Genetically informed ecological niche models improve climate change predictions

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Abstract

We examined the hypothesis that ecological niche models (ENMs) more accurately predict species distributions when they incorporate information on population genetic structure, and concomitantly, local adaptation. Local adaptation is common in species that span a range of environmental gradients (e.g., soils and climate). Moreover, common garden studies have demonstrated a covariance between neutral markers and functional traits associated with a species' ability to adapt to environmental change. We therefore predicted that genetically distinct populations would respond differently to climate change, resulting in predicted distributions with little overlap. To test whether genetic information improves our ability to predict a species' niche space, we created genetically informed ecological niche models (gENMs) using *Populus fremontii* (Salicaceae), a widespread tree species in which prior common garden experiments demonstrate strong evidence for local adaptation. Four major findings emerged: (i) gENMs predicted population occurrences with up to 12-fold greater accuracy than models without genetic information; (ii) tests of niche similarity revealed that three ecotypes, identified on the basis of neutral genetic markers and locally adapted populations, are associated with differences in climate; (iii) our forecasts indicate that ongoing climate change will likely shift these ecotypes further apart in geographic space, resulting in greater niche divergence; (iv) ecotypes that currently exhibit the largest geographic distribution and niche breadth appear to be buffered the most from climate change. As diverse agents of selection shape genetic variability and structure within species, we argue that gENMs will lead to more accurate predictions of species distributions under climate change.

Keywords: climate change, ecological niche models, ecotypes, foundation species, genetic differentiation, local adaptation, niche divergence, species distributions

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Introduction

Climate change is predicted to be a leading cause of species extinctions in the 21st century (Root *et al.*, 2003; Thomas *et al.*, 2006; Urban, 2015) and as an agent of selection, is expected to have major impacts on species distributions (Grant & Grant, 2002; Parmesan & Yohe, 2003; Brys *et al.*, 2004; Visser & Both, 2005; Aguilar *et al.*, 2006; Franks *et al.*, 2007; Aitken *et al.*, 2008; Sthultz *et al.*, 2009; Pías *et al.*, 2010). One consistent prediction is that changes along established temperature gradients (Epperson, 2003; Howe *et al.*, 2003) will lead to populations that are either locally adapted or locally maladapted (Holt, 2003; Hereford, 2009). The ability to respond to these changing gradients depends not only on the rate of environmental change (Loarie *et al.*, 2009), but also on intraspecific genetic variability,

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which is critical for an evolutionary response to climate (Evans *et al.*, 2016).

Although ecological niche modeling (ENM) has been widely used to predict species' distributions, one aspect of traditional ENMs is that they assume genetic uniformity (i.e., no variation or population structure) throughout a species' range and ignore the potential for local adaptation to specific biotic and abiotic conditions (Grady *et al.*, 2011, 2013; Smith *et al.*, 2011; Gotelli & Stanton-Geddes, 2015). While relatively few studies have incorporated genetics into niche modeling (Knowles *et al.*, 2007; May *et al.*, 2011; Joyce & Rehfeldt, 2013; Alvarado-Serrano & Knowles, 2014; Marcer *et al.*, 2016), to our knowledge no ENM studies to date have explicitly assessed whether incorporating information on genetic variation and local adaptation improves model performance (but see Marcer *et al.*, 2016). Simulation studies suggest that incorporating information on genetic variability and population structure can improve our ability to

predict species distributions under climate change (Ikeda *et al.*, 2014; Valladares *et al.*, 2014). Together, these studies underscore the hypothesis that species that are locally adapted to current environments (especially those with limited dispersal capabilities; Kawecki & Ebert, 2004) and in areas with high rates of change (Kunkel *et al.*, 2004) are likely to become maladapted in the future. For example, since 1895, the frost-free growing season in the region occupied by *Populus fremontii* has increased as much as 50 days, whereas in the eastern United States at the same latitude, the growing season has changed little (Kunkel *et al.*, 2004). Such variations in both population response and environmental change may greatly affect our ability to predict species distributions using traditional ENMs.

An important consideration for species distribution and ecological niche modeling is whether land management agencies will be able to use this information to plan for the future (Aitken & Whitlock, 2013). Hence, understanding the degree to which current, locally derived stock is matched or mismatched to future environmental conditions is of paramount importance. In fact, forest geneticists are making planting recommendations based upon local stock that is considered to be genetically appropriate for future environmental conditions (O'Neill *et al.*, 2008; Wang *et al.*, 2010; Duveneck & Scheller, 2015). The difficulty of making these decisions has prompted recent calls to incorporate both ecological and population genetic data, based on neutral molecular markers, and functional traits, to further inform ecological niche and species distribution models (Pauls *et al.*, 2012; Steane *et al.*, 2014; Fitzpatrick & Keller, 2015; Gotelli & Stanton-Geddes, 2015). This recognition is based on the fact that local adaptation allows species to occupy a wide range of environmental niches, especially ones with broad geographic distributions (Rundle & Nosil, 2005; Cushman *et al.*, 2014).

To evaluate the utility of incorporating genetic information into species distribution models, we focused our ecological niche modeling efforts on Fremont cottonwood (*P. fremontii*), a foundation species that is broadly distributed across riparian environments in the southwestern United States and is well known for its ability to both structure communities (Ferrier *et al.*, 2012; Bangert *et al.*, 2013) and influence ecosystem processes (Grady *et al.*, 2013; Fischer *et al.*, 2014, 2016). A recent study by Cushman *et al.* (2014) found that populations within the species exhibit significant genetic structure based on neutral molecular markers that define three genetically distinct clusters. Here, we refer to these clusters as distinct populations or 'ecotypes' (Hufford & Mazer, 2003; Bucharova

et al., 2016), likely resulting from adaptation to local environmental conditions that differ both in geography and climate among the clusters. Together, these ecotypes encompass the majority of Fremont cottonwood's distribution in the southwestern United States and occupy specific regions. Hereafter, individuals within these regions will be referred to as the Central California Valley, Sonoran Desert and Utah High Plateaus ecotypes (Fig. 1a). Additionally, several studies spanning the majority of the range encompassed by these ecotypes have demonstrated that populations within the distribution of Fremont cottonwood are locally adapted to temperature. Specifically, ecotypes varied in leaf phenology such that trees leafing out too early experienced severe frost damage at high elevations, while those that dropped their leaves too late at low elevations suffered a loss in growth (Grady *et al.*, 2013, 2015; Fischer *et al.*, 2016), and productivity (Grady *et al.*, 2011; Fischer *et al.*, 2016). These and other mismatches at a given site suggest there is strong selection pressure for local adaptation (see also Evans *et al.*, 2014, 2016 for examples with other *Populus* spp.). Thus, the wealth of genetics-based studies with this foundation tree makes it an ideal system for contrasting models with and without population genetic data and to develop the next generation of models that explicitly incorporate genetic information to forecast future distributions.

Materials and methods

Genetic groupings

The genetic basis of ecotypes used in this study was based on pairwise F_{ST} values derived from a recent region-wide study of 40 populations ($n = 743$) of Fremont cottonwood (Cushman *et al.*, 2014) (see Table S1). Samples from this study were collected in a stratified, nonrandom manner across the range of *P. fremontii* (Fig. 1a). Due to known instances of hybridization between *P. fremontii* and *P. deltoides*, populations showing genetic admixture between the two species were removed (Cushman *et al.*, 2014). Analysis of molecular variation (AMOVA) and Bayesian-based STRUCTURE (Pritchard *et al.*, 2000) analysis showed significant genetic structure among populations ($\Phi_{RT} = 0.26$, $P < 0.001$) occupying three distinct clusters. Based on the genetic analyses of Cushman *et al.* (2014), we classified these clusters as distinct ecotypes encompassed within the Central California Valley (CCV), Sonoran Desert (SD) and Utah High Plateaus (UHP) subregions, as defined by the ecological subregions of the United States delineated by the United States Forest Service (Cleland *et al.*, 2007) (Fig. 1b). We then used these genetically defined ecotypes to test for environmental niche differentiation using a large set of climate variables (see 'Environmental variables' below). For the gENMs, individuals that showed greater than 10% admixture with other ecotypes were removed before all
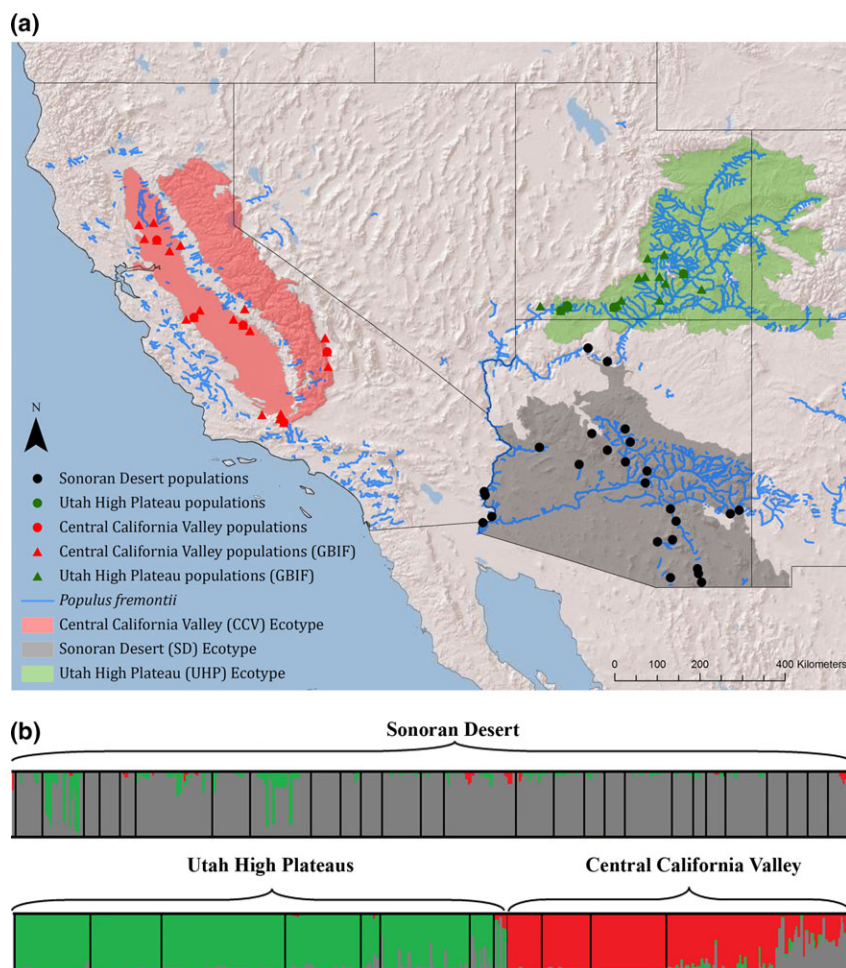
Fig. 1 (a) Map showing the range of collections (circles) from Cushman *et al.* (2014), and the locations from GBIF (triangles) that were used in the ecological niche models. Ecotypes are depicted by the red (Central California Valley), green (Utah High Plateaus) and gray (Sonoran Desert) backgrounds. The distribution of *Populus fremontii* is depicted in blue, which reflects the riparian corridors where this species is found (modified from Little, 1971). (b) STRUCTURE diagram showing the delineation of *P. fremontii* populations into three ecotypes. Vertical lines represent individuals within ecotypes, and those with more than one color share genetic information with other ecotypes. Further details of the genetic analysis can be found in Cushman *et al.* (2014).

analyses. As GPS points were only available on a per population basis, sample sizes were small for the Central California Valley ecotype (five population location points) and the Utah High Plateaus ecotype (seven population location points), which led to low partial receiver operator characteristic (ROC) scores in preliminary model runs. Thus, for these two ecotypes, we created a 50 km buffer around each ecotype and extracted species location points downloaded from the Global Biodiversity and Informatics Facility (GBIF), which fell within the buffer. We verified locations in the database through a process established in Ramirez-Villegas *et al.* (2012). We used both the original population location points in addition to those from GBIF in all subsequent analyses. The final location points covered a range of elevations across the distribution of *P. fremontii* and totaled 25, 28 and 29 location points for the Sonoran Desert, Central California Valley and Utah High Plateaus ecotypes, respectively (Table S1; Fig. 1a).

Environmental variables

Although Fremont cottonwood is a riparian species, and environmental variables besides climate are known to constrain its distribution (e.g., flood regime; Stromberg, 1997), numerous studies have reported significant physiological shifts to changes in climatic regimes (Hultine *et al.*, 2010; Grady *et al.*, 2011, 2013), which in turn can impact the distribution of the species (Ikeda *et al.*, 2014). We used WorldClim bioclimate variables (Hijmans *et al.*, 2005) downloaded from Global Climate Model data portal (www.ccafs-climate.org/data/) to project current and future niches for each ecotype. Current variables were averaged between the time periods 1961 and 1990 and were at a 30 arc-second (~1 km) spatial resolution. We conducted a preliminary model run without genetic information (NoGEN) and used Maxent's jackknife estimate to examine the permutation importance of each bioclimatic

variable in order to reduce the number of variables included in the final models. Bioclimatic variables with permutation scores less than five percent were removed from the final models (Sahlean *et al.*, 2014). As using different bioclimatic variables for each ecotype would likely inflate the probability that gENMs would outperform traditional ENMs, we used the same nine variables identified for the NoGEN model and in all subsequent gENMs.

We implemented a widely utilized (Kim *et al.*, 2013) conservative, moderate growth carbon emissions scenario, A1B (IPCC, 2007), and two future time frames, 2050 and 2080 (averaged from 2040 to 2069 and 2070 to 2099, respectively). As uncertainty in forecasting future climates is largely attributed to differences between general circulation models (GCMs) (Buisson *et al.*, 2010), we used five GCMs that are considered to most accurately reflect the climate of the southwestern United States (Garfin *et al.*, 2010): National Center for Atmospheric Research (NCAR), Community Climate System Model, version 3.0 (CCSM3), Max Planck Institute for Meteorology, Germany (ECHAM5/MPI), Commonwealth Scientific and Industrial Research Organisation, Australia (CSIRO-MK3), Centre National de Recherches Meteorologiques, Meteo France, France (CNRM-CM3), and Hadley Centre for Climate Prediction and Research, Met Office United Kingdom, and Hadley Centre Global Environmental Model, version 1 (HadGEM1). All models were statistically downscaled to a 30 arc-second resolution using the delta method (Ramirez-Villegas & Jarvis, 2010). Future bioclimatic variables were downloaded from the Global Climate Model data portal (www.ccafs-climate.org/data/).

Model calibration and evaluation

We used MAXENT version 3.3.3k (Phillips *et al.*, 2006) to determine whether three genetically defined Fremont cottonwood ecotypes are on different climate change trajectories. We ran a series of four MAXENT models to address this hypothesis; first with all species location points grouped together without genetic information ('NoGEN' model) in addition to three subsequent models using genetically defined ecotype groupings (Table S1). Maximum entropy (MAXENT) is a presence-only machine learning algorithm which approximates the ecological niche of a species by obtaining the distribution that is most spread out when constrained by environmental variables chosen *a priori* (Phillips *et al.*, 2006; Phillips & Dudik, 2008). Many studies have demonstrated Maxent to be one of the highest performing presence-background algorithms (Elith *et al.*, 2006; Kumar *et al.*, 2009). We restricted the selection of background points using a minimum convex polygon (Flory *et al.*, 2012), because the selection of sample points can influence model performance in Maxent (Phillips *et al.*, 2009; VanDerWal *et al.*, 2009). To avoid projecting into climates outside those in which the models were trained upon, we removed heavily clamped pixels from the final models using the 'fade-by-clamping' option in Maxent (Phillips *et al.*, 2006).

We used a tenfold cross-validation method, which uses 90% of the data for model training and 10% for model testing for 10 iterations (Elith *et al.*, 2010). We specified the output format

to a logistic form for easy interpretation. We evaluated model performance using partial ROC approaches, utilizing the partial receiver operator characteristics (pROC) software developed by Barve (2008). We followed the methods described in (Peterson, 2007), specifying 1000 iterations with the omission threshold set at ten percent (Peterson *et al.*, 2008). We examined the statistical significance of pROC values using *t*-tests. Traditional ROC area under the curve (AUC) scores were also included. Linear, quadratic, product, hinge and threshold functions of predictor variables were employed, and variable importance was assessed using a jackknife analysis (Phillips *et al.*, 2006). A binomial probability test was used to assess the accuracy of each predicted distribution (Phillips *et al.*, 2006). We evaluated variable importance by examining the permutation importance each bioclimatic variable had on the model building process. We specified a threshold that maximized training specificity plus sensitivity, as recommended by Liu *et al.* (2013), to convert the continuous probabilities into binary presence–absence maps.

Niche differentiation

An important issue in ecological niche modeling concerns how to quantify a species niche, and more importantly how to compare niches both across and within species (Soberón, 2007; Warren *et al.*, 2008). We used PCA analysis in R (Oksanen, 2007) to explore ecotype groupings in both climate space (E-space) and geographic space (G-space) (Soberón, 2007). The use of PCA allowed us to (i) test whether the previously identified ecotypes of Fremont cottonwood occupied significantly different climate niches and geographic distributions, (ii) explore the climate breadth of each ecotype and (iii) identify the climate variables that created among-ecotype differentiation in climate space (Soberón & Peterson, 2005; Rödder & Engler, 2011).

We also quantified the extent of niche overlap between populations in G-space using the metric Schoener's *D* (Rödder & Engler, 2011) executed in ENMTOOLS version 1.4.3 (Warren *et al.*, 2010). Following the methods suggested by Rödder & Engler (2011), we applied the maximum training sensitivity and specificity (MTSS) threshold prior to calculating niche similarities to eliminate biases associated with low probability values. Additionally, we used an identity test with 100 randomized pseudoreplicates to ascertain whether models generated from the three ecotypes were more different than expected if we assumed that ecotype points were drawn from the same underlying distribution (Warren *et al.*, 2008, 2010). As differences in projected suitable habitat could be due to differences between the habitats available to each ecotype, we conducted a background similarity test to assess whether the potential ecological niche of each ecotype is more similar (niche conservatism) or more different (niche divergence) than expected based on the environments in which they occur (Warren *et al.*, 2008).

In both the niche identity test and the background similarity test, we compared observed values of *D* to the randomized distributions using a one-tailed *t*-test (niche identity) and a two-tailed *t*-test (background similarity, Warren *et al.*, 2008).

For the identity test, niches were considered significantly different if the observed values of niche overlap were less than 95% or 99% of the overlap values derived from the randomized runs ($\alpha = 0.05$ and 0.01, respectively). Because the background selection can influence measures of background similarity (Warren *et al.*, 2008), we derived a minimum convex polygon using the location points for each population to specify a background (Warren *et al.*, 2008). We performed 100 pseudoreplicates for each pair of ecotypes tested.

Lastly, we used a series of binomial probability tests (Peterson *et al.*, 1999; Giles *et al.*, 2011) to evaluate the prediction that models developed using genetic data would better predict ecotype location points than the null model (using all location points, Table S1). Specifically, the number of test points for each ecotype and the null model were used as the number of trials, the number of correctly predicted test points was the number of successes, and the proportion of each predicted ecotype was the probability area (Giles *et al.*, 2011).

Results

Niche differentiation in environmental space

In support of our initial hypothesis that genetically distinct ecotypes occupy unique climate niches, we found that ecotypes differed significantly in climate niche space ($P < 0.0001$, Fig. 2a). The first three axes of the PCA explained 93% of the variation in climate between ecotypes (Table 1). When a correlation matrix was examined, we found that the climate variables that correlated with the first three principal components were minimum temperature of the coldest month (BIO6; -0.95), precipitation seasonality (BIO15; -0.92) and mean temperature of coldest quarter (BIO11; -0.37), respectively (Table 1). Specifically, the Utah High Plateaus and Sonoran Desert ecotypes occupied a similar winter precipitation niche, but Sonoran Desert was significantly warmer on average and has greater precipitation during the summer (Fig. 2a). The area occupied by the Central California Valley ecotype was dry in both seasons relative to Sonoran Desert and Utah High Plateaus, and occupied a temperature niche in between Utah High Plateaus and Sonoran Desert (Fig. 2a).

Niche differentiation in geographic space

We found that the ENM using all location points (NoGEN) was significant, with pROC scores greater than 1.0 (*t*-test, $P < 0.01$) (Table 2). Additionally, all three ecotype models were statistically significant, with pROC ranging from 1.18 to 1.80 (Table 2). Using a binomial probability test, we found support for our initial hypothesis that models using genetic information better predicted populations than do models without genetic information (NoGEN, Table 3).
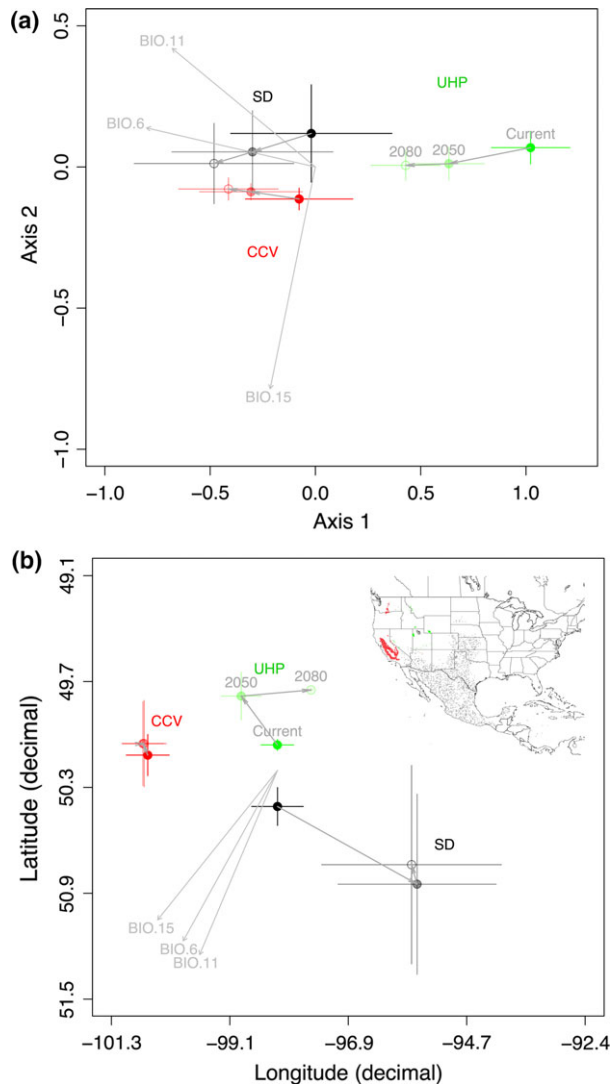

Fig. 2 Projections of ecotypes show climatic and geographic changes due to climate change of the Sonoran Desert (SD), Central California Valley (CCV) and Utah High Plateaus (UHP) ecotypes through time. Points (multivariate centroids $\pm$ 1 SD) closer together indicate more (a) climatically similar (PCA scores of environmental variables) or (b) spatially closer ecotypes. Arrows between points indicate the trajectory of ecotypes through time (current, 2050 and 2080) and arrows radiating from the center show the correlation of the original variables with the relevant axes (Table 1).

In agreement with our hypothesis that differences in the environmental niche of ecotypes would translate to differences in geographic space, we found current distributions derived from Maxent to be significantly different between ecotypes of Fremont cottonwood (Table 4; Fig. 2b). The Sonoran Desert model predicted large areas of suitable habitat east of the Rocky Mountain range, the Sonoran Desert and throughout México,

Table 1 Results from the correlation matrix showing the bioclimatic variables used in the final analysis, the associated correlation to each PCA axis and the contribution each made to explain the overall variation in the model

Variable	Correlation with PCA axes							
	1	2	3	4	5	6	7	8
Temperature seasonality (BIO4)	0.92	0.07	0.33	0.20	0.00	0.00	−0.02	0.03
Max. temperature of warmest month (BIO5)	−0.52	0.76	0.34	0.06	0.17	−0.10	−0.04	−0.03
Min. temperature of coldest month (BIO6)	−0.95	−0.10	0.18	0.22	0.02	0.06	−0.04	0.09
Mean temperature of coldest quarter (BIO11)	0.53	0.71	−0.37	0.13	0.23	0.04	0.05	0.03
Annual precipitation (BIO12)	−0.93	−0.07	0.23	0.24	−0.01	0.03	0.10	−0.04
Precipitation of driest month (BIO14)	−0.25	0.81	0.28	−0.44	−0.03	0.07	0.02	0.02
Precipitation seasonality (BIO15)	−0.21	−0.92	0.09	−0.24	0.19	−0.06	0.04	0.05
Precipitation of driest quarter (BIO17)	0.76	−0.51	0.36	−0.02	0.14	0.09	−0.02	−0.05
Precipitation of coldest quarter (BIO19)	0.92	0.19	0.29	0.06	−0.11	−0.06	0.07	0.05
Proportion of variance	0.52	0.32	0.08	0.05	0.02	0.00	0.00	0.00
Cumulative proportion	0.52	0.85	0.93	0.97	0.99	0.99	1.00	1.00

The three variables that had the strongest correlation to the first three principal components are shaded in grey.

Table 2 Maxent results showing the mean and range of percent contribution of all nine climatic variables, in addition to the partial receiver operator curve (pROC) for each of the four models

Bioclimatic variable	Ecotype			
	All ecotypes	Sonoran Desert	Central California Valley	Utah High Plateaus
Temperature seasonality (BIO4)	16.88 (20.05–7.76)	0.40 (2.79–0.00)	2.44 (4.29–1.11)	2.14 (6.33-0.32)
Max. temperature of warmest month (BIO5)	7.06 (18.82–1.45)	30.53 (40.53–23.16)	0.12 (1.18–0.00)	0 (0.00–0.00)
Min. temperature of coldest month (BIO6)	1.24 (4.86–0.00)	8.04 (19.80–2.98)	2.81 (4.87–0.24)	1.54 (4.53–0.00)
Mean temperature of coldest quarter (BIO11)	2.17 (5.73–0.16)	1.29 (2.49–0.00)	11.15 (16.24–7.16)	43.92 (77.73–35.06)
Annual precipitation (BIO12)	21.0 (27.83–15.5)	29.97 (37.63–19.17)	11.22 (15.36–4.50)	0 (0.00–0.00)
Precipitation of driest month (BIO14)	18.59 (24.74–10.14)	6.64 (13.92–3.14)	0.01 (0.11–0.00)	12.31 (26.62–0.00)
Precipitation seasonality (BIO15)	15.59 (19.81–12.41)	2.88 (5.39–1.01)	20.23 (34.92–7.20)	33.44 (49.13–17.97)
Precipitation of driest quarter (BIO17)	1.04 (4.51–0.00)	4.95 (11.83–0.49)	26.72 (42.48–3.80)	0.98 (5.82–0.00)
Precipitation of coldest quarter (BIO19)	16.42 (22.43–8.80)	15.29 (25.76–7.86)	25.30 (38.02–16.24)	5.66 (8.45–1.59)
pROC	1.47 (1.66–1.29)	1.18 (1.22–1.04)	1.80 (1.92–1.78)	1.77 (1.97–1.64)
AUC	0.77 (0.88–0.60)	0.87 (0.96–0.59)	0.93 (0.96–0.88)	0.90 (0.98–0.59)

as far south as the Yucatan Peninsula (Fig. 2b). Conversely, the Central California Valley model predicted a relatively small amount of suitable habitat, constrained to the coastal and central regions of California with a habitat encompassing south-central Baja California (Fig. 2b). The model based upon the Utah High Plateaus region predicted suitable habitat to be the least contiguous, with habitat classified as suitable from southwestern Texas as far north as Montana and Washington (Fig. 2b).

Additionally, we found that differences in suitable habitat between ecotypes are likely the result of differences in available environments. We measured niche overlap (D) for all pairwise comparisons of ecotypes and found that values ranged from 0.027 to 0.658 (Table 4). We compared these measures of overlap to values of overlap obtained from both the niche identity test and background similarity test. We rejected both the null hypothesis that niches were identical ($P < 0.01$, Fig. 3a–c, 'niche identity test') and that niches between ecotypes were conserved ($P < 0.01$, Fig. 3d–f, 'background similarity test') between the Utah High Plateaus–Central California Valley and the Central California Valley–Sonoran Desert as our observed measures of overlap fell outside the null distributions in both cases (Fig. 3d, f). However, niches between the Utah High Plateaus and Sonoran Desert ecotypes, while not identical, were conserved (Fig. 3e).

Impact of climate change on genetically distinct populations

As niche differentiation tests revealed that (i) ecotype models outperformed the full species model and (ii)

Table 3 Binomial probability test comparing the predictive success of correctly identifying location points as presence (true positive rate)

Ecotype predicted	Ecotype (test points)	Predictive success	Probability area	Binomial probability
Central California Valley	Central California Valley	20/22	0.1242	1.35E-16
	Sonoran Desert	0/25	0.1242	3.63E-02
	Utah High Plateaus	0/18	0.1242	9.19E-02
	All ecotypes	26/82	0.1242	2.75E-06
Sonoran Desert	Central California Valley	0/22	0.1278	4.94E-02
	Sonoran Desert	22/25	0.1278	3.37E-17
	Utah High Plateaus	0/18	0.1278	8.53E-02
	All ecotypes	21/82	0.0842	2.30E-06
Utah High Plateaus	Central California Valley	0/22	0.0842	1.45E-01
	Sonoran Desert	0/25	0.0842	1.11E-01
	Utah High Plateaus	15/18	0.0842	4.72E-14
	All ecotypes	21/82	0.0842	2.30E-06
All ecotypes	Central California Valley	17/22	0.2782	1.85E-06
	Sonoran Desert	18/25	0.2782	4.89E-06
	Utah High Plateaus	8/18	0.2782	6.03E-02
	All ecotypes	66/82	0.2782	4.81E-23

The null hypothesis, that the model without genetic information (NoGEN) more accurately predicts each ecotype's test points, is depicted in grey for each ecotype.

Table 4 Niche overlap measured using Schoener's *D* between ecotypes

	Ecotype			
Ecotype	All ecotypes	Utah High Plateaus	Sonoran Desert	Central California Valley
All ecotypes	1.000	0.345	0.658	0.340
Utah High Plateaus	–	1.000	0.180	0.027
Sonoran Desert	–	–	1.000	0.179
Central California Valley	–	–	–	1.000

Values close to 0 represent no overlap between species distribution models, while 1.0 indicates complete overlap.

differences in Fremont cottonwood distributions are likely due to differences in available habitat, we projected the climate niches of each ecotype into the future to explore how climate change will impact regions of Fremont cottonwood that are genetically and climatically distinct (Fig. 2). In agreement with our initial hypothesis that ecotypes would be differentially impacted by climate change, we found that while some ecotypes are projected to gain over 60% in suitable habitat by mid-century, others are projected to lose 100% of current suitable climate habitat by the end of the century (Table 5).

Differences between ecotypes were most pronounced in the extent and location of projected suitable habitat (Fig. 2b; Fig. S1). The Sonoran Desert ecotype had the greatest potential suitable habitat, with a projected distribution throughout México, the southwestern United States and in areas east of the Rocky Mountains (Fig. 2b). In contrast, the Central California Valley ecotype was projected to be the most constrained under climate change, with a small area concentrated in the Central Valley and east of the Cascade Range in Washington (Fig. 2b). The Utah High Plateaus ecotype was projected to have the most disjunct future distribution (Fig. 2b), in addition to experiencing the greatest habitat loss, with only small areas of habitat in Colorado, Utah and Wyoming being classified as suitable by 2080 (Table 5).

Discussion

Genetic relationships with ecotypes

The approach we advocate in our study is based on three major assumptions: (i) model improvement is attributed to intraspecific genetic variation in the species–climate relationship; (ii) adaptation to climate is driving ecotype responses to climate change; and (iii)
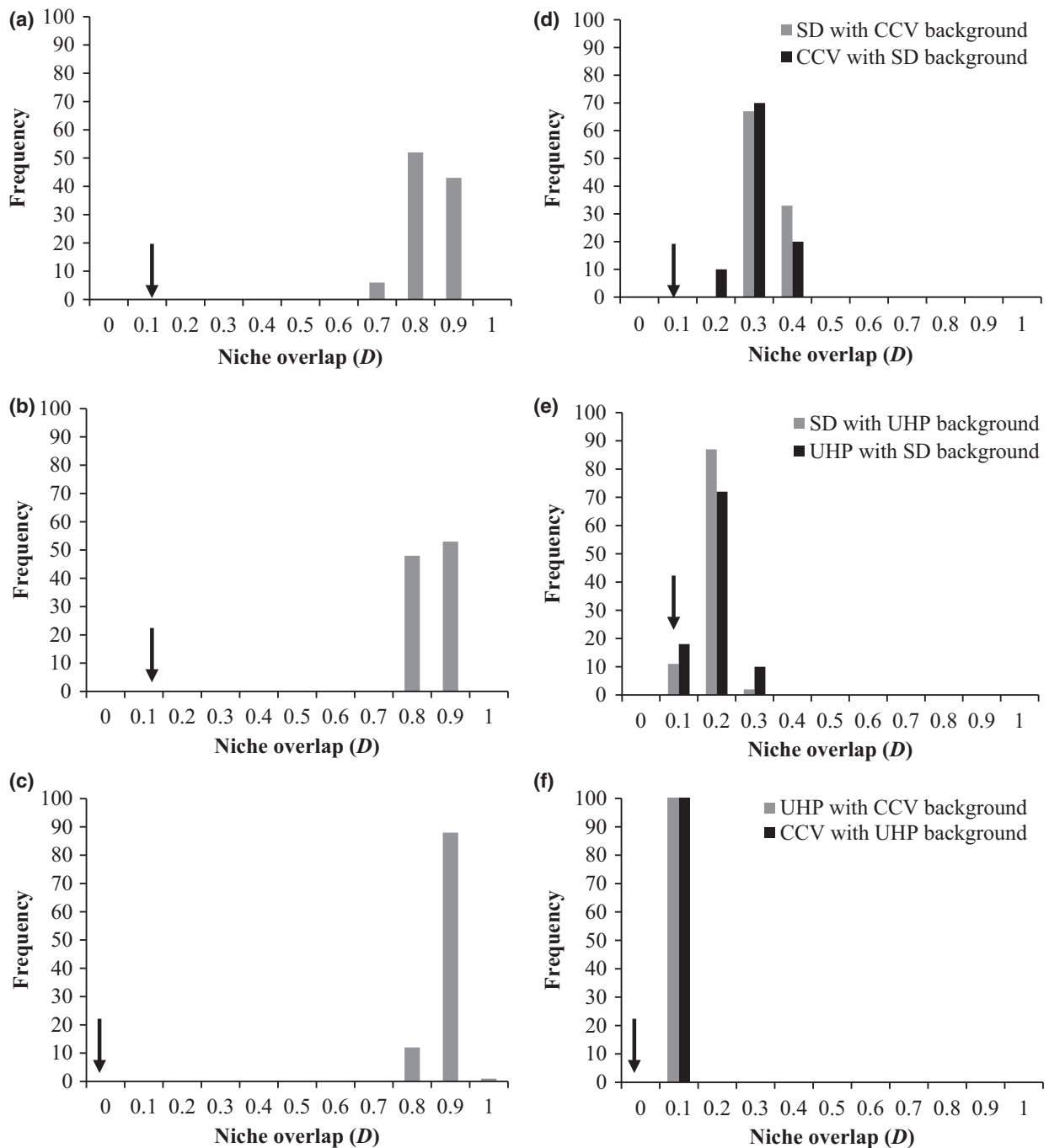
Fig. 3 Niche identity (a–c) and background similarity (d–f) tests between ecotypes. Observed measures of niche overlap (using Schoener's *D*) are indicated by the black arrows. In the niche identity test, null distributions were compared using current projected distributions between ecotypes [Sonoran Desert (SD) vs. Central California Valley (CCV) (a), Sonoran Desert vs. Utah High Plateaus (UHP) (b) and Utah High Plateaus vs. Central California Valley (c)]. The null distributions in the background similarity tests (d–f) were generated by comparing the niche model of a focal ecotype to 100 models generated from randomly drawn sets of points from a background range of the other ecotype. Measures of niche overlap that were outside the 95% confidence intervals in both tests were considered significant; however, overlap values significantly less than the null distribution in (d–f) (background similarity) indicate niche divergence.

neutral molecular markers are an appropriate surrogate for functional traits. Although ENMs generally improve in accuracy when modeling species with restricted

ranges or narrow niche breadth (Botts *et al.*, 2013), there are three lines of logic that affirm the accuracy of our approach. First, from a conceptual standpoint, there is

Table 5 The difference in projected suitable habitat between ecotypes in the time frames 2040–2069 (2050) and 2070–2099 (2080)

Ecotype	2050			2080		
	Gain (%)	Loss (%)	Same (%)	Gain (%)	Loss (%)	Same (%)
Sonoran Desert	38	3	97	21	3	97
Central California Valley	5	28	72	8	12	88
Utah High Plateaus	0	99	1	61	100	0

considerable research demonstrating the effect both climate and genetics have on the distribution of species (Rehfeldt *et al.*, 1999, 2002; Davis & Shaw, 2001; Savolainen *et al.*, 2007; O'Neill *et al.*, 2008; Wang *et al.*, 2010; Grady *et al.*, 2011). In Fremont cottonwood, for example, landscape genetic studies argue that genetic connectivity in these riparian corridors is affected by both river size and winter precipitation (Cushman *et al.*, 2014) and reciprocal common garden studies show that climate impacts productivity, functional traits and susceptibility to pathogens (Grady *et al.*, 2011, 2013, 2015; Fischer *et al.*, 2016). Furthermore, recent studies with the related species, *Populus angustifolia*, found significant divergent selection on phenology and growth traits that differ with climatic variables across its geographic range (Evans *et al.*, 2016). These studies indicate that, together with river order, strong climatic gradients are likely responsible for establishing and driving divergence among observed ecotypes. Second, given the above genetic relationships associated with ecotypes and climate, it is not surprising that we observed up to a 12-fold increase in predictive power when accounting for differences among ecotypes. Lastly, from a practical standpoint, there is a need to account for climatic differences in adaptation strategies if future restoration practices are to be successful (Millar *et al.*, 2007; O'Neill *et al.*, 2008; Aitken & Whitlock, 2013).

Our second major assumption, that climate adaptation accounts for the differences in ecotype response, invariably encompasses other sources of spatial variation that may influence an ecotype's response to climate shifts, such as demography and genetic drift. These forces typically act at a much finer spatial scale than the ecotype levels discussed here (Wright, 1943), but are nonetheless important when considering overall patterns of ecotype differentiation. Lastly, common garden studies have demonstrated that there is covariance between neutral markers and functional traits (Barbour *et al.*, 2009; Fischer *et al.*, 2016). Within the Fremont cottonwood system, common gardens with trees from different ecotypes have demonstrated pronounced differences in leaf phenology (early leaf-on and late leaf-fall timing) which is correlated with >80% of the variation in tree and forest productivity (Fischer *et al.*,

2016). Furthermore, reciprocal common gardens within a Fremont ecotype showed pronounced genetic variation in functional traits that affected survival and growth (Grady *et al.*, 2015). Due to these findings across and within ecotypes, we present our ecotype niche models as a first step in utilizing genetic information to inform ENMs (see also Marcer *et al.*, 2016), and suggest that future gENM modeling would benefit from the addition of functional trait variation.

Genetically informed models improve accuracy

We created a series of traditional ENMs and models that incorporate information derived from genetic population structure (gENMs) to explicitly test the hypothesis that gENMs will more accurately predict current species distributions compared to traditional ENMs. By comparing the accuracy of the gENMs and traditional ENMs in predicting population location points within each ecotype, we found that although the model without population genetic data significantly predicted all ecotypes (Table 2), gENMs predicted occurrence points with up to 12 times greater accuracy (Table 3). Our results indicate that ENMs that do not include information on genetic structure in geographically widespread or environmentally diverse species may vastly overestimate current and future suitable habitat. Although several studies have called for the integration of genetics into ENMs (Sork *et al.*, 2010; Fordham *et al.*, 2014; Valladares *et al.*, 2014; Gotelli & Stanton-Geddes, 2015), few have included either neutral genetic information (but see Sork *et al.*, 2010; Marcer *et al.*, 2016) or tested for local adaptation using reciprocal transplant trials (e.g., common gardens, provenance trials) (see Joyce & Rehfeldt, 2013; Oney *et al.*, 2013). As such, our study is one of the first to explicitly test whether model accuracy increases with the incorporation of genetic information consistent with local adaptation, together with past evidence that ecotypes differ in ecological tolerances based on common garden experiments (Grady *et al.*, 2011, 2013, 2015; Evans *et al.*, 2016; Fischer *et al.*, 2016).

Our finding that gENMs more accurately predict ecotype location points is likely a result of ecotypes occupying both unique climate niches and geographic distributions. The three ecotypes differed significantly

in their climate niche ($P < 0.0001$, Fig. 2a), with the first three axes of the PCA explaining 93% of the variation in climate between ecotypes (Table 1). When a correlation matrix was examined, we found that the climate variables that correlated most with the first three principal components were minimum temperature of the coldest month, precipitation seasonality and mean temperature of coldest quarter (Table 1). Specifically, the Utah High Plateaus and Sonoran Desert ecotypes occupy a similar winter precipitation niche, but Sonoran Desert is significantly warmer and has greater precipitation during the summer (Fig. 2a). The Central California Valley ecotype occupies a niche space that is dry in both seasons relative to Sonoran Desert and the Utah High Plateaus and occupies an intermediate temperature niche between these latter two ecotypes (Fig. 2a). In terms of breadth, the Sonoran Desert ecotype occupies a climatically broad niche, whereas the climate ranges of both the Central California Valley and Utah High Plateaus are distinctly narrower (Fig. 2a). Additionally, current projected distributions derived from Maxent were significantly different between ecotypes, indicating that each ecotype occupies a unique geographic space (Table 4; Fig. 2b).

Independent trajectories of genetic and climatic divergence of ecotypes

Differences in climate niche and geographic distribution have likely resulted in niche divergence between the Utah High Plateaus and Central California Valley and between the Central California Valley and Sonoran Desert ecotypes. The extent of niche overlap for all pairwise ecotype comparisons was measured (Table 4) and compared to values of overlap obtained from both the niche identity test and background similarity test. We rejected the null hypothesis that niches were identical ($P < 0.01$, Fig. 3a–c 'niche identity test') and that observed overlap between ecotypes is explained by regional similarities or differences in available habitat ($P < 0.01$, Fig. 3d–f; 'background similarity test') as our observed measures of overlap fell outside of the null distributions between the Utah High Plateaus–Central California Valley and the Central California Valley–Sonoran Desert (Fig. 3d, f). These findings are indicative of climate niche divergence, suggesting that populations comprising these ecotypes have adapted to different climate regimes, similar to that reported by Wellenreuther *et al.* (2012). This finding is consistent with a 'gradient' model (Rundle & Nosil, 2005) in which populations are expected to occupy different climate envelopes. In contrast, we found that, the Utah High Plateaus and Sonoran Desert ecotypes occupied a more similar climate space, indicative of niche conservatism (Fig. 3e).

Numerical models have demonstrated that cyclical, climatic oscillations promote speciation via niche divergence (Hua & Wiens, 2013). Climate oscillations stemming from the Quaternary period (2.6 to ∼ 0.01 Ma), characterized by cyclical glacial–interglacial periods (Zachos *et al.*, 2001) and reduced gene flow (Hua & Wiens, 2013) have likely imposed divergent selection pressures between the Utah High Plateaus–Central California Valley ecotypes and the Central California Valley–Sonoran Desert ecotypes, but this is less apparent between the Utah High Plateaus and Sonoran Desert ecotypes. This finding is especially novel suggesting that if these trends continue under climate change, the three ecotypes will likely continue on independent trajectories of genetic and climatic divergence.

Three major patterns emerged when we assessed the projected geographic and climatic distribution of the ecotypes under climate change (Table 5; Fig. 2). First, while the climate niche for each ecotype is projected to shift, only the Utah High Plateaus climate niche is expected to undergo significant changes (Fig. 2a). The climate niche for all ecotypes is projected to shift such that minimum temperature of the coldest month and mean temperature of the coldest quarter will increase and seasonal precipitation will decrease (Fig. 2a). Second, shifts in projected geographic distributions due to climate change are expected to be significantly different for the Sonoran Desert and Utah High Plateaus through time, indicating that populations comprising these ecotypes are unlikely to independently track climate change (Fig. 2b). Lastly, ecotypes that currently exhibit the largest geographic distribution and niche breadth were buffered the most from climate change (Sonoran Desert), with a three percent loss in suitable habitat by 2080. Conversely, ecotypes with the most geographically constrained current distributions (Utah High Plateaus and Central California Valley) are predicted to experience a 100 and 12% reduction in suitable habitat by 2080, respectively (Table 5). Differences in the extent of geographic distributions are likely attributed to differences in niche breadth between ecotypes (Treier *et al.*, 2009), with the Sonoran Desert occupying a broader climatic niche than either the Central California Valley or Utah High Plateaus (Fig. 2a). However, these differences could result from insufficient sampling across a range of environments, and thus, future studies would benefit from a more comprehensive sampling effort along the southern edge of the species distribution.

Conservation implications

Although we realize our data set is limited without the incorporation of functional trait data, it is clear that

model accuracy is substantially improved with the addition of genetic information. Thus, we argue that more data sets on foundation species for which genetic information is available need to be generated and evaluated in a 'gENM' model. Our findings have several important implications for conservation management and restoration prioritization. First, it has been estimated that the United States will spend an estimated one percent of gross domestic product by 2050, approximately $174 billion dollars, on climate change mitigation (Stern, 2006). On the lower Colorado River, $626 million is currently being allocated to riparian habitat restoration using Fremont cottonwood to mitigate land use practices that have resulted in the listing of sensitive species (Lower Colorado River Multi-Species Conservation Program: LCR-MSCP 2004). With such large expenditures, it is important that such projects achieve high success in both the short term and long term. Our findings argue that the success of these projects will rely in large part on accurate identification of current and future suitable habitat for each species, the identification of genetically based ecotypes and the use of genetically appropriate populations that are matched with projected suitable habitat in the future (Hufford & Mazer, 2003; Breed *et al.*, 2012). Thus, the lack of a genetic- and evolutionary-based perspective could diminish, or even greatly compromise the success of costly restoration projects.

Second, as productivity is correlated with both habitat suitability (Estes *et al.*, 2013) and biodiversity (Ikeda *et al.*, 2014), optimizing productivity for a given site or population can also increase associated community diversity (Ikeda *et al.*, 2014; Evans *et al.*, 2016). Toward this end, studies of how community diversity and structure relate to the spatial structure and associated genetic structure of foundation species should be evaluated (e.g., using common garden studies). This will help validate species distribution models and further quantify the relationship between foundation species and their relevant community members. Finally, most current management strategies use local seed sources for restoration in order to ensure that the seeds are locally adapted (Gustafson *et al.*, 2005), but our study and others (Crespi, 2000; Breed *et al.*, 2012) highlight the fact that what is locally adapted in the current environment is very likely to become locally maladapted in future climate regimes. Thus, the current practice of using local stock for restoration could result in species that are maladapted for tomorrow's environments (Aitken & Whitlock, 2013), especially where migration rates are slower than the rates of climate change. For example, planting with ecotypes better adapted for future climates can help ensure the future productivity and likely stability of foundation species and their dependent communities (Ikeda *et al.*, 2014).

Here, we demonstrate that the inclusion of population genetic information into ecological niche models significantly increases their accuracy and justifies modeling populations and their accompanying ecotypes as individual entities. Finally, given that we found that genetically differentiated regions of Fremont cottonwood are clearly on different climate change trajectories, our study has important implications for projecting species distributions in the face of climate change (review by Jump & Penuelas, 2005).

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Competing financial interests

The authors declare no competing financial interests.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Population location points.
Figure S1. Projected suitable future habitat of the three genetically distinct ecotypes: Sonoran Desert (a and d); Central California Valley (b and e); and Utah High Plateaus (c and f) in 2050 (a–c) and 2080 (d–f).