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RESEARCH ARTICLE

Landscape genomics of *Sphaeralcea ambigua* in the Mojave Desert: a multivariate, spatially-explicit approach to guide ecological restoration

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Abstract Local adaptation influences plant species' responses to climate change and their performance in ecological restoration. Fine-scale physiological or phenological adaptations that direct demographic processes may drive intraspecific variability when baseline environmental conditions change. Landscape genomics characterize adaptive differentiation by identifying environmental drivers of adaptive genetic variability and mapping the associated landscape patterns. We applied such an approach to *Sphaeralcea ambigua*, an important restoration plant in the arid southwestern United States, by analyzing variation at 153 amplified fragment length polymorphism loci in the context of environmental gradients separating 47 Mojave Desert populations. We identified 37 potentially adaptive loci through a combination of genome scan approaches. We then used a generalized dissimilarity model (GDM) to relate variability in potentially adaptive loci with spatial gradients in temperature, precipitation, and topography. We identified non-linear thresholds in loci frequencies driven by summer maximum temperature and water stress, along with continuous variation corresponding to temperature seasonality. Two GDM-based approaches for mapping predicted patterns of local adaptation are compared. Additionally, we assess uncertainty in spatial interpolations through a novel spatial bootstrapping approach. Our study presents robust, accessible methods for deriving spatially-explicit models of adaptive genetic variability in non-model species that will inform climate change modelling and ecological restoration.

Keywords Adaptive genetic variability · AFLP · Generalized dissimilarity model · Genome scan · Landscape genomics · Spatial interpolation

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Introduction

Evidence for local adaptation is widespread among plant taxa (Leimu and Fischer 2008; Alberto et al. 2013). There is growing recognition that adaptive genetic variability influences the responses of species to climate change (Davis and Shaw 2001; Jump and Peñuelas 2005) and the performance of seed used in ecological restoration (Hufford and Mazer 2003; Mijangos et al. 2015). Consequently, understanding the scale of local adaptation and developing spatial models to visualize patterns of adaptive genetic variability constitute major interdisciplinary challenges with practical implications (Holderegger et al. 2010; Schoville et al. 2012). Characterizing local adaptation with molecular markers may provide cost and time advantages over common garden experiments. However, this approach requires multivariate models that incorporate spatial covariance in both adaptive loci and environmental gradients (Thomassen et al. 2010; Fitzpatrick and Keller 2015). Recent studies highlight promising new avenues for visualizing adaptive genetic variability across the landscape

(Vandergast et al. 2008; Fitzpatrick and Keller 2015). Here, we extend these approaches to characterize adaptive genetic variability in Mojave Desert populations of *Sphaeralcea ambigua* (Malvaceae), a species important for restoring severely degraded desert landscapes.

Predicting species' responses to climate change is necessary for developing conservation strategies (Thuiller et al. 2008). Multiple factors complicate modelling of future range shifts, including leading-edge versus trailing-edge dynamics, migration rates, and context-dependent biotic interactions (Fordham et al. 2012; Svenning and Sandel 2013). Local adaptation also may drive intraspecific variability in species' responses to climate change at the population level (Davis and Shaw 2001; Aitken et al. 2008; Jay et al. 2012), as altered climatic means and extremes interact with species' life-history processes to shape local demographic trajectories (Parmesan 2006; Reusch and Wood 2007). Long-term outcomes depend in part on capacities for phenotypic plasticity and long-distance dispersal (Davis and Shaw 2001; Nicotra et al. 2010). However, adaptive genetic variability may lead to phenological or physiological asynchronies under novel climates (Valladares et al. 2014), or, conversely, provide the basis for evolution (Jump and Peñuelas 2005; Alberto et al. 2013). Adaptation is dictated by the interplay between gene flow and natural selection (Rieseberg and Burke 2001; Ellstrand 2014), and expressed as spatial variability in adaptive allele frequencies among populations (Manel et al. 2010; Schoville et al. 2012). In this context, landscape genomics seeks to identify environmental drivers of adaptive genetic variability and map patterns of local adaptation, enabling intraspecific-level predictions (Fitzpatrick and Keller 2015).

Landscape genomics is also broadly suited to guide ecological restoration. Widespread habitat changes caused by anthropogenic factors (Vitousek et al. 1997), often attended by novel disturbance regimes (Brooks et al. 2004), have greatly increased the need for ecological restoration across a range of ecosystems. Despite recognition that local ecotypes often have fitness advantages (Leimu and Fischer 2008), limited availability of local seed increases the potential for introducing genetic material from distant or unknown provenances during restoration (Johnson et al. 2010). Planting maladapted germplasm can result in low population fitness due to multiple processes: founder effects if seed stock is from a limited number of sources; outbreeding depression following intraspecific hybridization between indigenous and imported genotypes; and genetic swamping, leading to the replacement of local ecotypes (Lesica and Allendorf 1999; Hufford and Mazer 2003; McKay et al. 2005). By identifying drivers and patterns of local adaptation, landscape genomics can provide the genetic information needed to inform seed sourcing strategies (Breed et al. 2013; Mijangos et al. 2015).

Molecular markers have been used to characterize adaptation of alpine species (e.g., Manel et al. 2012) and forest trees (e.g., De Kort et al. 2014) to precipitation and temperature in numerous studies. Although desert species show marked phenological responses to environmental triggers (Beatley 1974) and narrow germination requirements (Meyer and Pendleton 2005), ecological drivers and patterns of intraspecific variability are little understood (but see Sandquist and Ehleringer 1997; Meyer and Pendleton 2005; Jones et al. 2014). Heightened climatic extremes (Dai 2013; IPCC 2013) and a novel fire regime (Brooks and Minnich 2006) both threaten the Mojave Desert over the next century, increasing the need for landscape genomics to inform predictive modelling and restoration decision making. While recent studies have elucidated patterns of genetic diversity and divergence for Mojave Desert fauna (Hagerty et al. 2011; Vandergast et al. 2013), genetic assessments are largely unavailable for flora.

Genome scans are a popular means for characterizing adaptive genetic variability among populations (e.g., Joost et al. 2007; Foll and Gaggiotti 2008; Poncet et al. 2010; Evans et al. 2014). Ecologically relevant loci (i.e., those linked to genetic regions under diversifying or balancing selection) are typically identified in two ways: (a) outlier locus detection, which identifies markers showing significantly higher genetic differentiation than expected under neutrality; and (b) direct identification of gene-environment correlations through modeling changes in allele frequencies along environmental gradients (Holderegger et al. 2008; Schoville et al. 2012). Developing landscape-scale spatial predictions for patterns of local adaptation requires accounting for covariance in both adaptive loci and environmental gradients, which is best accomplished through multivariate models (Thomassen et al. 2010; Fitzpatrick and Keller 2015). However, commonly used multivariate techniques, including constrained ordinations (redundancy analysis and canonical correspondence analysis) and canonical correlation, assume linear or uni-modal response structures that may limit inferences (McCune et al. 2002). A recent distance-based approach, generalized dissimilarity modeling (GDM), bridges this gap by modelling changes in adaptive allele frequencies as nonlinear functions of ecological covariates (Ferrier et al. 2002, 2007). GDMs account for both nonlinearity and non-stationarity (variation in the rate) in responses of allele frequencies to ecological gradients, which frequently characterize such associations (Bothwell et al. 2013; Fitzpatrick and Keller 2015). GDMs also enable spatial interpolations for

predicted patterns of local adaptation (Fitzpatrick and Keller 2015).

In this study, we demonstrate novel techniques for linking genome scans with a spatially-explicit GDM, and for visualizing uncertainty in multivariate spatial interpolations, using a dataset of amplified fragment length polymorphism (AFLP) markers typed in Mojave Desert populations of *S. ambigua* (Malvaceae). This species provides forage for the federally-listed desert tortoise (*Gopherus agassizii*; Barboza 1995), whose re-use of habitat burned by wildfire coincides with *S. ambigua*'s colonization (Drake et al. 2015). Hence, *S. ambigua* is particularly desirable for restoration. Our objectives were to: (1) identify ecologically relevant loci and relate these to important environmental gradients; and (2) develop spatial interpolations of adaptive genetic variability to guide restoration planning and predictive modelling.

Materials and methods

Study site, study species and genotyping

The Mojave Desert spans approximately 150,000 km^2 in the southwestern United States, forming a portion of the "Basin and Range" province characterized by north to south trending mountain ranges and interlaying basins (MacMahon 2000). Alluvial fans, bajadas, playas, and washes are common geomorphic features. Annual precipitation ranges from <50 to 300 mm (averaging 137 mm) with high inter-annual variability and a large proportion of winter rainfall (Hereford et al. 2004). However, the proportion of summer precipitation increases from west to east. The El Niño/Southern Oscillation (ENSO) drives episodic variability in the timing and amount of precipitation several times per decade. Temperatures range from <0 °C in winter to over 50 °C in summer (Turner 1994).

Sphaeralcea ambigua is a short-lived, drought-deciduous, insect-pollinated perennial forb or subshrub with a wide distribution across the Mojave Desert and surrounding ecoregions. Plants typically flower in early spring (February–March) and senesce during hot, mid-summer months. Green leaf tissue from 10 to 15 individual *S. ambigua* plants spaced at least 10 m apart was collected from 47 populations throughout the Mojave Desert ecoregion (Fig. 1; Online Resource 1). Leaf tissue was stored within sealed bags containing desiccant. GPS coordinates were recorded for each sampling location.

Genomic DNA from 446 *S. ambigua* plants was extracted using the MagAttract 96 Miniprep Core Kit (Qiagen Valencia, CA, USA) for AFLP genotyping. DNA (300 ng) was digested with three units each of EcoRI and MspI and 1× NEB #2 buffer in 40 µl reactions. After 1 h of incubation at 37 °C, the following ligation reagents, in a 10 µl mixture, were added to the digestion reaction and incubated for 3 h at 16 °C: 1.5 µM of double-stranded EcoRI adapter (combination of oligos 5′_CTCGTAGACTGCGTACC3′_ and 5′_AATTGGTACGCAGTCTAC3′_), 15 µM of double-stranded MspI adapter (combination of oligos 5′GACGAT GAGTCTAGAA′3_ and 5′CGTTCTAGACTCATC′3), 1× ligase buffer, and 0.1 µl of T4 ligase (NEB). The preselective AFLP amplification was carried out in a 20 µl reaction mixture containing 30 mM Tricine, 50 mM KCl, 2 mM $MgCl_2$, 5 % acetamide, 10 mM of each dNTP, 0.2 mM of each EcoRI primer (5′GACTGCGTACCAATTCA′3) and MspI primer (5′GATGAGTCTAGAACGGA′3), 0.6 µl of Taq polymerase, and 2 µl of the ligation reaction mixture using the following PCR program: 35 cycles of 30 s at 94 °C, 30 s at 55 °C, and 1 min at 72 °C. The selective AFLP amplifications were carried out in the same manner as the preselective reactions, except that 2 µl of a 1:20 dilution of the preselective amplification product was used as a template against four EcoRI–MspI primer combinations: Eact_Magat, Eatg_Matga, Eatc_Maaac, Eaca_Macc. Selectively amplified PCR products were separated on a 3730 DNA Analyzer (Applied Biosystems, Foster City, CA, USA) at Arizona State University. Electropherograms were viewed with GeneMapper software (Applied Biosystems), and all readily scorable, segregating fragments (loci) between 50 and 500 bp were manually typed as present (1) or absent (0) for each individual. A total of 153 AFLP loci were scored.

Characterizing environmental variability

We assembled 11 climatic and topographic layers in GIS as potential gradients driving adaptive genetic differentiation (Table 1). Winter precipitation, summer precipitation, winter minimum temperature, and summer maximum temperature were derived from PRISM climatic normals for the period 1981–2010 at a spatial resolution of 800 m^2 (Daly et al. 2008). Elevation, slope, and topographic index were derived from a 30 m digital elevation model and subsequently upscaled to a 1 km^2 resolution (National Elevation Dataset, http://ned.usgs.gov/). Three indices derived from the moderate-resolution imaging spectroradiometer (MODIS) satellite—also scaled to a 1 km^2 resolution—expressed seasonal surface temperature range (i.e., temperature seasonality), surface texture, and water stress (Inman et al. 2014; Table 1). MODIS indices were averaged across years from 2001 to 2010. We calculated pairwise correlation coefficients between all variables and excluded elevation a priori due to a strong correlation ($r = 0.95$) with summer maximum temperature.

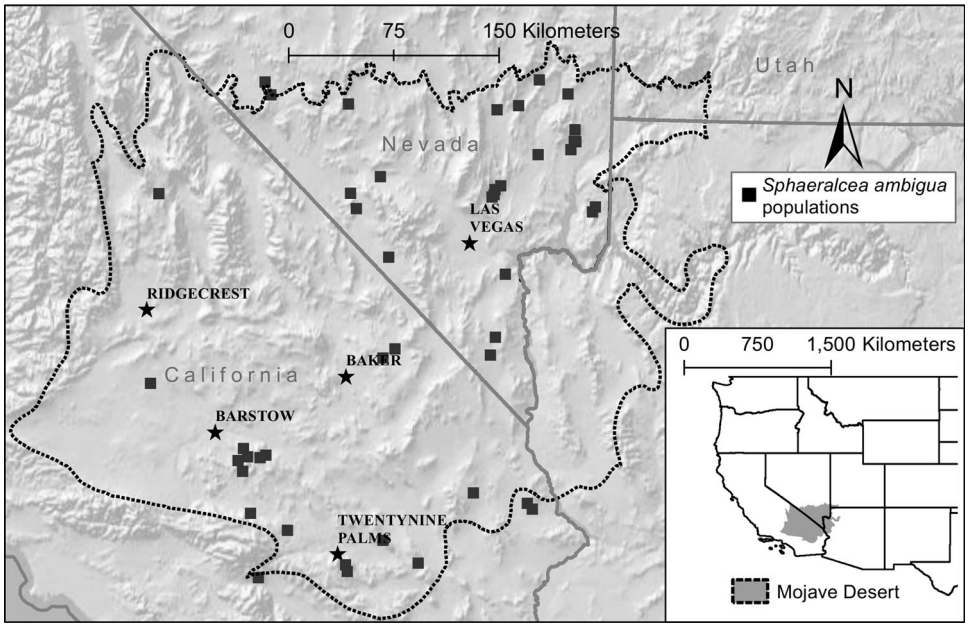

Fig. 1 Genotyped source populations of *Sphaeralcea ambigua* distributed across the Mojave Desert ecoregion in California and Nevada, USA

Table 1 Environmental variables derived for analysis of adaptive genetic variability in *Sphaeralcea ambigua* at a 1 km^2 spatial scale

Environmental layer	Description and source	Code
Elevation (m)	30 m digital elevation model (National Elevation Dataset, http://ned.usgs.gov/)	ELEV
Slope (°)	Rise in degrees, derived from 30 m digital elevation model (National Elevation Dataset, http://ned.usgs.gov/)	SLP
Winter precipitation (mm)	Average precipitation received from October to March, derived from PRISM 1981–2010 climatic normal (Daly et al. 2008, http://www.prism.oregonstate.edu/)	WP
Summer precipitation (mm)	Average precipitation received from April to September, derived from PRISM 1981–2010 climatic normal (Daly et al. 2008, http://www.prism.oregonstate.edu/)	SP
Winter minimum temperature (°C)	Average temperature minimum from November to February, derived from PRISM 1981–2010 climatic normal (Daly et al. 2008, http://www.prism.oregonstate.edu/)	WMT
Summer maximum temperature (°C)	Average temperature maximum from July to September, derived from PRISM 1981–2010 climatic normal (Daly et al. 2008, http://www.prism.oregonstate.edu/)	SMT
Precipitation ratio	Ratio of winter to summer precipitation, calculated from WP and SP layers	PRT
Seasonal thermal range (temperature seasonality)	Difference between summer and winter land surface temperature derived from MODIS MOD11A1 product (available from Inman et al. 2014)	STH
Topographic index	Area of hillslope per unit contour length draining into a given cell, following Moore et al. 1991 (available from Inman et al. 2014)	TOPIND
Water stress index	Shortwave and infrared water stress index (SIWSI; Fensholt and Sandholt 2003) derived from MODIS MOD09A1 product (available from Inman et al. 2014)	SWS
Thermal inertia (soil texture index)	Difference in daytime and nighttime surface temperatures from MODIS MOD11A1 (available from Inman et al. 2014)	TEXT

Statistical analysis

Population structure

Population differentiation was characterized using analysis of molecular variance (AMOVA) with 9999 permutations. AMOVA partitions variability within- and among-populations and results in phi-statistics, which are analogues of Wright's F-statistic for binary (dominant) data. Calculations were performed in GenAlEx version 6.501 (Peakall and Smouse 2012).

Identifying potentially adaptive loci

AFLP loci of potential ecological relevance (i.e., loci putatively linked to genetic factors contributing to adaptive

differentiation) were identified with two approaches: (a) outlier locus detection, which identifies a subset of loci that exhibit extreme differentiation relative to the full marker set, a pattern better explained by selection than drift; and (b) landscape genetics, which directly correlates environmental variability with allele frequency variation. Loci identified as potentially adaptive in either approach were combined into a matrix for multivariate analyses and are hereafter referred to as "potentially adaptive loci."

Outlier loci were identified using a hierarchical Bayesian approach based on the method of Beaumont and Balding (2004) and implemented in the program BayeScan V.2.1 (Foll and Gaggiotti 2008). This program estimates the posterior probability that a given locus is under selection by decomposing F_{ST} into population and locus-specific contributions in a logistic regression, assuming departure from neutrality when the locus-specific component best explains the observed pattern of genetic diversity. We performed three independent BayeScan iterations with sample locations as populations ($n = 47$). Loci under diversifying selection ($q < 0.05$) across all three runs were considered potentially adaptive. Each independent iteration comprised 20 pilot runs of 5000 and a 50,000 data burn in. While the genus *Sphaeralcea* is inferred to be predominantly allogamous (Hubbard et al. 1993), the inbreeding coefficient was allowed to vary between 0.0 and 1.0 to avoid biased F_{ST} estimation.

In the landscape genetics approach, population-level loci frequencies, calculated as the proportion of plants with a band present at each AFLP locus per sampling location, were tested for correlations with environmental predictors (sensu Manel et al. 2012). Outlying Mean Index ordination (OMI; Dolédec et al. 2000), as implemented in the R package "ade4" (Dray and Dufour 2007), was used to identify loci showing significant environmental correlations. OMI is a multivariate, non-parametric method for characterizing niche differentiation and can be used in a landscape genomics context to identify loci showing frequency clines along ecological gradients that deviate from chance expectation. OMI can identify both linear and nonlinear response distributions. Significance of correlations between loci and environmental gradients were assessed via permutation tests, and further adjusted using a false discovery rate (FDR) correction (Benjamini and Hochberg 1995). Loci showing significant ($q < 0.05$) correlations after P value correction were considered potentially adaptive.

Associations between environmental variables and potentially adaptive loci were further verified using general linear models (GLMs) with quasi-binomial errors to account for overdispersion in residuals. Variables were retained in reduced models based on the change in deviance from models fitted with and without each term. The deviance explained by each model was calculated as 1 − (residual deviance/null deviance). Significance was assessed via likelihood-ratio tests comparing reduced and null (intercept only) models.

Characterizing adaptive variability across the landscape

Multivariate models of adaptive genetic variability

Although exceptions exist, neutral genetic processes are expected to influence the entire genome (e.g., isolation-by-distance), while selection influences only certain regions. Consequently, adaptive loci should exhibit spatial autocorrelation that differs from neutral loci and corresponds to selective environmental gradients (Manel et al. 2010). To test these assumptions, we computed the following Mantel or partial-Mantel tests with 9999 permutations: genetic distance by geographic distance, genetic distance by environmental distance, genetic distance by environmental distance—geographic distance (partial-mantel), genetic distance by geographic distance—environmental distance (partial-mantel), and geographic distance by environmental distance. Tests were computed separately for neutral and potentially adaptive loci, where "neutral" loci include those not identified as potentially adaptive. Genetic dissimilarities were calculated as pairwise population Φ_{pt} matrices in GenAlex version 6.501 (Peakall and Smouse 2012), while a Euclidean distance metric was used to calculate geographic (based on latitude and longitude) and environmental (including all predictors from Table 1) distances. Additionally, we computed Mantel correlograms for neutral and adaptive loci to examine correlations in loci frequencies between populations as a function of increasing geographic distance (Legendre and Legendre 2012). Calculations were performed using the R package "vegan" (Oksanen et al. 2013).

Potentially adaptive loci were analyzed with a multivariate generalized dissimilarity model (GDM; Ferrier et al. 2002, 2007) implemented in the R package "Gdm01" (Manion et al. 2014). GDM is a distance-based approach accommodating non-linear relationships between compositional dissimilarities and ecological gradients, along with non-stationarity (variation) in the rate of compositional change (Ferrier et al. 2007; Fitzpatrick et al. 2013). This is accomplished through monotonic I-splines with two key properties: (1) the maximum height of each curve represents the total amount of compositional change explained by each ecological predictor; and (2) the slope of each curve indicates the rate of compositional change along the predictor's range (Fitzpatrick et al. 2013; Fitzpatrick and Keller 2015). GDM was run using the population Φ_{pt}

matrix for potentially adaptive loci as response, and thereby expressed the rate of change in allele frequencies with respect to environmental predictors. Significance of the model fit was assessed through a randomization procedure which permuted genetic distances (9999 permutations; Fitzpatrick et al. 2013). To assess uncertainty in model parameters (I-spline functions), we simulated 1000 bootstrap iterations of the GDM model leaving out 10 % of populations and sampling without replacement from the remainder. Standard deviations were calculated showing the variance of model parameters between bootstrap iterations and plotted as error bands for each I-spline.

Spatial interpolations

Two GDM-based interpolation methods were used to map potentially adaptive genetic variability in *S. ambigua*. First, we used the fitted GDM to directly predict pairwise genetic dissimilarities for a uniform 10 km^2 grid of points spanning the Mojave Desert ecoregion. Values for predictor variables were extracted at each point on the grid and input to GDM. Predicted pairwise dissimilarities were then input to the "single species genetic divergence tool" from the Genetic Landscapes GIS toolbox (Vandergast et al. 2011), which interpolated the dissimilarities into a continuous 1 km^2 raster grid through an inverse-distance-weighed (IDW) algorithm. Interpolated dissimilarity values for each cell on the raster grid were symbolized by color, allowing a visualization of the change in potentially adaptive loci frequencies through space.

The second technique involved mapping transformed predictors (i.e., model parameters) from the fitted GDM, which are scaled and weighted to best summarize variability in adaptive loci such that the scaled environmental distances provide the best fit between observed and predicted genetic dissimilarities (Fitzpatrick and Keller 2015). The fitted GDM was first used to transform environmental predictors extracted from a uniform 2.5 km^2 grid of points spanning the Mojave Desert. Next, we performed a principal component analysis (PCA) to reduce the transformed predictors into three principal components expressing major gradients of variability (sensu Fitzpatrick and Keller 2015). PCA axes were interpolated to a continuous 1 km^2 raster grid using IDW. Finally, the three resulting raster grids (PCA axes) were assigned to an RGB color palette in ArcGIS 10.1, such that the similarity of colors in the multiband raster corresponded to the similarity of predicted patterns of potentially adaptive loci frequencies.

Bootstrap simulations (as outlined above) were also used to visualize model uncertainty across the study region. After each bootstrap iteration (n = 1000), we calculated GDM-transformed predictors and compared the original and bootstrapped solutions in Procrustes analysis (function "procrustes" in R package vegan; Oksanen et al. 2013), a procedure for determining the similarity of two multivariate configurations (Peres-Neto and Jackson 2001). Procrustes errors for points on the 2.5 km^2 grid were averaged, normalized (range 0–1), and interpolated using IDW. The multidimensional climate space represented by sampled populations within the Mojave Desert study region was also mapped by overlying raster layers representing each environmental predictor.

Results

Population structure

AMOVA resulted in an overall Φ_{pt} statistic of 0.16 ($P < 0.0001$), indicating that 84 % of genetic variability was partitioned within populations. Pairwise population Φ_{pt} values ranged from 0.00 to 0.41, and 94.5 % of these values were larger than expected by chance ($P < 0.05$). Expected heterozygosity and the proportion of polymorphic loci for each population are provided in Online Resource 1.

Identifying potentially adaptive loci

Eleven loci were identified through BayeScan as under diversifying selection (Table 2). These corresponded with 5 of 31 loci showing significant ($q < 0.05$) correlations to environmental variables in OMI ordination (Online Resource 2; Table 2), for a total of 37 potentially adaptive loci. GLMs relating population-level allele frequencies with environmental predictors were significant ($P < 0.05$) for 33 loci, including all OMI loci and 7 of 11 BayeScan loci. Percentages of deviance explained by significant GLMs ranged from 0.20 to 0.52. Summer precipitation (SP) and winter precipitation (WP) were retained most frequently in GLMs (15 and 17 models, respectively), followed by summer maximum temperature (SMT; 13 models) and winter minimum temperature (WMT; 11 models) (Table 2). Slope and thermal inertia were not retained in GLMs.

Characterizing adaptive variability across the landscape

Multivariate models of adaptive genetic variability

Mantel correlations for neutral loci were significant between genetic and geographic distances, but not between genetic and environmental distances (Table 3). In contrast, Mantel correlations for potentially adaptive loci were significant in all tests (Table 3). In particular, the correlation

Table 2 Potentially adaptive loci identified through a landscape genetics approach (OMI) and outlier locus detection (BayeScan)

Locus	OMI	BayeScan	GLM model	Deviance
B52.5		×	SP	0.20*
B74.2	×		SP + SMT + STH	0.43***
B88.6	×		WPSPRT + STH	0.37***
B98.0	×		WP + SP + SMT + TOPIND	0.48***
B101.3		×	None	0.09
B116.0	×		WP + SP	0.23**
B122.1	×		SP + WMT + STH	0.31***
B129.8	×		WP + SP + WMT + TOPIND	0.37***
B130.5	×		WP + SP + SMT + SWS	0.41***
B146.3	×		SMT + STH	0.33***
B164.5	×	×	WP + SP	0.40***
B194.0	×		SP + SMT	0.28***
G62.6	×		WMT + TOPIND	0.35***
G67.0	×		SP + SMT + WPSPRT + SWS	0.33***
G83.4	×		WMT + SMT	0.18**
G111.0	×	×	SP + SMT + STH + TOPIND	0.51***
G139.7	×		WP + SP + WPSPRT + STH	0.34***
G151.2	×		WP + WMT + SMT + STH	0.27**
G157.4	×		WMT + WPSPRT + TOPIND	0.25***
G170.0	×	×	WP + SP + WMT + TOPIND	0.52***
G179.9	×		WP + SMT	0.22***
G231.5		×	None	0.19
R52.0		×	WP + WMT	0.21*
R85.7	×		WP + SP + WMT	0.40***
R87.0	×		SMT + WPSPRT + SWS	0.46***
R106.1	×		WMT + SMT + WPSPRT + SWS	0.44***
R118.8	×		STH	0.30***
R138.5	×		WP + SP + WPSPRT	0.25**
R141.5	×		WPSPRT + SWS	0.39***
R157.3	×	×	SP + STH + TOPIND	0.44***
R166.0	×	×	WP	0.38***
R184.5	×		WP + SMT + WPSPRT + TOPIND	0.38***
R189.0		×	None	0.11
Y71.4	×		SP + SWS + STH	0.49***
Y75.9	×		WP + TOPIND	0.25***
Y95.4	×		WMT + WPSPRT	0.30***
Y191.0		×	None	0.08

Terms that best explained allele frequencies at sampling locations in quasi-binomial GLM models are given, along with model goodness-of-fit measures

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

between genetic and environmental distance was significant after removing the effect of geographic distance ($r = 0.162$, $P = 0.015$). In Mantel correlograms, potentially adaptive loci showed stronger positive correlations than neutral loci at shorter distances, along with larger negative correlations at greater distances (Fig. 2).

GDM explained 28.41 % of the total deviance in potentially adaptive loci frequencies ($P = 0.009$), based on eight predictors (Fig. 3). Summing the I-spline basis coefficients for each predictor provides a means of comparing variable importance corresponding to the total height of each curve (Fitzpatrick et al. 2013). Based on this criterion, seasonal thermal range explained the most variability in adaptive loci frequencies (0.12), followed by water stress index (0.09) and summer maximum temperature (0.07). The association between potentially adaptive

Table 3 Mantel tests describing the relationship between genetic, environmental, and geographic distances

Mantel test	Neutral loci		Potentially adaptive loci	
	r	*P*	r	*P*
Genetic × environment	0.052	0.235	0.422	0.000
Genetic × geographic	0.088	0.032	0.571	0.000
Genetic × environment – geographic	0.005	0.425	0.162	0.015
Genetic × geographic – environment	0.071	0.093	0.449	0.000
Geographic × environment	0.543	0.000	0.543	0.000

Partial Mantel tests are indicated by "–", with the partialed-out term to the right of the dash

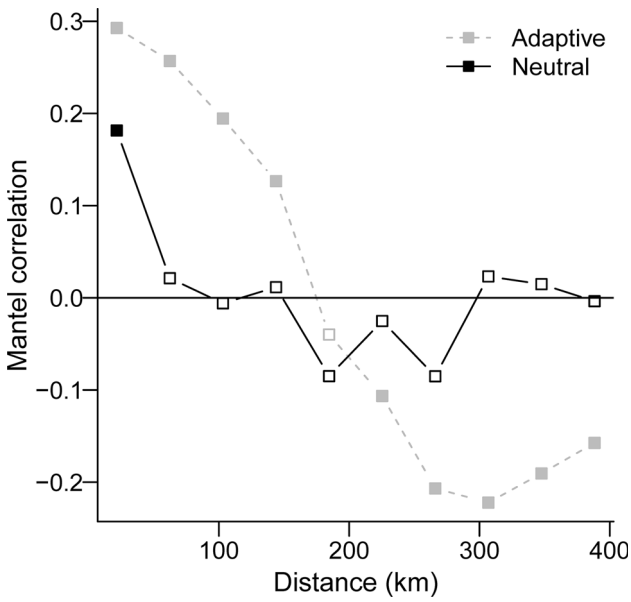

Fig. 2 Mantel correlograms showing the strength of correlations between genetic and geographic dissimilarity as a function of increasing geographic distance for neutral and potentially adaptive loci. *Filled squares* indicate significant ($P < 0.05$) Mantel correlations

loci and seasonal thermal range was predominantly linear, while associations with summer maximum temperature and water stress index were nonlinear. Higher temperatures and lower water stress index values (corresponding to drier conditions) contributed to greater variation in potentially adaptive loci.

Spatial interpolations

The interpolation of pointwise genetic dissimilarities showed that predicted changes in potentially adaptive loci were variable through space (Fig. 4a). Regions with high predicted genetic dissimilarities, corresponding to variation in influential ecological gradients (e.g., thermal range, water stress index and summer maximum temperature), included the northeastern Mojave Desert and Baker, CA (Fig. 4a). In contrast, much of the southwestern Mojave Desert exhibited low predicted genetic dissimilarities through space. The map of transformed ecological predictors (Fig. 4b) revealed patterns of local adaptation predicted for *S. ambigua* based on GDM splines. Low-lying basins with extreme temperatures and limited precipitation (e.g., the green-colored Death Valley trough extending northwesterly from Baker, CA) were distinguished from higher elevation areas with less extreme conditions (purple–pink coloration). Spatial bootstrapping of the GDM model (comparing successive interpolations in Procrustes analysis) revealed inconsistencies in model performance across the interpolated genetic surface (Fig. 5). Areas with higher Procrustes error were generally outside of the climate space represented by sampled populations. In contrast, areas within the sampled climate space exhibited low Procrustes errors.

Discussion

Using a combination of outlier locus detection, landscape genetics, and multivariate statistics, we identified correlations between potentially adaptive loci and environmental gradients in the desert species *Sphaeralcea ambigua*. Potentially adaptive loci were best associated with summer maximum temperature, water stress index, and seasonal temperature range, exhibiting both linear and nonlinear patterns of variation along these gradients. Adaptive divergence in alpine plants (e.g., Poncet et al. 2010; Manel et al. 2012) and forest trees (e.g., Evans et al. 2014; De Kort et al. 2014; Steane et al. 2014) has also been related to temperature and precipitation through genome scans. However, our study is unique in several ways: (1) we visualize the scale of adaptive divergence across the landscape, mapping regions of high genetic dissimilarities through space (Fig. 4a); (2) we interpolate predicted spatial patterns of local adaptation with respect to ecological gradients (Fig. 4b); and (3) we map uncertainty in spatial interpolations by comparing bootstrapped GDM iterations through Procrustes analysis (Fig. 5). These novel approaches will inform both ecological restoration and climate change modelling.

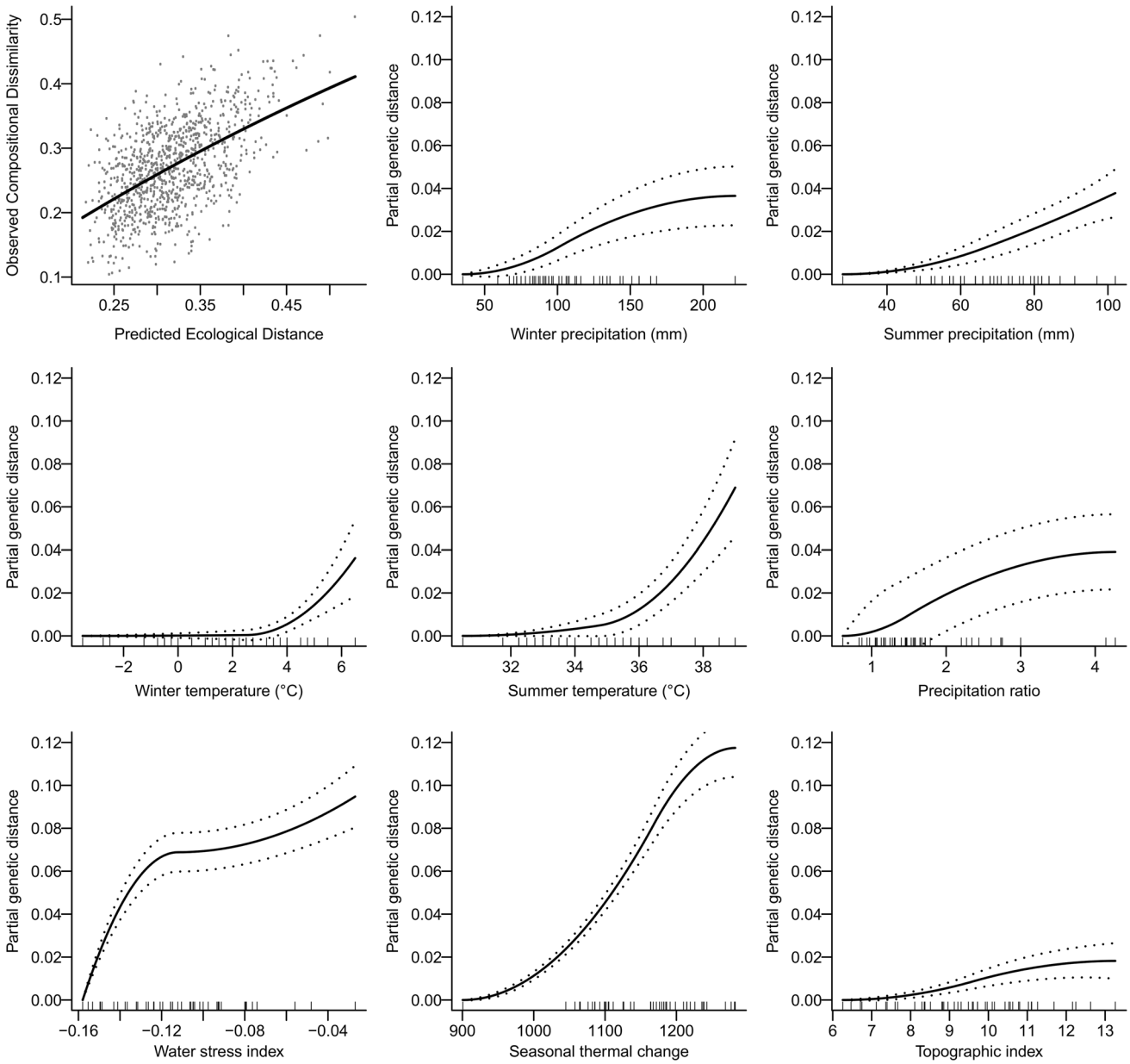

Fig. 3 I-splines derived from a generalized dissimilarity model (GDM) linking variability in potentially adaptive loci with environmental predictors. *Curve height* indicates the variability explained by each predictor, while *slope* indicates the rate of change in loci frequencies along each predictor's range. *Error bars* show bootstrapped standard deviations, while *rug plots* show environmental values at sampled populations. The *top left panel* shows the relationship between observed genetic dissimilarity and environmental dissimilarity

Landscape genomics and restoration

Associations between plant genotypes, phenotypes, and environmental gradients are reported in experiments combining marker-based genome scans with common gardens (e.g., Herrera and Bazaga 2008; Richardson et al. 2009; Hancock et al. 2011; De Kort et al. 2014; Steane et al. 2014) or genome-wide association studies (e.g., Fournier-Level et al. 2011; Evans et al. 2014), providing evidence that genome scans can distinguish phenotypes. Accordingly, molecular markers are increasingly used to guide ecological restoration, particularly for pre-treatment decision-making (e.g. seed sourcing; Mijangos et al. 2015), and may provide cost or time advantages over common garden experiments. However, this approach does not directly link potentially adaptive loci with phenotypic traits important in restoration, such as germination requirements or drought tolerance. Additional studies are needed to identify the

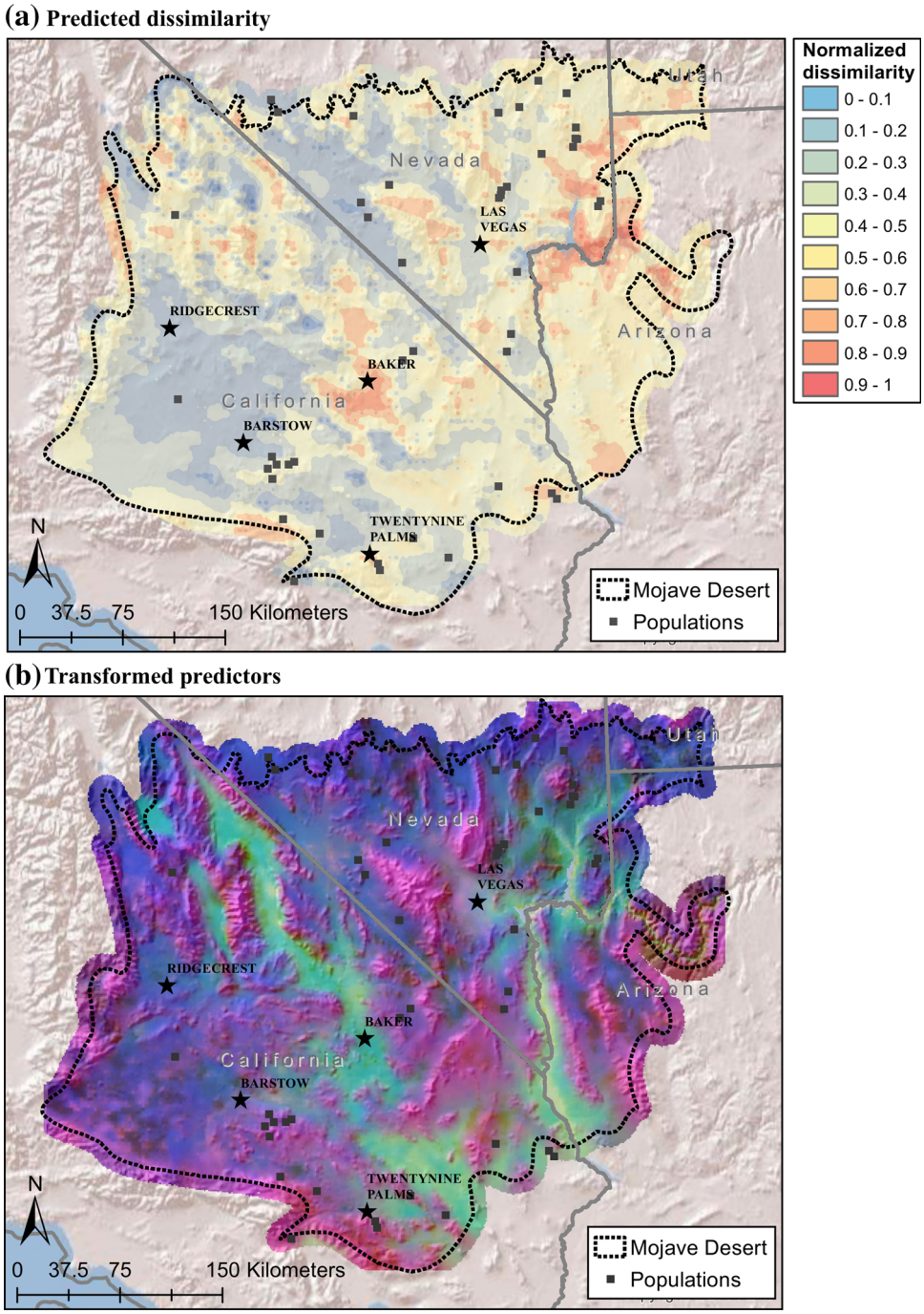

Fig. 4 Spatial interpolations of a generalized dissimilarity model (GDM) linking potentially adaptive loci in *Sphaeralcea ambigua* with environmental predictors. **a** Interpolation of the predicted pairwise genetic dissimilarities (normalized to range between 0 and 1) between points on a uniform 10 km^2 grid. **b** Interpolation of the multidimensional climatic space derived from a principal components analysis of GDM-transformed environmental predictors

range of conditions wherein molecular markers accurately characterize phenotypic differentiation in fitness traits, resulting in improved restoration outcomes (Bragg et al. 2015; Mijangos et al. 2015). Along these lines, *S. ambigua* is currently being evaluated in multiple common gardens located along a climatic gradient in the Mojave Desert.

Assuming potentially adaptive loci reflect true adaptive differentiation, our GDM approach is particularly suited to guide restoration. Risk of low survival in maladapted plantings has made the scale of local adaptation with respect to environmental gradients a central question (Hufford and Mazer 2003; McKay et al. 2005). Our GDM interpolation of predicted genetic dissimilarities (Fig. 4a) addresses this directly by contrasting regions where frequencies of potentially adaptive loci vary over short (red coloration) or wider (blue coloration) spatial gradients. The different spatial scales over which potentially adaptive loci diverged in *S. ambigua* suggest that ecological rather than

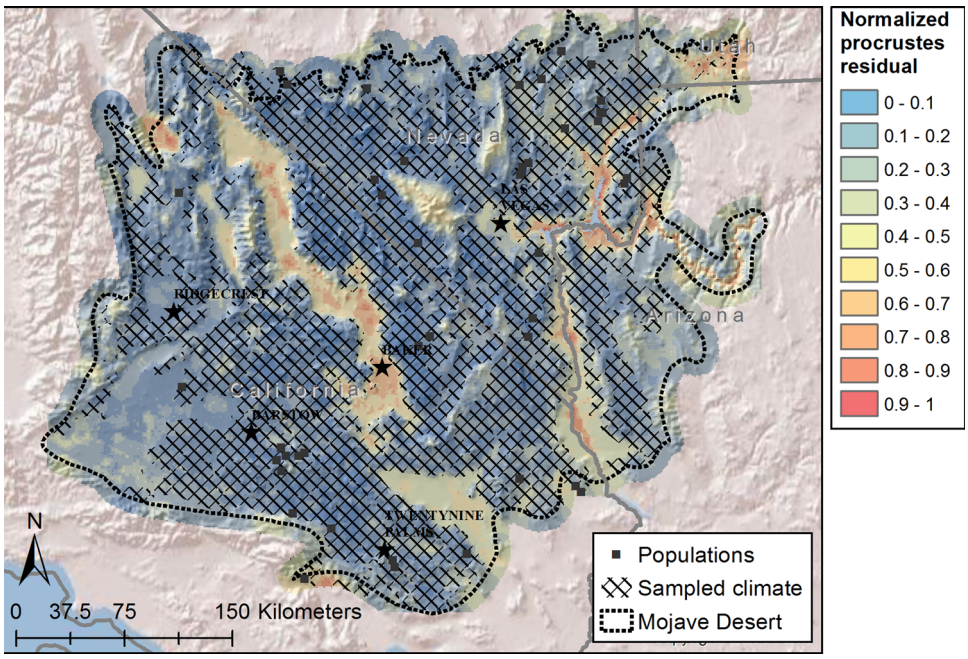

Fig. 5 Spatial uncertainty in a GDM model of potentially adaptive loci for *Sphaeralcea ambigua*. Procrustes analysis was used to compare successive predictions from bootstrapped GDM simulations (n = 1000). Hatching covers areas within the climate space represented by sampled populations

geographic distance criteria (e.g., "provenance threshold distances"; Stingemore and Krauss 2013) would best guide restoration. Moreover, ecological gradients driving changes in potentially adaptive loci—summer maximum temperature, seasonal thermal range, and water stress index for *S. ambigua* (Fig. 3)—could be matched between seed source and restoration sites.

Seed sourcing poses a considerable challenge for large-scale restoration. Recently, three approaches have been contrasted: (1) local provenancing based on seed transfer zones (distances within which seeds can be transferred without risk of maladaptation); (2) admixture provenancing using genetically diverse seed mixes to maximize evolutionary potential; and (3) predictive provenancing, or choosing seed sources to cope with future climates (Lesica and Allendorf 1999; Breed et al. 2013; Kettenring et al. 2014). While considerable debate exists surrounding these approaches (Breed et al. 2013), we propose that GDM-based spatial interpolations can guide all three. The map of GDM-transformed predictors (Fig. 4b) represents potential seed transfer zones, as areas with similar coloration are predicted to be similarly adapted. Alternatively, this map could support admixture provenancing if seed sources are collected from geographically separated but ecologically related (similar map coloration) areas, potentially increasing genetic diversity while minimizing maladaptation risks. Finally, comparisons between GDM models for current and projected future climates could inform predictive provenancing by revealing regions of greatest predicted disruption to adaptive loci/environment associations (e.g., Fitzpatrick and Keller 2015).

Landscape genomics and climate change

Plants in extreme environments may be particularly susceptible to changing climate because of their narrow distributions and potential exposure to rapid rates of environmental change (Walther et al. 2002; Parmesan 2006). Arid regions face warming along with changes in the frequency and intensity of extreme climatic events over the next century (Dai 2013; IPCC 2013). Whether desert plant populations, already adapted to harsh and variable climates, will remain viable under heightened extremes is uncertain (Brown et al. 1997; Salguero-Gómez et al. 2012) and depends on capacities for dispersal, evolution, or phenotypic plasticity (Reusch and Wood 2007). In the arid southwestern US, widespread plant population declines following recent droughts (Breshears et al. 2005; Miriti et al. 2007), along with long-term vegetation studies suggesting vulnerability to increased aridity (Munson et al. 2012; Munson 2013), cast doubt on phenotypic plasticity as the sole mechanism for maintaining populations. Adaptive genetic variability is therefore likely to shape population responses to future climate.

Desert plants have shown phenotypic divergence with respect to germination phenology (Meyer and Pendleton 2005) and drought response (Sandquist and Ehleringer 1997) in common gardens, traits likely to influence species' responses to climate change. Landscape genomics provides a basis for identifying ecological drivers of adaptive divergence across a wide number of species and populations, representing a useful step towards understanding intraspecific differences in climate change vulnerability.

We find evidence for adaptive genetic divergence in *S. ambigua* with respect to temperature (both maxima and annual range) and water stress index. Nonlinearities in GDM splines suggest that certain populations may experience greater genotype/environment asynchronies from changes in summer maximum temperature and water stress than others (note that slopes of GDM splines correspond to changes in loci frequencies). In contrast, the strong linear relationship between potentially adaptive loci and seasonal thermal range suggests that populations may be similarly affected by changes in temperature seasonality. These findings highlight how predictions of increased temperatures and drought may be interpreted in terms of population-level intraspecific variability. However, our GDM model points to potential adaptive divergence without identifying the quantitative traits or ecological mechanisms involved, for which common gardens (e.g., De Kort et al. 2014) or genome-wide association studies (e.g., Evans et al. 2014) are necessary.

Statistical considerations in the identification of potentially adaptive loci

Numerous processes may confound identification of adaptive loci and lead to false positives, including: historic population expansions, bottlenecks, or periods of secondary contact (gene flow) between previously isolated populations; hierarchical spatial genetic structure or isolation by distance (IBD); and divergence hitchhiking, where neutral alleles linked to adaptive loci show increased divergence (Excoffier et al. 2009; Feder and Nosil 2010; Holderegger et al. 2010; Manel et al. 2012; Schoville et al. 2012; Strasburg et al. 2012; Bragg et al. 2015). These processes may produce geographic clines in neutral allele frequencies resembling those expected under selection. Although outlier locus detection methods account for spatial genetic structure (Foll and Gaggiotti 2008; Excoffier et al. 2009), they assume that adaptive loci exhibit clines in allele frequency different from neutral loci, and may produce false positives when this condition is violated (De Mita et al. 2013; De Villemereuil et al. 2014). However, simulations incorporating complex spatial genetic structures have found BayeScan comparatively robust to Type I error (Pérez-Figueroa et al. 2010; Narum and Hess 2011; Vilas et al. 2012). In our analysis, BayeScan identified 11 of 153 AFLP loci (7.2 %) as under divergent selection, below the average of 8.9 % reported in Strasburg et al. (2012) from a review of genome scans in plants. Seven of these loci were also significantly correlated with environmental gradients in GLM models (Table 2), and five were identified by OMI, providing further evidence for selection. The four loci that did not correlate with environmental gradients may correspond to selective factors not accounted for in our study, such as fine-scale (<1 km^2) topographic variation, or are potential false positives.

Relative to outlier locus detection, landscape genetic methods correlating allele frequencies with environmental gradients have increased power to identify loci under selection, but also higher Type 1 error when correlations with environmental gradients arise from processes other than selection (De Mita et al. 2013; De Villemereuil et al. 2014). OMI identified 31 loci as potentially adaptive following p-value correction. GLMs confirmed the significant relationships between these loci and environmental gradients (Table 2). Although the proportion of potentially adaptive loci identified by OMI (20.3 %) is within the range (0.4–35.5 %) reported in Strasburg et al. (2012), it is well above average. Not accounting for spatial genetic structure may make OMI susceptible to higher rates of Type I error than BayeScan, as are landscape genetic methods involving linear or logistic regression (e.g., Joost et al. 2007; Manel et al. 2012). However, our interpretation of loci identified by OMI as potentially adaptive is supported by Mantel analyses showing: (1) different patterns of spatial autocorrelation for potentially adaptive versus neutral loci, including greater dissimilarities at larger distance classes, pointing to selective factors that do not have a genome-wide effect; and (2) a significant correlation between potentially adaptive loci and environmental variables after removing the effect of geographic distance between populations (Table 3), which generally corresponds with neutral genetic structure (e.g., IBD; Manel et al. 2010). Furthermore, relationships between potentially adaptive loci and environmental gradients in GDM were robust to simulations leaving out 10 % of populations (Fig. 3), suggesting that observed patterns were general rather than artefacts of sampling design or few isolated populations.

Both outlier locus and landscape genetic methods are single-marker analyses that do not account for multivariate relationships in adaptive portions of the genome. However, there are several scenarios where single marker analyses may fail to identify genomic signals of selection. First, quantitative traits directing plant responses to environmental cues are often polygenic, involving numerous small-effect loci spread throughout the genome (Le Corre and Kremer 2012; De Villemereuil et al. 2014). Second, soft sweeps (adaptation from standing genetic variation) are more likely to involve polygenic traits that are not distinguishable from background genomic variation (Barrett and Schluter 2008; Schoville et al. 2012). Third, selectively neutral loci may develop associations with environmental gradients due to isolation-by-environment (IBE), wherein propagule establishment is limited by environmental suitability (Orsini et al. 2013; Sexton et al. 2014); background genomic variation may then predict

establishment success (Schoville et al. 2012; Bragg et al. 2015). By incorporating complex inter-correlation patterns, multivariate models such as GDM may better account for genomic architectures of selection than single-marker analyses (Sork et al. 2013). Moreover, in cases of IBE or complex polygenic traits, multivariate models including both adaptive and neutral loci with environmental associations may still guide ecological restoration or climate change modelling (Bragg et al. 2015). In this respect, different methodologies may be appropriate in a restoration context than when characterizing the molecular architecture of adaptation (e.g., identifying quantitative trait loci).

Another important consideration in developing spatial models of adaptive genetic variability is the uncertainty in mapped interpolations with respect to sample size, geographic distribution of sample populations, and error in model parameters (Thomassen et al. 2010). Using a novel spatial bootstrapping approach that overlaid areas of high interpolation uncertainty with the climate space represented by sample populations, we found that GDM was robust within the climate space represented by *S. ambigua* populations, but less consistent between bootstrap iterations outside of this climate space (Fig. 5). Hence, caution is warranted when applying genetic or common garden data to applications such as the delineation of seed transfer zones, where it may be desirable to extend mapping regions beyond the environmental limits spanned by sample populations (e.g., St. Clair et al. 2013). Mapping of model uncertainty within sampled climates may also help to identify patterns of spatial autocorrelation in residuals that may reveal important artefacts of sampling design or spatial genetic structure.

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