Climate-associated genomic differentiation in Lemmon's willow, an important restoration species

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Data & code availability: Raw sequencing reads and metadata will be available from NCBI BioProject PRJNA1519925 (https://www.ncbi.nlm.nih.gov/bioproject/PRJNA1519925). Assembled reads, plus all other necessary data and code will be available on Figshare: 10.6084/m9.figshare.33503890.

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Abstract

Restoration practitioners are considering assisted gene flow to promote persistence of restored vegetation under future climatic conditions. However, for many important restoration species, the extent of climate-associated genomic differentiation remains unclear. Here, we examined climate-associated genomic differentiation in Lemmon's willow (*Salix lemmonii*), a key species in Sierra Nevada meadow restoration, across 40 montane meadows in California's Tahoe National Forest (mean pairwise distance = 31 km). Using ddRADseq-derived allele frequencies and 270 m-resolution climate data, we tested for associations between climate and genomic variation, while accounting for geography and population structure. Climate explained 10% of among-population allele-frequency variation. Two complementary genotype-environment association methods identified a shared set of 15 outlier loci, which were associated with spring snowpack, actual evapotranspiration, and potential evapotranspiration. Between-site differences in potential evapotranspiration were also associated with overall pairwise genetic differentiation. Together, these results reveal climate-associated genomic differentiation in an important restoration species and highlight multiple components of hydrology as important factors shaping genomic variation. The relatively fine spatial scale of climate-associated differentiation suggests practitioners may be able to access material for climate-informed restoration plantings within tens of kilometers or less.

Introduction

As climate change progresses, restoration practitioners are increasingly considering assisted gene flow to promote persistence of restoration plantings under future climatic conditions (Prober et al. 2015, Havens et al. 2015, Vernon et al. 2019, O'Neill & Gómez-Pineda 2021, Jordan et al. 2024). Successful implementation depends on the availability of plant material that is well suited to the anticipated future conditions of the restoration site (Aitken & Whitlock 2013). A common strategy is to leverage known associations between genomic variation and spatial climatic gradients, which can guide translocation between appropriate source and recipient sites (Aitken et al. 2024). Past work has documented climate-associated genomic differentiation in many plant species, but prior studies have focused strongly on

forest trees, as well as intensive climate adaptation studies in herbaceous model systems (Ahrens et al. 2018; Santos & Gaiotto 2020; Kooyers et al. 2025, Biaou et al. 2026). With a small number of valuable exceptions (e.g., Shryock et al. 2017, Faske et al. 2021, Grossfurthner et al. 2023), climate-associated genomic variation remains relatively understudied across the broader diversity of taxa used in ecological restoration, including woody shrubs used to restore non-forest ecosystems like montane meadows.

Mountain landscapes offer a particularly informative setting in which to test for climate-associated genomic differentiation because they compress large climatic disparities into short geographic distances (Rahbek et al. 2019). Populations separated by only a few kilometers may experience markedly different climatic environments and associated selective pressures (Ishizuka & Goto 2012, Anderson & Wadgymar 2020, Bachmann & Van Buskirk 2021). However, even strong climatic differences may not necessarily produce genetic differentiation, as gene flow among neighboring populations could overwhelm divergent selection (Lenormand 2002, Savolainen et al. 2007). If climate-associated genomic differentiation does emerge, then montane landscapes may provide opportunities to identify climatically differentiated source populations without requiring long-distance assisted gene flow.

Salix lemmonii Bebb (Lemmon's willow) provides an apt system for characterizing climate-associated genomic differentiation in a non-tree species of direct importance to restoration efforts. In the Sierra Nevada (western USA), *S. lemmonii* populations occupy naturally fragmented montane meadows distributed across steep climatic gradients (Argus 2007, Argus 2012), where clinal variation in drought resistance has previously been demonstrated (Rosenblad & Ackerly 2024). *S. lemmonii* is widely used in meadow restoration plantings, yet the extent and climatic drivers of genomic differentiation among potential source populations remain unknown. Characterizing this variation could therefore provide information relevant to climate-informed restoration sourcing.

Here, we examined associations between climate and allele frequencies in *S. lemmonii* across 40 montane meadows (mean pairwise distance = 31 km) in Tahoe National Forest, California, USA. Using ddRADseq genomic data and 270 m climate grids, we tested whether genomic variation was associated

with climate after accounting for population structure and geography. Individual loci showing associations with climate were identified via complementary multivariate and univariate genotype-environment association (GEA) methods. We further tested whether pairwise genetic differentiation increased with geographic and climatic distance via maximum likelihood population effects (MLPE) models.

Methods

Study system

Salix lemmonii Bebb is a woody shrub distributed across western North America (Argus, 2007). In the Sierra Nevada and southern Cascade mountain ranges, where conifer forest predominates, this species occupies naturally isolated wet montane meadows and riverbanks (Argus, 2012), which span steep climatic gradients that could potentially shape divergent selection regimes. *S. lemmonii* figures prominently in region-wide meadow restoration efforts due to its rapid growth and stabilizing effect on eroded streambanks (Vernon et al., 2019). Field observations during the 2012-2016 Sierra Nevada megadrought suggest that many populations may be vulnerable to increasing drought stress, which motivates interest among restoration practitioners in identifying planting stock better suited to future climatic conditions (R. Burnett, pers. comm.).

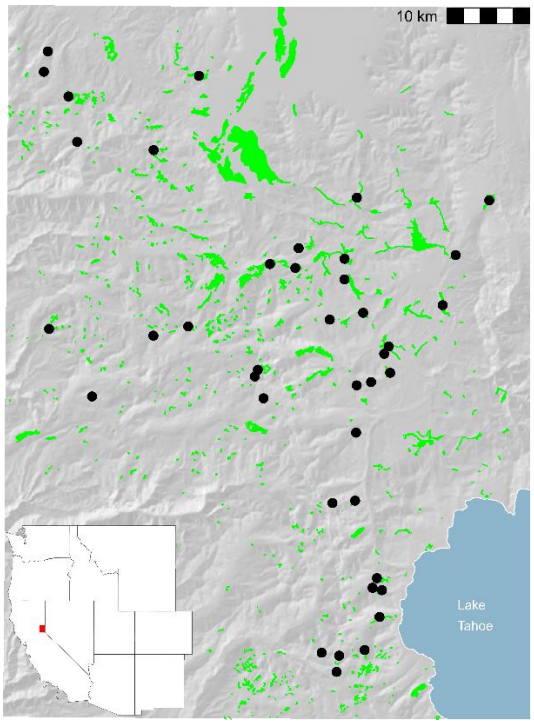

Fig. 1: *Map of study system. Green shows all montane meadows, the primary habitat of Salix lemmonii, across Tahoe National Forest. Points represent our 40 sampling sites. Inset shows general location (red) within western US.*

Genomic data

Young leaves were collected from 184 *Salix lemmonii* individuals across 40 sites in Tahoe National Forest during July 2021 (Table S1). Individuals were sampled throughout the occupied portion of each site. To minimize resampling of the same clonal genet, we only sampled plants separated by at least 10 m of willow-free ground. Leaf samples were immediately placed in paper envelopes and, within 8 h of collection, transferred to plastic bags containing silica gel for desiccation.

Genomic DNA was extracted from dried leaf tissue using a modified version of the CTAB protocol of Doyle and Doyle (1987; see Appendix S1).

Genomic libraries were prepared using a modified double-digest RADseq (ddRADseq) protocol based on Peterson et al. (2012). Genomic DNA was digested with *PstI*-HF and *MspI*, ligated to barcoded adapters,

PCR amplified, size-selected using a Pippin Prep system, and sequenced on an Illumina NovaSeq 6000 platform to generate paired-end 150-bp reads. Reads were demultiplexed by the QB3 Genomics Sequencing Laboratory (University of California, Berkeley) and assembled using ipyrad (Eaton & Overcast 2020) with default parameter settings.

Because *S. lemmonii* is tetraploid, the R package polyRAD (Clark et al. 2019) was used for SNP filtering and genotype estimation. Raw ipyrad outputs were formatted for polyRAD using Chafin et al.'s (2021) ipyrad2polyrad.py script. The reformatted assembly data were processed by polyRAD with settings that accommodate either auto- or allo-tetraploid inheritance. Loci were retained only if they were represented by sequence reads in at least 70% of individuals, and if the minor allele was observed in at least two individuals. Potential paralogous loci were identified using the Hind/He statistic (Clark et al. 2022), which compares observed within-individual heterozygosity against that expected under Mendelian inheritance. For tetraploids, the expected Hind/He value is 0.75. Loci with values exceeding this threshold were excluded. Genotype posterior probabilities were estimated separately within each sampling site to avoid shrinking genuine among-site allele frequency variation toward global means. The maximum a posteriori genotype for each individual at each locus was retained for downstream analyses.

Following genotype estimation, single-nucleotide polymorphisms (SNPs) were filtered for linkage disequilibrium using an R^2 threshold of 0.10. Genotypes were converted to site-level allele frequencies, and SNPs with missing data at 2 or more sampling sites (out of 40) were discarded, as were SNPs with a global minor allele frequency less than 0.05.

These processing steps (see Table S2) yielded 2,457 biallelic SNPs across 40 sampling sites.

Climate data

We characterized climatic variation among our 40 sites using 270 m-resolution climatologies for 1991-2020 from the Basin Characterization Model, version 8.0 (Flint et al. 2021). An initial set of candidate

climatic variables (Table 1) was reduced to minimize collinearity while retaining predictors with relevance to *Salix lemmonii*'s natural history.

Climate Variable	Used in final analyses
Max. temperature of warmest month (TMAX)	
Min. temperature of coldest month (TMIN)	Yes
Min. May temperature	
April snowpack (PCK)	Yes
Potential evapotranspiration (PET)	Yes
Actual evapotranspiration (AET)	Yes
Climatic water deficit (CWD)	
Summer (Jun/Jul/Aug) precipitation	

Table 1: *Climate variables considered for use in genotype-environment association analyses, as well as isolation by distance and environment analyses.*

April snowpack (PCK), an indicator of growing-season water availability, was retained because it was identified in previous work as an important driver of drought-related ecotypic variation in *S. lemmonii* (Rosenblad & Ackerly 2024) as well as allele frequency variation in other Sierra Nevada woody plants (Shu & Moran, 2023, Moran et al. 2024). PCK was strongly correlated with maximum temperature of the warmest month (TMAX; $r < -0.9$) and summer precipitation ($r > 0.9$), which were excluded from subsequent analyses.

Minimum temperature of the coldest month (TMIN) was retained as a widely recognized measure of cold exposure, which predicts allele frequency variation in other Sierra Nevada woody plants (Shu & Moran, 2023, Moran et al. 2024). May minimum temperature was excluded due to its strong correlation with TMIN ($r > 0.9$).

Climatic water deficit (CWD) and actual evapotranspiration (AET) were also strongly correlated ($r < -0.8$). We retained AET together with potential evapotranspiration (PET), as these variables represent complementary facets of ecosystem water balance: AET reflects joint availability of water and energy for plant growth, whereas PET reflects long-term atmospheric evaporative demand. In addition, AET was nearly uncorrelated with PET ($r = 0.04$), whereas CWD showed moderate correlation with PET ($r = 0.30$). Accordingly, CWD was excluded from subsequent analyses.

Fig. S1 provides maps of each climate variable used in downstream analyses. Table S3 provides a correlation matrix of all climate variables.

Population structure

We characterized population structure among our 40 sampling sites via genetic PCA. The resulting scree plot (Fig. S2) showed a breakpoint at the third principal component. Consequently, in downstream GEA analyses, we used the first three principal components as proxies for population structure (Capblancq & Forester 2021). Genetic principal components were calculated from the complete SNP dataset prior to identifying outlier loci.

GEA analyses

We characterized associations between allele frequencies and climatic variation using both a multivariate GEA method—redundancy analysis (RDA; Capblancq & Forester 2021)—and a univariate method, BayPass (Gautier 2015). These methods are complementary, as each entails different approaches to controlling for potential confounders of genotype-environment associations. BayPass accounts for population structure by modeling dataset-wide covariance among populations' allele frequencies (Gautier 2015), whereas the RDA approach we employed includes genetic principal components (as described above) as proxies for population structure, as well as distance-based Moran's eigenvector maps (dbMEMs) to account for isolation by distance (Capblancq & Forester 2021).

We used an RDA variance partitioning approach to quantify the proportions of genomic variation explained by climate, geography, and population structure. The variance partitioning approach entailed fitting a full RDA model containing all 10 predictor variables (four climate variables, three dbMEMs, and three genetic PCs), as well as three partial models using one set of variables as predictors and the other two sets as conditioning variables. RDA cannot accommodate missing data, so prior to RDA analysis, missing allele frequencies (2% of site-by-SNP combinations) were imputed using mean values among non-missing sampling sites.

For each GEA method, we designated a SNP as an outlier if it showed a strong signal of association between climate and allele frequencies. BayPass outliers were defined as loci with BF(dB) > 10 for at least one climatic variable. In the RDA analysis, we used the Mahalanobis distance-based approach implemented in Capblanqc et al.'s (2021) *rdadapt* R function with a Bonferroni-adjusted p-value threshold of 0.01. SNPs designated as outliers by both methods were considered to show strong evidence for genotype-environment associations.

Isolation by distance and environment

We used maximum likelihood population effect (MLPE) models (Clarke et al. 2002, Van Strien et al. 2012) to test for isolation by distance and isolation by environment, as represented by pairwise distances in each individual climate variable. The response variable was pairwise F_{ST}, which we computed using the polysat R package (Clark & Jasieniuk 2011) designed for polyploid data. The commonly used Gaussian error distribution yielded poor residual diagnostics, so we instead used a beta distribution with a log link function.

Results

Population structure

Global F_{ST} was 0.15 (95% CI 0.146, 0.155). The first two genetic principal components capture both smooth geographic gradients in allele frequencies, as well as several outlying populations (Fig. 2). A scree plot is given in Fig. S2.

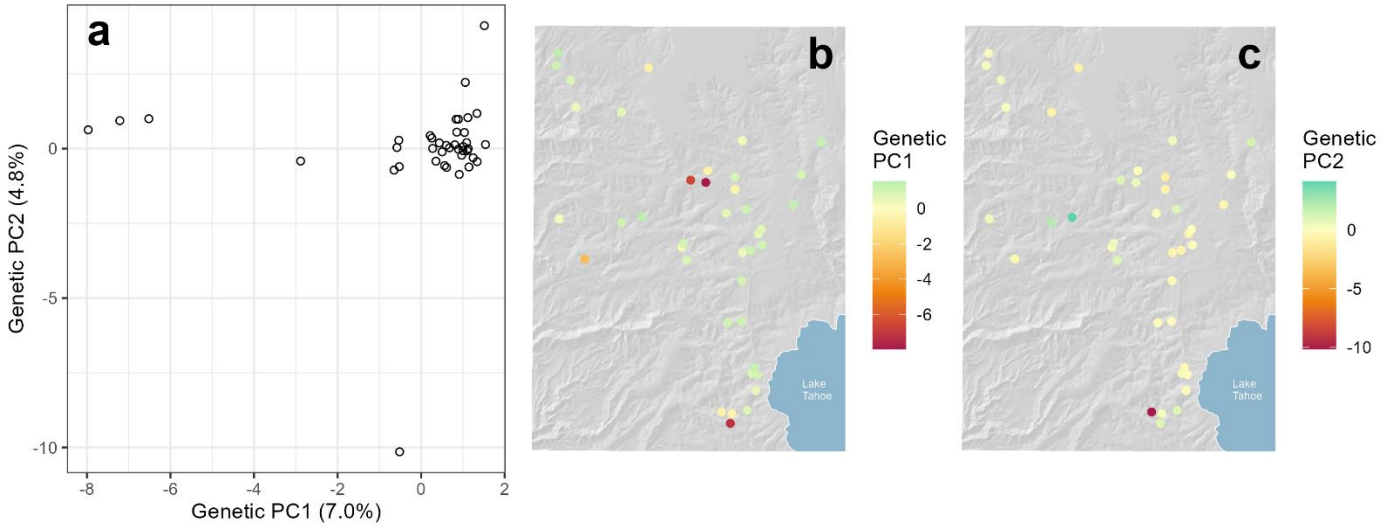

Fig. 2: *Summary of genetic PCA. Points represent our 40 sampling sites.* **a)** *Scatterplot of the first two genetic principal components.* **b-c)** *Maps of PC1 and PC2.*

GEA analyses

RDA showed a significant relationship between climate and allele frequencies, after accounting for geography and population structure (Table 2). Overall, our 10 predictors (4 climate variables, 3 dbMEMs, and 3 genetic PCs) explained 35% of allele frequency variation across our 40 sampling sites. 10% was attributable to pure climate (p=0.02), 15% to pure population structure (p=0.0001), and 8% to pure geography (p=0.09). Only 2% of variation was confounded among these three sets of predictors.

Model	Inertia	P (>F)	Proportion of Explainable Inertia	Proportion of Total Inertia
Full	25.1	0.0001	1	0.35
Pure climate	7.5	0.02	0.30	0.10
Pure geography	5.5	0.06	0.22	0.08
Pure structure	10.6	0.0001	0.42	0.15
Confounding	1.6		0.06	0.02
Total unexplained	46.9			0.65
Total inertia	72.0			1

Table 2: *Summary of RDA variance partitioning to quantify the roles of climate, neutral population structure, and geography in shaping allele frequency variation. The full model includes all variables as predictors, and partial RDA models were used to quantify variance explained by each of these three groups of variables while conditioning on the other two.*

RDA identified 148 outlier SNPs, and BayPass identified 90 (Table 3). A summary of all outlier SNPs is given in Table S4. 15 SNPs were identified by both methods (Fig. 3)—roughly 2.8 times more than expected if each method selected outlier SNPs at random ($p<0.001$). Among these 15 SNPs, 8 showed associations with AET in BayPass, 6 with PET, and 1 with PCK (Fig. 3).

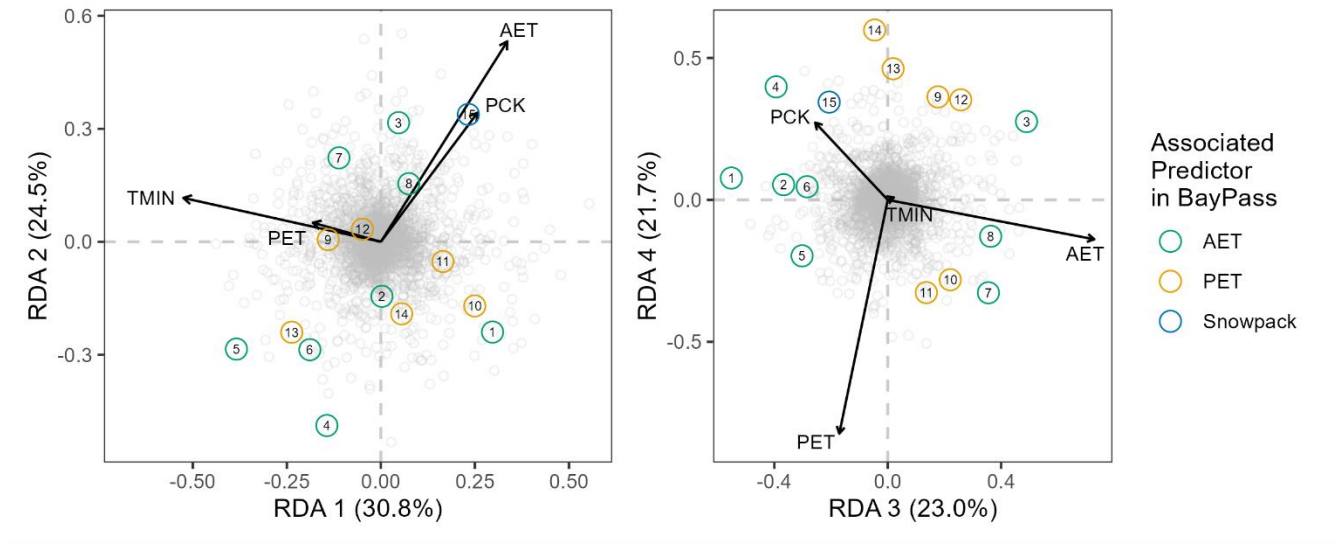

Fig. 3: *Summary of outlier SNPs identified by redundancy analysis (RDA) and BayPass, two complementary genotype-environment association approaches. Each panel shows an RDA biplot for two axes in the RDA model. Black arrows represent loadings of each climate variable on RDA axes. Percentages indicate variance in allele frequencies captured by each axis. Numbered, colored points represent SNPs identified as outliers by both methods. Gray, unnumbered points represent other SNPs.*

Climate Variable	SNPs with strong associations [BF(dB)>10] in BayPass
PET	29
AET	28
TMIN	23
PCK	10

Table 3: *Summary of outlier SNP associations with each climate variable in BayPass.*

Isolation by distance and environment

Pairwise F_{ST} increased with pairwise differences in PET (p=0.02) and geographic distance (p=0.004). (See Table 4). Pairwise differences in AET, TMIN, and PCK showed no clear association with F_{ST}.

Predictor	Standardized Effect Estimate	95% CI	p
D_{Geog}	0.020	(0.006, 0.034)	0.004
D_{PET}	0.015	(0.003, 0.028)	0.02
D_{AET}	-0.0058	(-0.021, 0.0095)	0.46
D_{TMIN}	-0.0032	(-0.020, 0.014)	0.71
D_{PCK}	-0.00057	(-0.013, 0.012)	0.93

Table 4: *Results summary for maximum likelihood population effect (MLPE) model of isolation by distance and isolation by environment.*

Discussion

Here we show that genomic differentiation is associated with climate in *Salix lemmonii*, a key species in restoration plantings, across a geographically compact montane landscape. After accounting for geography and population structure, climate explained 10% of among-population allele-frequency variation (Table 2, p=0.02). Two genotype-environment association methods identified a shared set of 15 SNPs associated with climate—particularly hydrologic variables—and pairwise overall genetic differentiation increased with differences in potential evapotranspiration (PET). Together, these results add new support for the hypothesis that steep climatic gradients compressed into small geographic areas can yield climatically structured genomic differentiation (Eckert et al. 2015, Gugger et al. 2021). This pattern of genomic differentiation can help inform planting strategies for this important restoration species.

Although further evidence is needed to determine the fitness consequences of genomic variation reported here, our findings are consistent with the hypothesis that local adaptation to climate shapes genomic

differentiation among montane meadows for *Salix lemmonii*. Genomic differentiation may have arisen due to strong selection, weak gene flow, or both (Lenormand et al. 2002, Richardson et al. 2014). Prior work suggests the naturally fragmented configuration of Sierra Nevada montane meadows may promote isolation and reduced gene flow (Storfer et al. 2007, Maher et al. 2017). Evaluating the relative strength of these processes will require experimental tests of local adaptation and direct estimates of gene flow.

If the climate-associated genomic variation we observed reflects local adaptation, then restoration efforts may benefit by tapping into this variation. Because climatically differentiated populations occur only tens of kilometers apart—and within a single management unit (Tahoe National Forest)—it may be possible to source plant material from climatically differentiated populations while reducing the risks and challenges of longer-distance translocation (Schwartz et al. 2012, Bucharova 2017, Baldwin 2019). Successful sourcing strategies will depend on determining how climate is predicted to change in the future, as well as which climatic gradients most strongly influence genomic variation (Aitken & Whitlock 2013).

In our analyses, the climatic gradients most strongly associated with genomic differentiation reflect multiple facets of plant water relations. Seasonal water supply (PCK), atmospheric evaporative demand (PET), and actual evapotranspiration (AET) all showed clear associations. These findings complement a common garden ecophysiological study of the same populations, which demonstrated that drought resistance varies systematically with PCK (Rosenblad & Ackerly 2024). PCK emerged here as a predictor of allele-frequency variation, while PET was associated with both a set of outlier loci and with overall genetic differentiation. AET was associated with the greatest number of outlier loci. Because several other climatic variables were excluded to minimize multicollinearity, the predictors reported here should be interpreted as representatives of broader hydrologic gradients rather than unique causal drivers. Nevertheless, multiple analyses highlight hydrology as a dominant factor shaping genomic differentiation across this landscape, consistent with prior studies of high Sierra Nevada tree species (Eckert et al. 2015, DeSilva & Dodd 2020, Shu & Moran 2023, van Mantgem et al. 2023, Moran et al. 2024) and woody shrubs of the adjacent Great Basin (Faske et al. 2021, Grossfurthner et al. 2023). This result is especially relevant for restoration planning because projected climate change in the Sierra Nevada is expected to

involve declining snowpack, increasing evaporative demand, and more frequent drought (Dettinger et al. 2018). Thus restoration efforts may benefit by sourcing plant material from more xeric sites where the current hydrologic environment resembles anticipated future conditions at the restoration site.

Several limitations should be noted in interpreting our results. First, GEA methods identify statistical associations rather than causal adaptive loci, and many candidate SNPs reported here likely represent linked markers rather than genuine targets of selection (Lasky et al. 2023). Second, strong correlations among climatic variables prevented simultaneous evaluation of all potentially relevant predictors, and thus the variables reported in our results must be regarded as proxies for larger sets of intertwined climatic gradients. Finally, the absence of a reference genome prevented functional annotation of candidate loci. More comprehensive genomic resources, along with further common garden or reciprocal transplant experiments, will be valuable for validating the adaptive significance of the patterns identified here.

Conclusions

These results reveal climate-associated genomic differentiation in *Salix lemmonii*, a key species in restoration plantings, across a geographically compact montane landscape in Tahoe National Forest. Hydrologic variables consistently emerged as the strongest climatic predictors of genomic variation, suggesting that plant water relations play an important role in shaping allele frequencies. As climate change brings declining snowpack, increasing evaporative demand, and more frequent drought to the Sierra Nevada, genomic variation along hydrologic gradients may prove valuable for sourcing plant material. These patterns emerged within a relatively small area (mean distance between sites = 31 km) comprising a single management unit, and thus suitable material for climate-informed plantings may be available within tens of kilometers or less from a given restoration site.

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