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Landscape genetic approaches to guide native plant restoration in the Mojave Desert

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Abstract. Restoring dryland ecosystems is a global challenge due to synergistic drivers of disturbance coupled with unpredictable environmental conditions. Dryland plant species have evolved complex life-history strategies to cope with fluctuating resources and climatic extremes. Although rarely quantified, local adaptation is likely widespread among these species and potentially influences restoration outcomes. The common practice of reintroducing propagules to restore dryland ecosystems, often across large spatial scales, compels evaluation of adaptive divergence within these species. Such evaluations are critical to understanding the consequences of large-scale manipulation of gene flow and to predicting success of restoration efforts. However, genetic information for species of interest can be difficult and expensive to obtain through traditional common garden experiments. Recent advances in landscape genetics offer marker-based approaches for identifying environmental drivers of adaptive genetic variability in non-model species, but tools are still needed to link these approaches with practical aspects of ecological restoration. Here, we combine spatially explicit landscape genetics models with flexible visualization tools to demonstrate how cost-effective evaluations of adaptive genetic divergence can facilitate implementation of different seed sourcing strategies in ecological restoration. We apply these methods to Amplified Fragment Length Polymorphism (AFLP) markers genotyped in two Mojave Desert shrub species of high restoration importance: the long-lived, wind-pollinated gymnosperm *Ephedra nevadensis*, and the short-lived, insect-pollinated angiosperm *Sphaeralcea ambigua*. Mean annual temperature was identified as an important driver of adaptive genetic divergence for both species. *Ephedra* showed stronger adaptive divergence with respect to precipitation variability, while temperature variability and precipitation averages explained a larger fraction of adaptive divergence in *Sphaeralcea*. We describe multivariate statistical approaches for interpolating spatial patterns of adaptive divergence while accounting for potential bias due to neutral genetic structure. Through a spatial bootstrapping procedure, we also visualize patterns in the magnitude of model uncertainty. Finally, we introduce an interactive, distance-based mapping approach that explicitly links marker-based models of adaptive divergence with local or admixture seed sourcing strategies, promoting effective native plant restoration.

Key words: drylands; ecological restoration; genome scan; landscape genetics; local adaptation; Mojave Desert; multivariate analysis; seed provenance strategy; seed transfer zones; spatial genetics.

Introduction

Dryland ecosystems worldwide are increasingly in need of ecological restoration due to synergistic disturbances, such as invasive species, novel fire regimes, shifting climates, and energy development (Reynolds et al. 2007, Verstraete et al. 2009). Local adaptation influences restoration outcomes if local genotypes are better able to establish and persist in a given environment (Hufford and Mazer 2003). Although plant populations frequently exhibit home-site advantages in reciprocal transplant experiments (Leimu and Fischer 2008, Hereford 2009), information about local adaptation is rarely available to guide restoration decision-making, particularly for dryland species. Identifying clines in adaptive genetic variability across heterogeneous environments is therefore both a consequential and a practical research objective. A growing body of work focuses on identifying the molecular basis of natural selection and attributing variation in adaptive loci to selective environmental gradients (reviewed in Schoville et al. 2012, Manel and Holderegger 2013, Bragg et al. 2015). Recent studies have also highlighted promising spatial approaches for visualizing adaptive genetic variability in non-model species (e.g., Thomassen et al. 2010, Fitzpatrick and Keller 2015, Shryock et al. 2015). However, techniques are needed to link landscape genetics with practical aspects of ecological restoration, particularly spatial planning tools

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that leverage models of local adaptation to inform seed-sourcing strategies.

Revegetating disturbed drylands is invariably challenging due to unpredictable precipitation (Chesson et al. 2004), high levels of granivory (Price and Joyner 1997, DeFalco et al. 2012), and, often, competition by invasive species (D'Antonio and Vitousek 1992, Abella et al. 2012). Use of maladapted seed stock could exacerbate these issues if propagules exhibit poor germination and seedling survival, low population fitness, or outbreeding depression (Hufford and Mazer 2003, McKay et al. 2005). Accounting for local adaptation in restoration designs is a promising approach for increasing revegetation effectiveness, particularly in drylands where stark environmental variation potentially drives high levels of adaptive divergence (Funk et al. 2012). Dryland plant species are adapted both to temporal climatic fluctuations, which lead to niche differentiation in seedling recruitment (Reynolds et al. 2004, Schwinning and Kelly 2013), and to extreme climatic events, which direct long-term population trajectories (Chesson et al. 2004, Miriti et al. 2007). Relatively few studies have characterized intraspecific variability in dryland species, but existing evidence points to adaptive divergence in germination and seedling emergence phenology (Meyer and Pendleton 2005), water-use efficiency (Schuster et al. 1992), and drought tolerance (Sandquist and Ehleringer 1997) along precipitation and temperature gradients. Use of local genotypes has long been favored as a means for maintaining gene–environment interactions in restored populations (e.g., McKay et al. 2005, Broadhurst et al. 2008). However, local provenancing may be problematic when populations are fragmented or lack sufficient genetic diversity (Breed et al. 2013). Hence, recent work has also favored use of genetically diverse plant materials in order to increase resilience to changing environmental conditions (e.g., Breed et al. 2013, Kettenring et al. 2014).

Currently, three seed sourcing strategies are broadly recognized: (1) local provenancing, possibly through seed transfer zones (geographic areas within which plant materials can be safely moved without disrupting gene–environment interactions), which is aimed at decreasing the risk of outbreeding depression; (2) admixture provenancing, in which genetic diversity is maximized by incorporating a broad range of genotypes, thereby increasing adaptive potential and reducing the risk of inbreeding depression; and (3) predictive provenancing, in which plant materials are selected based on their ability to cope with future environmental conditions (Lesica and Allendorf 1999, Broadhurst et al. 2008, Wang et al. 2010, Breed et al. 2013, Kettenring et al. 2014). While debate exists concerning the application of these approaches to different situations (e.g., Breed et al. 2013, Kettenring et al. 2014), a consistent limiting factor in the informed implementation of such designs is the lack of knowledge concerning the strength and scale of local adaptation and the ecological gradients driving these patterns (Mijangos et al. 2015).

Traditionally, spatial models of local adaptation have been derived for individual species through common garden experiments by linking variation in quantitative traits with climatic characteristics of source populations (e.g., Wang et al. 2010). However, dryland species have been infrequently incorporated in such experiments (but see Sandquist and Ehleringer 1997, Meyer and Pendleton 2005, Richardson et al. 2014), in part due to the difficulty of maintaining studies in arid environments. An alternative approach is to model local adaptation through molecular markers, which frequently correspond to quantitative traits measured in common gardens (Herrera and Bazaga 2008, Richardson et al. 2009, Hancock et al. 2011, De Kort et al. 2014, Steane et al. 2014). Genome scan techniques such as outlier locus detection (e.g., Foll and Gaggiotti 2008, Excoffier et al. 2009) and environmental-association methods that correlate marker frequencies with environmental gradients (e.g., Coop et al. 2010, Manel et al. 2012, Frichot et al. 2013) are now widely applied to detect adaptive divergence in both model and non-model species (e.g., Rellstab et al. 2015). One challenge is that neutral genetic structure can mimic selection, leading to false positives among putatively adaptive loci (Excoffier et al. 2009, Schoville et al. 2012, Strasburg et al. 2012, Bragg et al. 2015). Conversely, polygenic selection acting on numerous small-effect loci may reduce the statistical power to detect adaptive divergence across the genome (Le Corre and Kremer 2012, De Villemereuil et al. 2014). However, certain outlier locus detection techniques (e.g., BayeScan; Foll and Gaggiotti 2008), along with environmental association methods that account for neutral genetic structure (e.g., Coop et al. 2010, Frichot et al. 2013), have been effective in detecting adaptive loci while minimizing false positives in complex demographic scenarios (Pérez-Figueroa et al. 2010, Narum and Hess 2011, Vilas et al. 2012, De Mita et al. 2013), including polygenic selection (De Villemereuil et al. 2014). Spatial autocorrelation between environmental gradients can also bias identification of environmental variables that drive selection. However, multivariate statistical approaches account for spatial dependencies and can facilitate interpolations of adaptive genetic variability (Thomassen et al. 2010, Fitzpatrick and Keller 2015, Shryock et al. 2015, Forester et al. 2016).

In the absence of genetic information, the concept of "provisional seed zones," or those which incorporate environmental rather than genetic criteria to designate recommended seed transfer distances, has also gained traction (e.g., Hargrove and Hoffman 2005, Johnson et al. 2010). Provisional seed zones for the continental United States were recently proposed based on winter minimum temperature and an aridity index (mean annual temperature/mean annual precipitation; Bower et al. 2014) and have received limited validation for species of the Great Basin Desert (Bower et al. 2014, Kramer et al. 2015). However, the degree to which provisional seed zones based on limited combinations of environmental variables can serve as effective

surrogates for genetically derived models of local adaptation requires evaluation across a broader range of ecoregions, particularly in terms of selecting environmental gradients appropriate for different plant functional groups.

It has been argued that identifying analogous drivers of natural selection among separate species within a region constitutes strong evidence of adaptation to these drivers, given that different species are unlikely to share the same patterns of neutral genetic structure (Manel et al. 2012). We take such an approach here, applying genome scans to Amplified Fragment Length Polymorphism (AFLP) markers genotyped in two Mojave Desert species of restoration importance but contrasting life history and pollination biology: one, a short-lived, insect-pollinated angiosperm (*Sphaeralcea ambigua*); the other, a long-lived, wind-pollinated gymnosperm (*Ephedra nevadensis*). For each species, we identify potentially adaptive genetic loci and the corresponding selective environmental gradients. Previously, we demonstrated multivariate spatial analyses to visualize predicted patterns of adaptive divergence, as well as patterns of model uncertainty (Shryock et al. 2015). Here, we extend this approach to better control for neutral genetic structure and to facilitate effective native plant restoration. In particular, we introduce an interactive, distance-based mapping approach that links models of adaptive divergence with practical seed sourcing strategies. Finally, we address the extent to which a simple environmental classification can serve as a surrogate for more costly genetics-based models in predicting adaptive divergence.

Methods

Study site and species

The Mojave Desert (approximately 150000 km^2) encompasses portions of Nevada, California, Utah, and Arizona in the southwestern United States (Fig. 1). Throughout, arid basins are interspersed by a series of north-to-south-oriented mountain ranges, which enhance climatic variability. Common geomorphic features include mountaintops, vertical outcrops, hillslopes, alluvial fans, and basins. Interannual climatic variability is enhanced by the El Niño Southern Oscillation (ENSO), with both wet (El Niño) and dry (La Niña) phases (Hereford et al. 2006). Summer moisture from the Gulf of Mexico increases the proportion of warm-season precipitation (July–October) in the eastern Mojave Desert, while the western Mojave is dominated by winter (October–April) precipitation (Hereford et al. 2006). Annual precipitation averages 137 mm, with a range of approximately 30–300 mm (Hereford et al. 2006). Maximum summer temperatures may exceed 50°C, while minimum temperatures drop below 0°C in winter. Mean annual temperature is approximately 17.2°C.

Ephedra nevadensis S. Watson is a long-lived (>100 years), rhizomatous, aphyllous shrub with jointed, photosynthetic stems. A gymnosperm, the species is dioecious and wind pollinated. Populations do not typically flower every year, but instead flower synchronously during favorable climatic episodes, producing mast seed crops (Meyer 2008). The relatively large seeds (>20 mg) are dispersed short distances by scatter-hoarding rodents

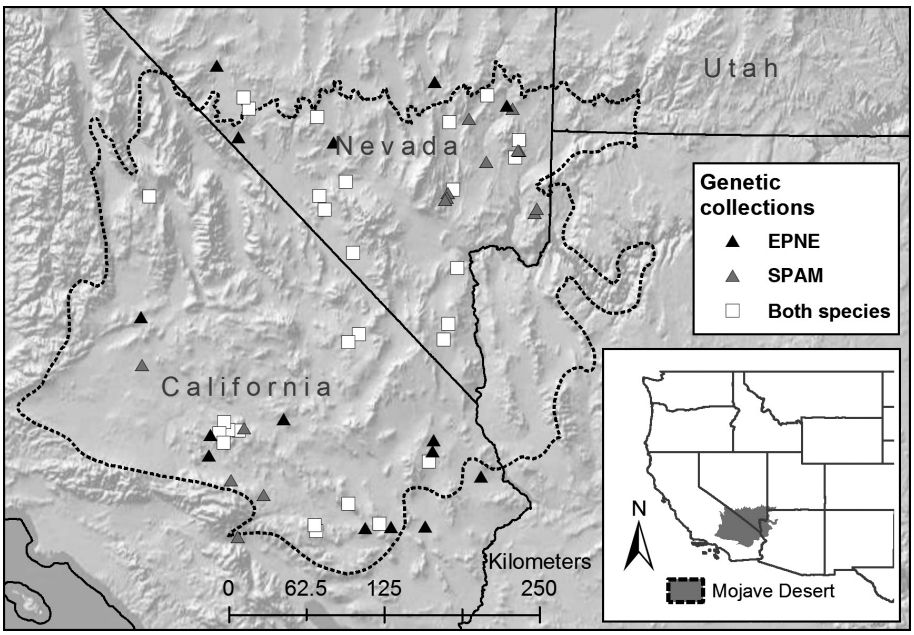

Fig. 1. Genotyped source populations of *Ephedra nevadensis* (EPNE) *and Sphaeralcea ambigua* (SPAM) in relation to the Mojave Desert ecoregion, USA. A total of 28 sampling locations were common to both species. Environmental variables are defined in Table 1.

(Hollander et al. 2010). *E. nevadensis* is a popular shrub used in dryland restoration due to its vigorous growth, wide distribution, high establishment success, and potential to serve as a nurse plant for other species while providing habitat structure for wildlife (Scoles-Sciulla et al. 2015).

Sphaeralcea ambigua A. Gray is a short-lived (<15 years), drought-deciduous, perennial subshrub. The species outcrosses and is insect pollinated. As with *E. nevadensis*, seeds do not possess a clear mechanism for anemochory but are dispersed short distances by rodents or ants (DeFalco et al. 2009). *S. ambigua* is a pioneer species following disturbance (Shryock et al. 2014) and more consistently flowers from year to year than *E. nevadensis*, despite fluctuations in precipitation (Beatley 1974). Other desirable traits, including high establishment success and fast growth, make *S. ambigua* a commonly used species for desert restoration. Moreover, colonization of burned areas by *S. ambigua* supports use of this habitat by the Mojave Desert tortoise (*Gopherus agassizii*), a threatened species (Drake et al. 2015).

Green leaf tissue from 10 to 15 individual plants spaced at least 10 m apart was collected during May–June 2011 from 47 populations of *S. ambigua*, and from 43 populations of *E. nevadensis*, located within and just outside of the Mojave Desert ecoregion (Fig. 1). Of these, 28 sampling locations contained populations of both species. Leaf tissue was stored within sealed bags containing desiccant, and GPS coordinates were recorded for each sampling location (Appendix S1).

Genotyping

Genomic DNA was extracted using the MegAttract 96 Miniprep Core Kit (Qiagen, Valencia, California, 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 μmol/L of double-stranded EcoRI adapter (combination of oligos 5′_CTCGTAGACTGCGTACC3′_ and 5′_AATTGGTACGCAGTCTAC3′_), 1× ligase buffer, and 0.1 μL of T4 ligase (New England BioLabs, Ipswich, MA, USA). The preselective AFLP amplification was carried out in a 20-μL reaction mixture containing 30 mmol/L Tricine, 50 mmol/L KCl, 2 mmol/L $MgCl_2$, 5% acetamide, 10 mmol/L of each dNTP, 0.2 mmol/L of each EcoRI primer (5′GACTGCGTACCAATTCA3′) and MspI primer (5′GATGAGTCTAGAACGGA3′), 0.6 μL of Taq polymerase, and 2 μL of the ligation reaction mixture using the following PCG 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, Eact_Maaac, Eaca_Macc. Selectively amplified PCR products were separated on a 3730 DNA Analyzer (Applied Biosystems, Foster City, California, 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. The AFLP markers for *S. ambigua* have been previously published (Shryock et al. 2015) and included 153 loci scored in 446 individuals. For *E. nevadensis*, we scored a total of 404 loci in 403 individuals.

Environmental variables

We assembled 14 environmental variables as potential drivers of adaptive divergence in our study species (Table 1). Annual precipitation and temperature variables were based on the normal period 1961–1990 and extracted using the program ClimateWNA (Wang et al. 2012), which downscales PRISM climate data (Daly et al. 2008) and corrects for elevational variation. Long-term precipitation variability was expressed as the coefficient of variation (CV) in winter/spring (WPCV) and summer/fall (SPCV) precipitation totals received annually from 1950 to 2000. Topographic variables were calculated from a 30-m digital elevation model and subsequently upscaled to a 1-km^2 resolution (data *available online*).[5] Elevation was not included among topographic variables due to its strong correlation with summer maximum temperature ($r = 0.95$).

Statistical analysis

Population structure.—Population differentiation was characterized by analysis of molecular variance (AMOVA) with 9999 permutations in GenAlEx version 6.501 (Peakall and Smouse 2012). To further evaluate population structure, genetic ancestry coefficients and the number of ancestral populations, K, were estimated across all loci from each species via admixture analysis through the sNMF algorithm (Frichot et al. 2014), as implemented in R version 3.2.4 (R Core Development Team 2016) in the package "LEA" (Frichot and François 2015). The sNMF approach provides least-squares estimates of ancestry coefficients and incorporates a cross-entropy criterion to evaluate model fit. The program provides comparable results to STRUCTURE and ADMIXTURE (Frichot et al. 2014, Boehm et al. 2015), but does not assume Hardy-Weinberg equilibrium and requires far less computation time (Frichot et al. 2014).

Identifying potentially adaptive loci.—Potentially adaptive loci were identified following a consensus approach incorporating both outlier loci and environmental-association analyses. Outlier loci (i.e., those with an F_{ST} larger than expected under neutrality) were identified using the hierarchical Bayesian approach implemented in BayeScan version 2.1 (Foll and Gaggiotti 2008).

[5] http://ned.usgs.gov/

TABLE 1. Environmental variables derived at a 1-km^2 resolution for the Mojave Desert.

Environmental variable	Code	Definition
Precipitation		
Summer/fall precipitation (mm)	SP	average precipitation received from May to Oct
Winter/spring precipitation (mm)	WP	average precipitation received from Nov to April
Mean annual precipitation (mm)	MAP	average annual precipitation
Precipitation seasonality (%)	PCV	coefficient of variation in monthly precipitation totals over the course of a year
Winter/spring precipitation variability (%)	WPCV	coefficient of variation in annual winter/spring precipitation received from 1950 to 2000
Summer/fall precipitation variability (%)	SPCV	coefficient of variation in annual summer/fall precipitation received from 1950 to 2000
Temperature		
Mean annual temperature (°C)	MAT	average of the monthly mean temperatures
Summer maximum temperature (°C)	SMT	maximum temperature of warmest month
Winter minimum temperature (°C)	WMT	minimum temperature of coldest month
Annual diurnal temperature range (°C)	TD	average of the monthly temperature ranges (monthly maximum minus monthly minimum)
Temperature seasonality (%)	TCV	coefficient of variation in monthly average temperatures throughout the course of a year
Topography		
Slope (°)	Slope	slope in degrees was derived from a 30 m DEM
Aspect northness	ASP	cos(Aspect × π/180), derived from 30 m DEM
Topographic wetness index	TWI	area of hillslope per unit contour length draining into a given cell, based on Moore et al. (1991)

Note: Climate variables are averages for the reference period 1960–1990 except where otherwise noted.

Assuming an island model where subpopulations are correlated through a common migrant gene pool, BayeScan decomposes F_{ST} into population and locus-specific components, estimating the posterior probability that the latter has arisen from selection (Foll and Gaggiotti 2008). For each species, we performed three independent BayeScan runs with sampling locations as populations and considered loci under divergent selection ($q < 0.05$) across all three runs as potentially adaptive. Each run comprised a burn-in of length equal to 50000 and 20 pilot runs of length equal to 5000 (program defaults). The inbreeding coefficient F_{IS} was allowed to vary between 0 and 1.

Two environmental association analyses were also used to identify potentially adaptive loci. First, we applied latent factor mixed models (LFMM) to identify loci showing significant correlations to environmental gradients while accounting for neutral population structure (Frichot et al. 2013, Frichot and François 2015). To run LFMM for each species, we reduced the set of 13 environmental variables into three principal components explaining 93% of the original variability for *E. nevadensis* sampling locations ($n = 43$), and 92% of variability for *S. ambigua* sampling locations ($n = 47$). The number of latent factors included in the analyses (representing neutral population structure), K, was set as the optimum number of ancestral populations identified through sNMF, plus or minus one population. Hence, LFMM was run three times for each PCA axis per species, once for each level of K. Loci with a z score >4 across all three values of K, based on a Gibbs sampling algorithm of 30000 sweeps and burn-in equal to 15000, were considered potentially adaptive.

In a second environmental–association approach, we applied the outlying-mean index ordination (OMI; Dolédec et al. 2000), as implemented in the R package ade4 (Dray and Dufour 2007), to population-level allele frequencies for each species, which were calculated as the proportion of plants positive (band present) for a given AFLP locus per sampling location (Shryock et al. 2015). Here, the full set of environmental variables (Table 1) was used for predictions. OMI is a nonparametric, multivariate, ordination technique that assesses the significance of niche differentiation via permutation tests and can be used in a genetic context to identify loci with frequency clines along ecological gradients that deviate from chance expectation. A strength of OMI is that it can identify nonlinear associations, which is a limitation of many other approaches (Rellstab et al. 2015). We applied a false-discovery-rate (FDR; Benjamini and Hochberg 1995) P value correction to the permutation test results, and considered loci with $q < 0.05$ as potentially adaptive.

Due to differences in the strengths and limitations of various methods, it is increasingly recommended to use a consensus approach for identifying potentially adaptive loci (e.g., De Villemereuil et al. 2014, Rellstab et al. 2015). Therefore, we considered loci potentially adaptive only if they were identified by two or more methods, resulting in data sets that are less dependent on individual model assumptions.

Multivariate spatial modelling.—To gain insight into the processes shaping neutral and adaptive genetic variation (e.g., Orsini et al. 2013), we partitioned the variability in neutral and adaptive loci for each species into components explained by geographic distance, ecological gradients, or their combination. This was accomplished through partial distance-based redundancy analysis (RDA) implemented in the R package vegan (Oksanen

et al. 2015). We next derived spatial interpolations of adaptive genetic variability along selective gradients by fitting generalized dissimilarity models (GDM; Ferrier et al. 2002, 2007), as implemented in the R package gdm (Manion et al. 2015), to potentially adaptive loci for each species. GDM is a nonlinear, multivariate distance-based approach that accommodates non-stationarity (i.e., variable rate of change) in allele frequencies along environmental gradients. Multivariate loci × environment associations are modelled through monotonic I-splines with two key properties: (1) the height of each spline represents the amount of genetic variability explained by each predictor; and (2) the slope of each spline indicates the rate of genetic differentiation along that predictor's range (Fitzpatrick et al. 2013, Fitzpatrick and Keller 2015). We used population-level allele frequencies of adaptive loci to calculate pairwise distance matrices based on the Jaccard index. As predictors, we included the set of environmental variables (Table 1), a Q matrix of ancestry coefficients derived from sNMF (aggregated to the level of sampling locations), and geographic distances between sampling locations. GDM models therefore represented environmental associations while accounting for residual variation due to neutral genetic structure or geographic distance. Model and variable significance were assessed via randomization tests involving permutations of genetic distances (Ferrier et al. 2007, Fitzpatrick et al. 2013). Only environmental predictors that resulted in a significant increase in deviance explained by each model were included. Uncertainty in model parameters (I-spline functions) due to sampling error was evaluated by simulating 1000 bootstrap iterations of each GDM model, leaving out 10% of populations. Standard deviations across bootstrap iterations were plotted as error bands surrounding each I-spline.

Continuous spatial interpolations of adaptive genetic variability for each species were calculated by using the fitted GDMs to transform significant environmental predictors (here excluding the Q matrix and geographic distance terms), extracted at a 1-km^2 spatial resolution across the Mojave Desert, into genetic importance values (Fitzpatrick and Keller 2015). These GDM-transformed environmental predictors 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, function gdm.transform in R package gdm; Manion et al. 2015). Next, a PCA was performed to reduce the GDM-transformed environmental predictors into three principle components, which were then converted to GIS raster grids. Finally, the three raster grids (PCA axes) were assigned to an RGB color palate, such that the similarity of colors in the multiband raster corresponded to the similarity in predicted patterns of adaptive genetic variability. By excluding the Q matrix and geographic distance terms at this stage, our approach maps environmental associations that are not confounded by neutral genetic processes.

Uncertainty in GDM spatial interpolations was assessed via a spatial bootstrapping procedure that enables a visual representation of model performance across the landscape (Shryock et al. 2015). Bootstrap simulations (n = 1000) were performed as outlined above, but after each iteration we calculated GDM-transformed environmental predictors for the 1-km^2 point grid. Next, and for each iteration, we performed a Procrustes Analysis between the original and bootstrap solutions (function procrustes in R package vegan; Oksanen et al. 2015), which measures the similarity of two multivariate configurations (Peres-Neto and Jackson 2001). Procrustes residuals for each point on the 1-km^2 grid were averaged across bootstrap iterations and converted to a raster grid for display.

Seed sourcing strategies.—We developed interactive distance-based visualization tools for mapping adaptive divergence in both study species, along with a provisional version incorporating only environmental distances, similar to the ecoregion-based approach in Hargrove and Hoffman (2005). For single or multiple user-supplied input points (e.g., restoration sites), these tools automatically calculate and map adaptive (for E. nevadensis and S. ambigua) or environmental Euclidean distance values from all other raster cells across the Mojave Desert to the input point(s) at a 1-km^2 resolution. Adaptive distances for our study species are based on the composite raster grids output from fitted GDMs (see Multivariate spatial modelling). Available as an ArcGIS (Environmental Systems Research Institute, Redlands, California, USA) toolbox or R script (see Appendix S2 for user guide, Data S1 for tools and scripts), these tools allow seed sources within the Mojave Desert ecoregion to be ranked in terms of suitability for specific restoration sites based on unique distance values.

We also generated discrete seed transfer zones by performing cluster analyses on GDM-transformed environmental predictors for each species. Partitioning-around-medoids, a robust version of k-means clustering (function clara in R package cluster; Maechler et al. 2015), was used to generate seed transfer zones of 6, 8, 10, and 12-zone resolution. The multiple resolutions allow managers to adjust seed sourcing decisions based upon seed availability. Additionally, provisional (i.e., incorporating only environmental information) seed transfer zones for the Mojave Desert were derived by performing cluster analysis on environmental variables that were linked with adaptation in either species. Zone performance was evaluated through permutational multivariate analysis of variance (perMANOVA [Anderson 2001], implemented in R package vegan [Oksanen et al. 2015]) with adaptive loci for each species as response matrices and zone membership as predictor. Finally, we compared predictive performance between our provisional seed transfer zones for the Mojave Desert and those for this ecoregion extracted from the recently proposed "generalized provisional seed zones" of the continental United States (Bower et al. 2014).

Results

Population structure

Both species showed moderate genetic differentiation in AMOVA, with Φ_{PT} statistics (an F_{ST} analogue for dominant markers) of 0.16 ($P < 0.0001$) for *S. ambigua* and 0.10 ($P < 0.001$) for *E. nevadensis*. Pairwise population Φ_{PT} values ranged from 0.00 to 0.41 for *S. ambigua*, and from 0.00 to 0.27 for *E. nevadensis*. In admixture analyses, sNMF converged on solutions of $K = 7$ and $K = 6$ ancestral populations for *S. ambigua* and *E. nevadensis*, respectively (Appendix S3: Figs. S1–S3).

Identifying potentially adaptive loci

For *S. ambigua*, a total of 19 loci (12.42%) were identified as potentially adaptive by two or more methods, including seven loci in BayeScan, 17 in OMI, and 19 in LFMM (Appendix S4). Of these, five loci were identified by all three methods. For *E. nevadensis*, 23 potentially adaptive loci (5.47%) were identified, including nine in BayeScan, 23 in OMI, and 22 in LFMM (Appendix S4). Eight of the 23 adaptive loci were identified by all three methods. For both species, OMI and LFMM shared greater overlap with each other than with BayeScan.

Multivariate spatial modelling

Variation partitioning indicated that neutral genetic loci in both species were largely unrelated to environmental gradients (Appendix S3: Fig. S4). Geographic distance explained a small portion of variability in neutral loci for *S. ambigua*, but only a negligible fraction for *E. nevadensis*. In contrast, variation in adaptive loci for both species was best explained by environmental gradients. However, geographic and environmental distances were related, complicating interpretation of the relative contributions of either.

The GDM model for *E. nevadensis* explained 57.35% of the variability in potentially adaptive loci ($P < 0.0001$; Fig. 2a). Taking the sum of I-spline basis functions as a measure of relative variable importance (i.e., corresponding to the total height of each curve; Fitzpatrick and Keller 2015), mean annual temperature was the most important predictor (0.382), followed by genetic ancestry (0.320), long-term winter/spring precipitation variability (0.300), and precipitation seasonality (0.245). Summer/fall precipitation, summer maximum temperature, and slope were also significant predictors. Higher values of precipitation variability (both annual and long-term) explained larger changes in adaptive loci than lower values, while areas with lower summer/fall precipitation or summer maximum temperature were differentiated from areas with moderate to high values for these variables.

For *S. ambigua*, GDM explained 57.42% of the variability in potentially adaptive loci ($P < 0.0001$; Fig. 2b). Genetic ancestry was the most important predictor (0.427), followed by mean annual temperature (0.267), mean annual precipitation (0.080), and annual temperature range (0.074). Summer/fall precipitation, temperature and precipitation seasonality, and long-term summer/fall precipitation variability were also significant environmental predictors (Fig. 2b). The slope of the I-spline for mean annual temperature suggested that both low and high values explained larger changes in potentially adaptive loci than moderate values. However, precipitation variables were most influential at their upper ranges.

GDM-transformed environmental predictors were used to generate spatial predictions showing patterns of adaptive loci along environmental gradients for each species (Fig. 3a for *E nevadensis*, Fig. 3c for *S. ambigua*). The spatial bootstrap analysis yielded low Procrustes errors across the Mojave Desert for *E. nevadensis*, indicating little spatial bias in model performance (Fig. 3b). The average Procrustes correlation between bootstrap iterations was 0.98 ± 0.01 (mean ± SD) for this species. For *S. ambigua*, an area of poor model performance was evident in the northern Mojave Desert, although errors were generally low elsewhere (Fig. 3d). The average Procrustes correlation between bootstrap iterations was 0.89 ± 0.02.

Seed sourcing strategies

Example output from the single and multi-point adaptive distance tools are shown for *E. nevadensis* (Fig. 4a for single point, Fig. 4b for multi-point), illustrating predicted adaptive distance values from the hypothetical input points indicated on the panels (see Appendix S2 for tutorial, Data S1 for tools and scripts). Discrete seed transfer zones of increasing resolution (6, 8, 10, and 12 zones) were calculated from GDM-transformed environmental predictors for each species as raster layers at a 1-km^2 scale (available in Data S2). Provisional seed zones for the Mojave Desert incorporating nine environmental predictors (MAT, SMT, TCV, TD, MAP, SP, PCV, WPCV, and SPCV; Table 1) were also calculated at multiple resolutions (6–12 zone) and are available for download (Data S2). As examples, we illustrate seed zones calculated for *E. nevadensis* (Fig. 4c), along with the Mojave Desert provisional seed zones representing environmental gradients (Fig. 4d).

In accuracy assessments, the proportion of adaptive genetic variability explained by seed transfer zones in perMANOVA models generally increased with zone resolution, ranging from 39.7% to 50.2% for *E. nevadensis* and from 35.2% to 44.1% for *S. ambigua* (Fig. 5). Our Mojave Desert provisional seed zones showed comparable performance to the species-specific versions, explaining from 33.0% to 45.7% of adaptive genetic variability for *E. nevadensis* and from 32.5% to 42.9% of variability for *S. ambigua*. In comparison, the generalized

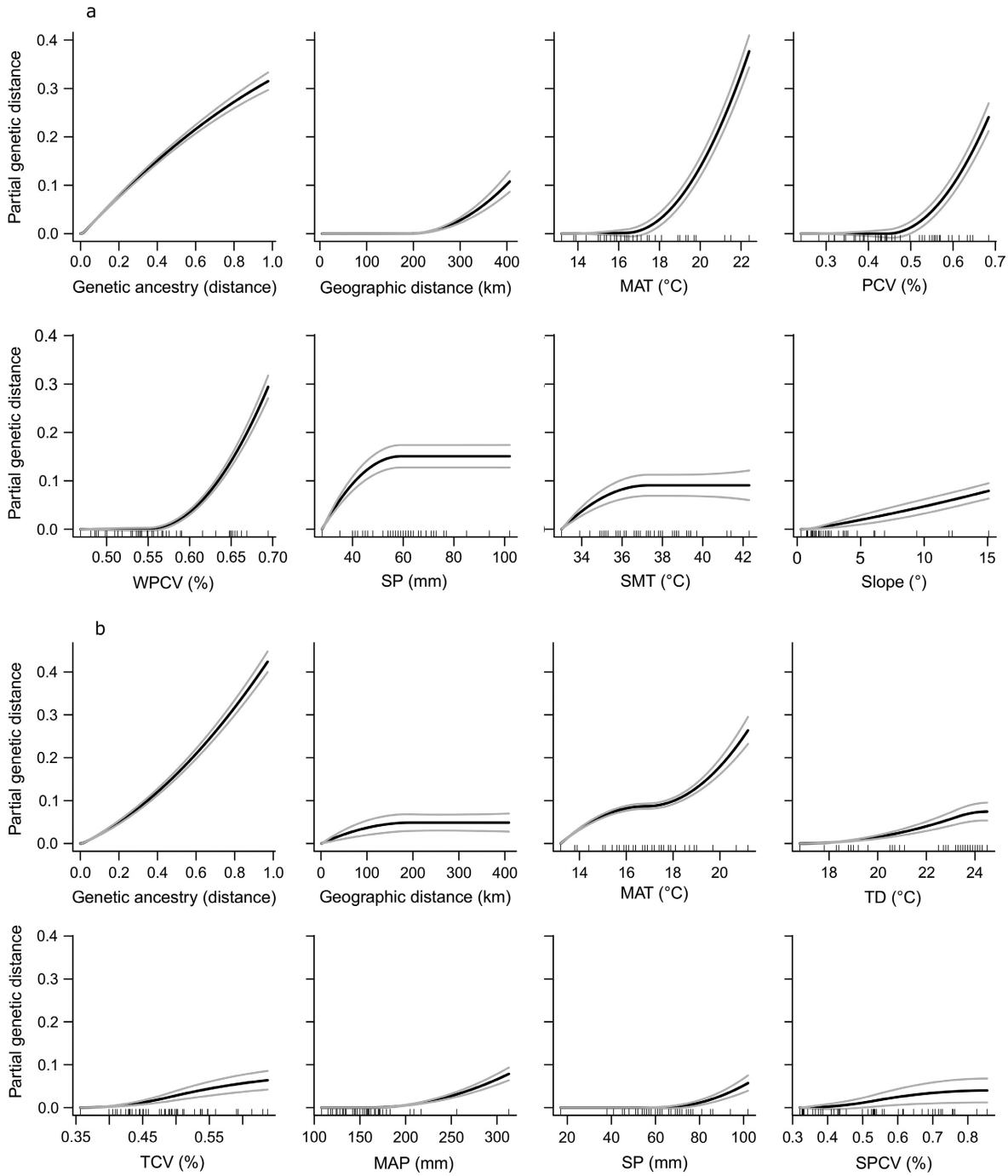

FIG. 2. Environmental gradients associated with potentially adaptive loci for (a) *Ephedra nevadensis* and (b) *Sphaeralcea ambigua* in generalized dissimilarity models (GDM). The GDM I-splines have two key properties: curve height indicates the total genetic variability explained by each predictor, 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 actual environmental values at sampling locations.

provisional seed zones for the Mojave Desert ecoregion derived from the national map of Bower et al. (2014) had lower predictive ability for our study species, explaining 25.5% of adaptive genetic variability for *E. nevadensis* and 16.1% for *S. ambigua* at resolutions of seven and six zones, respectively (Fig. 5).

DISCUSSION

Local adaptation and environmental gradients

Marker-based landscape genetic approaches represent an increasingly efficient means to identify and map adaptive divergence in non-model species (e.g., Fitzpatrick

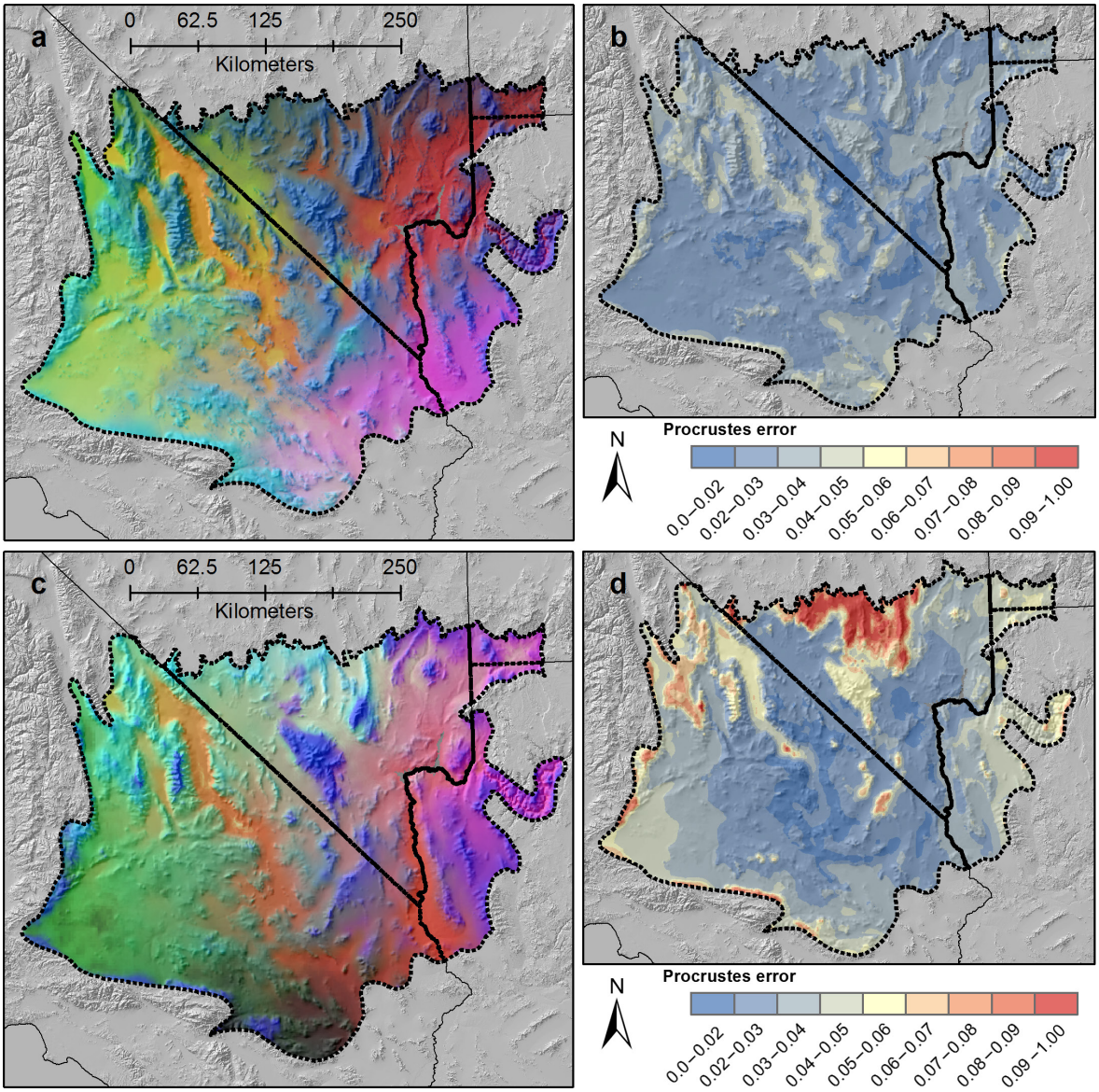

FIG. 3. Spatial interpolations of adaptive genetic variability and spatial uncertainty analyses for (a–b) *Ephedra nevadensis* and (c–d) *Sphaeralcea ambigua*. (a, c) RGB color composites derived from a principle components analysis of GDM-transformed environmental predictors, with the similarity of colors indicating similarity in predicted patterns of local adaptation. (b, d) Model uncertainty through space based on Procrustes analyses comparing bootstrapped spatial interpolations of GDM models for each species.

and Keller 2015, Rellstab et al. 2015, Forester et al. 2016), and a potentially powerful tool for guiding ecological restoration. We identified strong adaptive divergence with respect to mean annual temperature (MAT) for both of our study species (Fig. 2), suggesting that temperature may broadly predict patterns of adaptive divergence across plant functional types within the Mojave Desert. We also observed threshold responses of adaptive loci to precipitation variability (both inter- and intra-annual) for *E. nevadensis* (Fig. 2a), and to precipitation averages (MAP and summer/fall precipitation) for *S. ambigua* (Fig. 2b). These relationships were generally robust to bootstrapping, indicating their generality across populations (Figs. 2 and 3). Environmental associations were also predominantly nonlinear, suggesting that adaptive variation may be poorly explained by conventional linear approaches (e.g., redundancy analysis or RDA). GDM, in contrast, accounts for non-stationarity of loci frequencies along ecological gradients and is therefore well-suited for landscape genetic analyses (Fitzpatrick and Keller 2015).

Previously, we related adaptive divergence in *S. ambigua* to environmental indices derived from the MODIS satellite, including the shortwave infrared water

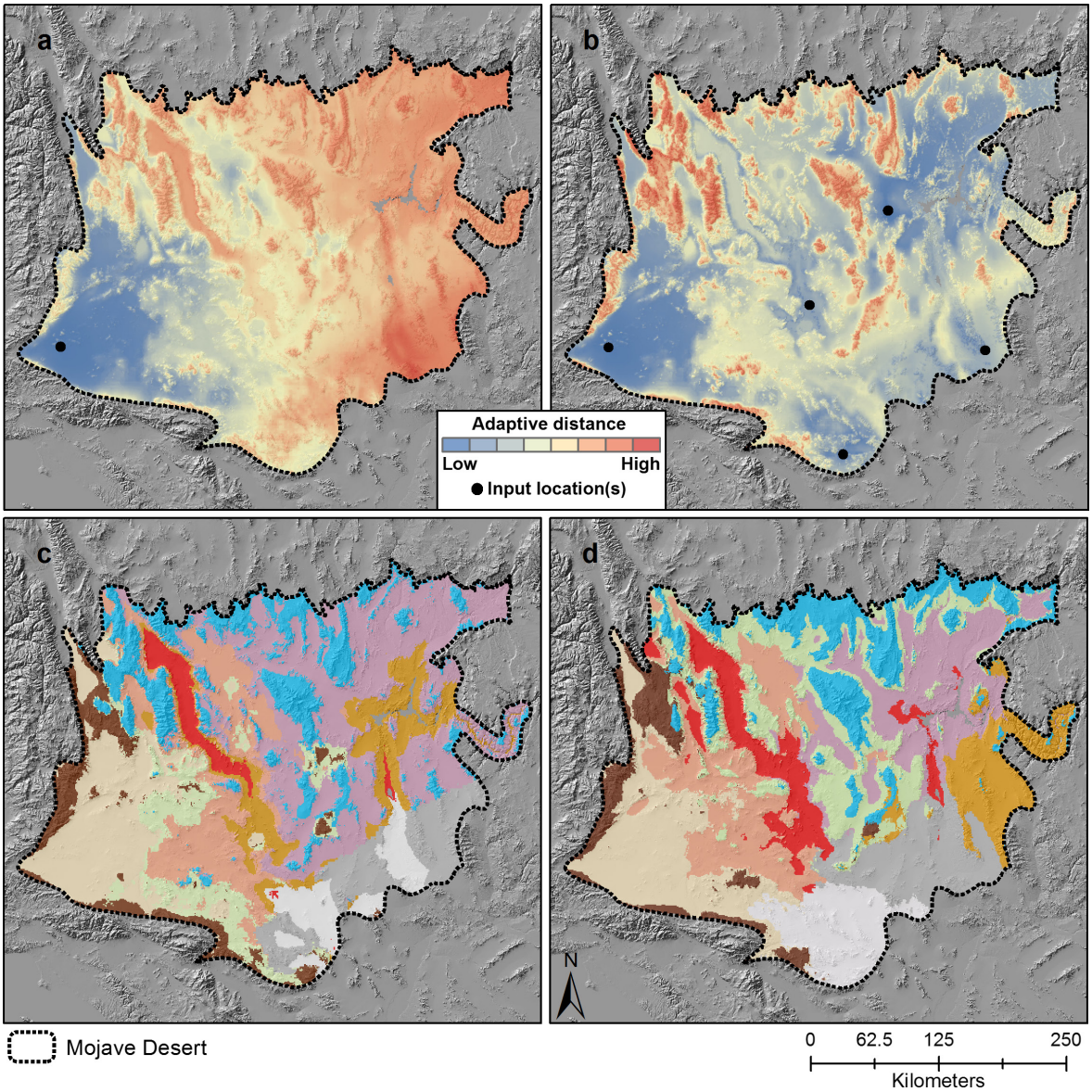

FIG. 4. Example output from (a, b) the adaptive distance tools and (c, d) seed transfer zones showing predicted patterns of adaptive divergence across the Mojave Desert. (a) The single-point adaptive distance tool was used to calculate predicted adaptive distances for *Ephedra nevadensis* from the example input point at bottom left. (b) The mulit-point adaptive distance tool was used to calculate the minimum adaptive distance from any raster cell to an input point, indicating areas that are not well represented by the points (i.e., areas with higher distance values). A tutorial for these tools is provided in Appendix S2, while tools and scripts are available for download in Data S1. (c) Seed transfer zones derived through cluster analysis on GDM-transformed environmental predictors are displayed for *E. nevadensis* at a 10-zone resolution. (d) Provisional seed zones are based on important environmental gradients and can guide seed sourcing when genetic information is not available. Seed transfer zones and provisional seed zones are available for download in Data S2.

stress index and seasonal temperature variability (Shryock et al. 2015). Here, we restricted analyses to climate variables that could be derived from global-circulation-model (GCM) predictions of future climate (e.g., IPCC 2013), precluding our use of MODIS indices. Our aim was to increase model transferability to future climate change scenarios, which is necessary for predictive provenancing. Despite this change in predictors, 16 of the 19 adaptive loci identified here were consistent with our previous study. While this points to robustness among genome scan methods at detecting adaptive divergence, it also highlights covariation among environmental variables that relate to the same loci. In heterogeneous environments, spatial dependencies among ecological gradients and their interactions with genetic processes may confound inferences regarding single environmental gradients or genetic processes taken in isolation (Thomassen et al. 2010, Orsini et al. 2013).

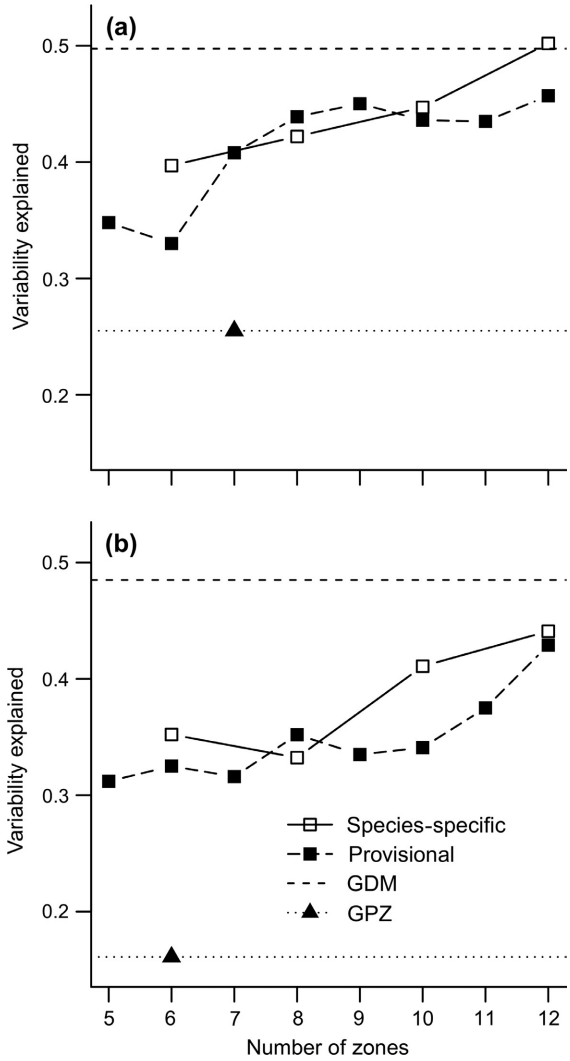

FIG. 5. Adaptive genetic variability explained by seed transfer zones of increasing resolution derived for (a) *Ephedra nevadensis* and (b) *Sphaeralcea ambigua*, compared to Mojave Desert provisional seed zones (Provisional) incorporating only environmental information, GDM-transformed environmental predictors (GDM), and the "generalized provisional seed zones" of the United States (GPZ; Bower et al. 2014). Percentages of variability explained are derived from perMANOVA models. For GPZ, *Ephedra* occurred in seven, and *Sphaeralcea* in six, provisional seed zones. As continuous variables rather than factors, GDM-transformed environmental predictors do not have multiple resolutions, and are represented as a horizontal line in the figures.

For this reason, we strongly advocate use of multivariate approaches that account for spatial dependencies among environmental variables and genetic loci. Moreover, we suggest bootstrapping spatial predictions as a means of visualizing model uncertainty through space (Fig. 3). This procedure was effective in identifying areas of poor model performance due to extrapolation beyond the environmental space represented by sample populations (Shryock et al. 2015).

Although our methods do not allow potentially adaptive loci to be linked with quantitative fitness traits, the contrasting life histories of our study species provide insight into the association of adaptive loci along environmental gradients. Mean annual temperature was strongly linked with adaptive loci for both species, potentially corresponding to phenological variation across the landscape. Evergreen dryland shrubs similar to *E. nevadensis* have shown genetic differences in seed dormancy, germination, and seedling emergence phenology (Meyer and Pendleton 2005), and flowering time (Barnes 2009) related to temperature differences between source environments. The adaptive genetic variability in *E. nevadensis* associated with precipitation variation may reflect strong selection on traits that maximize mast reproduction (Meyer and Pendleton 2015), seed dispersal, and seedling recruitment (Meyer and Pendleton 2005, Reynolds et al. 2012) more so than on physiological traits such as water-use efficiency, which promotes plant persistence regardless of environmental variability (Ehleringer and Cooper 1988, Gibson 1998). In contrast, short-lived deciduous dryland shrubs including *S. ambigua* have comparatively low water-use efficiency (Ehleringer and Cooper 1988), a physiological trait that has high intraspecific genetic variability and is potentially maintained through disruptive selection within temporally and spatially variable environments (Schuster et al. 1992). Genetic differences in water-use efficiency (Pennington et al. 1999, Housman et al. 2002), leaf pubescence, and the trade-off between water loss and carbon gain (Sandquist and Ehleringer 1997, 2003*a*, *b*, Carvajal et al. 2015) have been observed for other drought- and cold-deciduous dryland shrubs, and differentiate phenotypes from hotter, drier sites from those occupying more mesic conditions. Adaptive divergence in such traits could explain associations between adaptive loci in *S. ambigua* and environmental gradients that collectively determine aridity, such as precipitation, temperature, and soil water stress (Shryock et al. 2015).

Overall, 12.4% of loci in *S. ambigua* and 5.5% in *E. nevadensis* were identified as potentially adaptive, similar to values reported in other plants (Strasburg et al. 2012). Given that *E. nevadensis* exhibited less overall genetic divergence than S. *ambigua*, and likely experiences higher rates of gene flow due to wind pollination, its reduced percentage of adaptive loci relative to *S. ambigua* is not surprising. Adaptation in this species may occur from standing genetic variation (i.e., soft-sweeps, Schoville et al. 2012), which occurs under strong selective pressure even with high gene flow (Kremer et al. 2012). Local adaptation is often observed in wind-pollinated tree species exhibiting low overall genetic divergence (Alberto et al. 2013, De Kort et al. 2014). Somewhat counterintuitively, we also found that genetic ancestry was a strong predictor of adaptive divergence in GDM models for both species, indicating that neutral and adaptive loci were correlated. These correlations could arise through several processes. For example, isolation-by-adaptation (IBA) imposes environmental limits on

propagule establishment that influence the entire genome (Orsini et al. 2013, Sexton et al. 2014). However, weak associations between neutral loci and environmental gradients for both species do not support this pattern (Appendix S3: Fig. S4). Conversely, isolation by colonization (IBC) or distance (IBD), followed by local adaptation, could promote genetic divergence and lead to similar patterns of regional differentiation among neutral and adaptive loci, particularly if adaptation occurs from standing genetic variation (Schoville et al. 2012, Orsini et al. 2013) or if populations exhibit divergence hitchhiking (Feder and Nosil 2010). Admixture provenancing might then be supported to increase standing genetic variation, promoting the spread of advantageous alleles. Although a strong correlation between geographic distance and environmental distance within our study region limits our ability to differentiate purely spatial from environmental processes (Appendix S3: Fig. S4; Shryock et al. 2015), our analyses do suggest that adaptive loci are spatially structured along environmental gradients at a finer scale than are neutral loci, despite potential similarities in overall patterns of divergence. This interpretation is supported by our GDM framework, which accounted for neutral genetic structure and geographic distances in the identification of environmental associations.

Seed sourcing strategies

Seed provenance strategies that incorporate spatially explicit genetic information promote effective revegetation by reducing genetic risk factors, such as maladaptation, outbreeding, and inbreeding depression (Hufford and Mazer 2003, McKay et al. 2005, Breed et al. 2013, Kettenring et al. 2014). Molecular markers represent an increasingly robust and cost-efficient data source for uncovering patterns of adaptive divergence in support of restoration decision making. An important strength of this approach is that markers are not confounded by phenotypic plasticity (Kawecki and Ebert 2004, Gienapp et al. 2008), leading to relatively unbiased inferences of adaptive divergence as long as non-adaptive genetic structure is accounted for. Below, we discuss spatial analysis techniques aimed at increasing the accessibility of landscape genetics to restoration practitioners.

First, we propose interactive visualization tools based on "adaptive distances" (Fig. 4a, b; Appendix S2) as a flexible approach for guiding seed sourcing of known restoration sites, such as large-scale disturbances. For our study species, these tools incorporate marker-based GDM models to automatically interpolate predicted adaptive divergences, expressed as multivariate distance values, from any user-supplied input point(s) across the study region (e.g., Fig. 4a). A version based only on environmental distances (i.e., as a surrogate for adaptive divergence) is also provided for situations in which genetic information cannot be obtained. Different seed provenance strategies can be implemented based on the output distance values. For example, local provenancing may be accomplished by selecting seed sources with minimal adaptive or environmental distance values from the restoration site. Conversely, for admixture provenancing, a genetically diverse seed mix may be obtained by selecting geographically distributed seed source sites with up to moderate adaptive distance values, although avoiding extreme distances. This latter criterion reduces the risks of outbreeding depression associated with admixture provenancing approaches (Breed et al. 2013). The multi-point adaptive and environmental distance tool (Fig. 4b; Appendix S2) can also aid admixture provenancing by illustrating the extent to which seed collections represent overall patterns of adaptive divergence across our study region. However, this tool is also directed towards guiding large-scale seed collection and storage efforts, such as the federal Seeds of Success (SOS) program in the United States (Haidet and Olwell 2015), by enabling rapid identification of geographic areas that are underrepresented by existing seed collections in terms of adaptive or environmental diversity. Both the multi-point and single-point versions of the tools are scalable and could easily be adapted to other genetic data sets or study regions. Future versions will incorporate climate change predictions based on CMIP5 global circulation models (IPCC 2013), enabling comparisons between present and future adaptive distances in support of predictive provenancing.

In contrast to the interactive distance-based approach, which depends on specific input points, discrete seed transfer zones provide a static visualization of adaptive patterns across the landscape. Such layers may be particularly useful for the initial planning phase of broad-scale seed collections, and can also guide local or admixture provenancing (e.g., by maximizing zone coverage in the latter case). Through a multivariate cluster analysis of GDM model output, we derived discrete seed transfer zones for *E. nevadensis* and *S. ambigua* at multiple resolutions. These layers were nearly as effective at predicting adaptive divergence as the continuous GDM models at the highest resolutions (12 zones), but were less effective with fewer zones (Fig. 5). However, determining the ideal number of transfer zones for a species is difficult without supporting data on the fitness cost of movement along ecological gradients. Where resources are available, combined common garden/landscape genetic approaches afford an opportunity to assign fitness costs to distances along marker-based adaptive gradients (e.g., Steane et al. 2014), which could then inform both seed transfer zones and our distance-based mapping applications.

Provisional seed zones, which incorporate environmental but not genetic information, are also an important guide for restoration when genetic information is not available (Johnson et al. 2010). Bower et al. (2014) recently proposed generalized provisional seed zones for the continental United States by combining winter minimum temperature classes (5°F bands) with a discretized aridity index. Here, we derived finer-scale provisional seed zones for the Mojave Desert based on a multivariate cluster

analysis of nine environmental variables important to plant species within this ecoregion, including interannual and seasonal variability in temperature and precipitation (Fig. 4d, Data S2). These ecoregion-specific zones better predicted adaptive divergence in both study species than the national version (Fig. 5a–b), a notable result given that our study species come from different plant functional groups. For managers with limited resources, this suggests that environmental classifications lacking a genetic component may still provide adequate restoration guidelines across a range of species. We suggest the following steps for deriving ecoregion-specific provisional seed zones to guide localized restoration efforts: (1) incorporate a broad range of environmental variables that are known to drive adaptive divergence within the ecoregion, based upon existing evidence; and (2) apply a multivariate approach (e.g., cluster analysis) for delineating zones, which accounts for spatial dependencies among environmental variables and brings important natural gradients to the fore, rather than combining arbitrary spatial classes (e.g., temperature or precipitation bands at equal intervals).

Issues in modelling local adaptation

Genome scan methods are susceptible to false positives resulting from neutral genetic processes, including historic demographic events (population expansions, bottlenecks, or periods of secondary contact), hierarchical genetic structure, and isolation by distance (Excoffier et al. 2009, Feder and Nosil 2010, Schoville et al. 2012, Strasburg et al. 2012, Bragg et al. 2015). For this reason, and because genome scan methods exhibit optimal performance under different scenarios, we only considered loci potentially adaptive if identified by multiple methods. LFMM and BayeScan both account for neutral genetic structure and thereby limit false positives to reasonable levels (Pérez-Figueroa et al. 2010, Narum and Hess 2011, Vilas et al. 2012, De Mita et al. 2013, De Villemereuil et al. 2014). While OMI does not account for neutral genetic structure, this nonlinear technique may better reflect actual response distributions of loci under selection (Rellstab et al. 2015). Through the multivariate GDM analysis, we imposed an additional control for neutral genetic processes by including genetic ancestry as a predictor, and then partitioning out this component by mapping only the GDM-transformed environmental predictors. This combination of statistical approaches potentially reduces spurious inferences of selection beyond what any individual method is likely to achieve. However, our use of distance matrices calculated from population-level allele frequencies emphasizes broad-scale environmental gradients and is not expected to uncover microscale gradients that differentiate individuals within populations. This could explain the limited correspondence we observed between the outlier locus detection method, BayeScan, and the two environmental association methods (Appendix S4).

Polyploidy (i.e., whole-genome duplication) is increasingly regarded as a central force in plant evolution (Wood et al. 2009) and may drive ecological speciation or adaptation (e.g., Ramsey 2011). Both *S. ambigua* and *E. nevadensis* are known to exhibit variation in genome copy number (e.g., Webber 1936, Choudry 1984). Existing reports are based on small numbers of samples (<20 per species), thus, the prevalence of ploidy variation and its spatial patterns within these species is largely unknown, as are the underlying mechanisms (e.g., allopolyploidy vs. autopolyploidy). For the current study, ploidy of samples was not determined. Clearly, variation in ploidy, within and/or among populations, has the potential to impact standard and spatial population genetic analyses and their interpretation (Dufresne et al. 2014). Polyploidization in other desert species has been linked with environmental gradients and may be adaptive (e.g., Hao et al. 2013), however, there is currently limited understanding regarding the roles of genome duplication vs. post-duplication evolutionary change in directing patterns of adaptive divergence (Ramsey and Ramsey 2014). Moreover, it is unclear whether or how genome scan approaches for detecting adaptive loci should be modified to accommodate populations of mixed cytotype, given that genetic exchange between ploidy levels appears to be frequent (Dufresne et al. 2014). The majority of our statistical methods carry limited assumptions from genetic theory, and could therefore be well suited for a mixed-ploidy analysis. This could be evaluated by determining if ploidy levels in our study species vary spatially along the environmental gradients we identified as drivers of adaptive divergance. If variation in ploidy were to exist but was uncorrelated with the gradients we identified, this would suggest that our approach is robust.

Experimental evidence indicates that selection influences large portions of the genome (e.g., Gompert et al. 2014). The ability of genome scans to detect genomic regions under selection is therefore proportional to the density of genetic markers available. Consequently, our use of relatively low-density AFLP markers may limit the numbers of adaptive loci that we could potentially detect. High-throughput techniques such as RADSeq, which are derived from the AFLP protocol and thus share similar inferential limitations, yield far more markers. Yet, to our knowledge, no formal analysis has considered whether increasing marker number fundamentally alters spatial patterns identified through landscape genetic approaches. In general, AFLPs are more likely to identify large islands of genomic divergence (Caballero et al. 2013), although outlier AFLP loci may also mark small, independent, genomic regions (Wood et al. 2008). Genome scans with low-density markers are probably most effective where linkage disequilibrium and processes such as divergence hitchhiking (Feder and Nosil 2010) and isolation-by-environment (Orsini et al. 2013) are more pronounced, increasing the genomic footprint of selection. Where measured, AFLP markers have shown correspondence to phenotypic variation (e.g., Herrera and Bazaga 2008, Herrera et al. 2015), indicating that a certain proportion are linked to quantitative trait loci (e.g., Scalfi et al. 2004).

While AFLPs may still be more accessible to many research groups than high-throughput markers, next-generation sequencing technologies represent an increasingly cost-efficient option to generate high-throughput sequence data for non-model species. Hence, we expect that such data will become increasingly accessible to restoration practitioners. Along these lines, we note that the spatial analyses demonstrated here are applicable to any molecular markers from which distance metrics can be calculated, including microsatellites and, particularly, high-throughput SNP data sets.

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.1447/full

Data Availability

Data associated with this paper are available in Dryad: https://doi.org/10.5061/dryad.d48r5.