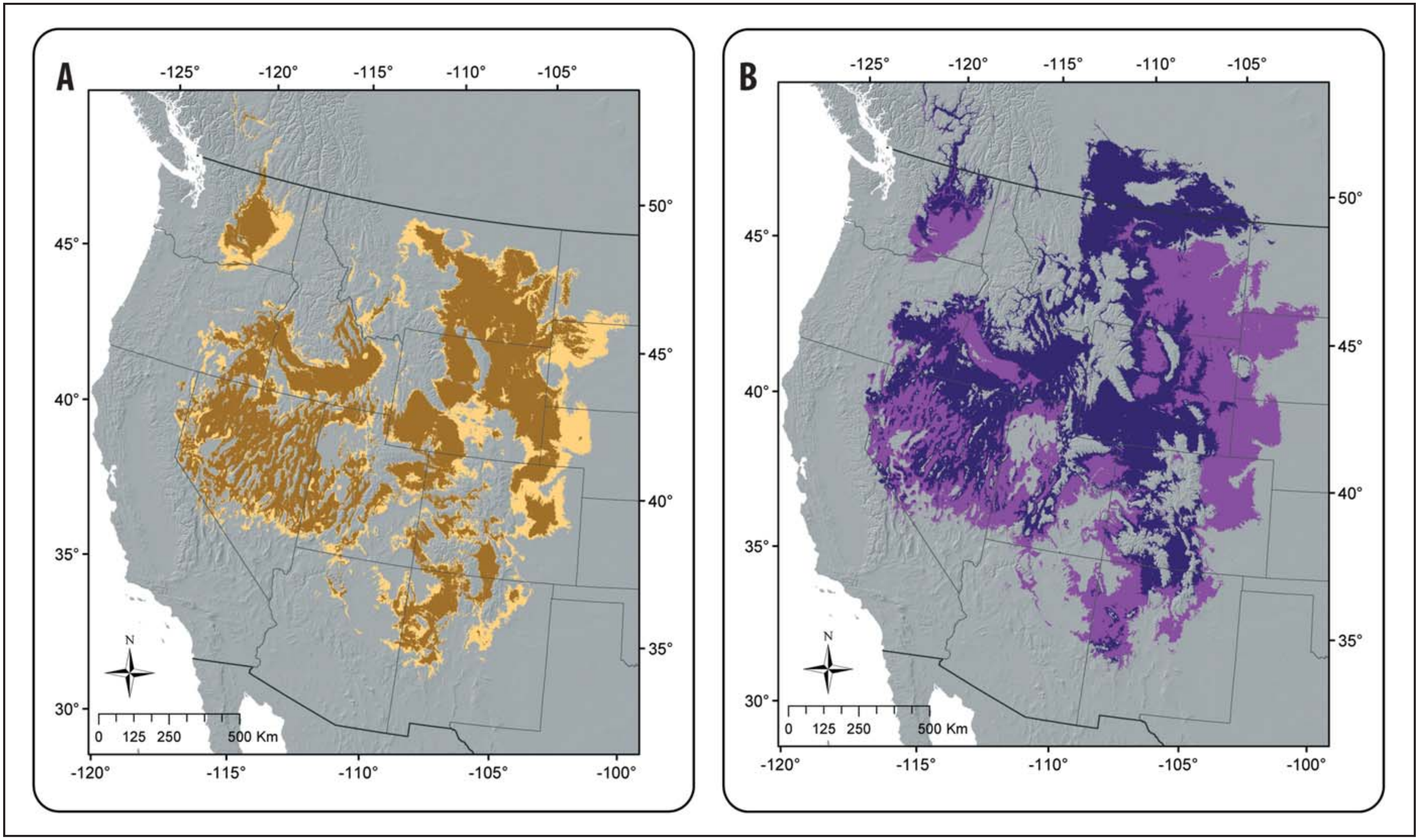

Figure 1. A) Mapped projection of the contemporary climate niche of *Artemisia tridentata* subsp. *wyomingensis*. Dark brown represents higher probability of occurrence (>0.75), whereas light brown represents lower probability (0.5 to 0.75). B) Mapped projection of the change in climate niche between contemporary and decade 2050. Dark purple represents areas that are predicted to have suitable climate for this subspecies in decade 2050 (i.e., stable or expanded), whereas light purple represents areas that are predicted to have unsuitable climates (i.e., contracted).

areas of the Great Basin was significantly different for SWP ($P < 0.0001$), and significantly large differences in SWP were observed between stable and contracting areas ($P < 0.0001$) within the Great Plains (Figure 2B and D).

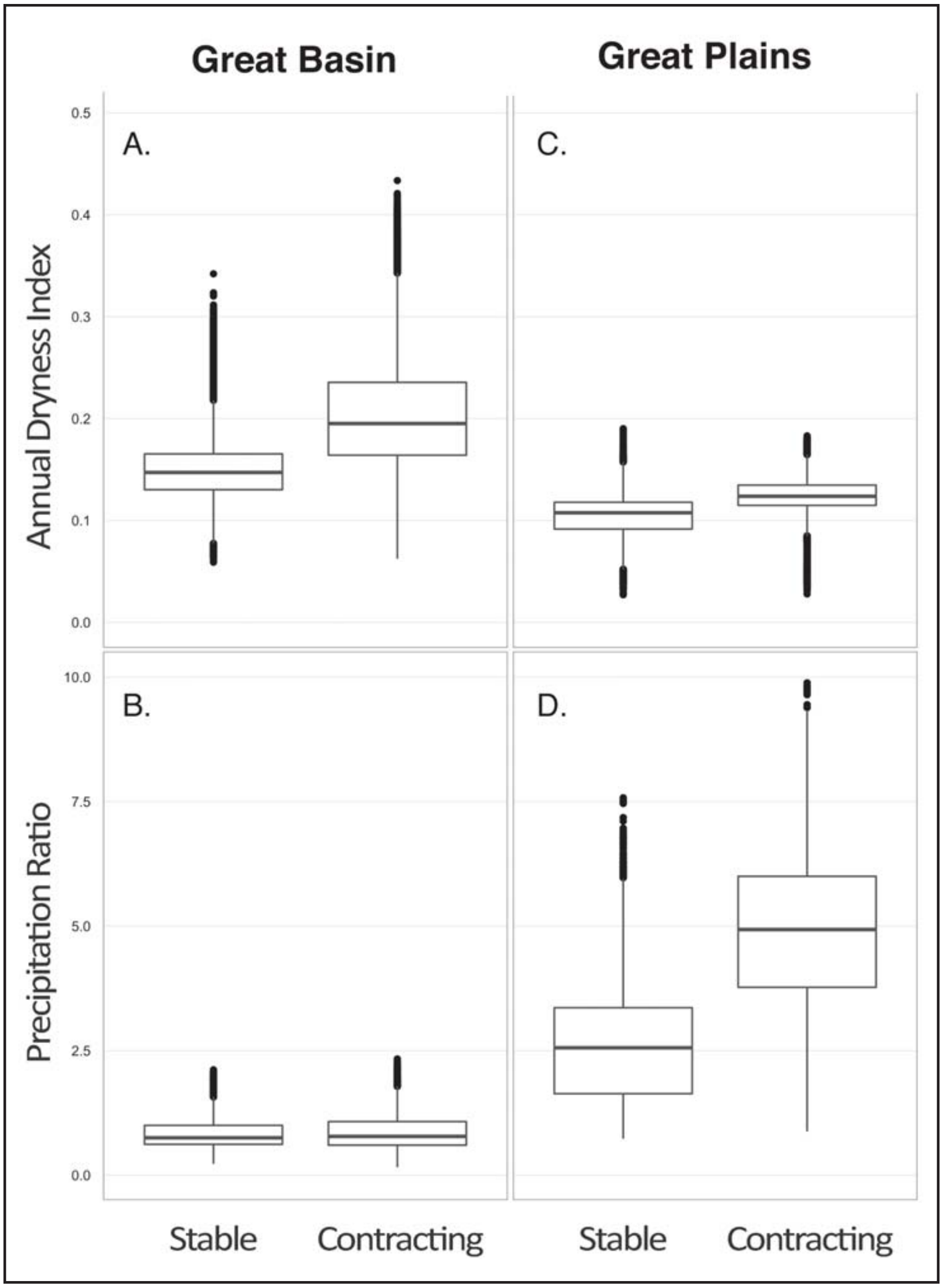

Figure 2. Boxplots illustrating the range of values for Annual Dryness Index (ADI) and summer-winter precipitation ratio (SWP) for stable and contracting areas of the contemporary climate niche of Wyoming big sagebrush (*Artemisia tridentata* subsp. *wyomingensis*). Increasing values of ADI indicate decreasing precipitation and / or increasing accumulating temperatures >5 °C. Increasing values of SWP indicate a higher ratio of summer relative to winter precipitation.

DISCUSSION

Model Development and Error

It is well known that big sagebrush subspecies are defined by climate and that Wyoming big sagebrush occupies the warmest and driest extent of this species distribution (Mahalovich and McArthur 2004). To be successful in the restoration of sagebrush ecosystems, it is imperative that subspecies are placed in the appropriate climate. Previous published bioclimatic models have used broader taxonomic hierarchies based on the constraints of GAP analysis data to define sagebrush climate niche (Bradley 2010; Schlaepher et al. 2012). In this study, our goals were to produce a management tool for contemporary and future restoration of Wyoming big sagebrush. Data were acquired from known occurrences that span much of the range of the subspecies and have been taxonomically identified to subspecies. Our strategy was to frame this subspecies' climate using targeted group absences using allopatric species in warmer and cooler climates (i.e., *Coleogyne ramosissima* Torr. and *Cercocarpus ledifolius* Nutt., respectively). A targeted group absence approach has been shown to be more accurate than pseudo-absences (Mateo et al. 2010). However, along the central and northern Great Plains, pseudo-absences were necessary because of the lack of suitable species to use as absence points.

As with any bioclimatic model, some modeling error can be expected. Sources of errors could come from the environment, including soil and small-scale topographic features. Ecological interactions (e.g., plant competition), disturbance, and land use histories could also be sources of error. Nevertheless, the resulting model generated low errors in the prediction of which much were due to commission. Geographically, we suspect the preponderance of commission errors occurs along the Great Plains and the boundary with the Chihuahuan Desert in New Mexico (Figure 1A). In these regions, Wyoming big sagebrush is less dominant. This is likely due to a change to increasing summer versus winter precipitation that favors grasslands (Ogle and Reynolds 2004). Here, soils and topography become more of an important influence on presence and absence, and thus predictive error based on a climate-only model.

Contemporary and Future Projections

Comparisons of contemporary and future projections show considerable loss (39%) of Wyoming big sagebrush climate niche good correspondence to the previously published bioclimatic modeling of North American-biomes (Rehfeldt et al. 2012) and blackbrush (Richardson et al. 2014), an ecotonal species occurring between warm and cold deserts. Rehfeldt et al. (2012) showed that midcentury Mojave Desert climates would replace cold desert biomes in some areas of the Great and Columbia Basins. These areas that show biome turnover from cold deserts to warm deserts (i.e., Great Basin Scrub to Mojave) are also areas that show major reductions in Wyoming big sagebrush climate niche (this study), the most prevalence of cheatgrass (Bradley 2010), and areas estimated to have very low restoration potential (Wisdom et al. 2005). Moreover, midcentury projections of blackbrush climate niche show expansion into contemporary Wyoming big sagebrush climate niche in the Lahontan and Columbia Basins and Lower Snake River Plain (Richardson et al. 2014).

Understanding the biological association between climate niche loss and life history traits of the target species is an important aspect of ecological and adaptive processes. While we do not have direct data supporting which life histories traits are critical to success or failure of this subspecies, previous research provides opportunity to speculate. The success of big sagebrush seedling establishment has been shown to be dependent on the timing and amount of precipitation. Snowpack appears to be a critical component for big sagebrush seedling recruitment. Studies have shown that snowdrifts, either caused by other plants or fencing, can greatly increase the recruitment of seedlings (reviewed in Meyer 1994). Another component of climate that affects the distribution of big sagebrush is the seasonality of precipitation. As discussed above, predominant summer precipitation favors grasslands, whereas winter precipitation favors shrublands (Ogle and Reynolds 2004; Brooks and Chambers 2011). Changes in climate that affect the longevity of snowpack and the seasonality of precipitation could greatly impact big sagebrush geographic distribution.

In this study, we examined the changes in two regions that support the highest predicted midcentury loss of Wyoming big sagebrush, the western Great Basin and the northern and central Great Plains. Based on these analyses, the climate conditions that result in the loss of Wyoming big sagebrush are different between the two regions (Figure 2). An interaction between increasing summer temperatures and reduced precipitation (ADI) appears to be an important component to climate niche loss in the Great Basin. Greater aridity differences were observed between stable and contracting areas. Differences were considerably smaller between stable and contracting areas in the Great Plains (Figure 2A and C). In contrast, the seasonality of precipitation events from less winter to more summer is expected in the Great Plains, whereas relatively minimal change is expected in the Great Basin (Figure 2B and D). Grassland ecosystems would likely prevail in the western Great Plains based on these projections.

As historical plant migration rates have been estimated to be 10–30 km per century (McLachlan et al. 2005; Yansa 2006), it is likely that the net loss will actually be more than 39% as a large portion of the expanding area is more than 30 km from current localities. Therefore, the species may not be able to expand into the new suitable range in the short period of time (ca. 30 to 40 years). If sagebrush is unable to colonize the expanded areas of niche in the shortened window of climate change, assisted migration is one possible solution to the problem (Ying and Yanchuk 2006; Kramer and Havens 2009; Vitt et al. 2010). In Havens et al. (this issue), assisted migration is defined as "the purposeful movement of individuals or propagules of a species to facilitate or mimic natural range expansion or long distance gene flow within the current range, as a direct management response to climate change." Successful assisted migration would need to ensure that the correct plant sources are transferred to the appropriate area. Such research in understanding the adaptive variation in Wyoming big sagebrush and other subspecies is ongoing.

Management Strategies and Planning

Restoration of Wyoming big sagebrush is a difficult and complex task. Restorationists will have to utilize a variety of management options and weigh a number of potential variables that can affect conservation and restoration outcomes (Chambers et al. 2013). Given the limited resources available, managers will have to focus on restoration sites that meet the most criteria for successful outcomes. Central among these criteria is an understanding of the impact of climate change. Our modeling focuses on the subspecies of the big sagebrush complex that is the most widespread and occupies the warmest and driest niche. The model suggests areas predicted to have an unsuitable climate niche in the upcoming decades (Figure 1B) would be poor choices for restoration of Wyoming big sagebrush; however, seed collected in these regions would be desirable for ex situ conservation or transfer to nearby suitable climates. Restoration should be focused on areas that are predicted to sustain Wyoming big sagebrush or areas of expansion.

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Appendix 1. Site name, study source and geographic coordinates of presence points used in the bioclimatic model of Wyoming big sagebrush (*Artemisia tridentata* subsp. *wyomingensis*).

No.	Site name	Study	Longitude	Latitude
1	Desert View	Richardson et al. 2012	-111.77287	35.91738
2	Williams	Richardson et al. 2012	-112.13125	35.82478
3	Rifle A	Richardson et al. 2012	-107.81	39.6127
4	Meeker	Richardson et al. 2012	-108.4555	40.1813
5	Old Oregon Trail Rd	Richardson et al. 2012	-115.6528	43.0931
6	Orchard Enc	Richardson et al. 2012	-116.0037	43.3274
7	Sommer Camp Rd	Richardson et al. 2012	-116.8531	43.4657
8	Powderville	Richardson et al. 2012	-105.1545	45.6545
9	Miles City	Richardson et al. 2012	-105.8261	46.3223
10	Pryor Mtn	Richardson et al. 2012	-108.7832	45.2066
11	Penistaja	Richardson et al. 2012	-107.2257	35.9802
12	San Luis Mesa	Richardson et al. 2012	-107.1478	35.7572
13	West of Juntura	Richardson et al. 2012	-118.2594	43.7853
14	Canyon V	Richardson et al. 2012	-112.5087	37.9933
15	La Sal W	Richardson et al. 2012	-109.4352	38.3279
16	Scooby	Richardson et al. 2012	-113.0499	41.8566
17	Crab Creek	Richardson et al. 2012	-119.2371	46.9488
18	Saddle Mtn	Richardson et al. 2012	-119.4727	46.7672
19	Burma Road	Richardson et al. 2012	-109.8341	42.6006
20	Westfall	Richardson et al. 2012	-117.7086	43.9928
21	Narrows	McArthur and Sanderson 1999	-118.958	43.2519
22	Fryburg	McArthur and Sanderson 1999	-103.4299	46.9127
23	Taos	McArthur and Sanderson 1999	-105.5739	36.272
24	Vale	McArthur and Sanderson 1999	-117.1861	43.9285
25	Amalia	McArthur and Sanderson 1999	-105.4567	36.9465
26	Costilla	McArthur and Sanderson 1999	-105.5203	36.9645
27	Murray Summit	McArthur and Sanderson 1999	-114.991	39.2053
28	Jakes Valley	McArthur and Sanderson 1999	-115.2112	39.4185
29	Ely	McArthur and Sanderson 1999	-114.884	39.2399
30	Baker	McArthur and Sanderson 1999	-114.123	39.0067
31	Ely 20 mi S	McArthur and Sanderson 1999	-114.7295	39.0577
32	Winnemucca 32 km SW	McArthur and Sanderson 1999	-117.9977	40.787
33	Salsbury Summit	McArthur and Sanderson 1999	-116.7466	38.1308
34	Calavada Summit	McArthur and Sanderson 1999	-118.1054	38.5994
35	Scott Summit	McArthur and Sanderson 1999	-116.9966	39.4577
36	Beowawe	McArthur and Sanderson 1999	-116.3002	40.6506
37	Monitor Valley	McArthur and Sanderson 1999	-116.6738	39.468
38	Warren	McArthur and Sanderson 1999	-108.6599	45.0616
39	Challis	McArthur and Sanderson 1999	-114.2215	44.4913
40	Mackay 4 km W	McArthur and Sanderson 1999	-113.6568	43.8941
41	Ridgway	McArthur and Sanderson 1999	-107.7532	38.1601
42	Harper	McArthur and Sanderson 1999	-117.6565	43.9138
43	Walden state line	McArthur and Sanderson 1999	-106.4016	41.0001

Continued

Appendix 1. (*Continued*)

No.	Site name	Study	Longitude	Latitude
45	Fredonia 14 km SE	McArthur and Sanderson 1999	-112.3787	36.9017
46	Blue Mesa	McArthur and Sanderson 1999	-107.2523	38.4706
47	Likely 2 km N	McArthur and Sanderson 1999	-120.5046	41.2545
48	Cerro Summit	McArthur and Sanderson 1999	-107.6513	38.4508
49	Dinosaur 3 km S	McArthur and Sanderson 1999	-108.9999	40.2176
50	Fort Benton	McArthur and Sanderson 1999	-110.6634	47.8116
51	Browns Park	McArthur and Sanderson 1999	-109.1806	40.8873
52	Gordon Crk	McArthur and Sanderson 1999	-110.9658	39.6514
53	Kane Springs	McArthur and Sanderson 1999	-117.4631	43.7764
54	Lewistown 32 km E	McArthur and Sanderson 1999	-109.0092	47.0625
55	Martin Draw	McArthur and Sanderson 1999	-109.2354	40.9776
56	Cottonwood Range	McArthur and Sanderson 1999	-117.7214	44.1215
57	Levan 12 km S	McArthur and Sanderson 1999	-111.905	39.4556
58	Tintic	McArthur and Sanderson 1999	-112.1397	39.8259
59	Scipio	McArthur and Sanderson 1999	-112.0925	39.2424
60	Clear Crk Canyon	McArthur and Sanderson 1999	-112.3708	38.5816
61	Glasglow 8 km E	McArthur and Sanderson 1999	-106.5093	48.1635
62	Piute Reservoir	McArthur and Sanderson 1999	-112.2071	38.3232
63	Lofgreen	McArthur and Sanderson 1999	-112.2901	40.0424
64	Diamond Fork	McArthur and Sanderson 1999	-111.4948	40.0362
65	Five Mile Pass	McArthur and Sanderson 1999	-112.2289	40.2202
66	Mercur-S	McArthur and Sanderson 1999	-112.2337	40.2636
67	Mayfield	McArthur and Sanderson 1999	-111.73	39.1346
68	Cove Fort	McArthur and Sanderson 1999	-112.5994	38.6101
69	Middlegate Summit	McArthur and Sanderson 1999	-118.0321	39.1775
70	Oasis	McArthur and Sanderson 1999	-114.4912	41.0283
71	Notch Peak Trl	McArthur and Sanderson 1999	-113.3643	39.1283
72	Greenwich	McArthur and Sanderson 1999	-111.9226	38.4354
73	Grassy Butte - 16 km W	McArthur and Sanderson 1999	-103.4867	47.4287
74	Loa	McArthur and Sanderson 1999	-111.6532	38.405
75	LT Murray	McArthur and Sanderson 1999	-120.5637	46.8401
76	Rest Stop	McArthur and Sanderson 1999	-120.4137	46.7115
77	Gable Mtn	McArthur and Sanderson 1999	-119.4533	46.5945
78	Ephrata 8 km E	McArthur and Sanderson 1999	-119.4591	47.2642
79	Coulee City 8 km SW	McArthur and Sanderson 1999	-119.382	47.5984
80	Odessa	McArthur and Sanderson 1999	-118.6847	47.3374
81	Petrified Forest	McArthur and Sanderson 1999	-120.0414	46.9493
82	Medicine Bow	McArthur and Sanderson 1999	-106.1916	41.9142
83	Kemmerer	McArthur and Sanderson 1999	-110.5305	41.8506
84	Daniel 2 km S	McArthur and Sanderson 1999	-110.0696	42.847
85	Kemmerer 30 km NE	McArthur and Sanderson 1999	-110.2863	41.9231
86	Boars Tusk	McArthur and Sanderson 1999	-109.1995	41.9616
87	Rock River 13 km N	McArthur and Sanderson 1999	-106.0358	41.8461

Continued

Appendix 1. (*Continued*)

No.	Site name	Study	Longitude	Latitude
88	Farson	McArthur and Sanderson 1999	-109.4433	42.0947
89	Pinedale	McArthur and Sanderson 1999	-109.8633	42.8776
90	Superior	McArthur and Sanderson 1999	-108.9559	41.7458
91	Cumberland	McArthur and Sanderson 1999	-110.578	41.5922
92	Newcastle	McArthur and Sanderson 1999	-104.1905	43.8324
93	Bitter Creek	McArthur and Sanderson 1999	-108.5578	41.5664
94	Pine Valley	Richardson unpublished	-113.7118	38.3713
95	Goshen	Richardson unpublished	-111.892	39.872
96	Lawson Draw	Richardson unpublished	-111.5104	39.8309
97	Cottonwood Pass	McArthur and Sanderson 1999	-107.5299	43.4957
98	Moneta	McArthur and Sanderson 1999	-107.4796	43.1252
99	Newcastle	McArthur and Sanderson 1999	-104.3195	43.6916
100	Cellar Loop Rd	McArthur and Sanderson 1999	-104.8676	43.6932
101	Exclosure 1960	McArthur and Sanderson 1999	-104.8852	43.7737
102	North of Bill	McArthur and Sanderson 1999	-105.2904	43.2549
103	Road 908	McArthur and Sanderson 1999	-105.3365	44.6456
104	S. Eden Canyon	McArthur and Sanderson 1999	-111.1913	41.9316
105	Curlew Valley	McArthur and Sanderson 1999	-112.732	42.0711
106	Hiledale	McArthur and Sanderson 1999	-113.0092	37.0071
107	Nucla	McArthur and Sanderson 1999	-108.5432	38.2769
108	Montrose	McArthur and Sanderson 1999	-108.0158	38.4907
109	Wilt-1	Wilt et al. 1992	-117.8415	41.6195
110	Wilt-2	Wilt et al. 1992	-119.8542	39.601
111	Wilt-3	Wilt et al. 1992	-119.8243	39.5257
112	Wilt-4	Wilt et al. 1992	-117.1032	39.4895
113	Wilt-5	Wilt et al. 1992	-114.6553	40.169
114	Wilt-6	Wilt et al. 1992	-115.9885	39.5235
115	Wilt-7	Wilt et al. 1992	-114.7555	39.4857
116	Wilt-8	Wilt et al. 1992	-117.8188	39.4885
117	Wilt-9	Wilt et al. 1992	-115.0343	39.141
118	Wilt-10	Wilt et al. 1992	-114.8233	38.4178
119	Patterson	McArthur and Sanderson 1999	-119.5416	45.9196
120	McCormack	McArthur and Sanderson 1999	-119.5774	45.8915
121	Rattlesnake	McArthur and Sanderson 1999	-119.7214	46.4989
122	McManamon	McArthur and Sanderson 1999	-119.287	46.8888
123	Simco	Richardson et al. 2012	-115.9717	43.1846
124	New Plymouth	Richardson et al. 2012	-116.8225	43.9148
125	Birds of Prey	Richardson et al. 2012	-116.4012	43.3242
126	Burns Junct	Richardson et al. 2012	-117.8617	42.7644
127	Rome	Richardson et al. 2012	-117.6111	42.8508
128	Camas 3	Richardson unpublished	-114.4008	42.9677
129	Camas 2	Richardson unpublished	-114.6725	43.1072
130	Idahome	Richardson unpublished	-113.3227	42.4153
131	Sharp Exp	Richardson unpublished	-113.2166	42.3273

Appendix 2. Pool of potential Target Group Absences (TGA) used in the bioclimatic modeling. The data sources include the California Consortium of Herbaria (CCH), the USDA Forest Service, Forest Inventory and Analysis (FIA), and two research studies.

Taxon	Common name	N	Data source
Adenostoma sparsifolium Torr.	redshanks	8	CCH
Cercocarpus ledifolius var. *ledifolius* Nutt.	curl-leaf mountain mahogany	959	FIA
Coleogyne ramosissima	blackbrush	2,925	Richardson and Meyer (2012), Esque et al. (unpubl. data)
Dendromecon rigida Benth.	bush poppy	31	CCH
Dendromecon harfordii Kellogg	island bush poppy	14	CCH
Rhamnus pilosa (Trel.) Abrams	hairyleaf redberry	1	CCH
Rhamnus pirifolia E. Greene	island redberry	16	CCH
	Total TGA	3,954	

Appendix 3. Definition of climate predictor variables.
Asterisk (*) = predictor variables used in the climatic niche model of Wyoming big sagebrush (*Artemisia tridentata* subsp. *wyomingensis*).

Climatic variable	Variable	Description
BIO1*	**Annual Mean Temperature**	
BIO2*	**Mean Diurnal Range**	**Mean of monthly (max. temp - min. temp)**
BIO3	Isothermality	(BIO2/BIO7) * 100
BIO4*	**Temperature Seasonality**	**Temperature SD * 100**
BIO5	Max Temperature of Warmest Month	
BIO6	Min Temperature of Coldest Month	
BIO7*	**Temperature Annual Range**	**BIO5 - BIO6**
BIO8*	**Mean Temperature of Wettest Quarter**	
BIO9	Mean Temperature of Driest Quarter	
BIO10*	**Mean Temperature of Warmest Quarter**	
BIO11	Mean Temperature of Coldest Quarter	
BIO12*	**Annual Precipitation**	
BIO13	Precipitation of Wettest Month	
BIO14	Precipitation of Driest Month	
BIO15	Precipitation Seasonality	Coefficient of Variation
BIO16	Precipitation of Wettest Quarter	
BIO17	Precipitation of Driest Quarter	
BIO18	Precipitation of Warmest Quarter	
BIO19	Precipitation of Coldest Quarter	

Appendix 4. Ranges for climate variables used to compare the Great Basin and Great Plains regions. PWQ = precipitation warmest quarter, PCQ = precipitation coldest quarter, ADI = annual dryness index.

		PWQ (BIO18)	PCQ (BIO19)	ADI
Contemporary	entire range	98 mm (60–135)	57 mm (33–75)	0.151 (0.120–0.171)
	Great Basin	56 mm (45–65)	74 mm (58–86)	0.179 (0.141–0.205)
	Great Plains	148 mm (128–169)	38 mm (28–41)	0.121 (0.112–0.133)
Stable	entire range	85 mm (61–107)	66 mm (41–86)	0.138 (0.115–0.159)
	Great Basin	60 mm (52–67)	80 mm (66–90)	0.150 (0.130–0.165)
	Great Plains	130 mm (116–142)	60 mm (40–76)	0.104 (0.092–0.118)
Contracting	entire range	107 mm (59–149)	51 mm (30–66)	0.159 (0.122–0.186)
	Great Basin	51 mm (40–62)	68 mm (52–80)	0.204 (0.164–0.236)
	Great Plains	152 mm (131–172)	33 mm (27–36)	0.125 (0.115–0.135)