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Climatic variation allows montane willows to escape an adaptive trade-off

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Summary

• Adaptive responses to climate change, based on heritable variation in stress tolerance, may be important for plant population persistence. It is unclear which populations will mount the strongest future adaptive responses. It may be fruitful to identify populations that have escaped trade-offs among performance traits, which can hinder adaptation. Barring strong genetic constraints, the extent of trade-offs may depend on spatial relationships among climate variables shaping different traits.

• Here, we test for climate-driven ecotypic variation and trade-offs among drought and freezing sensitivity, and growth, for Lemmon's willow (*Salix lemmonii*) in a common garden study of 90 genotypes from 38 sites in the Sierra Nevada, USA.

• *Salix lemmonii* exhibits ecotypic variation in leaf turgor loss point, a measure of drought sensitivity, from -0.95 to -0.74 MPa along a gradient of spring snowpack. We also find variation in spring freezing sensitivity with minimum May temperature. However, we find no trade-off, as the climatic gradients shaping these traits are spatially uncorrelated in our study region, despite being negatively correlated across the Sierra Nevada.

• Species may escape adaptive trade-offs in geographic regions where climate variables are spatially decoupled. These regions may represent valuable reservoirs of heritable adaptive phenotypic variation.

Introduction

Different populations of the same species can exhibit varying, sometimes counterintuitive responses to climate change (Compagnoni *et al.*, 2021; Oldfather *et al.*, 2021; Leites & Benito Garzón, 2023; Perret *et al.*, 2023). This variation may result partly from genetic variation among populations, with some harboring stronger adaptive potential than others (Hoffmann & Sgrò, 2011; Alberto *et al.*, 2013). However, for many species, it is unclear which populations are best positioned to mount adaptive responses to future climate change. Identifying these populations would be valuable for conservation, restoration, and assisted gene flow, whereby new genotypes are introduced in vulnerable populations to boost population mean fitness (Aitken & Whitlock, 2013).

Spatial patterns of adaptive potential might be clarified by exploring how climate shapes trade-offs among performance traits (Antonovics, 1976; Schluter, 1996; Fletcher *et al.*, 2022; Terasaki Hart & Wang, 2024). Climate change exposes organisms to multiple forms of abiotic stress (Anderegg *et al.*, 2019; Zohner *et al.*, 2020; Doughty *et al.*, 2023), and trade-offs can greatly impede adaptation to these stressors (Antonovics, 1976; Walsh & Blows, 2009; Kelly *et al.*, 2016). For example, population mean drought sensitivity might decrease along a gradient

from cooler to warmer locations, whereas freezing sensitivity might increase (Laanisto & Niinemets, 2015; Rueda *et al.*, 2017; McCulloh *et al.*, 2023; Pavanetto *et al.*, 2024). This trade-off could hinder future adaptive responses if climate change intensifies both drought-driven and freezing-driven selection. (Although global mean temperatures are increasing, the changing seasonality of freezing events is making them more dangerous for some taxa; Zohner *et al.*, 2020.) In this example, genotypes conferring low sensitivity to both drought and freezing are rare or absent. Consequently, if drought-induced and freezing-induced selection intensify, populations will struggle to adapt and persist unless genotypes conferring resistance to both stressors are produced sufficiently fast. Generating such genotypes requires introduction of novel alleles or realignment of genetic correlations, both of which may be prohibitively slow (Etterson & Shaw, 2001; Hellmann & Pineda-Krch, 2007; Walsh & Blows, 2009). Additionally, even if only one climatic stressor will impose strong future selection – for example drought – another may drive strong selection in the present – for example freezing – and assisted gene flow efforts must avoid maladaptation to both present and future conditions (Aitken & Whitlock, 2013). Lastly, stress resistance can trade off with other important performance traits like growth (Montwé *et al.*, 2016; Piper & Fajardo, 2023; Visakorpi *et al.*, 2024). Thus, populations that do not exhibit trade-offs
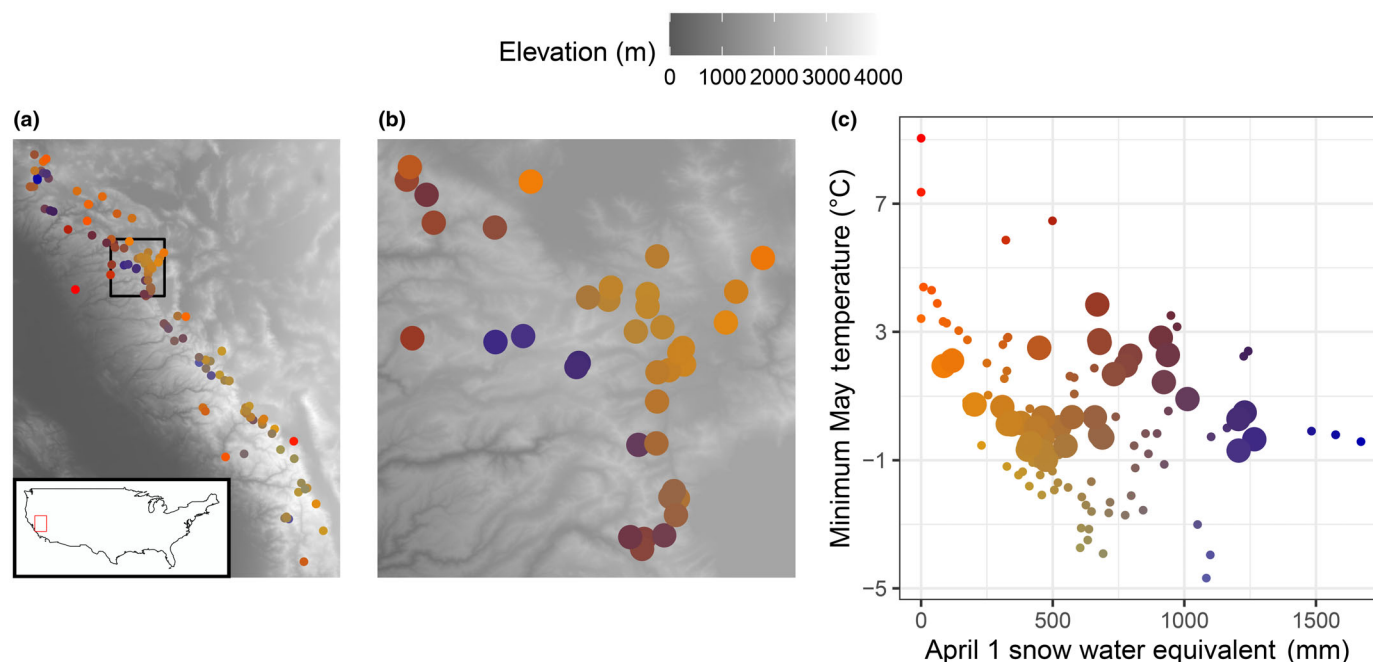
Fig. 1 Study region and climate data from a 1981–2010 climatology generated by the Basin Characterization Model. (a) Sierra Nevada, USA. Points are *Salix lemmonii* occurrences. Black bounding box shows our study region in Tahoe National Forest. Inset shows location of Sierra Nevada (red bounding box) in USA. (b) Zoomed view of our provenance sites in Tahoe National Forest. (c) Two-dimensional color legend for (a) and (b). Large points represent provenance sites in Tahoe National Forest. Small points represent occurrences outside Tahoe National Forest. Color varies continuously and two-dimensionally across the panel, with pure red, yellow, blue, and black delineating the four corners – that is combinations of extreme values. Red represents the least snowpack and the greatest temperature. Blue represents the opposite. Yellow represents the least observed values of both variables. Black represents the greatest observed values of both variables. Each combination of extremes may not necessarily occur in the data, hence the absence of, for example a pure yellow point in the lower panel left corner.

may constitute valuable sources for assisted gene flow. It remains unclear where populations that have avoided trade-offs might be found.

Adaptive trade-offs in performance traits can result from a spectrum of genomic mechanisms, which vary in prospects for escape (Garland, 2014). At one extreme is antagonistic pleiotropy, whereby a single genetic locus affects one trait positively (with respect to fitness) and another trait negatively (Caspari, 1950), possibly due to an organismal-level physiological trade-off (Bloom *et al.*, 1985). For example, one allele might confer low-drought sensitivity and high-freezing sensitivity, and an alternative allele might confer the opposite. This trade-off is inescapable without introduction of a new allele (e.g. via mutation). At the opposite extreme, adaptive trade-offs can result from spatially correlated selection gradients acting on unlinked loci (Anderson *et al.*, 2011, 2013) without any intrinsic physiological trade-off. For example, in hot, dry environments, an allele that decreases drought sensitivity might be strongly adaptive, whereas an allele at another locus that decreases freezing sensitivity might be neutral. In cold, snowy environments, this selection pattern might be reversed. Consequently, drought and freezing sensitivity are expected to vary in opposite directions among these environments (Garland, 2014). In principle, this trade-off could be avoided in an environment that has selected for resistance to both stressors (e.g. very cold and dry). However, such environments may be unavailable. This example illustrates that when

performance traits are free of strong genetic constraints (e.g. antagonistic pleiotropy), the strength of trade-offs among populations or ecotypes may depend at least partly on spatial variation in climate.

Here, we quantify climate-driven ecotypic variation in drought and freezing sensitivity, as well as growth, for Lemmon's willow (*Salix lemmonii*), a socially and ecologically important species in Tahoe National Forest, USA (Anderson, 2013; Vernon *et al.*, 2019). Our common garden study comprises 90 genotypes collected from 38 provenance sites. As a measure of drought sensitivity, we characterize ecotypic variation in leaf turgor loss point (Ψ_{TLP}) using pressure–volume curves. We quantify variation in spring freezing sensitivity with a postfreeze shoot viability experiment. Using a suite of climate variables (April snowpack, minimum May temperature, and actual evapotranspiration), we characterize the climatic gradient shaping each trait. April snowpack (an indicator of growing season moisture availability) and minimum May temperatures are negatively associated across *S. lemmonii*'s Sierra Nevada-wide range, suggesting that natural selection could have shaped an adaptive trade-off between adaptations to summer drought and spring freezes. However, these variables are spatially decoupled in Tahoe National Forest (Fig. 1), suggesting that natural selection may be less likely to produce a trade-off in this region. Finally, we test for population-level trade-offs among traits, and we explore the management implications of our results.

Materials and Methods

Study system

Salix lemmonii Bebb is a widespread, abundant woody shrub in western North America (Argus, 2007). In the high Sierra Nevada and southern Cascade ranges, *S. lemmonii* primarily occupies wet montane meadows and riparian corridors (Argus, 2012). It is integral to Indigenous cultural practices (Anderson, 2013), provides habitat for endangered wildlife, and features integrally in meadow restoration efforts due to its capacity for rapid growth and streambank stabilization (Vernon *et al.*, 2019). *Salix lemmonii* is dioecious and often reproduces from seed, but it can also reproduce clonally from shoot cuttings, facilitating common garden establishment. Field observations from the 2012–2016 Sierra Nevada megadrought suggest that many *S. lemmonii* populations may be vulnerable to intensifying drought under climate change (R. Burnett, pers. comm.). Restoration practitioners are seeking ways to increase resilience of new willow plantings to a more drought-prone future without compromising other important performance traits, like freezing sensitivity or growth (R. Burnett, pers. comm.).

The *S. lemmonii* genotypes sampled in this study come from 90 individuals in 38 montane meadows across Tahoe National Forest in the northern Sierra Nevada, USA (Fig. 1) occurrences outside Tahoe National Forest are from the Global Biodiversity Information Facility (GBIF, 2023). The 38 meadow provenance sites range from 86 to 1300 mm April 1 snow water equivalent ('spring snowpack'), an indicator of growing season moisture availability, which strongly influences seasonal greening of vegetation in Sierra Nevada meadows (Trujillo *et al.*, 2012; Albano *et al.*, 2019). (We recognize that in other studies, the term 'provenance' may refer to sites that are more spatially or climatically disparate than ours. We simply use this term to refer to sites that were sampled for our common garden, with no further implication.) Our provenance sites also range from −0.99°C to 3.9°C in minimum May temperature, which can be a strong predictor of plant populations' sensitivity to spring freezing events (Muffler *et al.*, 2016). Lastly, our provenance sites span 310–550 mm in actual evapotranspiration, which is often used as a predictor of plant growth (Aubry-Kientz & Moran, 2017). April snowpack and minimum May temperatures are negatively associated across *S. lemmonii*'s Sierra Nevada-wide range, but they are spatially decoupled in Tahoe National Forest. The least distance between provenance sites is 0.89 km, the greatest is 83 km, and the mean is 32 km.

Glasshouse common garden

In October–November 2021, we collected twig cuttings from 1 to 2 parent plants at each of our 38 provenance sites. Within each of the 38 provenance sites, the plants we selected were spaced approximately evenly across the portion of the site occupied by *S. lemmonii*. To avoid repeat sampling of a single clone, we only sampled plants separated by 10 m or more of willow-free ground cover. (Preliminary results from a genomic study of the same individuals suggest this strategy was likely sufficient.) Parent plants were mature and roughly 2–3 m tall. We collected 2–5 twig cuttings from each parent plant to account for the possibility that not all cuttings might be propagated successfully. Each parent plant was tagged so it could be relocated for field measurement of leaf turgor loss point in August 2022. Cuttings were grown in a glasshouse common garden environment in Berkeley, CA. Initial conditions were ambient photoperiod, 25°C : 20°C, day : night temperatures, continuous mist application, and a growth medium of 1 : 1 : 1 perlite : vermiculite : Sunshine #4 potting mix (Sungro, Agawam, MA, USA). Beginning in December 2021, plants were repotted in 3 : 3 : 4 compost : perlite : Sunshine #4, fertilizer was applied weekly (Osmocote slow release 19-6-12), photoperiod was lengthened to 16 h with supplemental light, mist irrigation ceased, and all plants were watered once daily to field capacity (i.e. until the soil was saturated and excess water drained freely). When necessary, plants were repotted in successively larger pots to ensure that none were pot-bound, culminating with 3-gallon (11.4 l) pots in September 2022. Each pot size transition occurred on the same date for all plants, ensuring treatment homogeneity.

Drought sensitivity

We quantified drought sensitivity by measuring the leaf turgor loss point (Ψ_{TLP}). This trait, measured in megapascals (MPa), quantifies the water potential at which a leaf fails to maintain turgor. Beyond this threshold, leaves may exhibit wilting, inability to open stomata, reduced photosynthesis, and other problems with important physiological functions (Lambers & Oliveira, 2019). Higher ('less negative') values indicate greater drought sensitivity. We chose this trait because it is known to play an important role in drought stress tolerance for *Salix* and close relatives (Dawson & Bliss, 1989; Moran *et al.*, 2023). Additionally, focusing on leaf traits allowed us to assay leaves grown from buds that were set in the glasshouse common garden environment. This approach helps to minimize maternal effects from the clonal parent plants' *in situ* environments, which might be a greater concern for traits measured in other tissues, like stem hydraulics. We quantified the turgor loss point for common garden plants in July 2022, when they were roughly 1–2 m tall. For one plant from each provenance site, we estimated the turgor loss point with a pressure–volume curve using the youngest fully expanded leaf on the dominant shoot. We sampled the 38 plants in random order. We followed the method of Tyree & Hammel (1972) to generate pressure–volume curves, and we used Williams *et al.*'s (2017) algorithm to compute the turgor loss point.

In August 2022, we measured the leaf turgor loss point on 37 of the 38 parent plants in the field (referred to here as '*in situ*'). (One *in situ* parent plant died after we established the glasshouse common garden.) For each plant, we cut off the distal 15 cm of the dominant shoot and recut *c.* 1–5 mm off the basal end submerged under water to minimize embolism. We then kept the cut end of the sampled shoot under water, with the full shoot in a dark container for 1–2 d before the sampled tissue arrived in our

laboratory. We followed the procedure described above to generate one pressure–volume curve for each plant. Note that this procedure began by cutting a single leaf, which was not submerged, from a roughly 15 cm shoot, of which only several centimeters at the basal end was kept submerged following collection from the field. The goal of this approach was to minimize 'plateau effects' that can result from saturated tissue (Parker & Pallardy, 1987). We also visually inspected each pressure–volume curve and saw no indication of plateau effects.

Growth

In September 2022, we separated 80 glasshouse common garden plants into groups of 39 and 41 for drought and control treatments. Note that not all common garden plants were used for growth measurements, as these measurements are destructive and thus prevent inclusion in the subsequent freezing sensitivity assays. Whenever possible, we included multiple replicates of individual genotypes within provenance sites, and for each genotype represented by multiple common garden clones, we included at least one glasshouse plant in the drought and control groups. An exception: one genotype represented by two common garden clones had both clones placed erroneously in the control group. See 'Data analysis' in the Materials and Methods section for further details regarding replication. The drought and control groups were subdivided into two spatial blocks each, and these blocks were rotated within the glasshouse room every 2 wk. We also reshuffled the locations of individual plants within blocks every 2 wk. (See 'Glasshouse common garden' in the Materials and Methods section for soil details.) Control plants continued receiving the same treatment described above, including daily watering to field capacity. Drought plants received thrice-weekly watering to field capacity for 2 wk, then twice weekly for 2 wk, then weekly for the remainder of the experiment, which concluded in November 2022 after 9 wk. At the conclusion of the drought experiment, we harvested all 80 plants for dry root, shoot, and leaf biomass quantification following Savage & Cavender-Bares (2011).

Freezing sensitivity

To characterize variation in freezing sensitivity among common garden plants, we exposed new spring shoots from each plant to a range of freezing temperatures (details below) and estimated LT50 – that is the temperature at which the probability of tissue viability is 50%. We timed the measurements in spring because this is when many temperate zone plants are most vulnerable to freezing (Vitasse et al., 2014; Muffler et al., 2016) and because prior studies of Salix indicate they are very resistant to freezing in winter, when they are fully acclimated (Sakai, 1970; Savage & Cavender-Bares, 2013). We focused on new spring shoots because these tissues are likely among the most vulnerable to freezing (Chamberlain & Wolkovich, 2021). We assessed each shoot's postfreeze viability according to its capacity to re-root in well-watered soil. This viability criterion takes advantage of Salix's well-known capacity to re-root from healthy shoot cuttings, thereby providing a less

labor-intensive and perhaps more direct measurement of true tissue viability than other methods like differential thermal analysis (DTA) and electrolyte leakage (Grossman, 2023). Furthermore, many Salix species do not appear to supercool (Neuner et al., 2019), so supercooling-based methods like DTA may be unhelpful for quantifying freeze tolerance in Salix.

Before measuring freezing sensitivity, we began inducing winter acclimation in December 2022 by moving all remaining common garden plants from the glasshouse to ambient outdoor conditions in Berkeley, CA, where the mean daily minimum temperature was 6°C. In January 2023, to further induce winter acclimation in a colder winter environment more similar to Tahoe National Forest, plants were moved to ambient outdoor conditions in Reno, NV, where the mean daily minimum temperature was −6°C. To induce spring deacclimation, all plants were returned to the glasshouse in Berkeley, CA in April 2023. (Glasshouse conditions are described in the 'Glasshouse common garden' in the Materials and Methods section.)

To assess freezing sensitivity, we sampled and froze four new 15 cm spring shoots from each plant on May 11, 2023. Visual inspection indicated that there was phenological variation among common garden plants – for example some had fully expanded leaves, whereas others did not. This was not a problem for our analysis, as our goal was not to compare genotypes' physiology at the same phenological stage. Rather, we aimed to quantify variation in the tissue viability responses of different genotypes to the same freezing event in a common environment, which can result from physiological variation, phenological variation, or both (Grossman, 2023). Variation could arise solely from physiological mechanisms – for example all genotypes might follow parallel temporal trends in spring deacclimation, with no variation in phenology, and variation in tissue viability could be driven by absolute, time-invariant differences among genotypes in cold-hardiness. Variation in tissue viability could also arise strictly from phenological mechanisms – for example all genotypes might follow the same progression of cold-hardiness levels, but with different timing. Alternatively, phenological and physiological mechanisms could both contribute. Our aim was to integrate across these possible mechanisms and characterize overall tissue viability responses to a spring freezing event.

The set of four shoots for each common garden plant was allocated randomly among four freezing treatment groups: −0.5°C, −5°C, −9.5°C, and −14°C. Shoots were wrapped in wet cotton balls at the bottom to avoid desiccation and loaded in a Vesta Precision blast chiller in a random (and periodically reshuffled) spatial configuration. Starting at 10:00 h, the temperature stepped down by 4.5°C each hour, starting at the ambient laboratory temperature of c. 22°C. We kept each treatment group in the chiller until it had spent 1 h at its treatment temperature. After each group was successively removed, we moved them to a 4°C refrigerator for 1 h for a gradual thaw before returning them to the ambient laboratory environment. The following morning, all shoots were planted using the initial propagation protocol described in the 'Glasshouse common garden' in the Materials and Methods section. Shoots were classified as viable if they produced roots within 6 wk and inviable if they did not.

With the four shoot viability data points for each plant, we estimated LT50, the temperature at which the probability of tissue viability is 50%, as the midpoint between the coolest temperature with viable shoots and the warmest temperature with nonviable shoots. In one case, in which viability was not completely separated by temperature, we used a least squares logistic regression model of viability vs temperature treatment to estimate the temperature at which the probability of viability was 50%.

Data analysis

In total, our study comprises 90 genotypes represented by 129 common garden plants. (39 of the 90 genotypes had two common garden clones that were propagated successfully, and the other 51 were represented by only one common garden plant.) Due to logistical constraints, each of our three phenotypic data sets – drought sensitivity, freezing sensitivity, and growth – contained different numbers of plants (Supporting Information Table S1). For our drought sensitivity measurements, we assayed one common garden plant from each of our 38 provenance sites – that is 38 common garden plants. Although more replication might have been desirable, we aimed to minimize seasonal variation by completing all measurements in the same month (July 2022), and this was approximately the maximum number of pressure–volume curves we could complete in that time. We took the same approach in measuring each common garden plant's *in situ* clonal parent plant during August 2022. In allocating plants to the growth and freezing sensitivity measurements, we aimed to strike a balance, as growth measurements (which occurred before freezing sensitivity) are destructive. Based on our observations *in situ* and in the common garden, we expected growth measurements to be noisier than freezing sensitivity, so we attempted to err on the side of greater replication for growth measurements. The growth dataset comprised 50 genotypes represented by 80 common garden plants, which were divided into 39 and 41 between the drought and control treatments, respectively. Thirty genotypes were represented by two common garden plants each, and 20 genotypes were represented by one common garden plant each. The 30 genotypes represented by two common garden plants each were all divided into one drought plant and one control plant, except for one genotype, for which both common garden plants were erroneously included in the control group. The freezing sensitivity dataset comprised 36 genotypes, each of which was represented by one common garden plant.

For each of our three phenotypic outcome variables measured in the common garden – drought sensitivity, freezing sensitivity, and growth – we built a regression model using climatic predictors to quantify the effects of provenance climate. (Growth was measured under both drought and well-watered control conditions, and these data were analyzed together.) See below for details of each regression model structure. We used three climate variables, represented as means over the period 1981–2010, from the Basin Characterization Model ('BCM'; Flint *et al.*, 2021): April 1 snow water equivalent ('snowpack'), minimum May temperature, and actual evapotranspiration ('AET'). The Basin Characterization Model is optimized for use in California, where our

provenance sites occur. Relative to other commonly used climate products, BCM data provide finer spatial resolution, which is useful for capturing small-scale climatic variation in topographically heterogeneous regions like Tahoe National Forest. Below, we provide an *a priori* justification for each choice of climate variable. We did not explore model selection approaches using additional climate variables because our goal was to test specific hypotheses, not to build an optimal predictive model. Prediction and inference are separate tasks, and model selection tools like AIC can bias inference for the independent variable(s) of interest (Arif & MacNeil, 2022). Testing too many climate variables can lead to high 'false discovery rates' of patterns that simply occur due to random chance (Roback & Askins, 2005). Instead, we defined *a priori* hypotheses regarding the climatic gradients that we expected to shape each phenotypic outcome variable. All three climate variables were used in each regression, so that the coefficient for each climatic predictor reflects the effect of that variable while holding the others constant.

We used April snowpack because in a recent study, measures of vegetation health and vigor for Sierra Nevada montane meadows (e.g. normalized difference vegetation index) were best predicted by this variable, compared to 16 other variables including precipitation, climatic water deficit, and potential evapotranspiration (Albano *et al.*, 2019). In the Sierra Nevada, most precipitation arrives as snow during winter, and growing season water availability is determined largely by snowmelt (Schoenherr, 2017). Consequently, we hypothesized that genotypes' drought sensitivity would increase with provenance snowpack – that is environments with low snowpack should select more strongly for low-drought sensitivity.

Minimum May temperature was chosen because this variable was the best predictor of sensitivity to a spring freezing event among northern hemisphere woody plant species in a large common garden study (Muffler *et al.*, 2016). Furthermore, our field observations suggest May is the month when plants in our study system are most likely to be growing new shoots. We hypothesized that genotypes' spring freezing sensitivity would increase with provenance minimum May temperatures – that is environments with extreme spring cold snaps should select more strongly for low-spring freezing sensitivity.

We used actual evapotranspiration (AET) because this variable reflects availability of both energy and water, which are critical for plant growth (Flint *et al.*, 2021). AET exhibits the greatest values in environments that are both warm and wet. For plants subjected to the well-watered control treatment, we hypothesized that genotypes' common garden biomass accumulation would increase with provenance AET – that is environments with high energy and water availability should select for more rapid growth. For plants subjected to the drought treatment, we hypothesized that biomass accumulation would decrease with provenance snowpack, based on the expectation that plants from drier environments would be better able to maintain critical physiological functions throughout the drought.

To quantify the effect of provenance climate on leaf turgor loss point among common garden plants, we used an ordinary least squares (OLS) multiple linear regression with Gaussian errors. As

each provenance site was only represented by one genotype, no clustering of errors was expected, and thus no random effects were used.

To quantify the effect of provenance climate on biomass accumulation, we used a maximum likelihood generalized additive mixed model (GAMM) with Gaussian errors. We included a linear term for each climate variable, as well as an intercept term for 'treatment' (drought vs control), as we hypothesized that growth would slow in response to the drought treatment. We included interactions between 'treatment' and each climate variable to account for the possibility that provenance climate might influence responses to the drought treatment. To control for differences in the initial sizes of cuttings, we included a thin plate regression spline for initial cutting volume, plus its interaction with 'treatment'. This approach allows for nonlinear effects of initial cutting size on the final biomass measurement. We included a random intercept for 'site', as some provenance sites were represented by multiple *in situ* parent plants (i.e. 'genotypes'), leaving open the possibility of clustered errors. We also included a random intercept for 'parent plant' (i.e. 'genotype'), as some *in situ* parent plants were represented by two common garden plants (one drought and one control). In some cases, multiple twigs cloned from the same *in situ* parent plant were propagated successfully in the common garden and included in the growth study.

To quantify the effect of provenance climate on LT50, the freezing temperature at which the probability of tissue viability is 50%, we used a maximum likelihood linear mixed effects model with Gaussian errors. We included a linear term for each climatic predictor. To account for possible clustered errors, we included a random intercept for 'site', as some provenance sites were represented by multiple *in situ* parent plants.

Our LT50 data have a 'binned' distribution (reflecting the midpoints between the four experimental temperatures), which may have strained the robustness of linear mixed effects models to non-Gaussian errors. To address this possibility, we also analyzed our LT50 data using a Bayesian ordinal generalized linear mixed model (GLMM) with a logit link function, in which each LT50 value is treated as an ordered category. This ordered categorical response variable is regarded as a function of a latent continuous variable defined by the linear predictor, which is identical to that of our linear mixed effects model described above. In other words, this model structure treats the true LT50 values as varying continuously (i.e. with infinitely fine resolution) and treats our LT50 measurements as 'rounded' versions of the unobserved true values.

Intensifying drought is the facet of climate change regarded by some management practitioners as most threatening to Sierra Nevada willows (Vernon *et al.*, 2019). Consequently, in addition to the analyses testing for effects of climate on common garden phenotypes, we used our glasshouse common garden and *in situ* drought sensitivity data to assess whether heritable phenotypic variation detected in the glasshouse translates to biologically meaningful phenotypic variation *in situ*. Toward this aim, we used an ordinary least squares (OLS) simple linear regression with Gaussian errors to quantify the effect of common garden

turgor loss point values on *in situ* values. Common garden phenotypes are assumed to reflect genetic variation (plus environmental noise), so a positive effect of the common garden phenotype on the *in situ* phenotype would indicate that genetic variation contributes to *in situ* phenotypic variation.

To visualize the role of climate in determining the extent of adaptive trade-offs, we reformulated our regression models of drought and freezing sensitivity using z-scaled responses (mean 0, SD 1) and replotted significant effects on the same axes. This approach creates a 'common currency' of effect sizes among different traits and helps show more clearly whether they vary in opposite directions along a climatic gradient, creating a trade-off.

To illustrate how multi-trait phenotypes vary across multidimensional climate gradients, we plotted our drought and freezing sensitivity data with a two-dimensional color scale on a grid of spring snowpack and temperature.

To test for direct trade-offs among traits, irrespective of climate, we built a ranged major axis regression model using provenance site-level mean phenotypes for each possible pairing of traits. Like a PCA, major axis (MA) regression techniques minimize errors perpendicular to the regression line, rather than the vertical errors that are minimized in ordinary least squares regressions (Legendre, 2018). This approach is useful for situations in which both variables of interest are measured with error, and there is no clear independent and dependent variable. 'Ranged' major axis regression is the MA method best suited for variables that do not share the same units or scale (Legendre, 2018). To account for the binned shape of the LT50 data we also used Kendall's tau tests, which test for rank correlations between variables, irrespective of the functional form of their relationship (Noether, 1981). We did not analyze the relationship between final biomass under drought vs control conditions because substantial biomass accumulation occurred before the controlled experiment, when all plants were receiving the same treatment. Consequently, final biomass under drought and control conditions are likely to show a positive association that simply reflects their shared history.

All regression analyses were performed in R (R Core Team, 2023). Continuous predictors were z-scaled (mean 0, SD 1). We used the GLMMTMB package (Brooks *et al.*, 2017) for linear mixed effects models, GAMM4 (Wood & Scheipl, 2020) for the GAMM, BRMS v.2.21.0 (Bürkner, 2017) for the ordinal GLMM, and LMODEL2 (Legendre, 2018) for the ranged major axis regression models. Model building and checking steps are shown in our publicly available R code (see the Data availability section).

Results

Drought sensitivity and climate

Genotypes from lower-snowpack provenance sites had less drought-sensitive leaves, as quantified by leaf turgor loss point. The turgor loss point of common garden plants increases (i.e. drought sensitivity increases) by 0.18 MPa per 1000 mm in April snow water equivalent (Fig. 2a,b; Table S2; $P < 0.01$). Conditional means range from -0.95 to -0.74 MPa along the snowpack gradient. Turgor loss point is not associated with
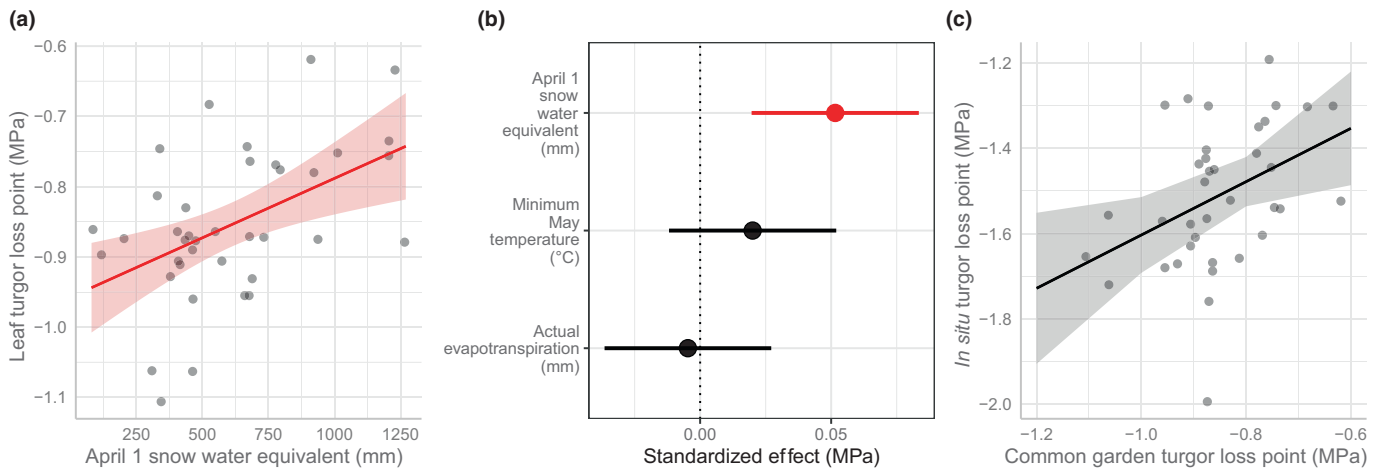
Fig. 2 Results for common garden and *in situ* studies of leaf turgor loss point, a measure of drought sensitivity, in *Salix lemmonii*. For consistency with Fig. 5, red represents the effect of provenance April snowpack on leaf turgor loss point. (a) Effect of provenance spring snowpack from multiple linear regression model. Ribbon shows 95% confidence interval. Each point represents one common garden plant from one provenance site. (b) 95% Confidence intervals for effect sizes of three climatic variables in a multiple linear regression model. (c) Effect of common garden phenotypes on *in situ* phenotypes from simple linear regression model. Each point represents one genotype from one provenance site, which is represented by an *in situ* parent plant and its common garden clone.
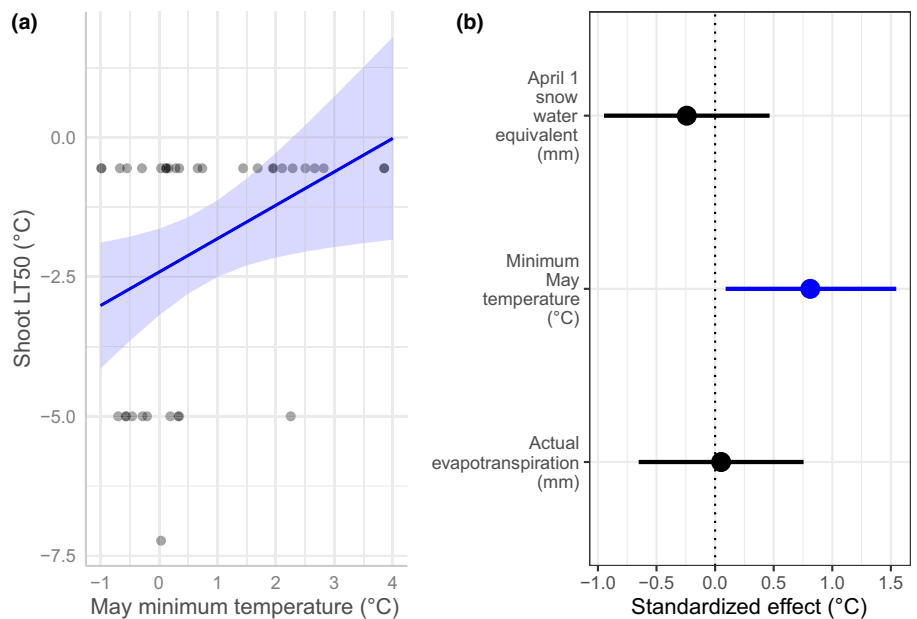

Fig. 3 Results for common garden study of shoot LT50, the freezing temperature at which the probability of tissue viability is 50%, in *Salix lemmonii*. This variable is a measure of freezing sensitivity. For consistency with Fig. 5, blue represents the effect of provenance minimum May temperature on LT50. (a) Conditional effect of provenance May minimum temperature from linear mixed effects model. Ribbon shows 95% confidence interval. (b) 95% Confidence intervals for effect size estimates of three climate variables in a linear mixed effects model. Qualitatively similar results were obtained from an ordinal logistic GLMM, which treats LT50 values as ordered categories to account for the 'binned' shape of the data.

provenance minimum May temperature or actual evapotranspiration (Fig. 2b; Table S2). For each 1 MPa increase in the common garden phenotype, the *in situ* phenotype increases by 0.62 MPa (Fig. 2c; Table S3; $P = 0.01$), indicating that genetic variation contributes to *in situ* phenotypic variation.

Freezing sensitivity and climate

Genotypes from colder provenance sites were less sensitive to freezing. Common garden plants' shoot LT50 increases (i.e. freezing sensitivity increases) by 0.60°C with each 1°C increase in provenance minimum May temperature (Fig. 3; Table S4; $P = 0.02$). LT50 is not associated with April snowpack or actual

evapotranspiration (Fig. 3b; Table S4). When we reanalyzed the data with a Bayesian ordinal logistic GLMM, which may account better for the 'binned' shape of the LT50 data, we again found a positive effect of minimum May temperature (95% CI 0.21–3.7) and no effect of the other climate variables (Table S5).

Growth and climate

Biomass accumulation was not associated with any of the climatic variables we tested under drought or well-watered conditions (Fig. 4; Table S6). The only significant effect was the overall influence of the drought treatment, which decreased biomass accumulation (Fig. 4; Table S6).
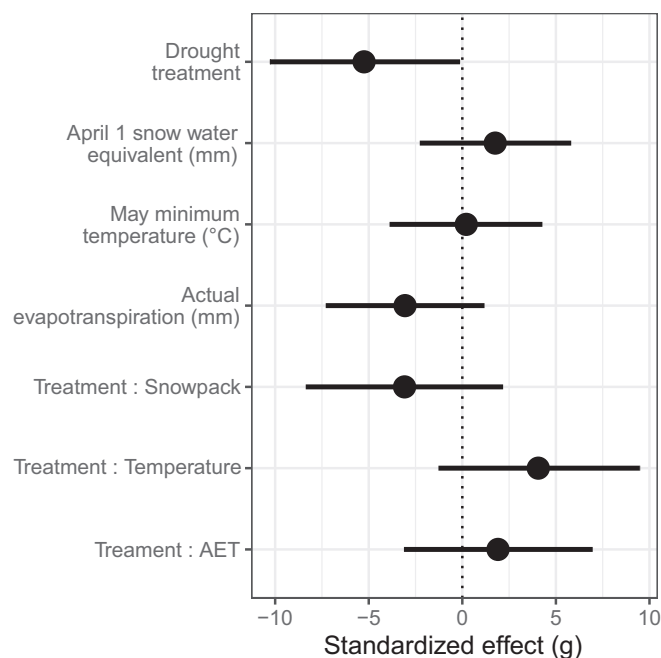
Fig. 4 95% Confidence intervals for effect sizes of provenance climate and drought treatment on common garden biomass accumulation for *Salix lemmonii* in a linear mixed effects model. AET, actual evapotranspiration.

Trade-offs

Drought sensitivity increases significantly with spring snowpack, whereas freezing sensitivity exhibits little trend (Fig. 5a). Freezing sensitivity increases significantly with minimum May temperature, whereas drought sensitivity exhibits a weak, nonsignificant positive trend (Fig. 5b). Consequently, in provenance sites with low-spring snowpack and minimum temperatures, site-level mean phenotypes are strong in both performance traits (Fig. 5c,d).

No significant negative relationship emerges for any two-trait pairing we analyzed among our four measured traits – drought sensitivity, freezing sensitivity, biomass accumulation under well-watered conditions, and biomass accumulation under drought conditions. This outcome is supported by ranged major axis regressions (Table S7) and Kendall's tau tests (Table S8).

Discussion

Summary

The results of this investigation show that populations of Lemmon's willow (*S. lemmonii*) in the northern high Sierra Nevada, USA do not exhibit an adaptive trade-off between drought and freezing sensitivity. In our common garden, genotypes' drought sensitivity increases with provenance April snowpack, an indicator of growing season soil moisture (Figs 2, 5). Freezing sensitivity increases with provenance minimum May temperature (Figs 3, 5). These climate variables are often negatively correlated (e.g. across the Sierra Nevada-wide realized niche of *S. lemmonii*; Fig. 1), so the trait-environment relationships we found would be

expected to produce trade-offs in regions that exhibit this climatic correlation (Garland, 2014). Although drought-freezing trade-offs are not universal, they occur in many other systems (Laanisto & Niinemets, 2015; Rueda *et al.*, 2017; McCulloh *et al.*, 2023). However, in our study domain, April snowpack and minimum May temperature are uncorrelated (see large points in Fig. 1c), and thus we find no trade-off between drought and freezing sensitivity (Fig. 5a,b). (Note that the existence of individual provenance sites with low-mean sensitivity to one stressor and high sensitivity to the other – for example the reddest and bluest points in Fig. 5c,d – does not indicate a trade-off. A trade-off is an association between traits at the level of the full dataset, which we did not find, as Fig. S1 also shows.) The absence of a trade-off suggests weak or absent genetic constraints on this trait pairing (Garland, 2014), as well as weak or absent organismal-level physiological trade-offs (Bloom *et al.*, 1985). Genotypes with relatively low sensitivity to both stressors occur in the coldest, driest provenance sites (yellowest points in Fig. 5c,d). These sites may represent reservoirs of strong adaptive potential under climate change, and assisted gene flow efforts may benefit by using them as sources (Aitken & Whitlock, 2013).

Drought sensitivity

In our drought sensitivity study, genotypes from lower-snowpack sites could withstand stronger drought without wilting. Among plants measured in the common garden, the mean turgor loss point increases (i.e. drought sensitivity increases) by 0.18 MPa with each 1000 mm increase in provenance April snow water equivalent (Fig. 3a,b; $P < 0.01$). Additionally, *in situ* phenotypes increase by 0.62 MPa with each 1 MPa increase in common garden phenotype (Fig. 2c; $P = 0.01$). This result indicates that genetic variation contributes substantially to *in situ* phenotypic variation. The turgor loss point measurements for the *in situ* parent plants were generally lower (i.e. less drought-sensitive) than the glasshouse common garden measurements. This phenotypic difference may reflect ontogenetic differences (mature plants vs saplings), phenological differences (August vs July), or overall environmental differences, irrespective of season. For example, the hydrologic regime in the common garden, with daily watering to field capacity, may have provided fewer of the cues that stimulate metabolic investment in osmolytes (Bartlett *et al.*, 2014). Overall, our drought study supports the expectation that wilting-resistant leaves carry greater adaptive value in dry conditions (Dawson & Bliss, 1989), and that dry sites harbor genotypes predisposed toward greater wilting resistance – that is low-drought sensitivity (Soliani *et al.*, 2021; Moran *et al.*, 2023).

Freezing sensitivity

Our freezing experiment shows that genotypes from provenance sites with colder spring temperatures have less freeze-sensitive shoots. LT50 of new spring shoots in the common garden increases by 0.60°C with each 1°C increase in provenance minimum May temperature (Fig. 3; $P = 0.02$). LT50 quantifies the temperature treatment at which posttreatment tissue viability is
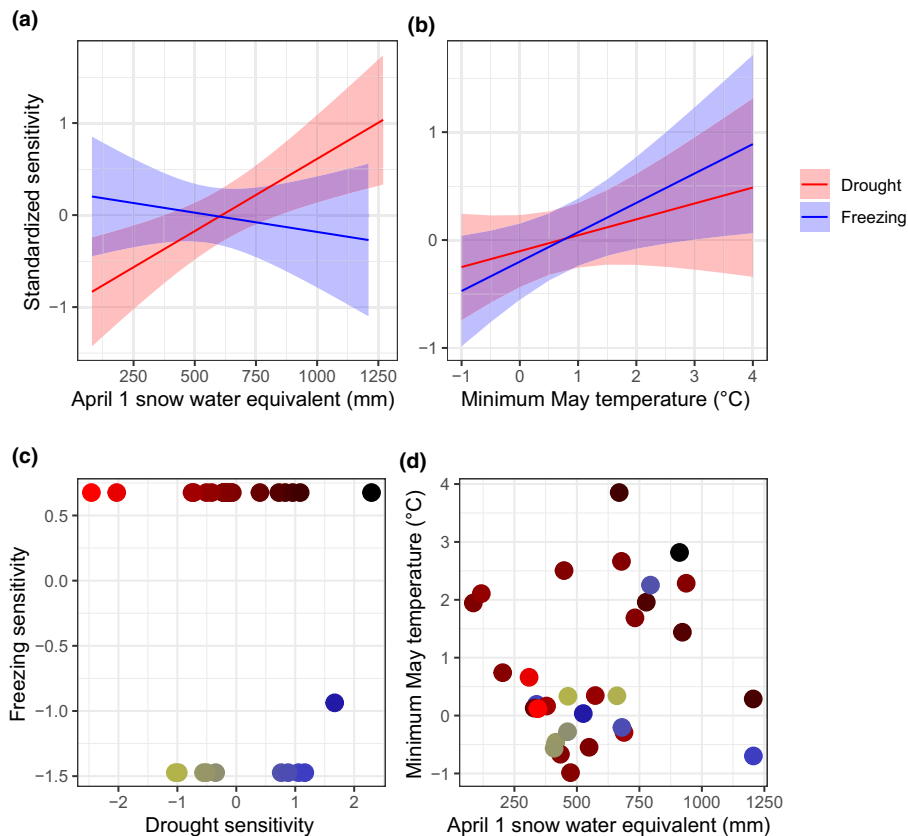
Fig. 5 Responses of drought and freezing sensitivity in *Salix lemmonii* to snowpack and minimum temperature. Drought and freezing sensitivity variables are generated by standardizing leaf turgor loss point and shoot LT50, the freezing temperature at which the probability of tissue viability is 50% (mean = 0, SD = 1). (a, b) Conditional effects of spring snowpack and minimum temperature on drought and freezing sensitivity from linear mixed effects models. (Points, which would represent mean trait values for provenance sites, are omitted to avoid visual clutter. Site-level mean trait values can be seen as points in (c, d) and Supporting Information Fig. S1.) Ribbons represent 95% confidence intervals. (c) Two-dimensional color legend for (d), in which a two-trait phenotype – drought and freezing sensitivity – is plotted against snowpack and temperature. Color varies continuously and two-dimensionally across the panel, with pure red, yellow, blue, and black delineating the four corners – that is combinations of extreme values. Red represents the least drought sensitivity and the greatest freezing sensitivity. Blue represents the opposite. Yellow represents the least observed values of both variables. Black represents the greatest observed values of both variables. Each combination of extremes may not necessarily occur in the data, hence the absence of, for example a pure yellow point in the lower panel left corner in (c).

50%, with greater values indicating greater freezing sensitivity. Our main qualitative result – that is LT50 increases with provenance temperature – is robust to reanalysis with an ordinal logistic GLMM, in which each LT50 value is treated as an ordered category. (We performed this analysis to account for the 'binned' shape of the LT50 distribution.) All genotypes were assayed simultaneously, so overall variation in LT50 may reflect both phenological variation (i.e. variation in the timing of spring cold deacclimation) as well as variation in postdeacclimation freezing sensitivity among genotypes that deacclimated quickly (Grossman, 2023). Overall, our results support the expectation that freezing resistance carries greater adaptive value in environments that have strong cold snaps in spring, when many plants are most vulnerable (Vitasse *et al.*, 2014; Muffler *et al.*, 2016).

Growth

Growth did not provide evidence of ecotypic variation or trade-offs. In our common garden, total biomass accumulation did not

vary with provenance climate under drought or control conditions (Fig. 4). When we examined direct relationships among population mean trait values, we also found little evidence for trade-offs (Fig. S1; Tables S7, S8). It may appear surprising that biomass accumulation among drought-treated plants did not increase with turgor loss point, as our leaf turgor loss point measurements show evidence of local adaptation to hydrologic conditions. Multiple factors might explain this result. First, it is possible that a relationship exists but is too subtle for our sampling design to detect. Second, genotypes with lower leaf turgor loss points (i.e. lesser drought sensitivity) may have had slower average growth rates during their growing season, but their growing seasons may have been longer (Berger *et al.*, 2016). We measured total biomass accumulation over the drought experiment – not shorter-term growth rates – and our observations in the common garden indicate that some drought-treated plants were likely at or approaching dormancy by the conclusion of the growth experiment. These observations suggest that only some drought-treated plants grew throughout the experiment. Trade-

offs between instantaneous growth rates and growing season length are known to promote coexistence among plant species in a Mediterranean climate (Levine *et al.*, 2024) like the Sierra Nevada, and it could be informative for future work to explore the implications of such trade-offs at the intraspecific level. In addition to these considerations, it is possible that other traits we did not measure, like herbivore defense or other forms of stress tolerance, might form trade-offs with the traits we measured. However, although trade-offs among performance traits are well-documented (Grime, 1974; Díaz *et al.*, 2016; Visakorpi *et al.*, 2024), they are not ubiquitous. Plants cope with multiple forms of abiotic stress through myriad mechanisms, and some of these mechanisms do not carry zero-sum physiological constraints in relation to growth rates (Savage & Cavender-Bares, 2013; Fletcher *et al.*, 2022).

Management implications

Our findings may help inform conservation strategies for *S. lemmonii* in the northern high Sierra Nevada and beyond. In the Sierra Nevada, climate change is making drought more frequent and severe (Dettinger *et al.*, 2018). Spring freezing events occur currently, and risks to plants may increase as seasonal and diel temperature fluctuations become more erratic (Arnold *et al.*, 2014). In Tahoe National Forest, we found that the coldest, driest provenance sites disproportionately harbor genotypes with low sensitivity to both drought and freezing. We also found no trade-offs with growth. Thus, populations at cold, dry sites may be valuable reservoirs of potential to respond adaptively to climate change. ('Cold' refers to minimum May temperatures, which do not necessarily reflect annual mean temperatures.) Although these populations' sensitivity to climate change may be less than others', their future exposure to climate-driven stress may be greater, as their current environments are relatively stressful (Williams *et al.*, 2008). Consequently, it is unclear whether the balance between exposure and sensitivity will translate to favorable outcomes *in situ*, although prior research suggests they might (Zohner *et al.*, 2020). Optimal outcomes might be achieved by translocating stress-tolerant genotypes to sites where future exposure will be milder, for example snowy sites with equable thermal regimes. Tahoe National Forest contains strong climatic variation within tens of kilometers (Fig. 1), so biologically meaningful translocation might be achievable over distances where legal, ethical, and other difficulties (Schwartz *et al.*, 2012) are minimized. If the combination of low drought and freezing sensitivity we found is exceptional in other parts of the range of *S. lemmonii*, then longer-distance translocation could also prove fruitful, although ethical, logistical, and ecological mismatch issues may apply (Bucharova, 2017; Baldwin, 2019).

Conclusions

Overall, our results suggest that adaptive trade-offs may be avoided in regions where key climate variables are uncorrelated. Multiple climatic stressors – for example drought and freezing – can coincide in certain sites to promote multiple stress adaptations – for example the yellowest points in Fig. 5(d). The fate of populations in these sites depends not only on their sensitivity to climate change but also their future exposure, which could be severe given their current exposure. However, regions of uncorrelated climate must also, by definition, contain less stressful sites. Assisted gene flow efforts might achieve the best of both worlds – that is low sensitivity and low exposure – by importing genotypes that have escaped adaptive trade-offs into these less stressful sites. To identify translocation opportunities for other taxa, further investigation is needed regarding the climate variables shaping key performance traits. However, ecotypic trait variation has already been studied extensively for some taxa (Mahony *et al.*, 2019; MacLachlan *et al.*, 2021; Prakash *et al.*, 2022; Capblancq *et al.*, 2023), so the trade-off-escape concept might be readily applicable in these cases. In general, conservation efforts may benefit by examining how multidimensional climatic gradients shape correlations among adaptive traits, which can have strong, persistent effects on populations' evolutionary trajectories (Schluter, 1996; Etterson & Shaw, 2001; Walsh & Blows, 2009; Terasaki Hart & Wang, 2024).

Competing interests

None declared.

Author contributions

KCR led study design with advice from DDA. KCR collected and analyzed the data. KCR wrote the first manuscript draft, and DDA contributed significantly to revisions.

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Data availability

All code and data are publicly available at doi: 10.5281/zenodo.10850900.

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Supporting Information

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

Fig. S1 Scatterplots of pairwise relationships among population mean trait values.

Table S1 Summary of replication for sites, genotypes, and clones in common garden.

Table S2 Regression results for common garden turgor loss point data.

Table S3 Regression results for *in situ* turgor loss point data.

Table S4 Main regression results for common garden freezing sensitivity (LT50) data.

Table S5 Ordinal regression results for common garden freezing sensitivity (LT50) data.

Table S6 Regression results for common garden biomass accumulation data.

Table S7 Kendall's tau results for population mean trait values.

Table S8 Ranged major axis regression results for population mean trait values.

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