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RESEARCH ARTICLE

Intraspecific trait variation in a dryland tree species corresponds to regional climate gradients

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Abstract

Aim: Intraspecific trait variation is fundamental to understanding a species' adaptive capacity. Assessing phenotypic variation at different ecological scales is useful for evaluating species' vulnerability to changing environmental conditions. Here, we quantify the ecological scale of variation of phenotypic functional traits for a widespread dryland tree species and evaluate the strength of trait-environment relationships across spatial gradients and in response to interannual variability in weather conditions.

Location: Western United States.

Taxon: Conifer tree (Pinaceae): *Pinus monophylla*.

Methods: Nine reproductive and foliar morphological traits were measured from 23 sampling locations in nine mountain ranges, stratified across broad-scale gradients of precipitation timing and quantity and local gradients of elevation. We partitioned trait variation within and among nested ecological scales (mountain range, site, tree, and tree growth year). We then used multivariate methods to quantify the association between environmental variables and ecological trade-offs associated with both reproductive and foliar traits.

Results: Most variation was explained at the scale of individual trees (18%–46%) and between growth years (20%–30%), with smaller but variable contributions at the scale of sites (8%–25%) and mountain ranges (0%–15%). Trait values had low correlation with environmental variables (13%); however, 94% of the trait-environment covariance was explained by two major axes of variation: (1) the drought-stress gradient covarying with reproductive traits, and (2) precipitation patterns covarying with foliar morphology.

Main conclusions: High levels of individual trait variation indicate within-population adaptive capacity. Consistent relationships among range-wide patterns of foliar and reproductive traits and broad-scale climate gradients provide indirect evidence of local adaptation and may inform seed sourcing for restoration or the potential for assisted migration efforts. Quantification of intraspecific trait variation across multiple ecological scales is important for understanding the potential climate change response of dryland tree species.

KEYWORDS
adaptive capacity, climate change, ecological scale, foliar traits, forest resilience, functional traits, intraspecific variation, pinyon pine, reproductive traits

1 | INTRODUCTION

Forest and woodland tree species are facing large-scale die-off events worldwide that are driven by drought and heat stress (Allen et al., 2010). In the western United States, current climate change projections predict that air temperatures will continue to rise with an overall reduction in soil moisture availability (Dai, 2013). Tree species from arid and semi-arid environments are expected to experience increasing physiological stress (Thorne et al., 2017) as droughts in these regions become more frequent and severe with increased evaporative demand and reduced precipitation (Dai, 2013). Understanding the vulnerability of tree species to conditions of increased drought is a necessary step in developing future management strategies to enhance the adaptive capacity of forests (Millar et al., 2007).

Adaptive capacity, as defined in the context of vulnerability assessment, refers to a species' ability to cope with, adjust to, and persist in current and future climate conditions (Beever et al., 2016). In general, a species will respond to climate change by either being able to 'persist in place' or 'shift in space' (Nicotra et al., 2015; Thurman et al., 2020). While some species are more capable of shifting their range in elevation according to changes in temperature or moisture (e.g. upslope movement with increased temperature), other species are dependent on the availability of suitable phenotypes within populations that can manage varying environmental conditions (Aubin et al., 2016; Nicotra et al., 2015; Thurman et al., 2020). For widespread species, there is increasing evidence that intraspecific trait variation will result in meaningful differences in climate change responses among different populations (Kuppler et al., 2020; Messier et al., 2010; Umaña & Swenson, 2019). Adaptive capacity may be greatest for species whose ranges encompass environmental heterogeneity across multiple ecological scales (Moran et al., 2016).

Partitioning functional trait variation across different ecological scales can provide context on how such species' adaptive capacity is structured. Broad-scale patterns of trait variation have implications for 'shifting in space.' Traits that co-vary consistently along broad-scale environmental gradients imply potential strategic trade-offs and provide indirect evidence of local adaptation (Albert et al., 2011; Kuppler et al., 2020; Laughlin, 2014; Westoby et al., 2002). Adaptive trait responses to environmental stress can allow species distributions to track directional climate change by providing pre-adapted propagules available for dispersal into adjacent sites whose conditions may have shifted to match those to which a population has adapted. In contrast, fine-scale variation among individuals within a population contributes to a species' capacity to 'persist in place' despite climatic stress (Jump & Peñuelas, 2005; Siefert, 2012). This strategy is often referred to as diversified bet-hedging, or the ability of a species to express several phenotypes to manage environmental variation (Philippi & Seger, 1989). At local scales, individual trait variation arises from microsite environmental heterogeneity, biotic interactions and genetic variation (Jung et al., 2010). Another component of this variation can be temporal, or the ability of traits to respond plastically to changes in the environment among and within years (e.g. intra- and interannual variation in growth rates of stem wood or needle tissues). These differences in trait expression can influence interactions among and between organisms, further contributing to higher-level variation in a species' response to environmental gradients (Funk et al., 2016; Siefert, 2012).

In this study, we investigated how intraspecific trait variation is structured within a widespread dryland tree species in the western U.S., singleleaf pinyon pine (*Pinus monophylla* Torr. & Frem). *P. monophylla* is considered the most xeric pine in the U.S. (Meeuwig et al., 1990); however, recent studies have documented an eight-fold increase in tree mortality across its range closely linked to drought severity and site aridity (Flake & Weisberg, 2019), making it a model species for studying the relationship between patterns of trait variation and adaptive capacity to climate change. By sampling trees within different mountain ranges, both along latitudinal and elevational gradients, we quantified trait variation across the broad range of environmental conditions where this species occurs. We measured key reproductive and foliar functional traits to compare phenotypic variation across ecological scales. Traits were selected to represent common trait trade-offs, including seed mass and number of ovules per cone, which represents a trade-off between seed quality and quantity known to vary in response to gradients of environmental stress (Cochrane et al., 2014; Laughlin, 2014; Muller-Landau, 2010), as well as specific leaf area (SLA), used to describe how plants manage resource availability (e.g. exploitative vs. conservative; Wright et al., 2004). This study addresses the following questions: (1) How is intraspecific trait variation in *P. monophylla* partitioned across four ecological scales: among mountain ranges, among sites elevationally-distributed within mountain ranges, among individual trees, and for foliar traits, among three consecutive growth years? (2) To what extent is broad-scale trait variation (e.g. among mountain ranges or elevationally-distributed sites) related to spatial gradients of seasonally available moisture? (3) To what extent is interannual variation in foliar traits related to deviations in annual weather conditions from site-level climate means?

We predicted that intraspecific trait variation would be observed across all ecological scales, with a null hypothesis of evenly partitioned variation across scales (e.g. Messier et al., 2010). Alternatively, one might expect to find the highest levels of variation explained at the individual tree scale, reflecting fine-scale heterogeneity in abiotic and biotic conditions (e.g. Jung et al., 2010). We predicted that broad-scale trait variation (among sites and mountain ranges) would coincide with known trade-offs associated with gradients of environmental stress, such that trees from drier locations would produce larger but fewer seeds, while trees from more mesic locations would produce lighter but more numerous seeds. Similarly, we predicted that trees from drier locations would have more resource-conservative foliar traits (e.g. denser needles with low SLA), compared to trees from more mesic locations. For foliar traits that could be compared across years, we predicted that annual growth would exhibit plastic responses to resource availability, such that years with greater precipitation (particularly during the summer) would produce larger needles, but that SLA, which reflects

general resource acquisition strategies, would remain relatively constant among years. Understanding how trait variation relates to climate gradients at multiple scales is important for assessing the vulnerability of widely-distributed dryland conifer species to projected increases in drought stress.

2 | MATERIALS AND METHODS

2.1 | Study area and site selection

The distribution of *P. monophylla* in the United States spans 8.02° of latitude and 8.34° of longitude and encompasses broad gradients of precipitation amount and seasonality (Figure 1; Table S1). To capture trait variation across the largest possible range of climate conditions, we stratified sampling locations across broad-scale gradients of mean annual precipitation and monsoonality (ratio of summer precipitation to annual precipitation), using PRISM 30-year climate normals (Daly et al., 1994). We categorized both mean annual precipitation and monsoonality evenly into thirds (tercile splits) and selected nine mountain ranges that contained each combination of the two climate variables and were distributed evenly in geographic space (Figure 1). The mountain ranges selected are distributed throughout Nevada, western Utah, and southern California, covering *P. monophylla*'s range.

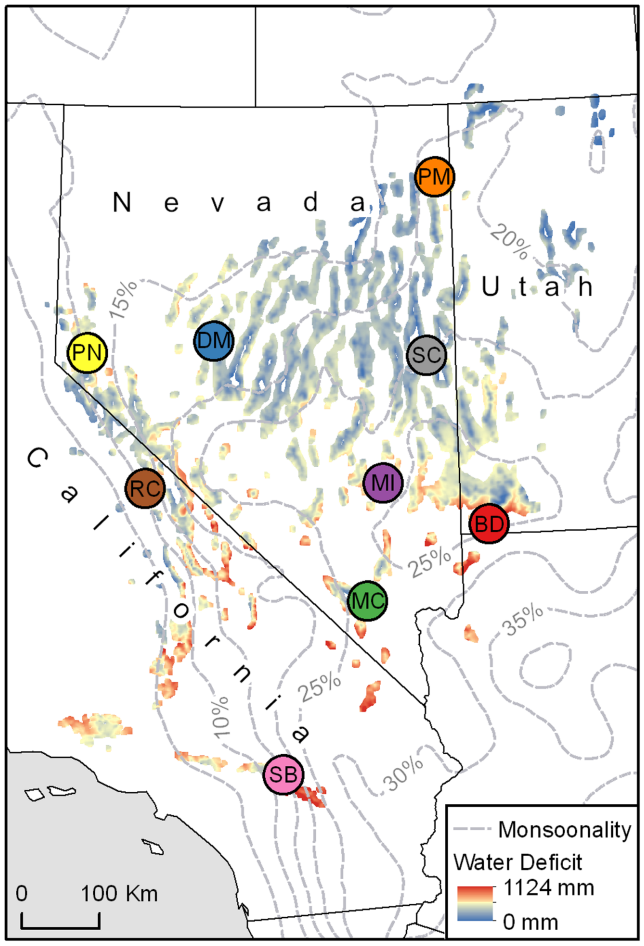

FIGURE 1 Map of site locations showing the species distribution of *Pinus monophylla* coloured according to climatic water deficit (red = higher water deficit; blue = less water deficit), overlaid with contour lines representing monsoonality (i.e. the percent of annual precipitation received in July, August and September). Nine sampled mountain ranges are indicated by coloured circles with two-letter codes: Pine Nut Mountains "PN" in yellow, Desatoya Mountains "DM" in blue, Pequop Mountains "PM" in orange, Schell Creek Mountains "SC" in grey, Beaver Dam Mountains "BD" in red, Mount Irish "MI" in purple, Mount Charleston "MC" in green, San Bernardino Mountains "SB" in pink, and the Rock Creek Range "RC" in brown.

At each mountain range, three sampling sites were selected along an elevational gradient, separated by at least 200 m (low, middle and high). The low elevation site represents the lowest elevation in which cone-bearing *P. monophylla* was detected, whereas the high elevation site represents the highest accessible elevation with cone-bearing trees. The middle elevation site was located at the approximate elevational midpoint of the low and high elevation sites. All sites were easily accessible from the road and were required to have a sufficient number of cones present (at least 30 cones from each of six trees). Sampling was limited to fewer than three sites in three of the mountain ranges, due to narrow elevation ranges (Schell Creek Mountains, two sites) or a lack of available cones (Beaver Dam Mountains, one site; and Pine Nut Mountains, two sites). Sampling sites ranged in elevation from 1515 to 2611 m, for a total of 23 sites (Table S1).

2.2 | Field data collection

All field collections took place in September of 2019, when *P. monophylla* cones were beginning to ripen. At each site, six cone-bearing trees were selected that were representative of the stand, based on tree size and cone production. Geographic coordinates, slope, aspect and elevation were collected for each tree. From each tree, we harvested at least 30 cones and three leaf branchlets from the upper ⅔ of the south-facing canopy using a telescoping pruner.

2.3 | Trait measurements

From each of six trees per site, we measured nine morphological traits including both reproductive (cone length, cone dry weight, seed mass, seed area and number of ovules per cone) and foliar (needle length, needle width, needle dry weight and SLA) traits. Cone traits were measured for ten cones per tree (60 cones per site). We first measured cone length and counted the number of ovules per cone, then weighed each cone after emptying all seeds.

To test for filled seeds, we bounced seeds on a hard surface to separate filled and hollow seeds based on their sound (Chambers, 2001). Twenty filled seeds per tree were weighed to the nearest 0.01 g and subsequently scanned for seed projected

area, measured to the nearest 0.0001 mm^2 (WinSeedle, Regent Instruments Canada Inc.).

Leaf branchlets were separated into annual needle cohorts at the annual bud scar nodes for three consecutive growth years (2016, 2017, and 2018 growth years). Twenty needles per growth year per tree were scanned and measured; thus, 60 needles total per tree were measured for needle straight length and needle straight width, measured to the nearest 0.0001 mm (WinSeedle, Regent Instruments Canada Inc.). Needles were air-dried to constant weight before weighing (measured to the nearest 0.001 g), and SLA was then calculated as the ratio of needle cross-sectional area to needle dry mass. Needles were weighed and measured individually to retain variation among needles within maternal trees.

2.4 | Climate and soil variables

For each of the 23 sites, we obtained six climate variables that we expected to relate to important trade-offs in ecological strategies for tree species in arid and semi-arid regions in response to drought stress. Cumulative total winter precipitation (December through February: prcpwin [mm]) and summer precipitation (June through August: prcpsum [mm]) represent the seasonality and amount of precipitation across *P. monophylla*'s range. Populations located just east of the Pacific Crest and in mountain ranges farther north receive most of their precipitation from winter snowmelt. Populations located in the southern portion of its range receive both winter snowmelt and infrequent pulses of summer rain during monsoonal precipitation patterns. The remaining variables represented different components of the seasonal water balance and were derived using methods described in Dilts et al. (2015). Cumulative actual evapotranspiration (CumlAET [mm]) estimates evaporative water loss as constrained by water availability over the course of the growing season and can be considered a proxy for net primary productivity when modelled at broad scales (Stephenson, 1998). Summer vapour pressure deficit (sumVPD [kPa]), the sum of the difference between monthly actual and saturation vapour pressure (May through July), is associated with increased evapotranspiration and reduced plant growth due to stomatal closure. Cumulative climatic water deficit (CumlCWD [mm]) is the amount by which potential evapotranspiration exceeds actual evapotranspiration over the growing season and represents the unmet evaporative demand for water (Stephenson, 1990). Available soil water storage capacity (AWC [cm]) integrates soil texture and depth and represents the amount of moisture the soil profile can store.

Winter precipitation, summer precipitation and summer vapour pressure deficit were calculated using 30-year normal (1981–2010) gridded PRISM climate data (PRISM Group, 2015) with 800-m cell size (Daly et al., 1994). Climatic water deficit was based on a Thornthwaite water balance model (Lutz et al., 2010), which incorporates 30-year monthly normals (800-m cell size) of temperature and precipitation, elevation, and soil water holding capacity. Soil available water storage was obtained from the POLARIS soil map at 90-m cell size resolution (Chaney et al., 2016).

To calculate interannual climate variation for the three tree growth years of 2016, 2017 and 2018, we downloaded PRISM monthly weather data (Daly et al., 1994) for each of the 23 site locations. We used the Climatic Water Deficit Toolbox for ArcGIS 10.1 (Dilts & Yang, 2015) to calculate the monthly weather variables for years 2016–2018. From these monthly weather variables, we computed annual values for each of the climate variables described above.

2.5 | Statistical analysis

2.5.1 | Ecological scale of trait variation

Trait measurements were compared across four hierarchical ecological scales: (1) mountain range, (2) site (elevational band within mountain range), (3) tree (individual trees within sites) and (4) tree growth year (annual needle growth for 2016, 2017, and 2018). All statistical analyses were performed in R v.4.0.2 (R Development Core Team, 2015).

To partition trait variation within and among nested ecological scales, we developed linear mixed-effects models for each trait with measurements at the scale of individual cones, seeds and needles (cone length, $n = 1367$; cone dry weight, $n = 1367$; seed mass, $n = 2712$; seed area, $n = 2748$; number of ovules per cone, $n = 1341$; needle length, $n = 7232$; needle width, $n = 7232$; needle dry weight, $n = 7232$; and SLA, $n = 7232$). We used intercept-only models with nested random effect terms for each ecological scale (following Messier et al., 2010) using the 'lme4' package (Bates et al., 2015). Cone and seed trait models included random effects of three nested ecological scales: mountain range, site, and tree. Needle trait models included a fourth random effect for tree growth year. Needle width and needle weight were log-transformed to normalize data prior to analysing. Variance partitioning was calculated using the *varcomp.mer* function from the 'HLMdiag' package (Loy & Hofmann, 2014), and 95% confidence intervals were calculated for each component using parametric bootstrapping (500 permutations).

2.5.2 | Trait variation with broad-scale environmental gradients

To evaluate the relationships between traits and broad-scale environmental gradients, we used two-block partial least squares analysis (2B-PLS; Rohlf & Corti, 2000). 2B-PLS analysis computes new latent variables (singular vectors) for each block (matrix), that when paired, form PLS dimensions that maximize explained covariance between the two blocks. We first calculated mean trait values for each tree ($n = 137$) to create the "Trait Matrix." We then extracted environmental covariate values for each sampling site ($n = 23$), replicating the site-level environmental values for each of the six trees

from each site (n = 137) to create the "Environmental Matrix." All observations from both environmental and trait matrices were then z-standardized by centring and scaling the matrices to standard deviation units. We computed the relative variance (RV) coefficient, describing similarity between the two matrices, using the 'MatrixCorrelation' package in R (Indahl et al., 2018).

To run the 2B-PLS analysis between the environmental and trait matrices, we used the *two.b.pls* function in the 'geomorph' package (Adams et al., 2020). The outputs of the function include the weights for the linear combinations of singular vectors in the calculated dimensions, the singular vectors (environmental and trait scores from the multiple dimensions) for each tree, the singular value decomposition of the cross-covariances (SVD), the total percent covariance explained, and the correlation coefficient for each dimension. We plotted the singular vectors (environmental and trait scores) against one another for the first two dimensions.

2.5.3 | Interannual variation in foliar traits

We used linear mixed-effects models to relate interannual variation in foliar morphological traits to ecologically relevant weather variables for the 3 years from 2016 to 2018. We calculated weather variable anomalies by taking the difference between the weather variable for that site/year and the 30-year climate normals. We also calculated anomalies for morphological traits by taking the difference between the needle measurement in that year and the average needle measurement for that site across all years.

Three weather anomaly variables were retained as predictors in the linear mixed-effects models: prcpwin, prcpsum and CumlCWD. Two additional weather anomaly variables were considered but not included in the models because of multicollinearity concerns: CumlAET and sumVPD. We included the nested random intercept terms for individual trees nested within site to account for the correlated structure of the data. Separate linear mixed-effects models were estimated for each trait using the 'lme4' package (Bates et al., 2015).

3 | RESULTS

3.1 | Ecological scale of trait variation

Variance partitioning across nested ecological scales (Figures 2 and 3) showed that much of the variation in traits occurred at the scale of individual trees (18%–46%). Differences among sites explained an additional 8%–25% of the variation. Differences among mountain ranges generally explained the least amount of trait variation (0%–15%), although some traits were partially explained by this scale. For needle measurements, tree growth year (17%–30%) was slightly more important than the individual tree scale (18%–26%). Residual variance, or variance not explained by any of the ecological scales, was between 22%–57% across the different traits. However, the

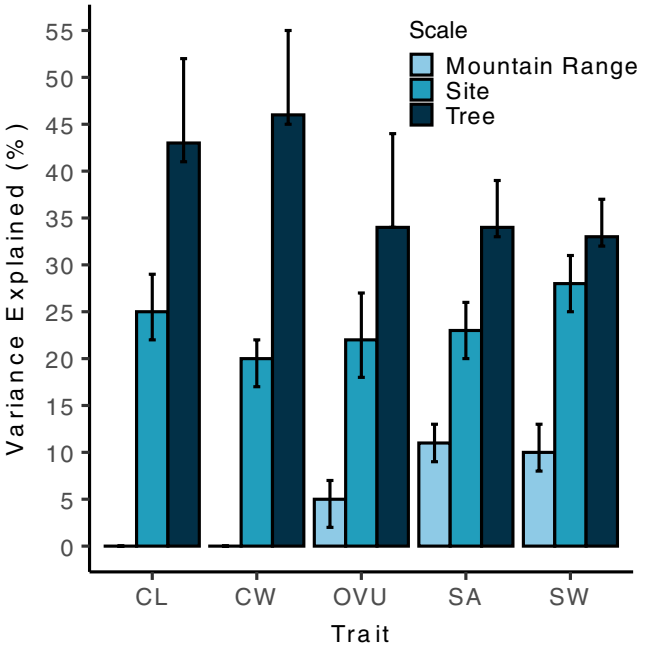

FIGURE 2 Variance components of five reproductive traits: Cone length "CL" (n = 1367), cone dry weight "CW" (n = 1367), number of ovules per cone "OVU" (n = 1341), seed projected area "SA" (n = 2748), and seed weight "SW" (n = 2712), explained by three ecological scales (mountain range, site, and tree). Error bars represent the 95% confidence intervals calculated by bootstrapping (500 runs with 'n' randomly sampled data points with replacement).

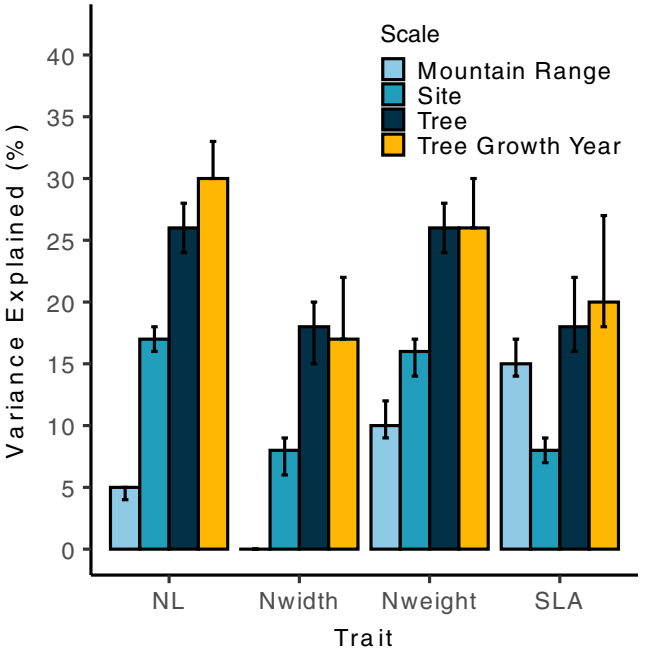

FIGURE 3 Variance components of four foliar traits: Needle length "NL" (n = 7232), needle width "Nwidth" (n = 7232), needle weight "Nweight" (n = 7232), and specific leaf area "SLA" (n = 7232), explained by four ecological scales (mountain range, site, tree, and tree growth year). Error bars represent the 95% confidence intervals calculated by bootstrapping (500 runs with 'n' randomly sampled data points with replacement).

ecological scale of trait variation differed in important ways among the types of plant traits.

Variance partitioning in reproductive traits differed for cones and seeds (Figure 2). The individual tree scale explained most of the variation for cone length (43%; 95% CI = 41–52) and cone dry weight (46%; 95% CI = 45–55), while about half as much variance was explained by site for cone length (25%; 95% CI = 22–29) and cone dry weight (20%; 95% CI = 17–23), and the mountain range scale did not explain any variance for either (0%; 95% CI = 0, 0). The number of ovules per cone showed similar variance partitioning across scales; however, individual trees explained less of the variation (34%; 95% CI = 34–44), site explained 22% (95% CI = 18–27), and mountain range explained a small percentage (5%; 95% CI = 2–7). Relative to cone traits, seed traits had less variance explained at the individual tree scale, similar variance explained at the site level, and more variance explained at the scale of mountain range. The individual tree scale explained 34% for seed projected area (95% CI = 33–39) and 33% for seed weight (95% CI = 32–37), while site explained 23% for seed projected area (95% CI = 20–26) and 28% for seed weight (95% CI = 25–31), and mountain range explained 11% for seed projected area (95% CI = 9–13) and 10% for seed weight (95% CI = 8–13). These results indicate that variation in seed traits was structured at broader scales than variation in cone traits (Figure 2).

Foliar traits differed in their variance partitioning compared to reproductive traits (Figure 3). For all traits, tree growth year and the individual tree scale explained nearly twice the variance as the site and mountain range scales. Comparing the four foliar traits for the remaining two ecological scales, site-scale variance was most explanatory for needle length (17%; 95% CI = 16–18), needle weight (16%; 95% CI = 14–17) and needle width (8%, 95% CI = 6–9) while mountain range was most explanatory for SLA (15%; 95% CI = 14–17). This shows that most of the variance in foliar traits was explained at local scales; however, foliar traits also differed along broad-scale gradients.

3.2 | Trait variation with broad-scale environmental gradients

Individual traits and environmental variables showed low correlation overall (Table S2), with 13% of the covariance in morphology explained by climate and soil conditions (RV = 0.1343, $p < 0.001$). In total, the first two dimensions in the 2B-PLS analysis explained 94% of the covariance between morphological traits and the environmental variables, with 62% of the total observed covariance summarized by the first latent dimension ($p < 0.001$) and 32% summarized by the second latent dimension ($p < 0.001$; Table 1).

The first 2B-PLS dimension was explained by the distribution of reproductive traits along the drought-stress gradient (Figure 4). Low dimension 1 trait scores (i.e. "negative" scores) describe trees with fewer, heavier and larger seeds, while the converse was true for high dimension scores (i.e. "positive" scores; Table 1; Figure 4). Specifically, the number of ovules per cone positively covaried in the first dimension (OVU = 0.3723), while seed weight and projected area negatively covaried (SW = −0.5270, SA = −0.5829). The corresponding environmental characteristics of the first dimension were described by high climatic water deficit and high summer

		Dimensions	
Matrix	Variable	1	2
Trait	Cone length	−0.0636	−0.3234
	Cone dry weight	−0.1849	−0.1217
	Number of ovules per cone	0.3723	−0.0963
	Seed weight	−0.5270	0.1190
	Seed projected area	−0.5829	0.2398
	Specific leaf area	0.0348	0.6478
	Needle width	0.0765	−0.2604
	Needle length	−0.3814	−0.1872
	Needle weight	−0.2304	−0.5195
Environment	Available water storage	0.5296	0.0904
	Cumulative actual evapotranspiration	0.2964	0.3346
	Winter precipitation	0.0735	−0.3443
	Summer precipitation	0.4425	0.5913
	Cumulative climatic water deficit	−0.5258	0.3101
	Summer vapour pressure deficit	−0.3924	0.5617
Percentage of total variance explained		62.17	32.26
Correlation		0.45	0.44

TABLE 1 Results of partial least-squares analysis of the trait-environment correlation matrix, quantifying the covariation between trait and environmental matrices for the first two dimensions. The scores associated with each trait and environmental variable represent the combination of the singular vectors from both matrices that explain the covariance for that particular dimension. Negative scores represent the low end of the dimension, while positive scores represent the high end of the dimension. 'Correlation' is Pearson's correlation coefficient between singular vector scores and *p*-values obtained from permutation testing ($n = 1000$) and estimates the strength of the relationship

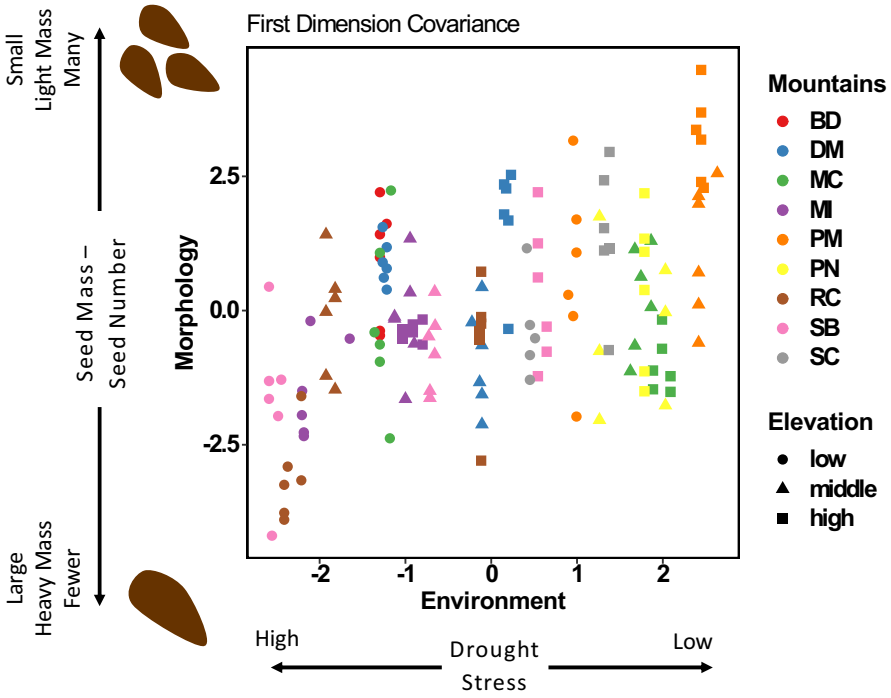

FIGURE 4 Covariance of morphological scores against environmental scores for the first dimension in 2B-PLS. Each point (n = 137) represents a tree from one of the three sampling sites (elevations) within each of the nine mountain ranges. The first dimension describes the relationship between the drought stress gradient (high vs. low; x-axis) and reproductive investments in seed size and number per cone (y-axis). Loadings of individual morphological and environmental variables on the first 2B-PLS dimension are given in Table 1.

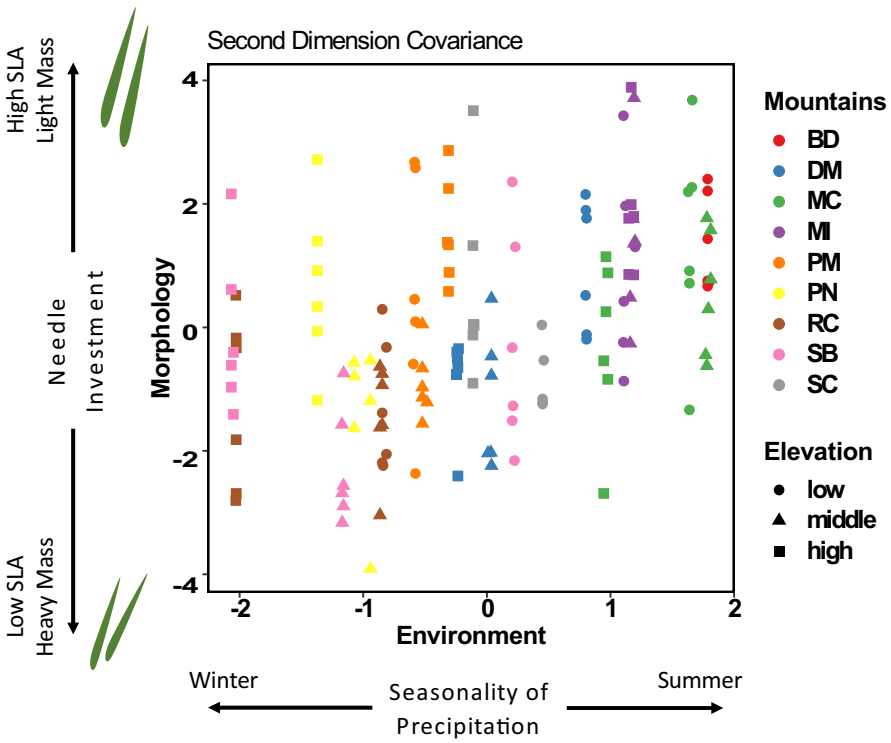

FIGURE 5 Covariance of morphological scores against environmental scores for the second dimension in 2B-PLS. Each point represents a tree from one of the nine mountain ranges (n = 137). The second dimension describes the relationship between the seasonality of precipitation (winter vs. summer; x-axis) and needle investment strategies (y-axis). Loadings of individual morphological and environmental variables on the second 2B-PLS dimension are given in Table 1.

vapour pressure deficit for the low end (CumICWD = −0.5258, sumVPD = −0.3924), and high available water storage and high summer precipitation for the high end (AWC = 0.5296, prcpsum = 0.4425; Table 1).

The second 2B-PLS dimension of trait and environmental space was explained by the distribution of foliar trait values along a gradient of precipitation seasonality, as defined by differences among sites that received high levels of winter precipitation (low scores on the second dimension) versus high levels of summer precipitation (high scores on the second dimension; Figure 5). Thus, the environmental condition of high winter precipitation (prcpwin = −0.3443) was associated with heavier needles (N_{Weight} = −0.5195), while high summer

precipitation (prcpsum = 0.5913) was associated with higher SLA (SLA = 0.6478; Table 1). Higher SLA was also associated with higher summer vapour pressure deficit and higher climatic water deficit (sumVPD = 0.5617, CumlCWD = 0.3101; Table 1).

3.3 | Interannual variation in foliar traits

Our results show significant effects of interannual weather variation on foliar morphology. Years that were drier-than-average overall (i.e. higher climatic water deficit) produced wider needles with higher SLA (Table 2). Conversely, in years with greater-than-average winter precipitation, needles were heavier and narrower, and with lower SLA, than average (Table 2). After accounting for the effects of overall aridity, years with greater-than-average summer (growing season) precipitation produced needles with substantially greater size in all dimensions, which were longer, wider and heavier, with higher SLA (Table 2).

4 | DISCUSSION

In this study, we evaluated the ecological scale of intraspecific trait variation for a widespread dryland tree species, *P. monophylla*. We found that the highest proportion of trait variation was explained at the scale of individual trees. However, a substantial portion of the variation occurring among sampling sites was strongly related to regional environmental gradients, which may provide indirect evidence that particular trait values are adaptive in different environments. For example, trees from drier sites produced fewer, larger seeds than trees from more mesic sites, suggesting trade-offs in reproductive investment across gradients of environmental stress. Additionally, seasonal precipitation patterns were correlated with variation in foliar traits associated with resource acquisition, such as SLA, and the trait-environment relationships observed across spatial gradients were consistent with foliar trait variation in response to interannual weather conditions. While this study does not demonstrate the adaptive value of traits, quantifying trait variation across multiple ecological scales and the strength of trait-environment relationships can inform our understanding of how populations may adapt to climate change.

4.1 | Ecological scale of trait variation

The results from the variance partitioning analysis generate three main takeaways. First, for *P. monophylla*, the largest portion of trait variance was explained at the individual tree scale (Figures 2 and 3). Phenotypic variation at local scales has been observed in other semi-arid species, including a closely related species (*Pinus edulis*), for which variation was attributed to genetic variation related to trade-offs in resistance to multiple stressors (Mopper et al., 1991). Conversely, local-scale variation may reflect plastic responses to abiotic and biotic heterogeneity (e.g. in microclimatic conditions, soil characteristics, and biotic interactions), although phenotypic plasticity is also known to have a heritable genetic basis (Scheiner, 1993). High levels of trait variation among *P. monophylla* individuals can indicate the presence of a broad range of phenotypes at local scales, which may facilitate the in situ persistence of local populations under climatic stress (Bolnick et al., 2011; Jump & Peñuelas, 2005; Siefert, 2012). Further studies, such as common garden experiments, could determine the adaptive value of each trait and help to disentangle the extent to which phenotypic variation is genetic or plastic (Violle et al., 2012).

Second, interannual variation in needle traits that were measured for three consecutive growth years explained a high proportion of total trait variation (Figure 3). These results suggest that some foliar traits expressed by *P. monophylla* are phenotypically plastic and respond to environmental variation. Given the potential for future increased aridity across *P. monophylla*'s distribution, plasticity in functional traits may augment the species' resilience to climate change (Funk et al., 2016; Nicotra et al., 2010). These results encourage further exploration into understanding how *P. monophylla* will respond to drought and increased temperature, possibly through mechanisms described in other studies like altering leaf chemistry or changing biomass allocation strategies (Ghalambor et al., 2007; Nicotra et al., 2010).

Finally, although the mountain range and site levels explained less variance compared to the individual-tree scale, our results show

TABLE 2 Regression coefficient estimates (±standard error) for linear mixed-effects models of annual needle trait anomalies in 2016, 2017, and 2018 in response to interannual weather variation. Trait anomalies were calculated for each year by subtracting the site-level mean needle measurement across all years from the average needle measurement in the respective year. Weather anomalies were calculated for each year by subtracting the site-level 30-year climate normal from the annual value in the respective year. Predictor variables were *z*-standardized to directly compare effect sizes

Trait	Winter precipitation anomaly	Summer precipitation anomaly	Climatic water deficit anomaly
Needle weight anomaly (g)	0.001 ±0.0002***	0.0007 ±0.0003**	−0.0009 ±0.0005
Needle length anomaly (mm)	0.07 ±0.07	0.99 ±0.10***	−0.19 ±0.18
Needle width anomaly (mm)	−0.03 ±0.01**	0.06 ±0.01***	0.13 ±0.02***
Specific leaf area anomaly (mm^2/mg)	−0.02 ±0.004***	0.01 ±0.006*	0.05 ±0.01***

*$p < 0.05$.; **$p < 0.01$.; ***$p < 0.001$.

that certain traits did vary over broader environmental gradients, influenced both by elevation and latitude. This was the case for seed size (weight and area), as well as for needle traits (weight and SLA). The second part of our analysis quantified the covariance between these particular traits and different environmental gradients.

4.2 | Trait variation with broad-scale environmental gradients

Although paleoecological studies on *P. monophylla* have suggested that the species' genetic makeup is relatively homogeneous due to a rapid late-Holocene migration (Cole et al., 2013), our findings show that there is high phenotypic variation within and among distinct provenances. The dominant axes of trait variation that we observed, which showed contrasts in reproductive investment allocations (cones with many small seeds vs. fewer large seeds) and foliar morphology (resource-conservative vs. resource-acquisitive traits), represent fundamental ecological trade-offs that are well documented in the literature (Westoby et al., 2002).

The first latent dimension in trait-environmental space showed the fundamental trade-off between seed size and seed number (Westoby et al., 2002) distributed across a drought-stress gradient (Figure 4). This describes the trade-off where investment in larger seeds can increase regeneration success in stressful environments, but at the cost of producing fewer seeds (Cochrane et al., 2014; Muller-Landau, 2010). Alternatively, plants may produce many seeds that have smaller mass (i.e. less tolerant of environmental stress), improving their ability to disperse greater distances from the parent and increasing regeneration rates in favourable environments (Laughlin, 2014). Similar to plant seed strategies for other arid *Pinus* species (Salazar-Tortosa et al., 2019), trees in the driest and warmest sites produced cones with the largest and heaviest seeds, but fewest in number. Importantly, our study assessed reproductive strategies at the scale of individual cones; among-tree comparisons of total seed production require multiple years of observations because *P. monophylla* is a masting species and total seed production is known to fluctuate synchronously among years.

The second dimension in trait-environmental space represented the well-known trade-off between leaf investment strategies (i.e. 'the worldwide leaf economics spectrum'), where along a continuum of resource availability, populations at the endpoints either rapidly acquire resources or maximize the conservation of resources (Albert et al., 2011; Wright et al., 2004). Our range-wide study of *P. monophylla* provenances showed that the propensity for either resource-conservative or resource-acquisitive foliar traits covaried with seasonal patterns of precipitation, which is not unexpected given that amount and timing of precipitation control many biological processes in arid ecosystems (Noy-Meir, 1973). Our results support the findings of previous studies from semi-arid regions with winter-dominated precipitation regimes where tree species typically have conservative growth strategies, producing heavy and wide needles with low SLA to reduce water loss (Greenwood et al., 2017; Grossiord et al., 2017; López et al., 2010). At the other end of the precipitation seasonality gradient, our southeastern mountain ranges are influenced by monsoonal precipitation patterns that create infrequent but large pulses of summer moisture. Despite experiencing generally hot and dry summer conditions, *P. monophylla* trees on these sites showed acquisitive growth strategies with lighter needles and higher SLA. The timing of moisture availability proved more important for needle traits than total water availability.

4.3 | Interannual variation in foliar traits

Annual changes in foliar morphology between years (2016–2018) indicated phenotypically plastic responses of *P. monophylla* trees to environmental variation, as has been observed for other pine species in arid environments (López et al., 2010; Sánchez-Gómez et al., 2011). The results of our analysis of trait responses to interannual variation in weather were generally consistent with our findings of trait-environment relationships at the regional scale. Years with higher-than-average winter precipitation produced heavier needles with lower-than-average SLA, whereas years with higher-than-average summer precipitation produced long needles with higher SLA. Although contrasting with to reported trends from other studies that observed reduced needle area in response to higher moisture stress (López et al., 2010; Sánchez-Gómez et al., 2011), drier years with greater water deficits produced needles with higher SLA, consistent with recent findings for *Pinus ponderosa* occurring in the same region as our study (Putz et al., 2021).

In the U.S. Intermountain West, winter precipitation recharges soil moisture and initiates spring photosynthesis. In contrast, summer precipitation can extend positive growth effects such as sustained leaf expansion into the post-melting period (Ziaco et al., 2014). This may explain why years with greater-than-average summer precipitation showed the greatest needle length. In a study that evaluated morphological needle traits for the closely related *P. edulis*, needle length increased with both pre-monsoon (e.g. winter precipitation) and monsoonal precipitation, but decreased with vapour pressure deficit (Guérin et al., 2018). These results are similar to our findings on the predicted effect of foliar growth during weather anomalies associated with seasonal patterns of precipitation and water deficit.

The fact that interannual variation in needle traits was consistent with the trait-environment relationships observed across spatial gradients suggests that some or all of the trait variation among sites and trees may simply reflect plastic responses to variation in the environment. Moreover, variation among populations in their level of phenotypic plasticity may influence their capacity to respond plastically to rapid environmental change (Schlichting & Smith, 2002). Ultimately, determining the extent to which plastic responses reflect adaptive, rather than passive, responses to the environment will require experiments comparing multiple seed sources in a common environment.

5 | CONCLUSIONS

Tree species worldwide are facing increasingly severe and frequent drought events associated with climate change (Allen et al., 2010). These effects are particularly evident in dryland forests and woodlands, where tree species already inhabit arid climates. Our finding that a high proportion of trait variation in *P. monophylla* occurs among individuals within sites suggests that within-population adaptive capacity may be possible, as the presence of a range of phenotypes can allow a population to persist in variable environments. However, the shifts in trait values that will be necessary to adapt to projected future conditions are still unknown, and recent canopy dieback and tree mortality observed across broad environmental gradients indicates that long-term persistence is uncertain (Flake & Weisberg, 2019).

We have also identified that variation in reproductive investment with seed mass and cone-level seed number responds to a broader aridity gradient, potentially providing indirect evidence of adaptation to local environmental conditions. This poses a unique situation when considering restoration or assisted migration for populations at risk of drought-induced mortality (McLachlan et al., 2007; Williams & Dumroese, 2013). While management interventions could prioritize seed collection from the driest populations (i.e. larger, heavier seeds), differences among individuals may provide sufficient in situ variation to recover from natural disturbances and adapt to changing conditions.

Our findings that functional traits in *P. monophylla* varied across multiple ecological scales suggest that using mean trait values to represent widespread species in predictive modelling may not adequately predict the range of potential responses. There remains a need for a better understanding of functional trait variation for other species, where knowledge of intraspecific variation in functional traits is lacking. Although there have been computational and data constraints in incorporating intraspecific trait variation into models (Moran et al., 2016), it is important that continued progress is made on the development of modelling frameworks to incorporate intraspecific trait variation (Chardon et al., 2019; Peterson et al., 2019) and the generation of necessary spatial datasets on functional plant traits along key ecogeographic gradients.

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CONFLICT OF INTEREST

The authors declare that they have no competing interests.

DATA AVAILABILITY STATEMENT

All data are publicly available on the Dryad Data Repository: https://doi.org/10.5061/dryad.69p8cz953.

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BIOSKETCHES

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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