Title: **Plasticity, geographic variation and trait coordination in blue oak drought physiology**

Running title: **Plasticity drives oak trait integration**

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**Summary**

Our ability to predict drought stress across the landscape remains limited. This uncertainty stems in part from an incomplete understanding of within-species variation in hydraulic physiology, particularly coordinated variation across multiple traits. This variation reflects genetic differentiation among populations (ecotypic variation) and phenotypic plasticity. We examined among-population differentiation in morphological and hydraulic traits in California blue oak (*Quercus douglasii*) using a 30 year-old common garden. We compared trait differentiation and trait-trait coordination in the garden to wild phenotypes from the original source populations. We found remarkably limited among-population differentiation in all traits in the common garden but considerable site-to-site variation in the field that could rarely be explained with site climate variables. Trait-trait relationships were also stronger in the field than in the garden, particularly links between leaf morphology, leaf hydraulic efficiency and stem hydraulic efficiency. Only four trait-trait relationship were present in both the wild and garden, but 12 of 45 relationships showed significant wild phenotypic correlations, with strong coordination among leaf and stem hydraulic efficiency apparently mediated by leaf size. Ultimately, we found limited evidence for ecotypic variation but considerable geographic in phenotypic integration in the wild, suggesting considerable acclimation potential in the face of climate change.

**Introduction:**

In the 21st century, trees living in a hotter, more variable and often drier world will need to acclimate or adapt to avoid local extirpation. Recent drought- or heat-induced forest mortality events highlight the vulnerability of even highly drought-adapted forests to climate change (Allen *et al.* 2010; Brodribb, Powers, Cochard & Choat 2020; Hammond *et al.* 2022). Unfortunately, despite multiple decades of concerted effort to understand the causes of drought-induced forest mortality, we still struggle to predict when and where trees will die off during drought (Trugman, Anderegg, Anderegg, Das & Stephenson 2021).

Part of the large uncertainty about drought vulnerability is a poor understanding of physiological variation within species (Trugman *et al.* 2021). Within-species variation can be substantial (Martinez-Vilalta *et al.* 2009; Mclean *et al.* 2014; Anderegg *et al.* 2021) and can decrease climate vulnerability in some populations (Laforest-Lapointe, Martinez-Vilalta & Retana 2014; Garcia-Forner, Sala, Biel, Savé & Martinez-Vilalta 2016). Drought resistance is the complex result of numerous plant traits, all of which potentially vary across populations within a species. Xylem resistance to embolism, often characterized by P50 or the water potential inducing 50% xylem embolism, has been identified as a key drought tolerance trait (i.e. a trait that allows a plant to experience drought stress without suffering physiological damage, (Levitt 1980; Anderegg & HilleRisLambers 2016)), that mediates mortality differences among species (Anderegg *et al.* 2016). However, within individual species, P50 is often quite consistent across populations (Lamy *et al.* 2013). For instance, in blue oak (*Quercus douglasii* Hook & Arn), a culturally and ecologically important tree species that dominates many of the oak savannas in California, USA, Skelton *et al.* (2019) previously found no evidence for local adaptation or plastic differences in leaf or stem P50 across blue oak's geographic range. This implies that the threshold for hydraulic damage is remarkably consistent across blue oak populations, despite large geographic differences in water availability (Fig 1).

How, then, do species such as blue oak adjust physiologically to deal with geographic variation in drought stress if their tolerance is fixed? The answer likely lies in coordinated adjustments of numerous traits, particularly drought avoidance traits (traits that allow a plant to avoid experiencing drought stress under water deficit). For example decreasing leaf area to sapwood area ratio ($A_L$:$A_S$) or increasing tissue-specific hydraulic efficiency can help plants avoid drought stress by minimizing the water potential drop required to maintain transpiration

fluxes (Gleason, Butler, Waryszak & Graham 2013; Mencuccini *et al.* 2019). Previous studies have found conflicting patterns of trait coordination within species, ranging from consistent increases in tissue robustness (leaf mass per area and wood density) and decreases $A_L$:$A_S$ in dry populations of multiple Australian tree species (Anderegg *et al.* 2021) to extremely unpredictable patterns of trait coordination within various Iberian tree species (Rosas *et al.* 2019). Indeed, the extent to which physiological and morphological traits are coordinated within species across different environments remains poorly understood (Blackman, Aspinwall, Resco de Dios, Smith & Tissue 2016). It remains an open question how individual species coordinate variation across many traits to develop drought resistant phenotypes in dry places, as broad evolutionary patterns of trait covariation among species often break down within species (Anderegg *et al.* 2018; Messier, Violle, Enquist, Lechowicz & McGill 2018; Rosas *et al.* 2019).

Equally important to the total amount of within-species variation are the drivers of this variation. Intraspecific variation can arise from two distinct processes with drastically different implications for near-term climate responses. First, genetic differentiation among populations can drive spatial phenotypic variation, caused be either neutral processes (e.g. drift, founder effects) or spatio-temporal variation in natural selection on heritable fitness-related phenotypes that leads to local adaptation of functional traits (Alberto *et al.* 2013). Substantial geographic variation in drought physiology due to genetic differentiation among populations would imply that certain populations or genotypes (and not others) are drought resistant and that gene-flow (assisted or natural) is necessary for other populations to manifest improved drought resistance (Hoffmann, Miller & Weeks 2021). Population-level genetic differentiation is widespread in plants, particularly species with large population sizes (Leimu & Fischer 2008; Savolainen, Lascoux & Merilä 2013). Indeed, provenance trials or common gardens (where multiple populations of a species are planted in a common environment) often detect genetic differentiation in performance (e.g. growth) among populations in trees (Alberto *et al.* 2013; Ramírez-Valiente, Santos del Blanco, Alía, Robledo-Arnuncio & Climent 2022). While phenotypic differences among populations growing in a common environment cannot demonstrate local adaptation *per se* (i.e. that among-population genetic variation is adaptive), traits showing among-population genetic differentiation that is related to the climate of the source population can highlight phenotypes that may show the fingerprint of past selection (Schwinning, Lortie, Esque & DeFalco 2022).

Alternatively, trait plasticity, or the ability of a genotype to manifest a broad range of phenotypes depending on environmental cues, can generate geographic variation in water stress-related traits (Blackman, Aspinwall, Tissue & Rymer 2017). If plasticity drives geographic trait variation (and plasticity itself does not differ among populations), all populations of a species could potentially manifest drought resistant traits given the right environmental cues. As sessile organisms that experience a range of environments over their lifetime and even in different parts of the same organism (e.g., light availability in different parts of the canopy), plants show marked plasticity in many traits (Poorter, Niinemets, Poorter, Wright & Villar 2009; Palacio-López, Beckage, Scheiner & Molofsky 2015; Keenan & Niinemets 2016). Indeed, substantial plastic responses to drought and cold stress have been observed in multiple tree species (Gimeno, Pías, Lemos-Filho & Valladares 2009; Gárate-Escamilla, Hampe, Vizcaíno-Palomar, Robson & Benito Garzón 2019).

We quantified the extent and drivers of geographic variation in drought-related traits within mature blue oak trees. Recent seedling experiments in blue oak (B. McLaughlin et al., 2022; B. McLaughlin et al. in prep) and other oak species (Ramírez-Valiente & Cavender-Bares 2017; San-Eufrasio *et al.* 2020) have revealed genetic variation in the performance of seedlings under drought related to their climate of origin. However, the extend of ecotypic variation in adult oaks remains largely unknown due to the difficulty of maintaining common garden experiments. Meanwhile, blue oak has also shown substantial plastic changes in leaf morphology during severe drought (Weitz 2018), hinting at its large potential for phenotypic plasticity. Thus, we investigated how blue oak, which grows across a huge range of water availability (Fig 1), manifests phenotypic variation across the landscape. This could manifest as geographic variation in drought avoidance traits such as hydraulic efficiency and leaf area:sapwood area ratios, as well as variation in drought tolerance traits beyond P50, such as leaf robustness (specific leaf area or SLA, leaf dry matter content or LDMC). We then attempt to disentangle the extent of among-population genetic differentiation versus plasticity in this phenotypic variation and trait coordination.

Specifically, we asked 1) how much do drought-related traits vary across the landscape, 2) in a 30 year old, reproductively mature common garden, is there evidence for among-population genetic variation underlying this landscape trait variation and 3) how is drought resistance coordinated across different traits and tissues, in common garden and wild

140 populations? We sought to disentangle the relative roles of population-level differentiation
141 versus plasticity by measuring drought-related traits in a common garden experiment compared
142 to the traits of the source populations in the wild. In the garden, trait differences between
143 populations are indicative of between-population genetic differentiation (genotype or G effects,
144 assuming limited non-genetic carryover such as maternal effects). Meanwhile, variation
145 measured in the wild source populations represents a combination of genetic and plastic effects
146 (G + environment or E effects + genotype-by-environment or GxE effects). Thus, the difference
147 between trait variation in the common garden (G only) and the wild (G + E + GxE) can provide
148 some inference about the extent of plasticity.
149
150 **Methods:**
151 Blue oak (*Quercus douglasii* Hook & Arn.) is a deciduous species, which is endemic to
152 California but widespread and abundant throughout the state in low elevation woodlands around
153 the California Central Valley (Fig. 1, Stahle et al., 2013). Blue oak experienced substantial and
154 spatially widespread mortality during a major drought from 2012-2016, particularly in the
155 southern portion of its geographic range (Brown, McLaughlin, Blakey & Morueta-Holme 2018;
156 McLaughlin *et al.* 2020). This mortality highlights the potential vulnerability of blue oak in a
157 changing climate, necessitating an improved understanding of blue oak drought tolerance in
158 space and time to support proactive oak management. We built on the work of Skelton et al.
159 (2019) on xylem vulnerability to embolism to quantify how morphological and hydraulic traits of
160 leaves and stems beyond P50 vary across seven populations of blue oak in the wild and in a ~30
161 year-old, reproductively mature common garden. These populations were selected to span the
162 geographic range and range of moisture availability of *Q. douglasii* (Fig. 1, Table S1), using only
163 populations whose original acorn source (for the common garden) had been accurately relocated,
164 and whose source populations were accessible based on current land tenure.
165
166 *Climate data*
167 Climate data for the source populations, both 1951-1980 climate normals and 2017-2018 water
168 year meteorology (the year of trait sampling), were extracted from the California state-wide
169 Basin Characterization Model (Flint, Flint, Thorne & Boynton 2013). Only historical source
170 population climate normals were used for garden analysis, while historical climate, sampling

171 year meteorology, and the sampling year anomaly (sampling year – 30yr normal) were used for
172 analysis of wild traits.
173
174 *Common garden sampling*
175 To investigate the amount of among-population genetic trait differentiation, we sampled an
176 existing provenance trial/common garden planted at the Hopland Research and Extension Center
177 (CA, USA), a fairly mesic site for blue oak (Figure 1). This trial was planted in 1992 with acorns
178 collected from 26 *Q. douglasii* populations across California and planted in a randomized block
179 design (J. McBride, pers. comm.; see also McBride *et al.* 1997). One year-old seedlings were
180 planted into the garden in six replicated blocks with nine sub-replicate individuals per population
181 per block. Individuals were grown from bulked acorns collected from 10 maternal trees per
182 population, and thus represent some combination of half sibs and more distant relatives (families
183 were not tracked at planting). In 2001-2002, six of the nine sub-replicate individuals per
184 population were thinned in each block to reduce competition. By 2018, mean tree height was
185 3.79 m, and 13 of the 468 planted individuals had died (Papper & Ackerly 2021). Due to the
186 time-intensive nature of hydraulic phenotyping, we subsampled seven populations, specifically
187 selected to capture as much of *Q. douglasii'*s aridity range as possible (Fig. 1). For each of the
188 seven populations, we sampled five to six individuals (one per block in 5-6 blocks) for hydraulic
189 traits, leaf traits and branch wood density. Between late-April and mid-June of 2018, we
190 collected one to three >1 m long branches to subsample for hydraulic measurements from the
191 sunlit, south-facing portion of the canopy in the early morning (before 9 am local time). We
192 relaxed the xylem by repeatedly recutting the stem underwater, and then placed the branches in
193 large plastic bags for immediate transport back to the lab. One to two individuals from each of
194 the seven sampled populations were collected from the garden at each sampling point (once or
195 twice weekly) to control for temporal variation in hydraulic traits. Three small terminal twigs
196 and subtending leaves were collected at the same time for the measurement of morphological
197 traits. Tree diameter at 50 cm and total tree height was also surveyed for every common garden
198 tree in the winter of 2017 and used to calculate the total stem volume of the largest stem
199 (assuming the stem was a cylinder) as a metric of total growth rate since planting.
200
201 *Wild population sampling*

We collected branches for trait measurement from six to eight mature trees from the source populations used in the garden. The exact maternal trees from which acorns were collected for the common garden could not be located, so the selected wild trees represented a sampling of reproductively mature, visibly healthy trees near the documented acorn collection location. Within a location, individuals were 5-50 m apart, often including all large trees present within a 500 m search area around the original collection site. Minimal ongoing or historic tree mortality (e.g., dead snags or stumps) were noted at the source populations and all wild trees were at least 30 yrs old, making adaptive evolution since seed collection unlikely. Large branches (typically >1.5 m long and >4 cm basal diameter) from the south-facing canopy were collected in the same manner as in the common garden. Short tree cores were also collected from the sampled trees for calculation of radial growth rates for the past decade. Sites were sampled between late April and early June 2018, roughly controlling for time since leaf out (i.e. earlier leafing sites were collected first so that all sites could be collected after full leaf expansion, ~1-2 months after leaf flush).

*Morphological Traits*

We selected three terminal branches from the south-facing sun-exposed canopy for morphological measurements (Table 1), cut at the prior year bud scar and including all current year stem and leaf tissue. Branches were rehydrated for >12 hrs using the 'partial rehydration' method (Pérez-Harguindeguy *et al.* 2013). We then measured specific leaf area (SLA, $cm^2$ wet leaf area per $g^{-1}$ leaf dry mass), leaf dry matter content (LDMC, g leaf dry mass per $g^{-1}$ leaf wet mass), mean leaf size ($cm^2$ fresh leaf area), leaf dry mass to stem dry mass ratio ($M_L$:$M_S$), and leaf area to sapwood area ratio ($A_L$:$A_S$, $cm^2$ leaf area per $mm^2$ stem area underneath bark, or the inverse of the Huber Value) on these current year terminal twigs and all of their subtending leaves using calipers, balances, and ImageJ image analysis software. We calculated mean leaf size as the average area per leaf for each terminal branch. We also measured wood density (WD, g dry mass per $cm^3$ wet volume) on one to five branch disks 2-5 cm in diameter cut from the basal end of branches collected for hydraulic sampling. Bark was removed from branch disks and wet volume was measured via water displacement on a balance.

For all analyses using individual or population average traits, we also included leaf and stem P50 values (the xylem tension causing 50% embolism) from Skelton *et al.* (2019), which

were measured on branches collected at the same time and using the same methods as branches collected for hydraulic efficiency measurements reported here. However, P50 measurements had few or no replicates per individual and were thus not suitable for branch-level analyses.

*Hydraulic traits*

Due to extremely long vessel lengths in oaks (often >1 m in branches of *Q. douglasii*, based on pressurized branches recut at the basal end until air bubbles were seen at the distal end; RPS and LDLA *pers. obs.*), classic hydraulic methods using stem segments were impossible without considerable open vessel artifacts. Instead, we performed hydraulic measurements on terminal branches of 1-2 mm basal diameter using the vacuum chamber method (Kolb, Sperry & Lamont 1996). We targeted current year growth when possible (similar to branch sampling for morphology), but included up to three years of growth when the current year was <2 cm long and stem diameter was not sufficiently large to fit in hydraulic tubing. For each terminal branch, all subtending leaves were cut under water at the petiole with a razor blade, and the entire stem was inserted into a vacuum chamber. Flow from a scale, through the branch and out the cut petioles was induced by subjecting the stem to a ~60 kPa vacuum. Nevertheless, any stem that was suspected of having an open vessel (i.e. any stem that had a high apparent conductance) was checked for open vessels by attaching to pressurized nitrogen for ~10 minutes and checking under water for air bubbles from the stem or petioles. The leaf area of all subtending leaves was measured via flatbed scanner and ImageJ (Schneider, Rasband & Eliceiri 2012), basal stem diameter calculated from 4 radii, and the length of the stem and all branches measured with digital calipers.

Raw stem conductance was standardized two different ways. First, raw conductance was standardized per unit leaf area, here termed $k_{stem}$, indicating leaf area-specific stem conductance (i.e. not standardized by path length, so including the effects of differential stem growth in long versus short stems, Table 1). Raw conductance was also divided by stem cross-sectional area and multiplied by total stem length (including length of branches if stem was branched) to produce sapwood area specific conductivity, or $K_s$.

Leaf hydraulic conductance was also measured on terminal branches (cut from the same >1 m long branch as stem conductance) using the 'rehydration kinetics' (RK) method (Brodribb & Holbrook 2003). Because leaves often had very small and irregular petioles, we measured

264 multiple leaves attached to a terminal twig. Leaf conductance was an order of magnitude lower
265 than stem conductance, meaning the effect of the stem in the conductance observed via the RK
266 measurements was negligible. Total leaf area for each sample was calculated via flatbed scanner
267 and ImageJ for each sample, and leaf-area specific leaf conductance, $k_{leaf}$ was calculated. Only
268 measurements from leaves with an initial water potential < −0.2 MPa and > −2 MPa were
269 analyzed to avoid large measurement errors in samples with small pressure gradients or potential
270 embolism. Skelton et al. (2019) measured leaf and stem xylem vulnerability to embolism on the
271 same individual using the optical method. Large (>1m) branches for vulnerability curves were
272 also collected in the spring of 2018, often on the same day as for hydraulic measurements
273 reported here. We include the P50 measurements (xylem potential causing 50% embolism) from
274 Skelton et al. 2019 for comparison with the traits measured here, but note that replication was
275 generally much smaller for P50 (1-2 replicates per individual as opposed to 3+ for all traits
276 reported here) so analyses could only be performed at the individual rather than replicate level
277 for P50.
278
279 *Growth rate:*
280 We calculated growth rates for the common garden individuals based on a survey of tree
281 diameter at 50 cm and stem height during the winter of 2017, when trees were approximately 27
282 years old. We tested for evidence of local adaptation by modeling height growth as a function of
283 'transfer distance' between the source location and the common garden using generalized
284 additive mixed models penalized spline smoothers for climate predictors (gamm function from
285 the *mgcv* package in R) with population as a random intercept. A concave down relationship
286 between growth and transfer distance that peaks at transfer distances near zero would indicate
287 'home site advantage' or that populations from climates most similar to the garden climate
288 perform best in the garden, though the fact that the garden was at the mesic edge of blue oak's
289 distribution decreases our power to detect this peak in transfer distance. 30 yr climate normals
290 for the seed sources were used as potential predictors and the best fit model was selected using
291 AIC. Results were qualitatively similar with height and 50 cm diameter, so only height is
292 reported.
293 Growth rates were calculated for the wild trees from tree cores, which were collected via
294 increment borer at 1.3 m height; cores were mounted and sanded, and 5 years worth of rings

identified using a dissecting microscope. The length of the 2013-2018 5-year growth period was measured via digital calipers and radial growth was converted to Basal Area Increment (BAI) based on tree DBH. Tree BAI is a function of tree size (Fig. S1), so BAI was standardized for tree size by calculating the percent of size-specific maximum Basal Area Increment (BAI) over the 2013-2018 period. Size-specific maximum BAI (the fastest rate a tree of a given DBH was observed to grow) was calculated for each tree's DBH based on the $90^{th}$ quantile regression of BAI versus tree DBH for all study trees (n=32) plus tree core data from 29 trees spanning five additional sites across California to expand the range of sampled tree sizes (total DBH range 7.8cm-104cm, Fig. S1). The observed BAI was then divided by the maximum BAI for each tree to produce '% max BAI'. Tree cores were collected in Oct of 2018, but could not be collected from one site due to loss of site access (n=6 sites rather than 7).

*Variance decomposition analysis:*

We performed variances decompositions, separately in the garden and the wild, on all branch-level trait measurements to quantify trait variation within canopy (among branches), among individuals within populations, and among populations. We fit linear mixed-effects models separately for the garden or the wild traits, with a fixed intercept term, a random intercept for population and a random intercept for individual nested within population. We employed the lmer() function from the *lme4* (v 1.1-28) and *lmerTest* (v 3.1-3) packages. We then extracted the random effect variance parameters, and calculated the proportion of total trait variance that was attributed to among-population differences (population random effect), individual differences within populations (individual random effect) or variation within individual tree canopies (residual variance). We also calculated the coefficient of variation (CV = trait mean / trait standard deviation) for each trait in the garden and in the wild. Finally, to compare the total trait variation in the garden versus in the wild while accounting for unequal sample sizes, we bootstrapped variance estimates, randomly sampling with replacement each dataset 1000 times with sample number set to the minimum sample size of the two datasets (wild versus garden) for each trait. We then compared the median bootstrapped trait variance for the wild versus garden.

*Among-population trait differentiation and climatic variation*

We tested for significant among-population trait differences by averaging trait values per individual and then performing one-way ANOVAs separately in the garden and in the wild, and calculated the omega-squared ($\omega^2$) as an estimate of the proportion of variance explained by among-population differences. Garden block was never a statistically significant factor in the garden, and was excluded from the final ANOVAs (fitted using the aov() function in the *stats* package, v 4.1.2). We then used AICc (Akiake's Information Criterion corrected for small sample sizes, AICc() function from the *MuMIn* package, v 1.43.17) to select the best single climatic predictors of among-population differences for each trait. First, we determined whether a random intercept for population was required to account for non-independence among individuals in a population by fitting an 'over the top' fixed effects structure (Zuur, Ieno, Walker, Saveliev & Smith 2009), including mean annual precipitation, mean annual potential evapotranspiration and mean minimum temperature, and using likelihood ratio test to determine whether the population random effect was needed (using the gls() and lme() functions from the *nlme* package, version 3.1-155). We then used AICc to select the best single climate predictor for each trait using linear models (lm in the *stats* package) or linear mixed models with a population random intercept (lmer in the *lme4* package) and assessed significance of the best predictor using t-tests, using Satterthwaite's degrees of freedom from the *lmerTest* package (Kuznetsova, Brockhoff & Christensen 2016). For the common garden, potential individual predictors included only source population 30 year climate normals (1951-1980) of mean annual precipitation ($PPT_{30yr}$), mean annual potential evapotranspiration ($PET_{30ry}$), mean annual actual evapotranspiration ($AET_{30yr}$), mean annual climatic water deficit ($CWD_{30yr}$=$PET_{30yr}$-$AET_{30yr}$), and mean annual minimum temperature ($Tmin_{30yr}$). For wild traits, potential univariate predictors included historic 30 year climate normal as well as growth year (2017-2018) weather information: wet season (Nov-May) minimum temperature ($Tmin_{gy}$), maximum temperature ($Tmax_{gy}$), precipitation ($PPT_{gy}$), potential evapotranspiration ($PET_{gy}$), actual evapotranspiration ($AET_{gy}$) and climatic water deficit ($CWD_{gy}$), as well as the anomaly of the 2018 water year from the site 30 year normal ($PPT_{anom}$, $PET_{anom}$, $AET_{anom}$, $CWD_{anom}$). We visually examined quantile-quantile plots and other patterns in the residuals to identify outliers and ensure model assumptions were met.

*Trait-trait coordination*

To examine the magnitude of phenotypic (genetic plus plastic variation in the wild) and genetic (variation in the garden) trait correlations, we calculated Pearson's correlation coefficients for all pairs of individual-averaged traits in the wild and in the common garden. We visualized the correlation structure using the corrplot() function in the *corrplot* package (v 0.92). We then used a similar procedure to the bootstrapped variance comparisons to test for significant differences between genetic and phenotypic trait correlations, randomly sampling individuals with replacement from the entire wild and entire common garden datasets to produce two populations of equal size to the smallest of the garden or wild complete pairwise observations, resampling 1000 times per trait combination. We then calculated the difference between the trait-trait correlations in each bootstrapped pair of garden and wild datasets and determined the two-tailed probability that the distribution of differences did not include 0 (e.g., alpha < 0.05 if either the 2.5$^{th}$ percentile of differences was greater than zero or the 97.5$^{th}$ percentile of differences is less than zero, alpha < 0.1 if the 5$^{th}$ and 95$^{th}$ percentile range did not include zero, and alpha < 0.2 if the 10$^{th}$ to 90$^{th}$ percentile range did not include zero).

All code for analyses and figure generation can be found at https://github.com/leanderegg/BlueOakGarden.git and all data are available on Dryad at [insert Dryad link upon acceptance](Data citation). *NOTE all data are currently in the github repository for peer review

# Results

Growth in the common garden showed relatively small among-population variation and little evidence of local adaptation. The historic PET of the seed source best explained among population differences in garden growth (using heights of all surviving individuals including all 26 original source populations), but only explained a small fraction of the variation in growth ($R^2$=0.05 for linear model, Table S2; $R^2$ = 0.06 for penalized regression spline, Fig. 1b). The relationship between climate transfer distance and growth was concave down but growth peaked at positive transfer distances (higher source PET than the garden), demonstrating little 'home site advantage' that would indicate local adaptation (Fig. 1b). Meanwhile, growth in the wild differed drastically among populations but was not strongly related to any climate variable (Table S2,

387 Figure 1c). Source environmental conditions did not appear to drive garden growth through
388 parental stress, as growth in the wild was uncorrelated with growth in the garden (Fig. S2).
389 Genetic variation among populations was low in all morphological, allocation and
390 hydraulic traits in the common garden (Fig. 2a). However, all traits except for stem sapwood
391 area-specific hydraulic conductivity ($K_s$) and leaf and stem vulnerability to embolism ($P50_{leaf}$,
392 $P50_{stem}$) showed substantial among-population variation in the wild. Among-population variation
393 in the wild was consistently 25%-30% of total trait variation in most traits, with SLA and LDMC
394 showing even larger among-population variation (46% and 40%, respectively, Fig. 2b).
395 Meanwhile, branch-to-branch variation within tree canopies consistently made up the majority of
396 trait variation in the common garden, constituting >50% of total variation in all traits except WD
397 (42% of total) and over 75% of total variation in $k_{leaf}$, $k_{stem}$, and $K_s$ (Fig. 2a). In the wild, within-
398 tree variation was typically less than 50% of total variation, except in $M_L$:$M_S$ and the three
399 hydraulic traits (Fig. 2b).
400 When traits were averaged to the individual, 40-60% of the total tree-to-tree variation in
401 almost all traits was between populations in the wild (Fig. 3a) and population differences were
402 significant in 8 of 11 traits (all but $K_s$, $P50_{leaf}$, and $P50_{stem}$) plus growth (ANOVAs $p < 0.05$, Table
403 S2). Meanwhile, typically <30% of tree-to-tree variation was between populations in the garden,
404 and population differences were only significant in 2 of 10 traits (SLA and leaf size) plus growth
405 in the garden (Table S2). Leaf size was the one notable trait that showed significant and similar
406 among-population differentiation in both the wild and garden.
407 However, despite the consistent among-population variation in wild traits, climate
408 predictors (historical climate normals, meteorology of the water year of sampling, or the
409 sampling year anomaly from historical climate) very rarely explained differences among
410 populations (Fig. 3b). Based on AICc of linear or linear mixed models (when there was support
411 for a site random intercept, see Table S2), univariate climate predictors were only statistically
412 significant for four wild traits (Fig 3b, Fig S3,S4, Table S2) with $M_L$:$M_S$ decreasing and $k_{stem}$
413 increasing with $Tmin_{gy}$, $P50_{stem}$ decreasing (growing more negative) with $AET_{30yr}$, and WD
414 decreasing with $AET_{anom}$ (though the relevance of annual anomaly for wood density of 5+ year
415 old branches is suspect). Meanwhile, in the garden three traits and growth were significantly
416 associated with source population climate (Table S2). In the garden, increasing $PPT_{30yr}$ was

417 significantly associated with decreasing wood density and increasing leaf size, while increasing
418 $PET_{30yr}$ was significantly associated with increasing SLA (Fig S3,S4).
419 The among-population variance was smaller in the garden than the wild for all traits
420 except leaf size (Fig. 4). However, the total among-individual variance was usually smaller in the
421 wild than the garden (garden:wild ratio <1), but only significantly so (alpha <0.05) for SLA,
422 LDMC, and WD based on bootstrapped variance estimates. Meanwhile, $M_L$:$M_S$, $k_{leaf}$ and $k_{stem}$
423 had similar total variances in the wild and the garden despite much larger among-population
424 variance in the wild. $K_s$, $P_{50[stem]}$ and $P_{50[leaf]}$ had similar variances in the wild compared to the
425 garden and no significant among-population differentiation in either location (Table S2), while
426 growth could not be compared because of differing metrics (% of max basal area increment vs 30
427 yr stem volume).
428 Norm of reaction plots suggest that trait values and variances may be an artifact of
429 ontogeny (younger trees in the garden than the wild) for two traits, with WD and $k_{leaf}$ having
430 consistently higher values in the garden than the wild for all populations (Fig. S5). For the
431 remaining traits, genotype x environment effects appeared prevalent (i.e. reaction norms often
432 cross). Leaf size was the only trait that did not show reaction norms of markedly opposing signs
433 across populations. As a result, population-average trait values were entirely uncorrelated in the
434 garden and in the wild except for $M_L$:$M_S$ (Fig. S2), even for the traits with similar amounts of
435 total variation in the two settings.
436
437 *Trait coordination*
438 Trait-trait coordination was much stronger in the wild than in the common garden,
439 suggesting phenotypic correlations are driven by coordinated plasticity. Only six of 55 possible
440 trait-trait correlations were significant in both the garden and the wild (Fig. 5), almost all of
441 which are unsurprising (e.g., $A_L$:$A_S$ ~ $M_L$:$M_S$, SLA ~ LDMC) or mathematically related ($K_s$ ~
442 $k_{stem}$ or $K_s$~$A_L$:$A_S$ because $K_s$ was calculated as $k_{stem}$ * $A_L$:$A_S$ * branch length). The main notable
443 correlations consistent in both the garden and the wild were positive relationships between
444 average leaf size and leaf vs stem allocation on both an area basis ($A_L$:$A_S$) and a mass basis
445 ($M_L$:$M_S$). Moreover, average leaf size was much more strongly associated with variation in
446 $A_L$:$A_S$ than number of leaves per branch in both the garden and the wild (Fig. S7), suggesting
447 that plastic leaf expansion may be a key regulator of leaf-to-stem allocation.

448 Beyond these correlations, only three additional trait correlations were significant in the
449 garden, while 10 additional trait correlations were significant in the wild (Fig 5). The change in
450 trait-trait correlations from garden to wild was significant or marginally significant ($\alpha$ <0.05 or
451 <0.1 respectively, based on 5000 bootstrapped correlation comparisons) in five trait pairs (Fig
452 S8). In four of these pairs, this trend was driven by a strengthening of correlation in the wild: a
453 increasingly negative leaf size ~ $k_{stem}$ correlation, and increasingly positive $k_{leaf}$~$k_{stem}$; $K_s$~$M_L$:$M_S$
454 and $M_L$:$M_S$~SLA correlation. Notably, hydraulic integration, namely correlations among leaf and
455 stem conductance, leaf size and $A_L$:$A_S$ was strong in the wild but almost completely absent in the
456 common garden. This plastic increase in hydraulic integration in wild trees appears to be driven
457 by leaf size, which is strongly negatively correlated with $k_{leaf}$ and $k_{stem}$ in the wild (change in
458 correlation is statistically significant for $k_{stem}$). Across the landscape, trees with smaller leaves
459 had lower $A_L$:$A_S$, but consequently greater $k_{leaf}$ and $k_{stem}$. We found no evidence for a tradeoff
460 between safety and efficiency in either leaves or stems (Fig S11).
461
462 *Trait-Growth relationships*
463 In the garden, traits were generally not strongly related to population average growth (27
464 yr height). LDMC was positively and $k_{stem}$ negatively correlated with growth rates. This
465 conflicts with expectations, if traits are presumed to drive growth (and that trait values predict
466 the past trait values that drove growth). Leaf size and $M_L$:$M_S$ were the only traits correlated with
467 growth in the expected direction, with populations with larger leaves and higher allocation to leaf
468 mass having higher average growth rates (Fig. S9), though $M_L$:$M_S$ was only marginally
469 significant.
470 In the wild, we found very little evidence for relationships between traits and growth
471 (calculated as the percent of maximum size-specific Basal Area Increment), despite much larger
472 among-population trait differentiation. The only significant relationship was a decrease in growth
473 with increasing $K_s$, which may be consistent with increasing drought avoidance in the driest
474 populations (Fig S10). However, growth was only measured in six of the seven populations due
475 to lost access at one site after initial trait sampling (due to threats from nearby illicit marijuana
476 growers). Moreover, both traits and environmental conditions and resources differ among
477 populations, making it difficult to disentangle cause versus effect.
478

## Discussion

We found very little among-population genetic differentiation but consistent among-population variation across the landscape in morphological and hydraulic traits of a widespread oak species. This landscape-scale variation, likely due to environmentally driven plasticity, could not be easily explained using gridded climate or annual meteorological data, but drove trait-trait coordination – particularly of leaf and stem hydraulic traits – that was otherwise lacking in the common garden.

*Traits in the common garden: little population-level differentiation*

The limited evidence for genetically based trait variation that we found in a relatively mesic common garden (978 mm of mean annual precipitation, greater than all but two of the sampled populations, Table S1) contrasts with the fairly widespread experimental evidence of ecotypic variation in many trees (Leimu & Fischer 2008; Alberto *et al.* 2013), other oak species (Sáenz-Romero *et al.* 2016; Ramírez-Valiente & Cavender-Bares 2017; Browne, Wright, Fitz-Gibbon, Gugger & Sork 2019; Ramírez-Valiente *et al.* 2022), and blue oak itself (McLaughlin, pers. comm.). This contrast could potentially indicate that population-level differentiation is less common in hydraulic traits than in growth and morphological traits or that differentiation is less common in reproductively mature adult phenotypes compared to the more commonly studied seedlings/saplings. Due to the difficulty of measuring physiological traits, our sample sizes were also smaller than true quantitative genetic studies of morphological traits, and thus we way have lacked the statistical power to detect subtle among-population genetic variation. However, we note that our sample sizes are similar to or larger than prior studies that have detected among-population genetic variation in hydraulic traits (e.g. in *Corymbia callophyla*, (Blackman *et al.* 2017)). We also had sufficient power to detect significant among-population differentiation in almost all traits in wild trees. Thus, even if we missed subtle among-population genetic variation in the garden, this genetic variation must be substantially smaller than plasticity.

Among individual trees in the common garden, there was also remarkably little trait coordination, even though many of these traits are correlated across species (Mencuccini *et al.* 2019; Sanchez Martinez, Martinez-Vilalta, Dexter, Segovia & Mencuccini 2020).This lack of coordination was not necessarily an artifact of limited total trait variation in the common garden. Only three of 11 possible traits showed significantly smaller total trait variation in the garden

510 than in the wild (Fig. 4), despite all traits showing less among-population variation in the garden.
511 Thus, the trait variation manifested in the garden was not merely the wild trait variance minus
512 among-site plasticity. Neither the lack of trait coordination nor the lack of correlation between
513 wild and garden trait values (Fig. S6) was thus driven by restricted garden trait variance (i.e.
514 limited statistical power). Moreover, there was limited evidence of populations converging on
515 wet-adapted trait values in the garden (Fig. S5), and only WD and $k_{leaf}$ showed offsets between
516 the wild and garden traits that might suggest that size- or age-related effects drove garden trait
517 values relative to wild trees. Rather, the garden trees growing in a relatively wet environment
518 manifested a large range of phenotypes, but this variation was uncoordinated across traits and not
519 structured by population.
520 At the same time, the only traits that showed expected relationships with growth rates in
521 the common garden were leaf to stem allocation traits (leaf size and potentially $M_L$:$M_S$), with
522 leafier populations showing faster growth. We conclude that changes to allometry were the
523 primary drivers of functional differences among populations in the common garden in line with
524 classic predictions about the drivers of growth rate variation (Lambers & Poorter 1992), and that
525 this variation in allocation was linked in part to genetically determined variation in leaf size (Fig.
526 S7). Meanwhile, leaf dry matter content (LDMC) and leaf-specific stem conductance ($k_s$) were
527 significantly correlated with growth rates, but in a direction contrary to expectations if lower
528 tissue construction costs or higher hydraulic efficiency support faster growth (Hajek, Leuschner,
529 Hertel, Delzon & Schuldt 2014). For LDMC, we interpret this as a consequence rather than a
530 cause of growth rate variation (faster growing trees had accumulated more photosynthate in their
531 leaves per unit leaf water by the sampling period and thus had higher LDMC), and for $k_s$, results
532 were driven by the two the two most arid populations that grew slowly in the garden but had high
533 $k_s$.
534
535 *Traits in the wild*
536 Meanwhile, based on the wild phenotypes it appears that spatial variation in drought-
537 related physiology is substantial in blue oak, and is likely driven by trait plasticity. In contrast to
538 the common garden results, all traits except $K_s$ and $P50_{stem, leaf}$ showed substantial among-
539 population trait differentiation across *Q. douglasii*'s geographic range. While all traits exhibited
540 large branch-to-branch variation within a canopy (in both the garden and the wild), among-

541 population trait differences were as large or larger than differences among trees in the wild (Fig
542 2b, 3a). Experimental evidence for plastic drought responses is reasonably common in the
543 literature for other oak species (Gimeno *et al.* 2009; Ramirez-Valiente, Sanchez-Gomez, Aranda
544 & Valladares 2010; Ramírez-Valiente & Cavender-Bares 2017; Ramírez Valiente, Lopez, Hipp
545 & Aranda 2019; Ramírez-Valiente *et al.* 2022), our results highlight this plasticity as a key driver
546 of trait variation across the landscape.

547 Surprisingly, this site-to-site trait variability was not strongly related to historical site
548 climate data nor meteorology of the sampling year (absolute or anomaly relative to historical
549 climate, Table S2, Fig. S3,S4). Even for the four traits that were significantly predicted by site
550 climate, water limitation was not the driver of variation. Winter minimum temperatures ($Tmin_{gy}$)
551 was the best predictor for two traits ($M_L$:$M_S$ and $k_{stem}$), perhaps indicating an early season
552 developmental temperature constraint, and a water balance metrics (some actual
553 evapotranspiration metric, $AET_{anom}$ and $AET_{30yr}$) was only a significant predictor for two traits
554 (WD and $k_{leaf}$, respectively). We hypothesize that these weak trait~climate patterns are the result
555 of *Q. douglasii*'s deep rooting strategy, which combined with the substantial geologic and
556 edaphic variation among the sampled sites to largely decouple the actual water availability (the
557 'weather underground', sensu (McLaughlin *et al.* 2020)) from above-ground climate.

558 Strikingly, the plasticity-driven trait variation across California resulted in strong trait-
559 trait coordination, particularly between hydraulic efficiency and allocation traits. Leaf and
560 branch morphology (SLA, LDMC, WD) and P50 were largely uncoupled from other traits in
561 both the wild and the common garden (Fig 5). However, $k_{leaf}$ and $k_{stem}$ significantly changed their
562 correlation strength from uncorrelated in the garden to positively correlated in the wild, and both
563 traits showed a strong correlation with both leaf size and $A_L$:$A_S$ in the wild. Collectively, this
564 resulted in strong integration across a leaf and stem 'hydraulic module', wherein trees with small
565 leaves had small $A_L$:$A_S$ ratios and high leaf area-specific leaf and stem hydraulic conductance.
566

567 *Leaf size-driven hydraulic coordination*

568 In theory, the coordination or integration of plant traits across tissues should optimize
569 whole-plant function (Reich 2014). However, across species this coordination is not universally
570 observed among tissues (Vleminckx *et al.* 2021) or types of traits (Sanchez Martinez *et al.* 2020),
571 and the actual mechanisms of this coordination (e.g., coordinated evolution, developmental

constraints, etc.) remain elusive. The leaf and stem hydraulic integration that we found across wild populations suggests that, within individual species, plastically determined leaf size, presumably coordinated by leaf expansion, may be a key mechanism coordinating hydraulic efficiency across tissues.

In the garden we saw quite weak phenotypic trait coordination. While we are not able to directly assess genetic trait correlations (as opposed to phenotypic correlations) with this historic garden, as it was not designed for quantitative genetic analysis, our results suggest that the signal, either for genetic correlations among traits or local adaptation in these phenotypes (with the exception of leaf size) is not strong. Leaf size was the only trait that showed similar among-population variation in the wild and garden (Fig 3) and evidence of local adaptation: populations from wetter source climates grew larger leaves in the garden (Fig S3) and populations with larger average leaf sizes grew faster in the garden (Fig. S9). This hints at leaf area's potential adaptive importance.

However, wild and garden leaf size were uncorrelated (Fig. S5,S6), suggesting strong environment and likely environment-by-genotype effects on leaf size. At the same time, wild trees showed strong hydraulic integration between the leaf area-specific hydraulic conductance of leaves and stems across wild populations. This coordination seems to be mediated by allocation to leaf area, relative to stem area ($A_L$:$A_S$), which was largely driven by the average size of leaves (rather than leaf number, Figure S11). Average leaf size had a larger coefficient of variation than stem diameter (0.41 versus 0.31, respectively), and had a stronger negative correlation with both $k_{leaf}$ ($\rho = -0.43$) and $k_{stem}$ ($\rho = -0.54$) than $A_L$:$A_S$ itself did with either trait ($\rho = -0.39$ and $\rho = -0.30$ for $k_{leaf}$ and $k_{stem}$ respectively). Further supporting the importance of plasticity, average leaf size was uncorrelated with either $k_{leaf}$ or $k_{stem}$ in the garden, and the increase in the correlation from garden to wild was strong for both traits and statistically significant for $k_{stem}$ ($p < 0.05$). Meanwhile, the more commonly measured sapwood-specific branch conductivity ($K_s$), which is standardized for branch xylem conductive area and path length, was highly variable but not differentiated among populations (Fig. 2) and unrelated to either leaf size or $k_{leaf}$ in the wild. This may partly be due to the difficulty of measuring path length for our $K_s$ estimates. In order to avoid open vessels in this long-vesseled oak species we measured the conductance of whole terminal branches cut at the petioles (rather than branch segments) and estimated the path length imperfectly from the total branch length. Thus, $k_{stem}$

603 (conductance of the whole branch per unit leaf area) was likely a more accurate measurement of
604 hydraulic efficiency than $K_s$ (conductivity per sapwood area for a 1cm stem length) in this study.
605 Ultimately, it appears that whole-branch conductance of terminal branches and leaf
606 conductance were coordinated in the wild not by changes in xylem efficiency itself but rather by
607 changes in leaf size, regulated partly by ecotypic variation but largely by environmental cues
608 governing spring leaf expansion. $K_s$, or sapwood area-specific hydraulic efficiency, did not differ
609 among populations either in the garden or the wild (Fig 1) and therefore could not drive this
610 pattern. A developmentally fixed hydraulic architecture (in both leaves and stems) that then gets
611 allocated to supply a variable amount of leaf area based on leaf expansion presents a
612 parsimonious mechanism for regulating whole-tissue hydraulic resistance, as regulation of
613 transpirational area may be much easier to regulate in response to environmental cues through
614 turgor driven leaf expansion than anatomical changes to xylem efficiency. Moreover, the
615 negative relationship between leaf size and $k_{leaf}/k_{stem}$ documented here contrasts with the lack of
616 relationship between $k_{leaf}$ and leaf size among species (Sack & Frole 2006)and suggests a
617 developmental constraint rather than adaptive mechanism.
618
619 *Caveat to management implications*
620 On their face, our results from mature trees might indicate that genetically informed
621 management or restoration of blue oaks may not require strong consideration of the aridity of the
622 seed source. Mature tree drought resilience appears to be determined by canalized physiological
623 damage thresholds of xylem vulnerability to drought (Skelton *et al.* 2019) and largely plastic
624 adjustments to drought avoidance-related traits (e.g. $k_{branch}$ and $k_{leaf}$). While we could not predict
625 trait variation across the landscape based on site climate (Fig 2b), the substantial among-
626 population variation in leaf-to-stem allocation and hydraulic efficiency are presumably adaptive
627 and therefore constitute plastic adjustments to drought exposure by increasing plant hydraulic
628 efficiency. This decreases the minimum leaf water potential required to attain a given rate of
629 transpiration (Whitehead & Jarvis 1981; Trugman *et al.* 2019; Mencuccini *et al.* 2019) and is
630 quite consistent with within-species adjustments to promote drought avoidance in numerous
631 other systems (Mencuccini & Grace 1995; Martinez-Vilalta *et al.* 2009; Anderegg &
632 HilleRisLambers 2016; Rosas *et al.* 2019; Anderegg *et al.* 2021).

633 Our findings of limited among-population differentiation are also consistent with the
634 relatively small amount of local adaptation found in blue oak growth rates (Fig 1) and phenology
635 (Papper & Ackerly 2021), and the relatively high rates of gene flow in blue oak (Papper 2021).
636 While other California oak species have been found to show strong genetic structure across their
637 range (Sork *et al.* 2013; Gugger, Fitz-Gibbon, Albarrán-Lara, Wright & Sork 2021), evidence
638 suggests that blue oak population differentiation across its broad geographic distribution is more
639 limited. Given the strong potential for plastic adjustments to plant hydraulics documented here,
640 this might suggest that most populations can (and may) manifest more drought avoidant
641 phenotypes in a warmer and drier future climate, regardless of their climate history.
642 However, we encourage caution in this interpretation, as there are two important caveats
643 to our finding of limited drought-related among-population differentiation. First, we only studied
644 reproductively mature trees, and our results strongly contrast with emerging results from the
645 seedling stage that show more ecotypic differentiation (B. McLaughlin et al., 2022; B.
646 McLaughlin in prep). Local adaptation or population-level differentiation at the earliest life
647 stages may be the most immediately relevant for restoration, and limited differentiation in adult
648 phenotypes does not guarantee limited differentiation in juvenile phenotypes. Indeed, explicit
649 contrasts of among-population differentiation in adult vs juvenile phenotypes is important before
650 we generalize across common garden results for different life stages.
651 Second, we were only able to perform trait measurements in a relatively wet common
652 garden, and may not have detected important genetic differentiation in plasticity itself. If the
653 expression of genetic differences depends on the environment – e.g., if there are strong
654 genotype-by-environment or GxE interactions for drought-related phenotypes– then our results
655 could differ entirely in a drier common garden location. It remains possible that genotypes from
656 drier populations have larger potential for plasticity (as documented in a *Eucalyptus* species,
657 Mclean *et al.* 2014), which could imply that the same source populations planted in a dry
658 location could show substantial among-population variation due to the dry-adapted populations
659 manifesting more plasticity than wet-adapted populations. Thus, our results do not obviate the
660 need for proactive stewardship of genetic resources from range edge populations (McLaughlin *et*
661 *al.* 2022).
662
663 **Conclusion**

In a study of range-wide trait variation in blue oak (*Quercus douglasii*), we found little evidence for population-level differentiation in any of numerous morphological or hydraulic traits but substantial realized trait variation across the landscape. Our results suggest that this landscape-scale trait variation involved plastic trait adjustments, and that this plasticity drove among-tissue trait coordination. Thus, plastic adjustments, likely during the process of leaf development and expansion, drive the coordinated manifestation of drought avoidant phenotypes with high hydraulic efficiency in leaves and stems and increased carbon investment in stems relative to leaves. However, these phenotypes could not be predicted by site climate and were poorly linked to growth rates, indicating that our understanding of blue oak drought exposure and integrated performance remains limited.

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**Data Availability**

The data from this study are publicly available in Dryad at [insert Dryad DOI] (data citation). All code to replicate the statistical analyses and generate the paper figures are in the Github repository https://github.com/leanderegg/BlueOakGarden.git.

**Author contributions**

LDLA, RPS, PP, DDA and TED conceived of the project ideas; LDLA, RPS and PP designed the methodology; LDLA, RPS and JD collected the data; LDLA analyzed the data and lead the writing of the manuscript. All authors contributed to editing the manuscript.

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**Table 1:** Trait definitions and abbreviations as employed by this study.

| Trait | Definition |
|---|---|
| SLA | Specific leaf area ($cm^2\ g^{-1}$) |
| LDMC | Leaf dry matter content (g dry mass per g fresh mass) |
| WD | Wood density |
| $M_L$:$M_S$ | Terminal branch leaf dry mass to stem dry mass ratio (g/g) |
| $A_L$:$A_S$ | Terminal branch leaf area to sapwood area ratio ($cm^2\ mm^{-2}$) |
| Leaf size | Average area of a single leaf based on all leaves on a terminal branch ($cm^2$) |
| $k_{leaf}$ | Leaf conductance per unit leaf area (mmol $m^{-2}\ s^{-1}\ MPa^{-1}$) |
| $k_{stem}$ | Leaf area-specific stem conductance of full current year terminal branch (mmol $cm^{-2}\ s^{-1}\ kPa^{-1}$) |
| $K_s$ | Sapwood area-specific stem conductivity per branch length (k[stem] * Al:As * length, mmol $cm^{-1}\ s^{-1}\ kPa^{-1}$) |
| $P50_{leaf,\ stem}$ | Leaf and stem P50 measured with optical technique from Skelton et al. 2019 |
| Growth | **Garden**: stem volume attained at 30 yrs, based on basal diameter and height of largest stem assuming cylindrical stem.<br>**Wild**: percent of size-specific maximum basal area increment (based on rangewide 90$^{th}$ percentile BAI at a given DBH) |

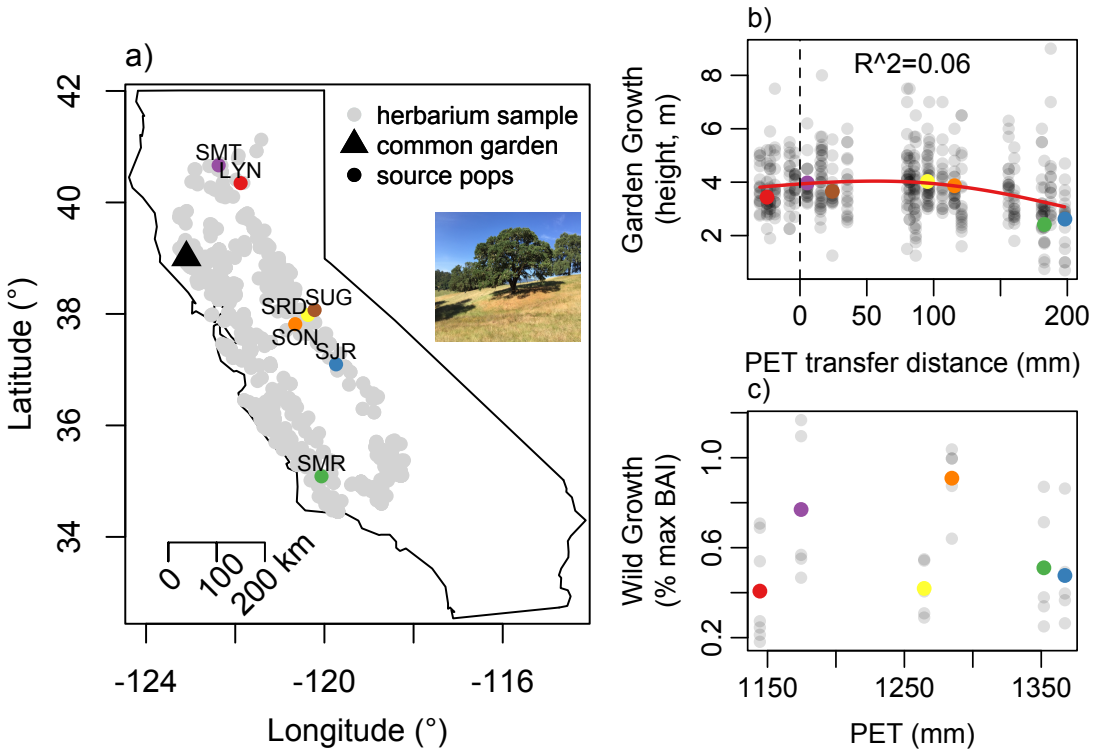


**Figure 1:** *(a) Geographic distribution of blue oak (Quercus douglasii* Hook & Arn) *based on herbarium specimens, with focal source populations and common garden location. (b) Height growth in the common garden (gray points show all individuals from full 26 populations, colored points show population means of seven focal populations) as a function of the potential evapotranspiration (PET) 'transfer distance' (difference between garden and source locations). Garden growth shows little evidence of home-site advantage, with only subtle among-population growth differences and maximum growth reached at positive transfer distances. (c) Wild growth as % of maximum Basal Area Increment (BAI) standardized for tree size as a function shows no significant relationship with site climate variables (plotted against PET for illustration).*

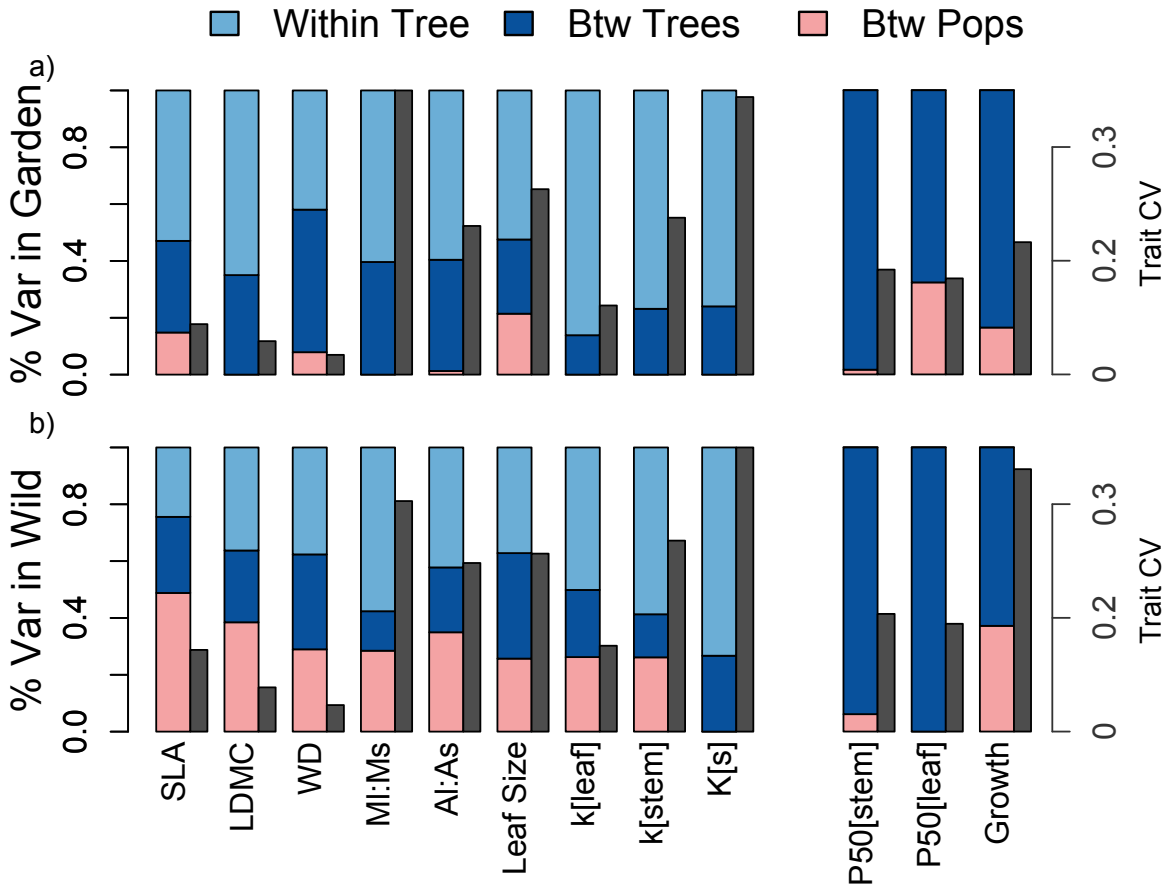


**Figure 2:** *Variance decomposition of all branch-level measurements in the common garden (a) and wild source populations (b). Grey bars beside the colored bars show the magnitude of the trait coefficient of variation. $P50_{stem}$, $P50_{leaf}$ and Growth do not have replicates within tree, so only contain between tree and between population variance components.*

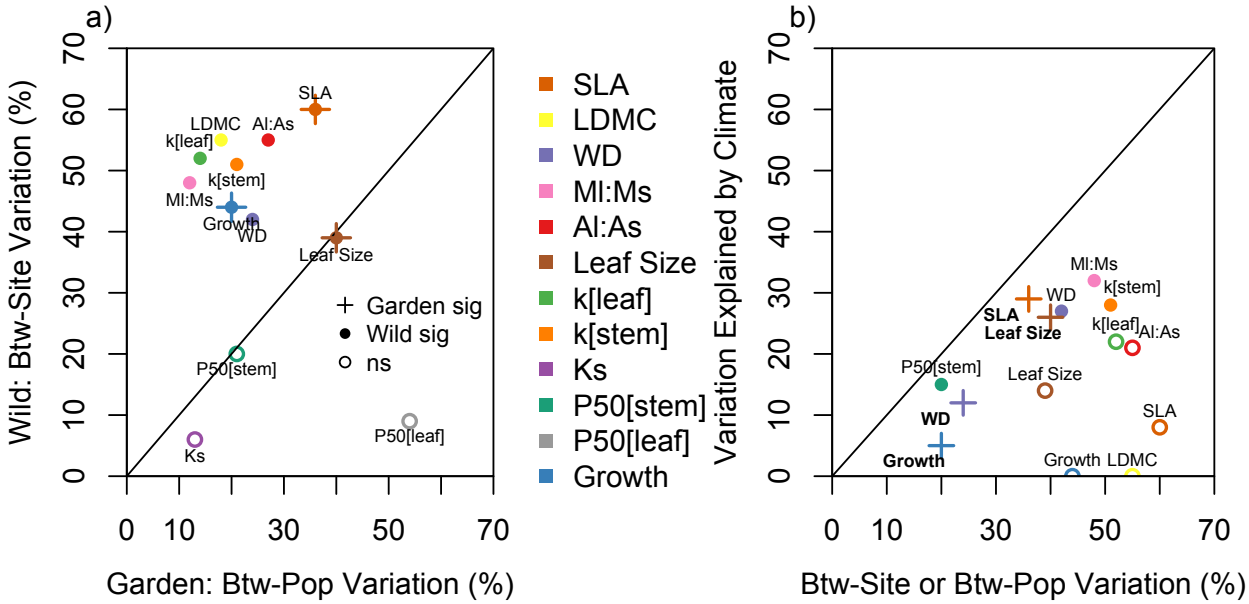


**Figure 3:** *(a) % of the total tree-to-tree variation attributable to population in the garden versus attributable to sites in the wild. Traits with significant between-site variation (ANOVA p <0.05) in the wild are shown as filled points, while traits with significant between population variation in the garden are shown with crosses. (b) The among-population and among-site variation that could be explained with climate variables, including only traits with significant among-population variation (ANOVA p<0.05). Y-axis shows* $R^2$ *of best climate predictor based on AICc, filled points indicate predictors that are statistically significant for wild traits, open points show traits with significant among-population differentiation but non-significant climate predictors, and crosses with bold text labels show garden traits with significant climate predictors (Table S2). Black line shows 1:1 relationship.*

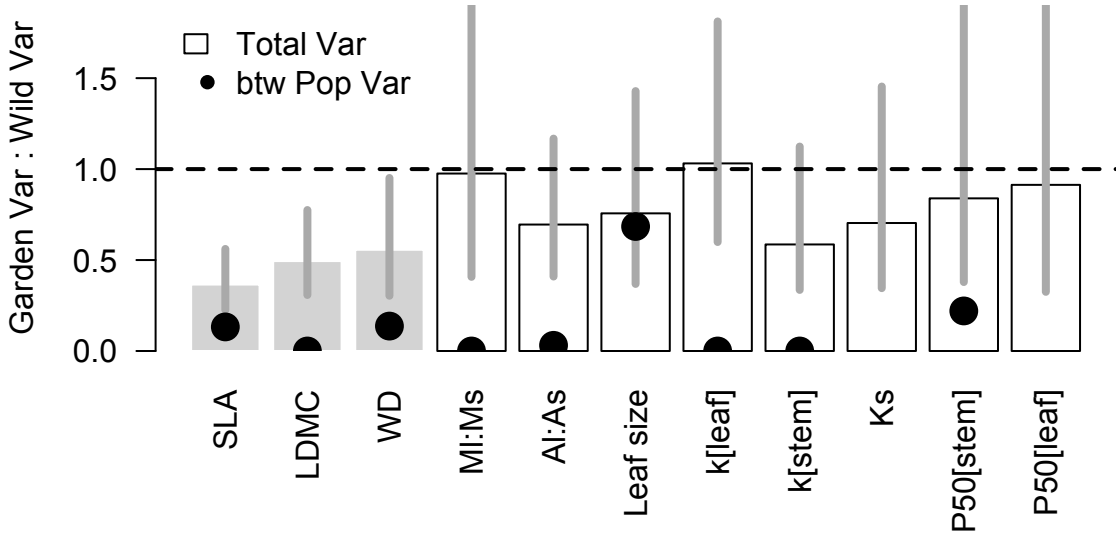


**Figure 4:** *Ratio of trait variance in the common garden compared to the wild (values <1 indicating more trait variance in the wild). Bars show the ratio of total trait variance (median of 1000 bootstrapped variance estimates, lines show 5$^{th}$ – 95$^{th}$ percentile of ratio), gray bars indicate significantly lower variance in the garden. Points show the ratio of the between-population variance component alone (Ks and P50$_{leaf}$ had 0 estimated between-population variance in the wild and thus no points).*

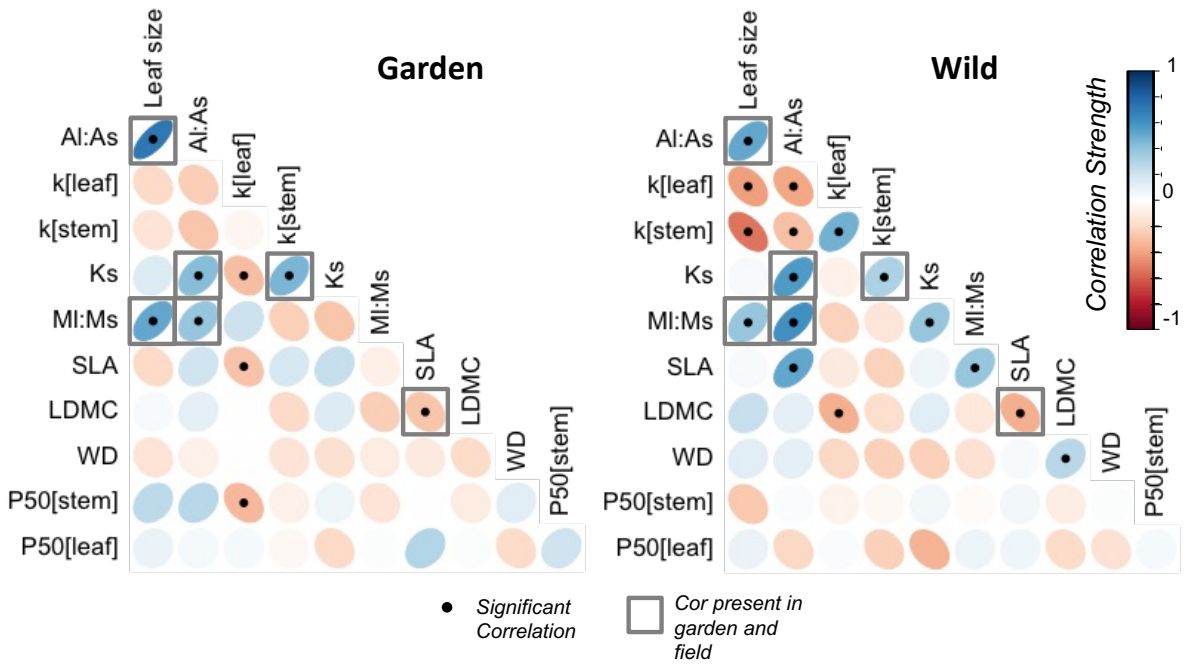


**Figure 5:** *Trait integration was stronger in wild trees. Tree level trait-trait correlations in the garden (a) and in the wild (b). Ellipses and color show direction and strength of the correlation, points show statistically significant relationships, and grey boxes show relationships that are significant in both the garden and the wild.*