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Contrasting climate niches among co-occurring subdominant forbs of the sagebrush steppe

Sarah C. Barga[1,2] | Thomas E. Dilts[1] | Elizabeth A. Leger[1,2]

[1]Department of Natural Resources and Environmental Science, University of Nevada, Reno, Reno, NV, USA

[2]Program in Ecology, Evolution, and Conservation Biology, University of Nevada, Reno, Reno, NV, USA

Correspondence
Sarah C. Barga, Leger Lab, NRES Dept., 1664 N. Virginia Street, Mail Stop 186, Reno, NV, 89557.
Email: sarahcatherinebarga@gmail.com

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Abstract

Aim: Abiotic conditions are key components that determine the distribution of species. However, co-occurring species can respond differently to the same factors, and determining which climate components are most predictive of geographic distributions is important for understanding community response to climate change. Here, we estimate and compare climate niches of ten subdominant, herbaceous forb species common in sagebrush steppe systems, asking how niches differ among co-occurring species and whether more closely related species exhibit higher niche overlap.

Location: Western United States.

Methods: We used herbarium records and ecological niche modelling to estimate area of occupancy, niche breadth and overlap, and describe characteristics of suitable climate. We compared mean values and variability in summer precipitation and minimum temperatures at occurrence locations among species, plant families, and growth forms, and related estimated phylogenetic distances to niche overlap.

Results: Species varied in the size and spatial distribution of suitable climate and in niche breadth. Species also differed in the variables contributing to their suitable climate and in mean values, spatial variation and interannual variation in highly predictive climate variables. Only two of ten species shared comparable climate niches. We found family-level differences associated with variation in summer precipitation and minimum temperatures, as well as in mean minimum temperatures. Growth forms differed in their association with variability in summer precipitation and minimum temperatures. We found no relationship between phylogenetic distance and niche overlap among our species.

Main conclusions: We identified contrasting climate niches for ten Great Basin understorey forbs, including differences in both mean values and climate variability. These estimates can guide species selection for restoration by identifying species with a high tolerance for climate variability and large climatic niches. They can also help conservationists to understand which species may be least tolerant of climate variability, and potentially most vulnerable to climate change.

KEYWORDS

climate variability, conservation, ecological niche modelling, herbarium, niche breadth, restoration

1 | INTRODUCTION

Identifying factors that influence differences in the geographic distribution and ecological niche among species is a core goal of ecology (Gaston, 1996; MacArthur, 1972), and one that is vital for predicting responses to global climate change (Parmesan & Yohe, 2003). Climate is a primary force shaping the distribution of plant species (Gioia & Pigott, 2000; Hocker, 1956; Woodward, Lomas, & Kelly, 2004), with geographic and interannual variation in precipitation and temperature acting as potential selective forces influencing the occurrence of individual species (Rehfeldt, Crookston, Warwell, & Evans, 2006; Woodward & Williams, 1987). While differences in mean climate are often used to describe the climate preferences of plant species, such as mean annual precipitation or mean annual temperature, measuring species-level variation in tolerance for interannual and spatial climate variability may also be useful for understanding plant responses to climate change scenarios (Adler et al., 2006; Reyer et al., 2013). In addition, soil and topographic characteristics can also affect availability of water and other resources (Dyer, 2009). These variables are increasingly being used to create niche models that focus on plant ecophysiological processes using a water balance approach (Dilts, Weisberg, Dencker, & Chambers, 2015; Lutz, Van Wagtendonk, & Franklin, 2010), producing models that are functionally more closely related to the physiological needs of plants.

While environmental variables are frequently important for determining geographic distributions, different species, even co-occurring or closely related ones, can have different environmental associations, which affect their distribution and abundance (Anacker & Strauss, 2014; Hernández, Vilagrosa, Pausas, & Bellot, 2010; Silvertown et al., 2006). Studies of niche conservatism in the distribution of plants across environmental gradients have found, at broad scales, evidence of more similar environmental associations in more closely related species (Burns & Strauss, 2011; Prinzing, Durka, Klotz, & Brandl, 2001). However, the strength of these relationships is not always consistent across taxa, meaning that phylogenetic relatedness may not necessarily predict niche overlap for a given pair of species. Additionally, the strength of niche conservatism can vary by particular environmental variables (Prinzing et al., 2001), and thus depending on the environmental factors important for species distributions in a particular ecosystem, relatedness may or may not be a strong predictor of overlap in environmental niche.

Spatial and temporal variation in the availability of resources and species-level differences in tolerance for variability may facilitate the coexistence of sympatric plant species through the evolution of niche separation (Silvertown, 2004). In arid environments, where precipitation is limited and the timing and quantity is highly variable, plant species can potentially partition their use of water resources as a way to avoid competition, maintaining species coexistence (Chesson et al., 2004). For example, species can evolve differences in phenology (Aronson, Kigel, Shmida, & Klein, 1992; Beatley, 1974) or seed germination cues (Forbis, 2010) that may enable them to differentiate the timing of their resource use from other overlapping species. Due to these differences in timing, species can co-occur at a site, but not overlap in resource use. Year-to-year variation in environmental conditions can also mediate species diversity and coexistence within arid land plant communities, where different species germinate and grow (Venable, Pake, & Caprio, 1993) or achieve higher reproductive success (Pake & Venable, 1995) in different years.

Here, we explore bioclimatic factors influencing subdominant plant distributions within western US shrublands. The Great Basin desert of North America is an arid region within the western United States that contains large areas dominated by sagebrush steppe shrublands. Landscape-scale disturbances from the invasion of exotic species, such as cheatgrass (*Bromus tectorum* L.), the increase in frequency and size of wildfires and other human activities in this region have caused degradation of native plant communities throughout the Great Basin, putting hundreds of species at risk (Billings, 1994; Chambers, Roundy, Blank, Meyer, & Whittaker, 2007; Knapp, 1996; Wisdom et al., 2003). Studying subdominant, herbaceous plants can be challenging due to their smaller size, patchy distribution or ephemeral nature (Abella, 2009; Mulroy & Rundel, 1977; Thompson & Grime, 1979). However, these plants provide important forage and shelter resources for wildlife (Beale & Smith, 1970; Connelly, Rinkes, & Braun, 2011; Gregg & Crawford, 2009; Petersen & Best, 1987; Siegel Thines, Shipley, & Sayler, 2004) and pollinators (Cane & Love, 2016; Gathmann & Tscharntke, 2002) in this region and furnish the understorey diversity which is essential for ecosystem functioning (Anderson & Inouye, 2001; Hooper et al., 2005). Consequently, there is increasing interest in understanding the ecology of herbaceous species and their current and potential distribution (Dumroese, Luna, Richardson, Kilkenny, & Runyon, 2015; Haidet & Olwell, 2015; Shaw, Lambert, Debolt, & Pellant, 2005; Shaw, Pellant, Fisk, & Denney, 2012). Currently, most range maps available for non-dominant plant species are at a coarse scale, indicating only county or state boundaries (Kartesz, 2015; USDA NRCS, 2017). These coarse boundaries can be misleading when investigating the ecology of specific plant species and their potential uses in restoration, as they almost certainly overestimate potential habitat. Using herbarium data to model the area of occupancy for understudied plant species can provide a way to approximate appropriate habitat (Doherty, Butterfield, & Wood, 2017; Elith et al., 2006; Hernández & Navarro, 2007). Although museum records present some challenges, such as identification error and collection biases (Newbold, 2010), they also provide a wealth of information describing the distribution of species over large areas (Newbold, 2010). This is especially useful for ephemeral annual species, which may not be present during field surveys in a given year (Mulroy & Rundel, 1977; Rathcke & Lacey, 1985).

Our goal was to estimate suitable climate for a suite of ten subdominant forbs commonly found in sagebrush-dominated ecosystems and to examine similarities and differences between the geographic distribution of suitable climate and the climate niches

of these species, asking the following: (1) Which climate variables are most influential for predicting the suitable climate for our target species? (2) How do relationships between highly influential climate variables (Question 1) and predicted climate suitability vary among species? (3) How do climatic niche characteristics vary by species, family and growth form? and (4) Is there a relationship between phylogenetic relatedness and niche overlap among our target species?

Although our species occur in sympatry in some areas (Williams, Howell, True, & Tiehm, 1992), we know from collection records that their overall area of occupancy varies greatly (Kartesz, 2015). We used maximum entropy (Maxent) models to estimate the area of climatic suitability for each species, and calculated niche breadth and overlap between the predicted areas of occupancy among species. Next, we assessed similarities and differences in the climate niches of our species, using Maxent results to identify the climate variables most predictive of the suitable climate for each species and the species–specific relationships between abundance and climate variables. We then calculated annual and seasonal values for precipitation and temperature variables across occurrence records for each species, asking how niches differed in mean values and their level of spatial and interannual climate variability. We expected that species would differ in the relative importance of specific climate variables and in their tolerance for climate variability, as well as in niche breadth and the size and distribution of their predicted area of occupancy. We also expected that annual species would exhibit more within-species variation in niche characteristics, due to their potential for rapid evolution in response to local conditions. Finally, we predicted that plant families would differ in their niche characteristics, and that more closely related species would exhibit higher niche overlap, consistent with niche conservatism (Burns & Strauss, 2011; Prinzing et al., 2001). We conclude by discussing how these predictions could be tested using field studies and how this information can be used in conservation and restoration efforts.

2 | METHODS

2.1 | Environmental variables

We considered 29 biologically relevant variables for inclusion in our modelling efforts (see Table S1). These included measures of annual and seasonal precipitation and temperature, as well as a suite of bioclimatic variables (Booth, Searle, & Boland, 1989). All variables were derived from 64-year averages of monthly temperature and precipitation values obtained from PRISM data for the western United States from 1950 to 2014, the period of herbarium record observations (Daly et al., 2008). We used a Thornthwaite water balance approach to calculate variables that take into consideration the simultaneous availability of water and energy for plants (Lutz et al., 2010; Stephenson, 1998). Several of these variables were derived from climographs of actual evapotranspiration (AET), potential evapo-transpiration (PET), water supply (WS), soil water balance (SWB) and climate water deficit (CWD), using methods outlined in Dilts et al. (2015). We selected a subset of ten uncorrelated (Pearson's correlation coefficient > ± 0.70) variables to include in Maxent models to describe the suitable climate of each species and to allow for comparisons across species (Table S2). Variables included the following: mean maximum and minimum temperature, temperature range, annual and summer precipitation, precipitation seasonality, fraction of AET from precipitation, soil water balance, AET:CWD and spring water availability (Table 1). For simplicity, we use the term "climate variables" to include all of these responses, including variables such as

TABLE 1 Ten soil and climate variables used in ecological niche models. All water-based variables are in units of millimetres and all temperature-based variables are in units of degrees celsius

Variable	Biological relevance
SWB—annual soil water balance[a,b]	Quantity of water stored in the soil from one month to the next
Coefficient of variation in annual precipitation	Seasonality of precipitation
AET:CWD ratio[a]	Relative CWD; values > 1 are more mesic, values < 1 are more xeric
Positive difference between AET and SWB[a]	Fraction of AET from month's precipitation, not from soil water
Spring ratio of WS and the greater of AET or SWB[a]	Spring water available for runoff or deep percolation
Annual Precipitation[b]	
Summer Precipitation[d]	
Temperature range[c]	
Annual Minimum temperature[c]	
Annual Maximum temperature[c]	

[a]See Dilts et al. (2015) for method of calculation.
[b]Summed for all months.
[c]Averaged for all months.
[d]Summer (June, July, August).

TABLE 2 Species-specific evaluation of the best ecological niche model results for (A) perennial and (B) annual species. Values were obtained from Maxent models using environmental variables (Table 1) calculated for herbarium collection locations. AUC values are an indicator of model prediction accuracy, with values closer to 1 indicating higher predictive power

Species	Acronym	Family	*n*	Training AUC[a]	Test AUC[a]	Niche Breadth	Predicted area of suitability[b] (1,000 km^2)
(A)							
Agoseris grandiflora	AGGR	*Asteraceae*	141	0.926	0.905	0.323	552
Chaenactis douglasii	CHDO	*Asteraceae*	456	0.799	0.768	0.682	1,348
Crepis intermedia	CRIN	*Asteraceae*	173	0.755	0.749	0.741	1,322
Phacelia hastata	PHHA	*Boraginaceae*	468	0.776	0.810	0.732	1,053
(B)							
Blepharipappus scaber	BLSC	*Asteraceae*	80	0.889	0.904	0.435	325
Collinsia parviflora	COPA	*Scrophulariaceae*	554	0.790	0.746	0.675	1,540
Cryptantha pterocarya	CRPT	*Boraginaceae*	401	0.865	0.858	0.417	1,074
Gilia inconspicua	GIIN	*Polemoniaceae*	214	0.815	0.807	0.530	774
Mentzelia albicaulis	MEAL	*Loasaceae*	568	0.707	0.715	0.827	1,340
Microsteris gracilis	MIGR	*Polemoniaceae*	515	0.735	0.722	0.802	1,442

n = number of herbarium record locations used for modelling the species distribution.
[a]Test points for all models were better predicted than random prediction with the same fractional predicted area ($p < .001$).
[b]The area of suitable habitat was determined using the Maximum Test Sensitivity Plus Specificity threshold value produced by the ecological niche model for each species and converting to presence–absence binary maps.

SWB that are derived from an interaction between soil and climate characteristics.

2.2 | Species and occurrences

We selected four perennial and six annual forbs that are commonly found in sagebrush steppe ecosystems in the western Great Basin. As a guild, understorey forbs are important forage and cover for imperilled sagebrush-obligate wildlife, such as the greater sage-grouse (*Centrocercus urophasianus*) (Connelly et al., 2011; Gregg & Crawford, 2009) and pygmy rabbits (*Brachylagus idahoensis*) (Green & Flinders, 1980). We selected these ten species in particular either because they have been specifically documented as important for wildlife diets or important species for pollinators (Drut, Pyle, & Crawford, 1994; Dumroese, Luna, Pinto, & Landis, 2016; Dumroese et al., 2015; Gregg & Crawford, 2009; Stiver et al., 2015). Perennials species included *Agoseris grandiflora* (Nutt.) Greene, *Chaenactis douglasii* (Hook.) Hook. and Arn., *Crepis intermedia* A. Gray, and *Phacelia hastata* Douglas ex Lehm.; annual species included *Blepharipappus scaber* Hook., *Collinsia parviflora* Lindl., *Cryptantha pterocarya* (Torr.) Greene, *Gilia inconspicua* (Sm.) Sweet, *Mentzelia albicaulis* (Hook.) Torr. and A. Gray, and *Microsteris gracilis* (Hook.) Greene. These species differ in phenology (Table S3), with annual species generally flowering earlier in the year and for a longer window (March–July), while these perennial species generally have a shorter bloom period (May–July). These species are primarily distributed within the western United States, and we obtained occurrence records from three herbaria with coverage spanning this region (Table 2): The Intermountain Region Herbarium Network (http://intermountainbiota.org/portal/) (accessed: 01 December 2014), The Consortium of California Herbaria (http://ucjeps.berkeley.edu/consortium/) (accessed: 30 April 2015), and the Burke Museum herbarium at the University of Washington (http://www.burkemuseum.org/research-and-collections/botany-and-herbarium/collections/database/) (accessed: 22 October 2015). There was frequent uncertainty about location information provided for older specimens, especially collections from the 1940s and earlier. Thus, we limited our points to collections from 1950 to the present, a range that allowed us to maintain our sample size (between 80 and >500 records per species; Table 2) while eliminating many early records with imprecise information. We then identified spatial outliers, verified the accuracy of location information and removed any questionable records from the dataset.

We focused our analysis on points within the Western United States., as this represents the core of the range for our focal species. We performed geographic filtering of occurrence points for each species in order to reduce collection bias (Boria, Olson, Goodman, & Anderson, 2014; Kramer-Schadt et al., 2013), using the SDM Toolbox for ARCGIS (Brown, 2014) to remove duplicate points within a 20-km buffer. This practice also attempts to reduce spatial-autocorrelation when measuring environmental variables and improves model generalizability (Kramer-Schadt et al., 2013). We used variograms to assess whether a 20-km buffer would reduce spatial-autocorrelation among climate variables. We began by performing a principal components analysis in ArcMap 10.1 using the ten uncorrelated variables used to describe the climate niches of species, then created variograms using 351,506 random points spanning the study area to determine the range of variability for the principal components axes. The first principal components axis corresponded to moisture and elevation-related variables and accounted for 99.9998% of the variation in the climate variables across the study area, with a range of just

over 7 km. Thus, the 20-km buffer acted as a conservative measure for reducing spatial-autocorrelation among our climate variables. We used the spatially thinned set of occurrence points to perform the Maxent modelling, as removing spatially autocorrelated points has been shown to improve the performance of the presence-only modelling methods (Fourcade, Engler, Rödder, & Secondi, 2014; Hijmans, 2012; Veloz, 2009). We then randomly partitioned the thinned dataset for each species into a set used for model training (65%) and a set used for model validation (35%). After performing geographic thinning, clear visible differences in sampling effort across states remained. To account for these differences in sampling effort across jurisdictional boundaries, we built a bias file and included it in our Maxent modelling framework (Phillips & Dudík, 2008). The Target Group Sampling approach of Ponder, Carter, Flemons, and Chapman (2001) was used to estimate sampling density for each state relative to the region-wide average. Bias was calculated by dividing the density of occurrences of all species in each state by the average density of occurrences across all states.

2.3 | Estimating area of occupancy, niche breadth and overlap

Due to the lack of absence data for our species and the large number of presences available from herbarium records (Table 2), we used a presence-background modelling approach. Among presence-background modelling approaches, Maxent modelling is one of the best performing and most commonly used approaches for estimating potential habitat (Elith et al., 2006). We used Maxent (version 3.3.3k, Phillips, Anderson, & Schapire, 2006) to identify the best model(s) of the potential habitat for our focal species across the western United States, relying on Maxent's internal variable selection to identify which combination of variables had the most predictive power for each species (Elith et al., 2011). We selected 10,000 random background points using either the entire study area, for more widely distributed species, or buffer areas around occurrence points, for species with more restricted distributions (see Appendix S1). Background selection can affect model performance (Chefaoui & Lobo, 2008; Fourcade et al., 2014), and the background used to analyse the suitable climate for each species was optimized using methods outlined by VanDerWal, Shoo, Graham, and Williams (2009) and Iturbide et al. (2015) (Table S4). Model selection included species-specific optimization by varying the regularization parameter (1–5) and the feature types (linear, quadratic, product, threshold and hinge) (Anderson & Gonzalez, 2011; Warren & Seifert, 2011). We selected the best model(s) for each species using Akaike's information criterion (AIC) score, calculated using ENMTOOLS (Warren, Glor, & Turelli, 2010). The model with the lowest AIC score was considered the best model, and models with AIC scores less than two points higher than the lowest AIC score were considered comparable. We created binary maps for all best models using the threshold value associated with maximum sensitivity plus specificity of the test data (Liu, White, & Newell, 2013) (Figures S1 and S2). For species with multiple best models, we averaged the predicted probabilities of occurrence and the threshold values across all best models, and we created binary maps using these estimates (Figures S1 and S2). We used ArcMap 10.1 (ESRI, 2012) to calculate the relative percent overlap for each species pair by dividing area of overlap by total area occupied (Table S5).

Niche breadth was calculated for each species using ENMTOOLS and the output of the top Maxent models (Warren et al., 2010). The niche breadth function determines the amount of ecological niche space available by applying the Levins' inverse concentration metric (Levins, 1968). Niche breadth values range from 0 to 1 and are comparable among species, with lower values indicating a more narrow environmental tolerance and higher values indicating a broader environmental tolerance. Niche overlap between pairs of species (*D*) was calculated using the Schoener's *D* statistic (Schoener, 1968; Warren, Glor, & Turelli, 2008). *D* values range from 0 to 1, with 0 indicating no overlap in environmental space and 1 corresponding to complete overlap. Finally, we performed a pairwise niche equivalence test using ENMTOOLS 1.4 (Warren et al., 2010), to determine whether niche spaces were interchangeable among species. *D* values were compared to a null distribution of 100 overlap values, and niches were determined to be non-equivalent if overlap was significantly lower than observed in the null distribution.

2.4 | Comparing climate niches

We made climate niche comparisons among our species using the best model for each species as identified by our model selection procedures. Although alternate best models existed for some species, all were very similar to the best model as indicated by the AIC values, and for computational simplicity, we picked only one best model per species. We report area under the receiver-operator curve (AUC) values for the best model for each species (Table 2); AUC values are threshold-independent measures of model prediction accuracy, measuring the probability that a randomly chosen presence is ranked higher than a randomly chosen background (Merow, Smith, & Silander, 2013). The permutation importance values and the ecological response curves were used to identify the climate variables most predictive of the distribution of each species (Phillips & Dudík, 2008).

We focused our analysis of climate variation on two variables of interest: mean summer precipitation (mm) and mean annual minimum temperature (C); these variables were selected based on their importance for predicting the suitable climate for our study species. PRISM monthly precipitation and temperature rasters were downscaled from a 4 km^2 to a 500 m^2 grid size using the Climate Water Deficit Toolbox (Dilts, 2015), and were used to extract monthly precipitation and temperature data for each occurrence point from 1950 to 2014. Downscaling was performed with the delta method using the difference in the values between the monthly PRISM data for the variables and the 30-year PRISM normals at an 800 m^2 spatial resolution. We then calculated summer (June–August) precipitation totals and mean annual minimum temperatures for each year. We used these values to calculate the mean and standard deviation for each of the variables at each occurrence point through

TABLE 3 Results of the permutation importance analysis for a set of 10 uncorrelated variables performed in Maxent. Values indicate the percentage of variable contribution to the ecological niche model for (A) perennial and (B) annual species. Variables with a contribution >8, an arbitrary cut-off selected by assessing the values, are presented in bold

Variable	*Agoseris grandiflora*	*Chaenactis douglasii*	*Crepis intermedia*	*Phacelia hastata*	Percent of species affected
(A)					
Maximum temperature	7.7	**22.9**	**26.4**	**56.7**	75
Minimum temperature	0	**12.3**	**9.6**	**20.7**	75
Temperature range	0.2	0	0	3.6	0
Annual precipitation	0.3	1.3	5.6	0	0
Summer precipitation	**57.2**	**32.4**	**49.4**	6.5	75
Precipication seasonality	**31.7**	**18.2**	6.3	1.5	50
Fraction of AET from precipitation	1.5	**9.8**	0	**11**	50
Soil water balance	0	0.7	0	0	0
AET:CWD	0	0	0	0	0
Spring water availability	1.5	2.3	2.2	0	0

Variable	*Blepharipappus scaber*	*Collinsia parviflora*	*Cryptantha pterocarya*	*Gilia inconsipcua*	*Mentzelia albicaulis*	*Microsteris gracilis*	Percent of species affected
(B)							
Maximum temperature	6.3	7.6	0.2	0	**11.9**	2.4	17
Minimum temperature	**29.4**	3.8	**67**	**30.3**	3.4	3.4	50
Temperature range	0	0.2	4	2.6	0	**11.3**	17
Annual precipitation	**20.1**	7.4	**11.4**	0	**14.1**	0	50
Summer precipitation	**33.7**	11.5	**8.6**	27.6	**45.3**	0	83
Precipication seasonality	0.4	**26.1**	2.3	**28**	3.5	0	33
Fraction of AET from precipitation	4.9	**14.4**	3.4	4.6	0	0	17
Soil water balance	1.6	**24.9**	0	6.2	**21.7**	**78.9**	50
AET:CWD	0	0.2	0	0	0	0	0
Spring water availability	3.5	3.9	3	2.1	0	3.9	0

time (year-to-year variation) and for each year across each collection point (spatial variation).

We calculated the coefficient of variation (CV-standard deviation/mean) as a measure of climate variability for each variable across the occurrence points for each species. In order to account for unequal sample sizes for occurrence data among species, we calculated an unbiased CV using the methods of Abdi (2010), as follows:

$$CV_{unbiased} = \left(1 + \frac{1}{4 \times N}\right) \times CV$$

where N is the number of samples from the group being measured.

We used Program R (R Development Core Team, 2016) to determine statistical differences in the mean values and climate variability for summer precipitation and mean annual minimum temperature among species, plant families and growth forms (annual/perennial). For the analysis of plant families, we included only families that were represented by more than one species (Asteraceae, Boraginaceae and Polemoniaceae). First, we performed Type 2 ANOVAs to compare means and CVs using the CAR package (Fox & Weisberg, 2011). If differences were detected, we performed Tukey's Tests using the AGRICOLAE package (de Mendiburu, 2016) to determine significant differences among groups.

2.5 | Calculating relatedness among species

We estimated the phylogenetic distances between our focal species using gene sequences for the region associated with *Internal Transcribed Spacer 1* from sequence data available at GenBank (AF386493.1 *Agoseris grandiflora*, GU818511.1 *Chaenactis douglasii*, EU363616.1 *Crepis acuminata*, AY630299.1 *Phacelia hastata*, AF229316.1 *Blepharipappus scaber*, AF385340.1 *Collinsia parviflora*, KU927680.1 *Cryptantha pterocarya*, KJ159385.1 *Gilia inconspicua*, HM357418.1 *Mentzelia* sp., EU339823.1 *Microsteris gracilis).* We found sequences for eight of our species, and were able to represent the remaining two species using sequences for regionally appropriate members of the same genera, *Crepis* (*C. acuminata*) and *Mentzelia* (*M. longiloba*). The sequences (788 base pairs) were aligned using ClustalW. We used Program R (R Development Core Team, 2016), package PHANGORN (Schliep, 2011), to create a distance matrix for our species. We then performed a Mantel test with 9999 replicates, package ADE4 (Dray & Dufour, 2007), to test for a significant relationship between phylogenetic distance and niche overlap.

3 | RESULTS

When performing the background optimization process for our climate suitability models, we found that four species (*A. grandiflora*, *B. scaber*, *G. inconspicua* and *C. intermedia*) required the selection of a smaller background than the full study area (Table S4). In addition, model outcomes for the two most restricted species, *A. grandiflora* and *B. scaber*, were different when comparing the results obtained using the buffered background relative to the entire study area. More specifically, for *B. scaber*, we found that while minimum temperature and annual precipitation were important for predicting suitable climate at smaller buffer distances, they reduced in importance at higher buffer distances; conversely, the fraction of AET from precipitation was only important for predicting suitable climate at the largest buffer distance (Figure S3). These results support previous research indicating that the spatial extent of the model background can affect model predictions and performance (VanDerWal et al., 2009); therefore, we used the optimum background area for each species for all analyses.

3.1 | Identifying highly influential climate variables

Species varied in the climate variables that contributed most to predicting their suitable climate (Table 3). For perennials, maximum temperature, minimum temperature and summer precipitation were most important (Table 3A). For annuals, summer precipitation was highly influential (affecting 83% of species), followed by minimum temperature, annual precipitation and soil water balance (affecting 50% of species; Table 3B).

3.2 | Relationships between climate and environmental suitability

In general, the direction of the relationship and the degree of influence on predicted climate suitability varied across species for the bioclimatic variables used in our models (Figures 1 and 2). More specifically, increased summer precipitation had a slight positive effect on climate suitability for *C. parviflora* and *C. pterocarya*, whereas increased summer precipitation had a negative effect on potential climate suitability for *A. grandiflora*, *C. douglasii*, *C. intermedia*, *B. scaber*, *G. inconspicua* and *M. albicaulis*. Summer precipitation was not highly predictive of the suitable climate for either *P. hastata* or *M. gracilis*. In addition, decreasing annual minimum temperatures had a negative effect on potential climate suitability for *C. douglasii*, whereas *C. intermedia*, *P. hastata*, *B. scaber*, *C. pterocarya* and *G. inconspicua* all had different optimal minimum temperatures that characterized their suitable climate. Annual minimum temperature was not highly predictive of the suitable climate for *A. grandiflora*, *C. parviflora*, *M. albicaulis* or *M. gracilis*.

3.3 | Niche differences among species, plant families and growth forms

Species varied in the size of their potential area of occupancy (calculated from binary maps, see Figures S1 and S2) and niche breadth (Table 2). *C. parviflora* possessed the largest area of occupancy (1,540,000 km^2) and *B. scaber* possessed the smallest

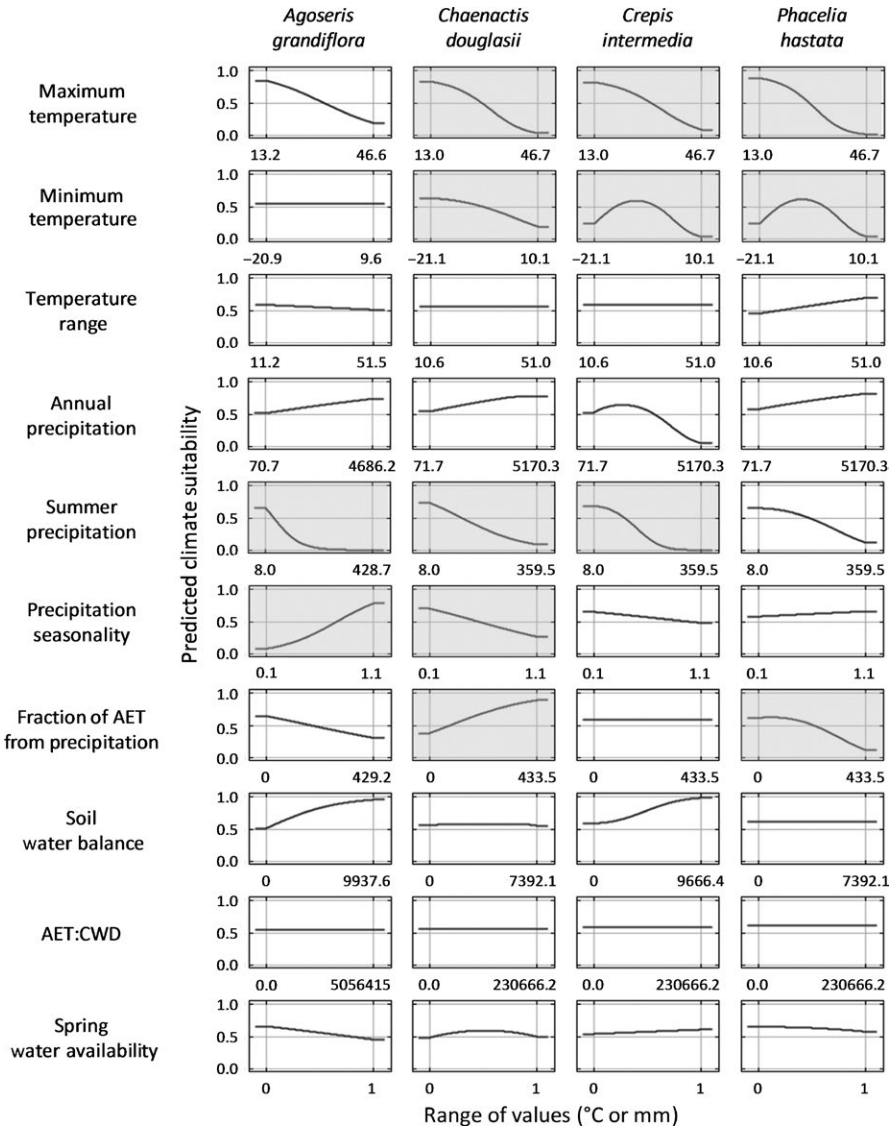

FIGURE 1 Ecological response curves demonstrating relationships between environmental variables and predicted climate suitability for each perennial species. Response curves are based on the results of ecological niche models using ten uncorrelated variables. The *x*-axis for each variable represents the range of that variable across the geographic background used in the model, with all water-based variables in units of millimetres and all temperature-based variables in units of degrees celsius, and the *y*-axis represents the predicted climate suitability ranging from 0 (unsuitable) to 1 (suitable). Grey boxes indicate variables that were important for describing suitable climate for a particular species (permutation importance > 8)

area of occupancy (325,000 km^2), with an average area of occupancy of 1,077,000 km^2 (Table 2). The predicted area of occupancy for our species overlapped in some areas, including parts of the Great Basin, but our estimates indicated that the extent and spatial distribution of suitable climate differed greatly among most species (Figures 3 and 4). Niche breadth values varied from 0.827 (*M. albicaulis*) to 0.323 (*A. grandiflora*), with higher numbers indicating a broader climatic range of suitability (Table 2). Pairwise niche comparisons suggested that only one pair of species occupied an equivalent niche (*C. douglasii* and *C. intermedia*- overlap of 0.884), despite the fact that some species overlap geographically across a large portion of their predicted area of occupancy (see Table S5).

Our species occupied areas that differed significantly in both their mean level of summer precipitation ($F_{(9,3568)} = 55.24$, $p < .001$) and their mean annual minimum temperature ($F_{(9,3568)} = 219.58$, $p < .001$). Species also differed in the level of variation in summer precipitation and annual minimum temperatures across their range (summer precipitation: $F_{(9,640)} = 86.55$, $p < .001$, annual minimum temperature: $F_{(9,640)} = 1027716$, $p < .001$) and year-to-year variation at collection locations (summer precipitation: $F_{(9,3568)} = 71.01$, $p < .001$, annual minimum temperature: $F_{(9,3568)} = 81.78$, $p < .001$) (Figures 5 and 6). For example, the perennial *A. grandiflora* was collected from locations that experienced much lower quantities of summer precipitation than other species, and had relatively high levels of spatial and year-to-year variation in summer precipitation. In contrast, the annual *C. parviflora* occupied areas that experienced low quantities of summer precipitation with low levels of spatial and year-to-year variation relative to other species. Similar patterns were seen for minimum temperature, where the annual *C. pterocarya* was found in areas that experienced relatively high minimum temperatures with high spatial variation and low year-to-year variation in minimum temperature. In comparison, the perennial *C. douglasii* grew in areas that experienced relatively low minimum temperatures with moderate spatial variation and high year-to-year variation in minimum temperature. The perennial *A. grandiflora* grew in areas that were notably different in environmental characteristic than the other perennial species.

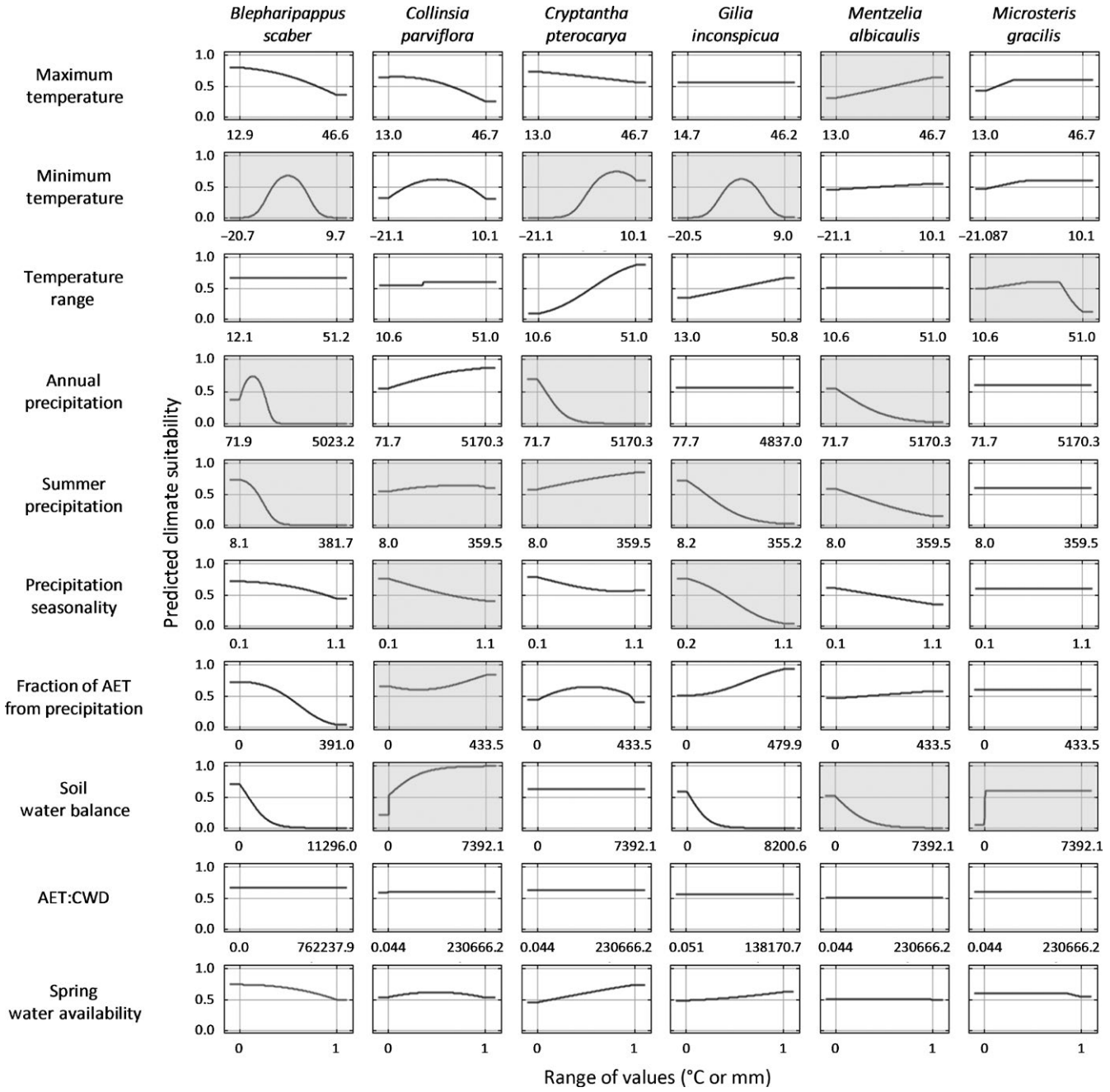

FIGURE 2 Ecological response curves demonstrating relationships between environmental variables and predicted climate suitability for each annual species. Response curves are based on the results of ecological niche models using ten uncorrelated variables. The *x*-axis for each variable represents the range of that variable across the geographic background used in the model, with all water-based variables in units of millimetres and all temperature-based variables in units of degrees celsius, and the *y*-axis represents the predicted climate suitability ranging from 0 (unsuitable) to 1 (suitable). Grey boxes indicate variables that were important for describing suitable climate for a particular species (permutation importance > 8)

We did not find family-level differences in the mean values for summer precipitation ($F_{(2,2448)} = 0.95$, $p = .387$) or for temporal environmental variation associated with summer precipitation ($F_{(2,2448)} = 1.34$, $p = .261$). We did find family-level differences in spatial variation associated with summer precipitation ($F_{(2,517)} = 6.62$, $p < .01$). Members of *Polemoniaceae* grew in areas with higher levels of spatial variation in summer precipitation, while members of *Boraginaceae* grew in areas of moderate spatial variation in summer precipitation. Members of *Asteraceae* exhibited the lowest level of spatial variation in summer precipitation across the locations where they grow.

We found family-level differences in the mean values for annual minimum temperatures ($F_{(2,2448)} = 74.45$, $p < .001$) and the levels of spatial and temporal environmental variation associated with annual minimum temperature (spatial: $F_{(2,517)} = 118.56$, $p < .001$, temporal: ($F_{(2,2448)} = 22.36$, $p < .001$). Members of *Boraginaceae* grew in areas

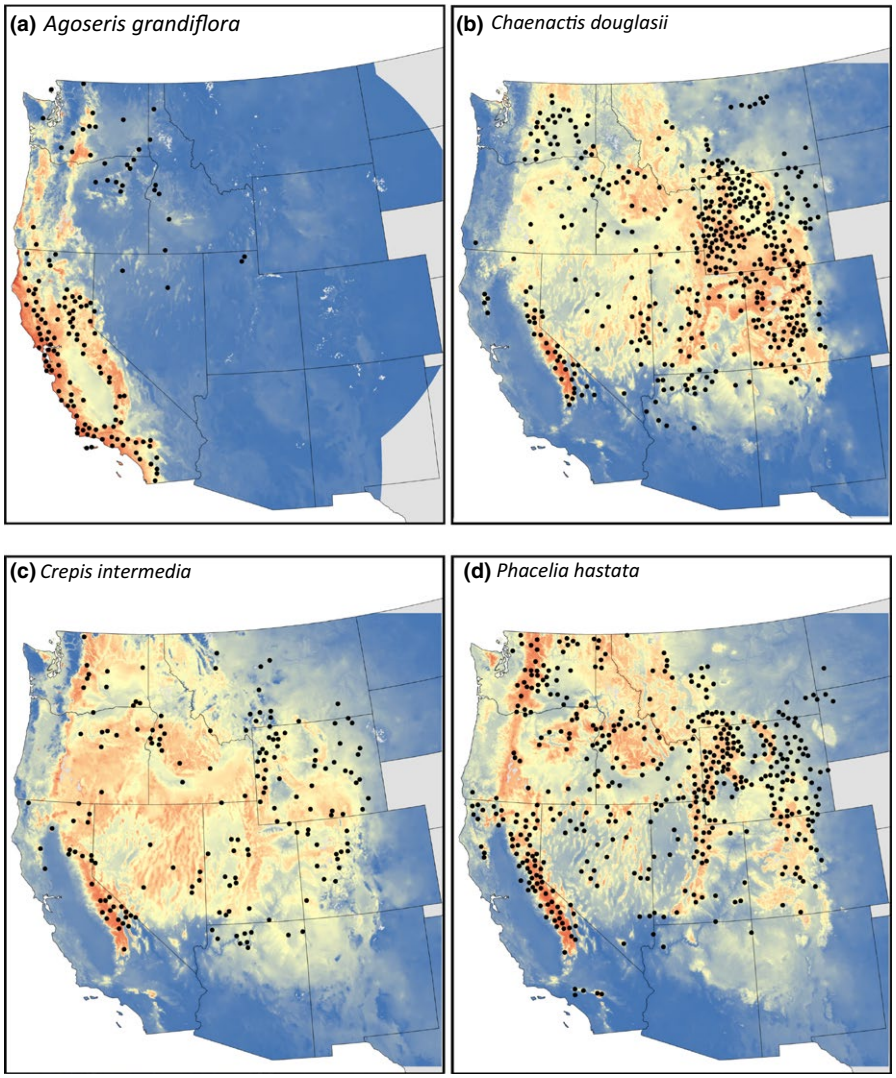

FIGURE 3 Estimated suitable climate for perennial species. Maps depict environmental suitability using a red–yellow–blue colour ramp, with red indicating a high probability and blue indicating a low probability of suitable climate relative to a minimum–maximum stretch type based on the Maxent output probabilities for each species. These maps were created using Maxent modelling based on herbarium records (shown as points on the maps) and 10 uncorrelated environmental variables

that experienced relatively high annual minimum temperatures with high spatial and low year-to-year variation in annual minimum temperature. Members of *Polemoniaceae* grew in areas experiencing relatively moderate minimum temperatures and moderate levels of environmental variation. Finally, members of *Asteraceae* grew in areas that experienced relatively low minimum temperatures with relatively low levels of spatial variation and relatively high levels of year-to-year variation.

We found differences between annuals and perennials in both mean values of summer precipitation ($F_{(1,3576)} = 41.89$, $p < .001$) and the level of temporal environmental variation associated with summer precipitation ($F_{(1,3576)} = 32.00$, $p < .001$). We did not find a difference in the level of spatial variation in summer precipitation associated with the different growth forms ($F_{(1,648)} = 0.12$, $p = .734$). Perennial species grew in areas that experienced higher quantities of summer precipitation with relatively low year-to-year variation in summer precipitation.

Annuals and perennials differed in both the mean values of annual minimum temperature ($F_{(1,3576)} = 407.11$, $p < .001$) and the levels of spatial and temporal environmental variation associated with annual minimum temperature (spatial: $F_{(1,648)} = 33.54$, $p < .001$, temporal: ($F_{(1,3576)} = 169.89$, $p < .001$). Perennial species grew in areas that experienced lower annual minimum temperatures with relatively low spatial variation and relatively high year-to-year variation in minimum temperature.

3.4 | Relationship between phylogenetic distance and niche overlap

We did not find support for a relationship between phylogenetic distance and niche overlap (rM = 0.115, $p = .212$).

4 | DISCUSSION

Predicting suitable habitat for subdominant species can be challenging due to the ephemeral nature of some species and the lack of apparency for others. Here, we used herbarium records to estimate the climate preferences of Great Basin forbs, identifying potentially contrasting niches for a suite of understorey species. Although our focal

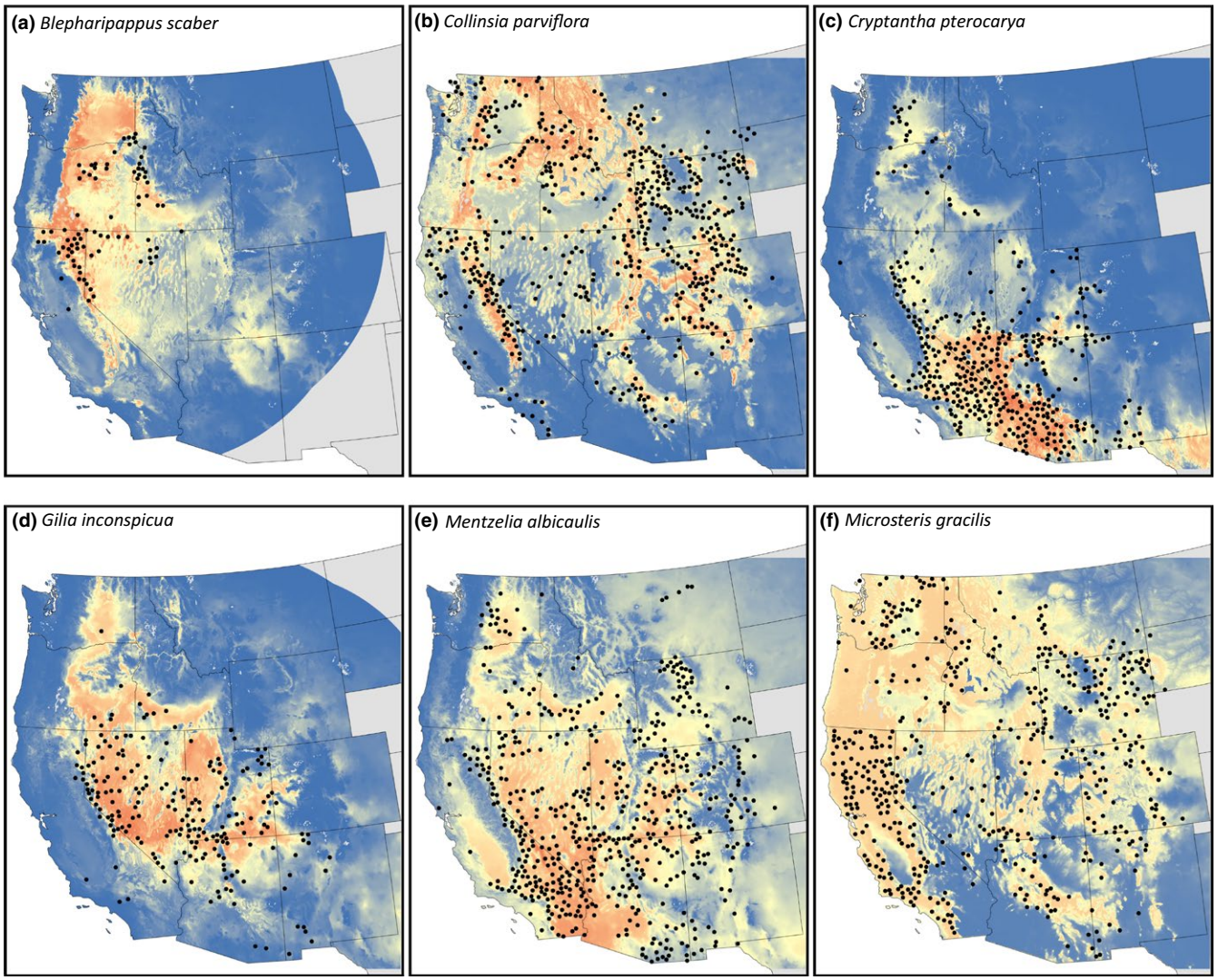

FIGURE 4 Estimated suitable climate for annual species. Maps depict environmental suitability using a red–yellow–blue colour ramp, with red indicating a high probability and blue indicating a low probability of suitable climate relative to a minimum–maximum stretch type based on the Maxent output probabilities for each species. These maps were created using Maxent modelling based on herbarium records (shown as points on the maps) and 10 uncorrelated environmental variables

species displayed some overlap in the environmental characteristics associated with potential habit and in the spatial distribution of their suitable climate (Figures 3 and 4), they appeared to possess very different climate niches. In fact, our results indicate that only one pair of species, *C. douglasii* and *C. intermedia*, possessed overlapping climate niches. Some variables, such as summer precipitation and annual minimum temperature, were important predictors for multiple species, but even then, these environmental variables differed in the direction of their influence (i.e., positive, negative) or in the quality of their relationship (i.e., linear or threshold) when predicting suitable climate. Despite extensive species-level differences in climate niche, there were commonalities in climate preferences among species from the same families, indicating potential niche conservatism. We also found commonalities among annuals and perennials, with annual species more likely to grow in areas with higher temporal variability in summer precipitation and higher spatial variability in minimum temperatures, indicating consistent selection for particular life history characteristics in particular environments (Díaz et al., 2004; Hastings & Caswell, 1979).

Although species in the same family shared some characteristics, we did not find support for a relationship between phylogenetic relatedness and niche overlap among our species. Other studies have explored this question with contrasting results. Several studies have found evidence of high levels of niche conservatism among related taxa in general (Burns & Strauss, 2011; Koniak & Everett, 1982; Lord, Westoby, & Leishman, 1995; Prinzing et al., 2001) and among co-occurring sister species (Anacker & Strauss, 2014). Other research has found no evidence of a relationship between niche overlap and species coexistence (Godoy, Kraft, & Levine, 2014; Silvertown et al., 2006). In studies like ours, which compare characteristics of relatively few species, phylogenetic relatedness may not be strong enough to predict overlap among particular groups of

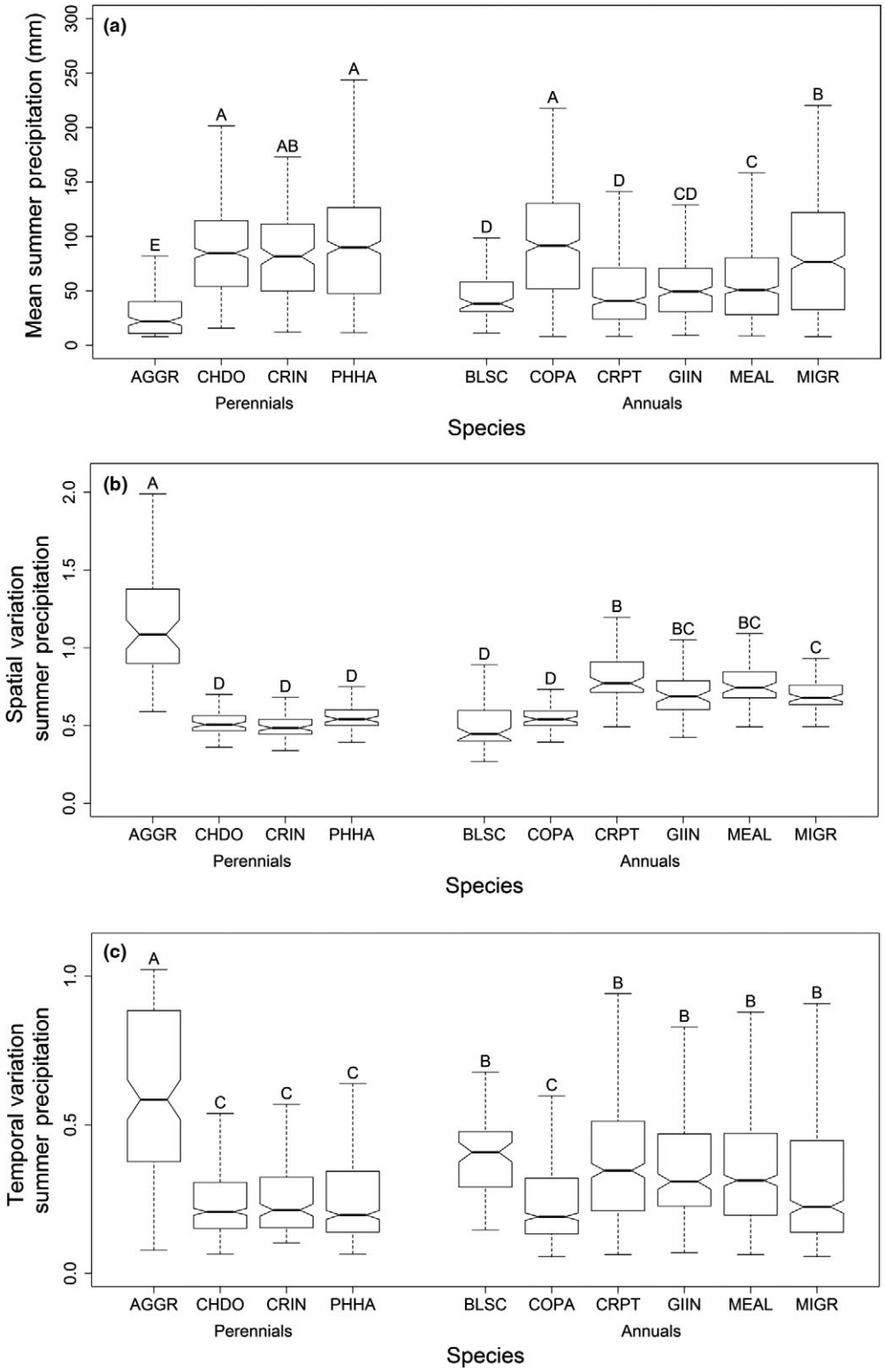

FIGURE 5 Boxplots of mean (a), spatial variation (b), and temporal variation (c) of annual precipitation at herbarium collection locations. Variation is measured using the coefficient of variation (CV) for total annual precipitation for each year. Spatial variation is measured across the collection locations for each species from 1950 to 2014 and temporal variation is measured across all years from 1950 to 2014 at each location. See Table 2 for species acronyms. Letters that appear above each boxplot indicate the results of Tukey's tests that differentiate significant differences in means between species by assigning them a different letter

species. For example, while our two species with overlapping climate niches were in the same plant family (Asteraceae), another perennial plant in the same family displayed contrasting relationships with environmental variables (Figures 1, 5 and 6). Another explanation for these results could be that competition is occurring between closely related species, and that character displacement is driving the lack

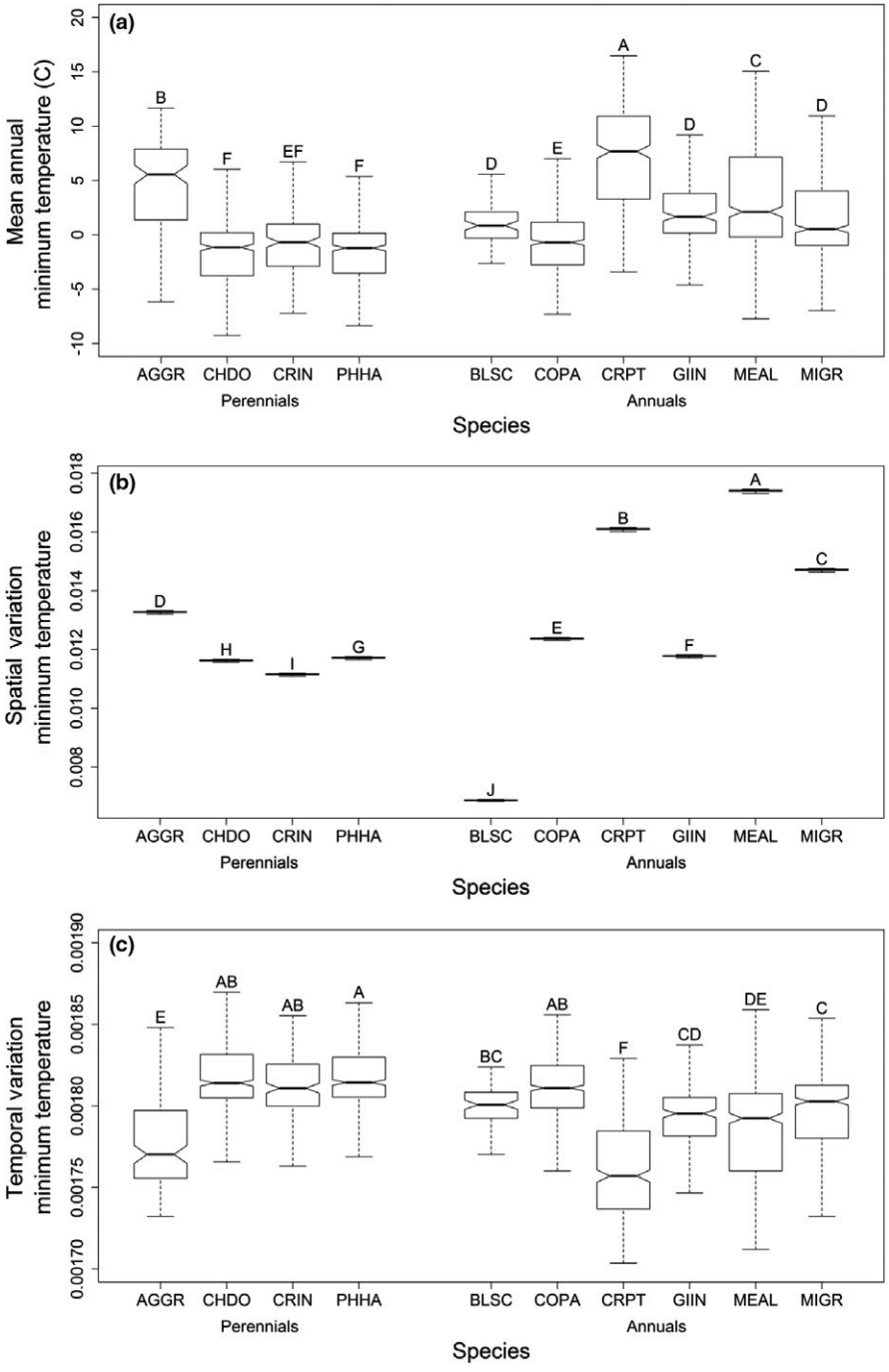

FIGURE 6 Boxplots of mean (a), spatial variation (b), and temporal variation (c) of summer precipitation at herbarium collection locations. Variation is measured using the coefficient of variation (CV) for total summer precipitation for each year. Spatial variation is measured across the collection locations for each species from 1950 to 2014 and temporal variation is measured across all years from 1950 to 2014 at each location. See Table 2 for species acronyms. Letters that appear above each boxplot indicate the results of Tukey's tests that differentiate significant differences in means between species by assigning them a different letter

of phylogenetic patterns (Silvertown, 2004). This process could result in similar climate niches and coexistence at a regional scale, with niche partitioning occurring at a more local scale (Brown & Wilson, 1956). Ultimately, while there may be evidence of broad relationships between phylogenetic relatedness and niche overlap, understanding the potential for coexistence between individual species likely requires more detailed information for more species.

Our models did produce testable hypotheses about environmental conditions that should favour particular species, and thus can serve as a foundation for further experiments to understand plant species coexistence, community diversity and adaptation to climate. For example, while *M. albicaulus* and *B. scaber* might occur at the same location, our modelling results suggest that *M. albicaulus* would grow better in warmer, drier years (supported by Leger, 2013) while *B. scaber* would perform better in cooler years (Figure 2). Identifying sympatric species with similar growth forms can be useful for examining how variation in climate niches among species may result from the temporal partitioning of resources through the storage effect (Angert, Huxman, Chesson, & Venable, 2009; Chesson & Warner, 1981), reflected in variation in species composition and performance on the landscape from year-to-year. Additionally, using niche modelling to identify areas that vary in species diversity may be useful for examining diversity–stability relationships through mechanisms such as the portfolio effect (Chalcraft, 2013; Tilman, Lehman,

Bristow, & Circle, 1998). This approach can also help to identify and explore strong abiotic predictors of species distributions. For example, it seems counter-intuitive that summer precipitation should be influential for species that do not typically survive long enough to be present during the summer season; the importance of summer precipitation has also been seen for the annual invader *B. tectorum* (Bradley, 2009). Thus, summer precipitation may be an important indirect indicator of future resource availability or stronger competitive pressures from late season species (Bradley, 2009).

Future work could involve testing the importance of genotype–environment relationships for producing patterns observed here, using field collections and reciprocal transplant studies across a range of environments. Such studies could indicate whether species with larger climate niches are persisting in disparate areas through phenotypic plasticity, that is responding to local conditions by adaptive changes in phenotype, or show fixed differences in phenotypic traits, that is they persist via populations that are adapted to specific local conditions. Climate is not the only factor shaping the realized niches of these species (Silvertown, 2004), and further experiments could ask to what degree competition, facilitation and other interactions are affecting species distributions (Wisz et al., 2013).

Because of the conservation value of desert shrublands, our results are also relevant for conservation and restoration. From a land management perspective, this research establishes that herbarium records can be used to create estimated maps of suitable climate for species that lack detailed habitat information, and also to identify species with high tolerance for climate variability and relatively large climate niches. Land managers could use these results to select appropriate restoration species based on the environmental conditions at the location being restored, or to prioritize planting of species with high tolerance for year-to-year climate variability. This approach could be used in conjunction with recently developed tools built to help direct the effort of land managers to efficiently and appropriately select climatically representative sites for specific restoration needs (Doherty et al., 2017). This type of information is especially important for species where seed availability is limited and can be expensive to procure (Shaw et al., 2012). This work is also of value for conservation efforts, as it can identify species with narrow climate niches or low tolerance for environmental variation, which may be the most vulnerable to climate change (Thuiller, Lavorel, & Araújo, 2005; Williams, Araujo, & Rasmont, 2007). Modelling efforts such as those used here could be used retrospectively to ask if species showing the largest contemporary decreases under climate change are also those with the lowest tolerance to environmental variation. Herbarium collections represent hours of fieldwork, preservation and digitization efforts, and using these records to estimate potential habitat and isolate important variables is an excellent way to begin to understand relatively understudied elements of community diversity.

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ORCID

Sarah C. Barga http://orcid.org/0000-0002-1466-8170

Thomas E. Dilts http://orcid.org/0000-0003-4234-0698

Elizabeth A. Leger http://orcid.org/0000-0003-0308-9496

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BIOSKETCHES

Sarah C. Barga values basic research that can provide solutions for conservation and restoration problems. Her research examines the influence of environmental heterogeneity on the specialist–generalist balance in life history responses displayed by natural populations of native plants in the Great Basin using three aspects of plant life history: seed germination, seed bank dynamics and mature plants.

Thomas E. Dilts is a research scientist in the Great Basin Landscape Ecology Lab at the University of Nevada Reno. His interests are in the application of geographic information systems, remote sensing and species distribution modelling techniques for understanding vegetation dynamics, habitat for wildlife and for conservation planning.

Elizabeth A. Leger studies native plant ecology and restoration in arid ecosystems, asking how understanding patterns of selection in altered systems can improve restoration outcomes, as well as contribute to our understanding of the strength of natural selection in the wild.

Author contributions: SCB is the corresponding author. SCB and EAL conceived and designed the experiment. SCB acquired the herbarium data. TED generated climate data and assisted with analyses using geospatial information and tools. SCB analysed the data. SCB and EAL wrote the manuscript, and TED edited the manuscript.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information section at the end of the article.

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