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Population-level response to past and future climate change across the native range of California

poppy

A Dissertation submitted in partial satisfaction of the requirements
for the degree Doctor of Philosophy

in

Biology

by

Elizabeth M. Ryan

Committee in charge:

      Professor Elsa Cleland, Chair
      Professor Andrew Barton
      Professor Ronald Burton
      Professor Joshua Kohn
      Professor Kaustuv Roy

2022

The Dissertation of Elizabeth M. Ryan is approved, and it is acceptable in quality and form for publication on microfilm and electronically.

University of California San Diego

2022

DEDICATION

For my parents, who work incredibly hard to allow their four children to have the

education they could not.

And for Ryan, who does the same for our daughter.

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ACKNOWLEDGEMENTS

Chapter 1, in full, is a reprint of the material as it appears in Climate Change Ecology 2021. Ryan, Elizabeth and Cleland, Elsa. The dissertation author was the primary investigator and author of this paper.

Chapter 2, in full, is currently being prepared for submission for publication of the material. Ryan, Elizabeth and Cleland, Elsa. The dissertation author was the primary researcher and author of this material.

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PUBLICATIONS

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Heard, M., Smith, K., Ripp, K., Berger, M., Chen, J., Dittmeier, J., Goter, M., McGarvey, S., and **Ryan, E.** 2013. The threat of disease increases as species move toward extinction. Conservation Biology, 27: 1378–1388.

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ABSTRACT OF THE DISSERTATION

Population-level response to past and future climate change across the native range of California

poppy

by

Elizabeth M. Ryan

Doctor of Philosophy in Biology

University of California San Diego, 2022

Professor Elsa Cleland, Chair

Increased aridity and temperatures are expected worldwide in the coming decades. Under predicted levels of climate change, threatened organisms that cannot move must either adapt, respond plastically, or depend on non-climatic factors to avoid extinction. Predicting how certain species will respond to climate change can be complicated by population-level differences in fitness-related traits, population growth rates and demography. We investigated 20 populations of *Eschscholzia californica* (California poppy) distributed across a fourfold gradient in annual precipitation. In a greenhouse and field common garden, plants received precipitation treatments

approximating the wettest and driest sites, crossed with either the presence and absence of a 1.5°C warming treatment or home soil inoculum. We documented strong clinal variation across populations, with southern arid populations exhibiting the most drought tolerance. Populations, especially from arid sites, had higher growth rates, seed set, biomass and rates of survival to flowering under warm and wet conditions We also found that plants grown in home soil inoculation produced 10% more biomass than when grown in common garden soil; however, the influence of soil was small relative to the 13-fold variation across populations in fitness responses to drought. Assisted gene flow sourced from arid population would be most likely to allow populations to persist in the face of increasing warming and more extreme precipitation trends. We also investigated evidence of evolution of traits, over a 60-year period of climate change by comparing data sets from a 1958-1960 common garden and field collection by Stanton A. Cook with a 2017 re-survey. This data set included 74 populations of *E. californica* distributed across a sixfold gradient in annual precipitation. Seed diameter decreased over time, consistent with expectations based on increasing aridity over the past 60 years. While percent germination and stamen number did not change significantly over time. Our results suggest that plant traits may be responding to a complex suite of climatic and non-climatic changes over the past 60 years.

CHAPTER 1: Clinal variation in phenological traits and fitness responses to drought across the native range of California poppy

Abstract

Increased aridity, associated with climate change, is predicted worldwide in the coming decades. Species persistence in the face of climate change is thought to be influenced by plasticity, potential for adaptation, and dependence on non-climatic factors, but their relative importance has rarely been quantified. We investigated 13 populations of *Eschscholzia californica* (California poppy) distributed across a fourfold gradient in annual precipitation. In a greenhouse, plants received precipitation treatments approximating the wettest and driest sites, crossed with the presence and absence of soil inoculum from their collection location. We documented clinal variation across populations; plants from southern populations (arid sites) emerged later, flowered earlier, had shorter growing seasons, higher mean fitness, higher reproductive effort, and were more drought tolerant than plants from northern populations (mesic sites). A second experiment demonstrated clinal variation in biomass allocation, with higher root allocation in northern populations. We found no evidence of adaptive phenological plasticity to drought; instead, the drought treatment decreased fitness and growing season length (maladaptive phenological plasticity) more for plants from mesic than arid sites. Individuals grown with home soil inoculation produced 10% more biomass than when grown in common garden soil; however, the influence of soil was small relative to the 13-fold variation across populations in fitness responses to drought. Our results suggest that restoration efforts involving California poppy may benefit from assisted gene flow; sourcing seeds from arid parts of the species range may improve individual fitness and population persistence of this iconic species in the face of future climate change.

1. *Introduction*

Under predicted levels of climate change, threatened organisms must either adapt, move, or respond plastically, to avoid extinction (Anderson et al., 2012; Parmesan, 2006; Reed et al., 2011; Shaw & Etterson, 2012; Urban, 2015). While individual species have already experienced range shifts in concert with climate change in recent decades, they vary widely in their responses (Chen et al., 2011), making it critical to develop better predictions regarding the potential for species to both shift their ranges, and adapt evolutionarily in situ (Parmesan & Hanley, 2015; Walther et al., 2002). Plants that cannot disperse rapidly across long distances may be at heightened risk from rapid climate change (Huntley, 1991; Loarie et al., 2009). For these plants, the ability to rapidly adapt will be even more crucial (Davis & Shaw, 2001).

Phenological traits are likely to be particularly important for predicting plant responses to climate change. Previous work has shown that phenological traits are closely tied to fitness and are often under strong natural selection (Anderson & Gezon, 2015; Franks et al., 2007; Wilczek et al., 2010). Phenological traits also display significant phenotypic plasticity and are sensitive to climate change (Donohue et al., 2010; Munguía-Rosas et al., 2011; Parmesan, 2006; Wolkovich et al., 2012). The influence of warming has often been a focus of phenological research, but other significant components of climate change, such as drought, can also cause plastic (Gugger et al., 2015) and rapid evolutionary (Dickman et al., 2019) responses in plants. Because phenology is linked to plant fitness, and is often climatically driven, if shifts in the specific timing of biological events do not occur quickly enough to track climate change, species may suffer declining fitness (Miller-Rushing et al., 2010).

Plasticity in both traits and fitness may promote species persistence, until adaptation can occur, via short-term phenotypic responses to future climate change (Bradshaw, 1965; Ensing & Eckert, 2019; Ghalambor et al., 2007; Lande, 2009; Nicotra et al., 2010; Reed et al., 2011; Robinson & Dukas, 1999; Schlichting, 1986). For instance, in a synthesis of warming experiments, species that accelerated their vegetative or reproductive phenology with warming had higher average fitness than species with less phenological plasticity (Cleland et al., 2012). While plasticity is often assumed to be adaptive, there are important instances when plasticity is neutral or mal-adaptive (Bradshaw, 1965; Chevin & Lande, 2010; Schlichting, 1986). In these cases, plasticity may still provide novel phenotypes for future evolution to act on (Nicotra et al., 2010).

Within plant species, climatic and edaphic conditions across geographic space can lead to clinal variation, and even local adaptation (Clausen et al., 1948; Endler, 1977; Hall & Willis, 2006; Peterson et al., 2016; Turesson, 1922). Clinal variation in key fitness-related traits can reveal how climate has influenced the history of past selection and provides a window into the potential for species to adapt to modern climate change (Etterson et al., 2016). Hence, experiments that evaluate the response of populations to climate manipulations may help predict species' responses to future climate change (Pearson & Dawson, 2003; Thuiller et al., 2008). In addition to climatic factors, biotic interactions can affect population persistence under novel conditions (Afkhami et al., 2014; Bueno de Mesquita et al., 2016). For example, mutualistic interactions, like those with co-evolved specialist soil microbial communities, can promote local adaptation (Pregitzer et al., 2010; Smith et al., 2012). Plants that are locally adapted to their native microbial community may be less likely to establish when growing without such soils (Johnson et al., 2010; Koziol et al., 2018; Schultz et al., 2001). Thus, both clinal variation and

local adaptation to biotic interactions, may constrain a species' ability to effectively move or adapt to climate change and thus modify the predictions of species' response to climate change (Kelly et al., 2012).

There are both practical and theoretical motivations for evaluating the relative importance of plasticity, clinal variation in relation to climate, and local adaptation to non-climate factors for predicting population persistence in the face of climate change. Practically, restoration and revegetation efforts may be more successful if they anticipate climate change by sourcing seeds from populations in warmer and drier parts of the species range (Hufford & Mazer, 2003; Rehfeldt et al., 1999). This type of "assisted gene flow" (AGF) may also accelerate adaptive evolution through the introduction of favorable alleles (Aitken & Whitlock, 2013). Understanding the relative importance of these factors is also important for our theoretical understanding of the basis of species range limits (Sexton et al., 2009), which are frequently limited by climatic and non-climatic factors (Stanton-Geddes et al., 2012). Species distribution models (SDMs) are often used to predict current species ranges, and future distributions under future climate scenarios (Hijmans & Graham, 2006; Kearney et al., 2010). However, if populations have narrower climatic tolerances than the species as a whole, then accurate predictions of future species distributions will need to incorporate these parameters (Atkins & Travis, 2010; Oney et al., 2013; Pearman et al., 2010; Peterson et al., 2019). Experiments evaluating climatic versus non-climate (e.g. biotic) impacts on population persistence can act as proof-of concept tests of SDMs (Dixon & Busch), and can identify the factors underlying species range limits (Briscoe Runquist et al., 2020). Few studies, however, have specifically evaluated how clinal variation and local adaptation to non-climate factors, such as soils, interact to predict

population and species responses to climate change (Compagnoni & Adler, 2014; Kardol et al., 2014; Macel et al., 2007).

Here, we investigated clinal variation in traits (phenological and allocation), fitness, and plastic responses to drought and the presence of home soil, for 13 populations of California poppy (*Eschscholzia californica*) distributed across a climate gradient characterized by a fourfold difference in precipitation. We should note that while this study took place in the native range of California poppy, it is invasive in other regions (e.g. 73). Driven by rising global temperatures, aridity is expected to increase in nearly all terrestrial regions of the globe (except Northern Africa and high latitudes), even in areas where precipitation is expected to rise, due to increased evaporative demand with higher temperatures (Berg et al., 2016; Cook et al., 2014; Dai, 2013; Feng & Fu, 2013; Scheff & Frierson, 2015). This makes adaptation to increased aridity one of the most globally relevant aspects of plant responses to future climate change. Our study was conducted in the Mediterranean-climate region of California, a region expected to become warmer and drier, with increasingly severe drought periods (Cayan et al., 2008; Dai, 2013). Climatic changes have already caused local and regional declines in the diversity of California wildflowers (Harrison et al., 2015), and they are likely to exert significant directional selection pressures on extant populations (Jump & Peñuelas, 2005). Further, in this region the effects of a changing climate are compounded by habitat loss and fragmentation (Underwood et al., 2009), limiting the ability of organisms to migrate in response to these environmental changes (Davis & Shaw, 2001).

California poppy, the state flower, exhibits large intraspecific variation across its range. Prior studies have found geographic variation in longevity and higher potential for seed dormancy in drier sites (Cook, 1962), variation in below-ground allocation (Boucher, 1985), and

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evidence of local adaptation to climate (Leger & Rice, 2007). We expanded on prior work in this model system to: 1. document population-level differentiation in phenological traits, root allocation and plant fitness, and tested the hypothesis that this population-level variation was associated with the aridity gradient across California, consistent with a history of past selection in relation to climate. 2. quantify population-level plasticity in phenological traits, root allocation and fitness in response to drought. 3. evaluate evidence for local adaptation to soil factors, via biotic interactions with associated microbial communities and/or other soil chemical or physical properties, by growing plants with or without soil inoculum from their home collection site.

We expected to find population level variation in traits and fitness in response to both drought and presence of home soil inoculum. Under drought conditions, we expected populations from southern arid sites would have higher fitness than those from northern mesic sites, and vice versa under high precipitation conditions, consistent with past meta-analyses documenting frequent local adaptation to climate in plants (Leimu & Fischer, 2008). We expected populations from more arid sites would have higher instances of delayed germination, an adaptation to variable environments (Venable & Brown, 1988). We also expected populations from more arid sites would flower earlier and have shorter growing seasons than those from more mesic sites, because dry conditions should favor earlier reproductive phenology to avoid late season stress (Aronson et al., 1992; Franks, 2011; Franks et al., 2007; Hall & Willis, 2006; Sherrard & Maherali, 2006). With respect to biomass allocation, we expected to find higher allocation to roots in mesic-site populations, consistent with prior observations from three populations in central California (Boucher, 1985). By subjecting individuals from different populations to a drought treatment, we evaluated variation in plasticity (i.e. genotype x environment interactions) (Schlichting, 1986; Sultan, 1987). We expected the greatest plasticity in populations from arid

sites that historically experienced higher levels of environmental variability both within and across years (Bradshaw, 1965; Chevin & Hoffmann, 2017; Gugger et al., 2015; Pratt & Mooney, 2013; Schlichting, 1986). Finally, we expected the potential benefits of local adaptation to home soil inoculation would help ameliorate the negative fitness effects of drought (Pregitzer et al., 2010; Smith et al., 2012). Together, by identifying populations that have the greatest potential for persistence under future climate conditions and assessing whether soil inoculations are an important complement to support AGF, we aimed to use these findings to improve restoration success in the face of climate change.

2. Materials and Methods

2.1 Collection and preparation of seeds

Between April and July, 2017, we collected *E. californica* seeds from 30 natural (non-planted) populations in California. Thirteen of the original 30 sites were chosen as the focus of this study; these populations had an annual life history when grown under common garden field conditions between 2018 and 2020 (Ryan & Cleland, in preparation). Populations with the potential for perennation were excluded because they preclude a direct comparison of lifetime fitness within the timeframe of a greenhouse experiment. The collection sites for these 13 populations are distributed over 700km in southern, central, and northern California (32.8-38.9 latitude) and span a climatic gradient with a fourfold increase in precipitation (Figure 1, Table 1). Within a collection site, seed pods were collected across the population from 10 maternal plants spaced at least 5 meters apart, and subsequently bulked, so the maternal lines were fully randomized within the population seed source. Seeds were stored at room temperature until planting. Seeds were surface sterilized with a 5,000 ppm concentration of Clorox Household

Bleach (8.25% active chlorine) and treated with a 500 pm concentration of gibberellic acid to help break dormancy (Cook, 1961; Fox et al., 1995). Populations from arid sites have a higher instance of seed dormancy (Cook, 1962; Montalvo et al., 2002), even after gibberellic acid treatment (Cook, 1961). Five soil cores (20 cm deep, 2.5 cm diameter) were taken at each collection site, 15cm away from five evenly dispersed maternal plants, and subsequently homogenized to a single sample for soil inoculation.

2.2 Common garden design and home soil treatment

The greenhouse common garden was located at the University of California San Diego Biological Field Station in La Jolla, CA (32.8855, -117.2299). This site is coastal, and like all the collection sites has a winter growing season (average annual precipitation: 26.7cm, average annual temperature: 16.9°C; full list of sites in Table 1). Although winter rains often start in November, the onset of the growing season has been delayed in recent years due to lower than normal fall precipitation, a trend expected to continue in the future (Pierce et al., 2018). Seeds for this greenhouse experiment were planted on January 24, 2018, following the start of the rainy season in January. The 13 populations of *E. californica* were planted in 5 Liter tree pots (Stuewe & Sons CP512) in a randomized block design and grown under 4 experimental treatments (factorial combinations of rainfall and soil inoculation treatments), with eight replicates of each population by treatment combination (a total of 416 pots, Data S1). Tree pots were filled 95% with sterilized soil from Oceanside, CA. A total of 2.01 metric tons of soil was autoclaved for this purpose. Half of these pots were then filled 5% with un-sterilized soil from the same source in Oceanside, referred to as "common" soil. The remaining half of the pots were filled with 5% of un-sterilized soil from the source populations, referred to as "home" soil (i.e. each of the 13

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populations received a unique "home" soil). Seeds were pre-treated with a 500ppm gibberellic acid solution 24 hours before planting to break dormancy. Three seeds were planted in each pot, 1cm below the surface, because light inhibits germination of *E. californica* (Fox et al., 1995). The first seedling to emerge was the focal individual, and any later emerging seedlings were removed. The eight blocks were separated by 0.5m and rotated every three weeks to minimize the effect of greenhouse environmental variation.

2.3 Experimental drought treatments

The high precipitation and drought treatments approximated the annual precipitation totals of the wettest (McLaughlin UC Natural Reserve, 98.1cm annually) and driest sites (Motte Rimrock UC Natural Reserve, 26.72cm annually). Plants were watered 75 mL every 2 days in the high precipitation treatment, and 40 mL every 4 days in the drought treatment. At the start of the experiment, plants were watered at an intermediate level, halfway between the drought and high precipitation treatments for two weeks to ensure sufficient germination.

2.4 Soil moisture data collection

Soil moisture levels were measured every two weeks from March-June with a Field Scout TDR 100 Soil Moisture Sensor, which measures volumetric water content at a depth of 12cm, to assure the precipitation treatments were influencing soil moisture as expected (see supplementary figure S2).

2.5 Phenology Data collection

We conducted daily phenology surveys on emergence, day to first flower and senescence. Flowering was calculated as the number of days between emergence and day to first flower, to represent time to reproduction. The growing season for an individual started at emergence and ended at senescence when there was no longer any above ground living biomass. Individuals were harvested at this time and the root was examined to confirm the plant was not dormant. Because of the high degree of variation in population senescence, harvesting was staggered based on end of growing season to avoid above-ground decomposition before drying and weighing for accurate plant performance measurements. Biomass was harvested between May 20, and September 21, 2018.

2.6 Plant Performance Data collection

We used total seed mass and above ground plant biomass as proxies for fitness. Individual *E. californica* plants grown under our greenhouse conditions can produce over 10,000 seeds, and we found seed number was strongly predicted by seed mass (see supporting Figure S1). *E. californica* is self-incompatible [82, 85], and our greenhouse is screened and maintained to be free from insects. Flowers were hand pollinated (every 1-2 days) by transferring pollen on a cotton swab from individuals within the same population. After harvesting, above ground biomass was dried at 40°C, before weighing. Above ground biomass, as reported in our analysis, is the addition of dried vegetative biomass and dried seed pods, with all seeds removed. Reproductive effort % for a plant is total seed mass/above ground biomass.

2.7 Aridity Calculations, and correlations among environmental variables across collection sites

To examine patterns in mean annual Aridity we used the Thornthwaite function in SPEI v1.7 to calculate monthly potential evapotranspiration (PET) (R Core Development Team 2019). The Thornthwaite formula is a standard calculation that uses temperature and daylength (via latitude and month) to estimate the water needs of plants in a specific environment (Thornthwaite, 1948). Aridity index (AI) values that are low indicate arid environments, while high values indicate mesic environments (Data S2). See Supplemental Material for detailed methods of the Aridity index calculation. Correlations among the environmental variables listed for each population collection site in Table 1 were evaluated using Pearson correlations from the Hmisc package in R (Harrell et al., 2019). As expected, the environment becomes colder, wetter, and more mesic (higher AI values) with increasing latitude across our sites going from south to north. The collection sites also become warmer, drier, and more arid with decreasing longitude from west to east, representing a coastal to inland gradient (see statistical summary of environmental correlations in Table S1).

2.8 Organic matter loss on ignition (LOI)

We measured soil organic matter from the field collected soils, because SOM is strongly associated with soil water holding capacity. We sequentially dried three replicates of 5.0 grams of soil collected from each site in a muffle furnace. First, samples were dried for 12 hours at 100°C to remove water. Samples were then dried at 550°C for four hours, an optimal temperature and duration for measuring organic matter loss in soil, and then cooled and weighed (Heiri et al., 2001; Santisteban et al., 2004).

2.9 Below ground versus above ground allocation

Using the same populations and planting methods as the main experiment, we performed a second experiment, planted October 16, 2019, and harvested between May 21 and September 19, 2020. For this second experiment all plants were grown under the high rainfall treatment. Root biomass was collected by passing the entire contents of each pot through a 4 mm sieve, immediately following above-ground biomass collection. The root biomass was subsequently submerged in tap water to remove mineral soil, transferred to an envelope, and dried at 40 degrees C to constant mass (at least 72 hours). We calculated the root mass fraction as belowground biomass divided by total biomass (above- plus belowground biomass).

2.10 Statistical analysis

All analyses were conducted in R version 3.6.2 (R Core Development Team 2019). Analysis of phenological traits and fitness in relation to aridity, precipitation treatment, and soil inoculum were conducted with linear mixed effect models using the *lme* call in the package *nlme* (Pinheiro et al., 2013), where population was included as a random factor (see Supplemental Material for R code). Statistical significance for fixed effects was evaluated with type-II tests using the *Anova* function in the *car* package (Fox & Weisberg, 2019), based on a Wald Chi-square tests. Significant effects of aridity indicated clinal variation in the response variables; significant main effects of precipitation treatment and soil inoculum indicated plasticity in response to these treatments when averaged across all populations; and significant aridity by precipitation or soil inoculum treatments indicated clinal variation in plasticity in response to these factors. In other words, the site aridity by treatment interaction is akin to genotype x environment interaction that varies across populations, and is a test of the hypothesis that greater phenotypic plasticity evolves in more arid (harsh and unpredictable) environments.

We evaluated whether clinal variation (mean traits) or plasticity (change in traits) were adaptive to rising aridity by correlating traits with plant fitness (above ground biomass or total seed production) under the drought treatment, where each population was an observation in the analysis (i.e. N=13 for the correlations). Analysis of the root mass fraction data used the same method, except that the precipitation and inoculum treatments were not included in the model. We visually inspected quantile-quantile plots of all model residuals for normality using the qqnorm function (see Supplementary figures S5-S11 for plots). We further compared our results to models specifying a Poisson error structure in the glmmadmb package (Fournier et al., 2012), for days to emergence, seed mass, and reproductive effort. In all cases models assuming Gaussian errors had lower AICs than those with alternate error structures; hence we proceeded with our analyses as described.

3. Results

3.1 Clinal variation and association between phenological traits and fitness

Across all treatments we documented clinal variation in phenological traits (i.e. emergence timing, flowering timing, growing season length) and fitness (i.e. biomass, seed production, reproductive effort) in relation to site aridity (Figure 2 A, B, C, D, E, F, Table 2). Southern populations from more arid sites emerged later, flowered earlier, had shorter growing seasons, and had higher fitness than northern, mesic, populations (Table 2). When averaged across all experimental treatments, the most arid site had 130% more above ground biomass than the most mesic site (1245 mg for Motte Rimrock UC Natural Reserve versus 541 mg for McLaughlin UC Natural Reserve). Therefore, variation in phenological traits (emergence,

flowering, growing season length) and fitness were correlated when considered across populations (Table 3).

3.2 Plasticity and its association with fitness under drought

Clinal variation in plasticity in phenological and fitness traits was evident in relation to site aridity. The drought treatment decreased growing season length more for plants from northern populations in more mesic sites (Figure 2C, Table 2), and these more plastic northern populations had lower fitness under drought (Table 3). The drought treatments decreased fitness and reproductive effort three-fold when averaged across all populations (Table 2). The negative impact of drought was expected; however, contrary to our expectations, populations from arid sites had higher plasticity in fitness response to the drought treatment, increasing their above ground biomass and seed mass more than northern populations did under high precipitation conditions (Figure 2 D, E, Table 2). Plasticity in growing season length was associated with fitness responses to drought (Table 3); populations with a greater decline in growing season length had lower fitness under drought. Flowering time plasticity was not associated with fitness differences among populations under drought. (Figure 2B, Table 3).

3.3 Influences of home vs away soil inoculations

When averaged across all populations and precipitation treatments, individuals grown with home soil inoculation emerged and flowered earlier (1 and 3 days respectively), had longer growing seasons (4 days), and produced 10% more above ground biomass (866 mg versus 957 mg) than individuals grown in pots filled entirely with common garden soil (Figure 3, Table 2). These responses to home soil inoculation were not correlated with the quantity of organic matter

in the soil (supporting Table S2), nor soil moisture levels across the course of the experiment (supporting Figure S2). There were no interactions between home soil inoculum and precipitation treatment for any variable (Table 2).

3.4 Below ground versus above ground allocation

Our additional experiment shows clinal variation in root allocation, with increasing root allocation associated with increasingly mesic sites (Figure 4). While mesic site populations have higher belowground biomass, this experiment again showed their above ground biomass was significantly lower than arid site populations (supporting Figures S3 and S4).

4. Discussion

4.1 Summary

Our experiment revealed striking clinal variation in phenological traits, belowground allocation, mean fitness, and response to drought, across the range of California poppy. Populations from more arid sites emerged later, flowered earlier, had shorter growing seasons, and had higher average fitness than populations from more mesic sites. The drought treatment also decreased growing season length and fitness more for populations from mesic than arid sites. Our results did not show evidence of adaptive phenological plasticity to drought, but instead suggested maladaptive phenological plasticity in response to drought in mesic site populations. Inoculation with home soil increased biomass by a modest 10%, but this potential influence of local adaptation to soils was small in relation to the large clinal variation in performance between the extreme arid and mesic sites (130% greater biomass of the most arid as compared to the most mesic site population). Together these lines of evidence support the idea

that promoting gene flow from arid to mesic sites during restoration efforts (i.e. AGF) could improve the potential for population persistence in the face of drought. These results further suggest clinal variation may be more important for improving predictive models than local adaptation to soils, at least for widespread species such as California poppy.

4.2 Clinal variation and association between phenological traits and fitness under drought

The clinal variation in phenological traits we observed in California poppy is consistent with patterns of genetic variation in relation to climate observed for other widespread species in California (Clausen et al., 1948; Peterson et al., 2016; Pratt & Mooney, 2013). We predicted that populations from southern, more arid sites, would have higher fitness under drought, while populations from northern, more mesic sites, would have the highest fitness under the high precipitation treatment. Contrary to expectations, the southern arid populations out-performed mesic populations under both precipitation treatments, and the arid populations had a more positive fitness response to high precipitation than the mesic populations. Leger & Rice (Leger & Rice, 2007) documented clinal variation in *E. californica* populations both in the native range in Northern California and in the invasive range in Chile. In both regions plants from more arid locations grew larger and produced more seeds in a common garden, although they did not evaluate population-level variation in response to experimental manipulations.

Our study also documented greater plasticity in fitness in the populations from more arid sites, which showed greater gains in biomass and seed set under high rainfall compared to populations from more mesic sites. In a common garden experiment with rainfall treatments, Pratt and Mooney (Pratt & Mooney, 2013) found similar results with populations of the shrub *Artemisia californica* collected from coastal California; plants from southern populations had a

higher fitness gain under high precipitation than northern populations (see Figure 2 D & E). Southern California experiences greater interannual rainfall variation than the northern part of the state, and is the most climatically variable part of the U.S. (Dettinger et al., 2011b). The capacity for populations from more arid and climatically variable locations to capitalize on favorable conditions to improve fitness is consistent with theory suggesting these environments should favor plasticity (Bradshaw, 1965; Chevin & Hoffmann, 2017; Gugger et al., 2015; Pratt & Mooney, 2013; Schlichting, 1986).

We also documented an almost 75-day longer growing season in populations from mesic sites compared to arid sites. Populations varied by approximately three days in time to emergence: populations from arid sites had delayed germination, as well as a greater potential for seed dormancy [Ryan, unpublished data], both adaptations to highly variable environments (Rees, 1994; Venable & Brown, 1988). However variation in time to senescence contributed the most to the longer growing season of the populations from mesic sites, suggesting that populations adapted to short growing seasons may have developmental programs, such as programmed cell death, that prevent them from taking advantage of late-season soil moisture (Thomas et al., 2000).

In sum, we found strong correlations between the average phenology of a population and its fitness; the populations from the more arid collection locations, with fast growth and flowering, and short growing seasons, had the highest fitness under drought. However, the populations from arid sites also had the highest fitness under all conditions; potentially reflecting the fact that our common garden was in located in Southern California, where factors such as daylength would be most similar to the conditions experienced by Southern populations. Regardless, our results suggest that clinal variation in phenology and fitness are strongly

associated with climate (in our case aridity). Consistent with our results, Kooyers et al. (Kooyers et al., 2019) found that the timing of flowering was key to the fitness advantage of local adaptation with respect to drought escape in *Erythranthe guttata,* a widespread species in California and Oregon.

4.3 Phenology is key to understanding variation in life-history across species ranges

The significant variation in flowering phenology across our populations is likely related to significant life history variation across the range of *E. californica*; a perennial life history is more common in mesic locations and an annual life history is more common in arid locations (Cook, 1962). Similar to other studies, populations in the arid portion of the range flowered faster and had a shorter growing season than populations from the mesic portion of the range (Aronson et al., 1992). In general, fast flowering and an ability to produce seeds in a short growing season are traits associated with an annual life history; theory suggests an annual life history should evolve in environments that are unfavorable to adult survival, such as arid environments with short seasons favorable to plant growth (Schaffer & Gadgil, 1975; Stearns, 1992). Consistent with theory, recent experimental work has shown the potential for rapid evolution of earlier phenology in response to drought (Dickman et al., 2019; Franks, 2011; Franks et al., 2007; Sherrard & Maherali, 2006).

The findings reported in this study were from populations with annual life histories, allowing us to compare lifetime fitness across the populations. One prediction of life-history theory is that plants with a shorter time to reproduction will invest proportionally more in reproduction, i.e. have higher reproductive effort (Primack, 1979), and indeed we observed higher reproductive effort in the populations on the more arid end of the range. However,

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populations from the northern, more mesic portion of the range displayed traits such as longer time to flowering and greater allocation to roots, both strategies associated with perenniality (Moriuchi & Winn, 2005). Hence, even though our populations are functionally annual, there is likely gene flow between annual and perennial populations, especially in the more mesic portions of the species range; molecular genetic studies could confirm this. While classic views on life-history theory have traditionally considered discrete life-history categories such as annual versus perennial, (Charnov & Schaffer, 1973; Cole, 1954), we suggest that continuous phenological and allocation traits which are tightly linked to fitness support a more nuanced view of life-history evolution (Friedman & Rubin, 2015; Thomas et al., 2000).

4.4 Evidence for maladaptive phenological plasticity in response to drought

In this experiment we found no significant plasticity in flowering phenology in response to drought within populations. However, we did see evidence of maladaptive plasticity in growing season length, where a shorter growing season in response to drought was associated with a decline in fitness, a response previously documented in annuals (Aronson et al., 1992). Our results also show that the populations from more arid sites displayed less plasticity in growing season length, and hence, a higher fitness in response to drought. More work is needed to determine the conditions, taxa, and populations where plastic phenological responses are key for understanding fitness responses to a changing environment (Fox et al., 2019; Nicotra et al., 2010).

4.5 Home soil advantage

We found plants emerged and flowered earlier, had longer growing seasons, and produced more above ground biomass when grown with home soil inoculum, regardless of population source. On average, there was a 10% increase in biomass when plants were grown with home soil inoculum, which was consistent across populations. Neither soil organic matter content nor soil water holding capacity of the home soils was associated with the biomass increase, suggesting the microbial community may have been responsible for the increase in fitness of plants growth with home soil inoculum, although we cannot rule out the possibility that the common soil was lower in nutrients than all home soils. Broadly, our findings are consistent with other research suggesting local adaptation of plants to their soil microbial communities (Pregitzer et al., 2010; Smith et al., 2012), and that restoration outcomes can be improved by inoculating soil with microbial communities that benefit target plants (Johnson et al., 2010; Koziol et al., 2018; Schultz et al., 2001).

Presence of home soil inoculum did not modify population responses to drought (i.e. there was no interaction between precipitation and soil inoculum treatments), indicating that while plants benefited from home soil inoculation, inoculation did not ameliorate fitness declines caused by drought. We should also note that the 10% increase in biomass with soil inoculation is small relative to the 130% difference in biomass between populations with the highest versus lowest fitness in the experiment. Together we conclude that sourcing seeds from populations with high drought tolerance will have a greater impact on restoration success (as measured by plant fitness), compared with home soil inoculations.

4.6 Caveats of our study

We acknowledge some important caveats regarding our experimental approach which limit the generality of our findings. First, plant growth is sensitive to precipitation timing, in addition to the magnitude of precipitation events (Fay et al., 2003). While the greenhouse approach enabled us to sterilize and inoculate soils, this limited the realism of our precipitation treatments. We watered more frequently than plants would experience rainfall events in the field, which was necessary because soil moisture declines quickly due to evapotranspiration for plants grown in pots. Additionally, we used field-collected seeds for this experiment, and hence maternal effects likely contributed to the variation in traits and fitness (although the inclusion of population as a random effect in our statistical models accounted for unmeasured site variation, such as soil fertility). Similarly, we acknowledge that we pre-treated our seeds with gibberellic acid, a standard method to induce germination, and hence the timing of germination in our experiment was likely accelerated (by about one day) compared to the timing of germination for untreated seeds (Fox et al., 1995). Another caveat is that our plants were grown without supplemental lighting, and hence experienced southern California daylength, which would have been longer in the winter, and shorter in the summer, than the population locations in northern California. Daylength is a significant cue for flowering in *E. californica* (Lyons & Booze-Daniels, 1986), but we do not yet know the importance of daylength relative to other germination cues across populations. Although we attribute clinal variation in *E. californica* populations to variation in site aridity, we cannot preclude that other drivers (such as daylength or specific climatic factors) could be selective agents responsible for clinal variation in this species, due to the strong correlations among latitude (which correlates with daylength), the aridity index, and other climatic variables across our seed collection sites (see Table S1). Finally, it is important to note that our study is aimed at understanding how clinal variation might improve restoration

efforts for species within their native range, such as *E. californica*, which is commonly used in restoration. However, care should be taken when moving any species outside of its historical range, including *E. californica*, which has the potential to be invasive.

4.7 Implications for species distributions under future climate change, and conservation efforts

Species distribution models (SDMs) are commonly used for projecting biodiversity loss due to climate change, and hence conservation priorities (Trisos et al., 2020; Warren et al., 2018). The significant clinal variation we observed across the range of California poppy in relation to site aridity and drought response support efforts to improve projections of future species ranges by including population variation (Hällfors et al., 2016; Marcer et al., 2016; Oney et al., 2013; Pearman et al., 2010) and adaptive potential (Hamann & Aitken, 2013) in SDMs. Experiments such as ours can also provide important tests of these models. For instance, the populations from arid sites had higher fitness under precipitation levels found far from their home sites, violating a basic SDM assumption that potential suitable habitat for a population is found only within its current local climate (Hijmans & Graham, 2006; Kearney et al., 2010). Efforts to improve SDMs, such as the development of demographic distribution models (DDMs) focus on population level persistence (Merow et al., 2014). Experiments such as this one can provide important data on population-level fitness in different environments, key for the parameterization and testing of these DDMs.

Our results also have important implications for restoration and revegetation efforts seeking to identify seed sources with the highest potential for successful establishment (Breed et al., 2013). Although populations with the closest geographic proximity are often recommended, they may not optimize restoration success (Jones, 2013; McKay et al., 2005). Experimental

crosses have demonstrated that gene flow from populations in the warmer parts of the range results in higher fitness of offspring at range edges under warmer conditions (Bontrager & Angert, 2019; Sexton et al., 2011). The results from our experiment suggest that in California, populations from the warmer, drier end of the range would be promising candidates for restoration locations predicted to experience rising aridity and long-term drought.

Assisted gene flow (AGF) is a promising conservation strategy, aiming to introduce favorable alleles into target populations, and hence speed adaptation through contemporary evolution (Aitken & Whitlock, 2013). However, if populations are locally adapted to non-climatic factors, the introduction of non-local genotypes could decrease population fitness (Aitken & Whitlock, 2013; Weeks et al., 2011). Our results suggest that local adaption to soils has a small influence on plant performance, compared with the genetic variation across populations in relation to historic climate, as has been found previously (Kardol et al., 2014; Macel et al., 2007). A potential challenge to restoration efforts seeking to employ AGF hinges on the dramatic clinal variation in phenology we observed; our studies and others (Wadgymar et al., 2015) suggest that phenological differences among populations could limit successful gene flow, if the introduced individuals don't flower synchronously with the target population. Regardless of these challenges, species that are economically or culturally valuable but are at a low risk of local extinction, such as *E. californica,* might be promising candidates for early, experimental, AGF efforts. Even if local extinction is unlikely, a decline in fitness due to climate change in such widespread iconic species, could have ecological and tourism-related economic effects that would likely exceed the risks of AGF (Aitken & Whitlock, 2013; Mooney et al., 2009).

5. *Conclusion*

Our study joins a small number of other studies which have compared the relative importance of local adaptation (clinal variation in our case) to climate and non-climate factors for predicting population responses to climate change. In our case, clinal variation in relation to aridity was a stronger predictor of response to drought than local adaptation to home soils. A strength of this study lies in the large number of sampled populations (13) compared with prior studies that have quantified the relative importance of local adaptation to climate and non-climate factors such as soils (Kardol et al., 2014; Macel et al., 2007) (3 population sources each) or competition from neighbors (Compagnoni & Adler, 2014; Stanton-Geddes et al., 2012) (3 and 7 populations respectively). In the future, data from experiments could improve predictions of species persistence in the face of climate change by incorporating clinal variation into integral projection models (Merow et al., 2014), thus incorporating demographic variation across populations with varying genetic potential to respond to climate (Metcalf & Pavard, 2007).

Further, our findings highlight that species are unlikely to respond consistently to climate change across their geographic range; clinal variation in relation to climate is likely in many widespread species. However, experiments such as these are time-consuming, and would be infeasible to conduct for the large number of species and populations at risk for declines with climate change. The strong association we documented between phenological traits and fitness provides a potential path forward. For instance, phenological observation networks are documenting variation in phenological sensitivity to climate across species ranges (Crimmins et al., 2017), and when paired with observations of species abundances could help document whether the association between population-level phenology and fitness is also found in other widespread species.

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Table 1.1. Collection locations, climate means, and elevations for the 13 focal populations of *E. californica* in California, USA. Greenhouse location and environmental conditions for the two precipitation treatments are provided for comparison. Abbreviation is the number used to label points in Figures in this manuscript, which correspond to a given population.

Site Name	Abbreviation	Mean Annual Precip. (cm)	Mean Annual Temp. (C)	Aridity Index	Latitude	Longitude	Elevation (m)
Motte Rimrock UC Reserve	1	26.72	17.8	0.2765	33.7985	-117.2545	502
Torrey Pines State Park	2	27.25	16.9	0.3377	32.9233	-117.2586	42
Mission Trails Regional Park	3	33.55	18.1	0.3672	32.8449	-117.0467	181
Dawson UC Reserve	4	32.18	17.2	0.3710	33.1490	-117.2578	130
Wildomar (Clinton Keith Rd.)	5	40.41	18.4	0.3911	33.6017	-117.2312	387
Antelope Valley State Nat. Reserve	6	36.30	16.4	0.4048	34.7338	-118.3786	828
Point Mugu State Park	7	41.66	17.2	0.4515	34.0880	-119.0343	91
Carrizo Plains National Monument	8	37.99	15.2	0.4721	35.2125	-119.8765	597
Fort Ord UC Reserve	9	37.72	13.8	0.5603	36.6868	-121.7784	46
Sedgwick UC Reserve	10	57.61	16.3	0.6738	34.7054	-120.0560	425
Blue Oak Ranch UC Reserve	11	58.87	14.6	0.6901	37.3808	-121.7384	542
Hastings UC Reserve	12	53.80	14.5	0.7947	36.3855	-121.5551	659
McLaughlin UC Reserve	13	98.10	14.6	0.9292	38.8602	-122.4166	701
Greenhouse – High Water		98.10	17.9	0.9040	32.8855	-117.2295	60
Greenhouse - Drought		26.72	17.9	0.2598	32.8855	-117.2295	60

Table 1.2. Summary statistics from linear mixed effects models evaluating how Aridity of collection site and experimental treatment (Precipitation and Inoculum) influenced phenological traits and fitness in 13 populations of *E. californica*.

	Days to Emergence		Days to Flowering		Growing Season Length		Biomass		Seed Mass		Reproductive Effort	
	X^2	P	X^2	P	X^2	P	X^2	P	X^2	P	X^2	P
Aridity	30.32	<0.001***	13.11	<0.001***	21.80	<0.001***	19.54	<0.001***	10.04	0.0015**	7.95	0.0048**
Precip.	N/A	N/A	1.27	0.2589	519.54	<0.001***	700.89	<0.001***	130.33	<0.001***	67.46	<0.001***
Inoculum	18.21	<0.001***	5.66	0.0149*	4.66	0.0308*	5.79	0.0162*	1.31	0.2516	0.30	0.5824
Aridity*Precip.	N/A	N/A	0.72	0.3971	88.67	<0.001***	11.81	<0.001***	18.34	<0.001***	1.82	0.1771
Aridity*Inoculum	0.01	0.9214	3.08	0.0793	0.35	0.5552	0.23	0.6338	0.46	0.4953	0.25	0.6190
Precip.*Inoculum	N/A	N/A	0.0002	0.9899	0.60	0.4368	0.36	0.5487	1.66	0.1975	1.67	0.1967

P-value significance: * <0.05, ** <0.01, ***<0.001.

Table 1.3. Pearson correlations between fitness (biomass and seed mass) under drought conditions and mean population-level phenological traits, or mean population-level plasticity in those traits (see Methods for details). Plasticity metrics were calculated as the difference between the population mean trait value under the drought treatment and the high precipitation treatment.

	Biomass		Seed Mass	
Phenological Trait	R	P	R	P
Emergence	0.72	0.0055**	0.77	0.0021**
Flowering	-0.79	0.0014**	-0.69	0.0088**
Growing Season	-0.78	0.0017**	-0.74	0.0041**
Plasticity in Emergence	0.14	0.6438	-0.22	0.4739
Plasticity in Flowering +	0.18	0.6136	0.62	0.9517
Plasticity in Growing Season	-0.86	0.0002***	-0.66	0.0143*

P-value significance: * <0.05, ** <0.01, ***<0.001 Positive R values indicate a positive correlation. +N=10 for Change in flowering due to no flowering in 3 sites under drought conditions. N=13 for all other correlations.
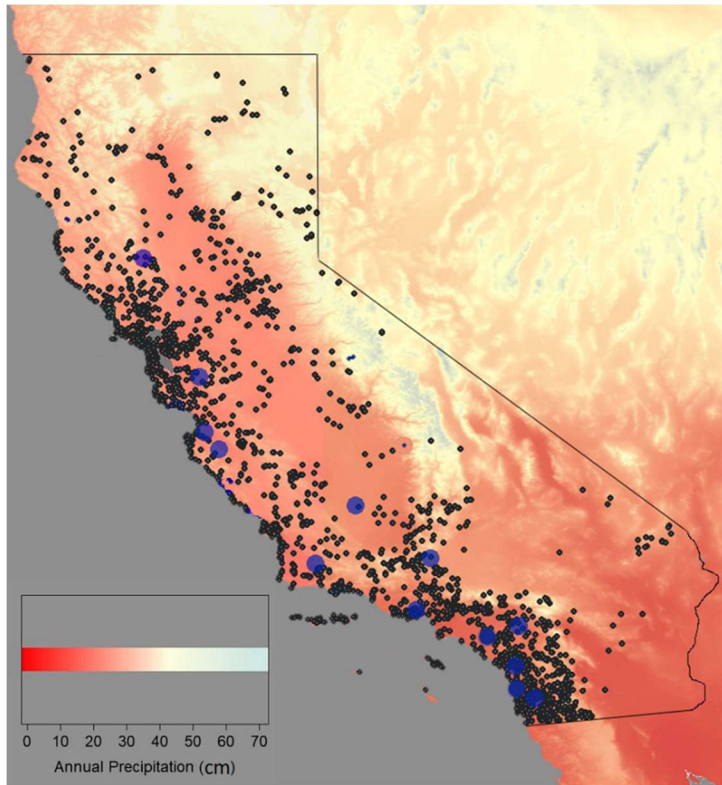
Figure 1.1. Occurrences (black dots) of *E. californica* in California, based on specimen collection locations from the Consortium of California Herbaria database. The full species range extends north to southern Washington state, and south to Baja Sur, Mexico. Background colors indicate mean annual precipitation, where darker red colors indicate higher mean annual precipitation values (see legend). Blue dots indicate our 13 seed collection sites for *E. californica*.
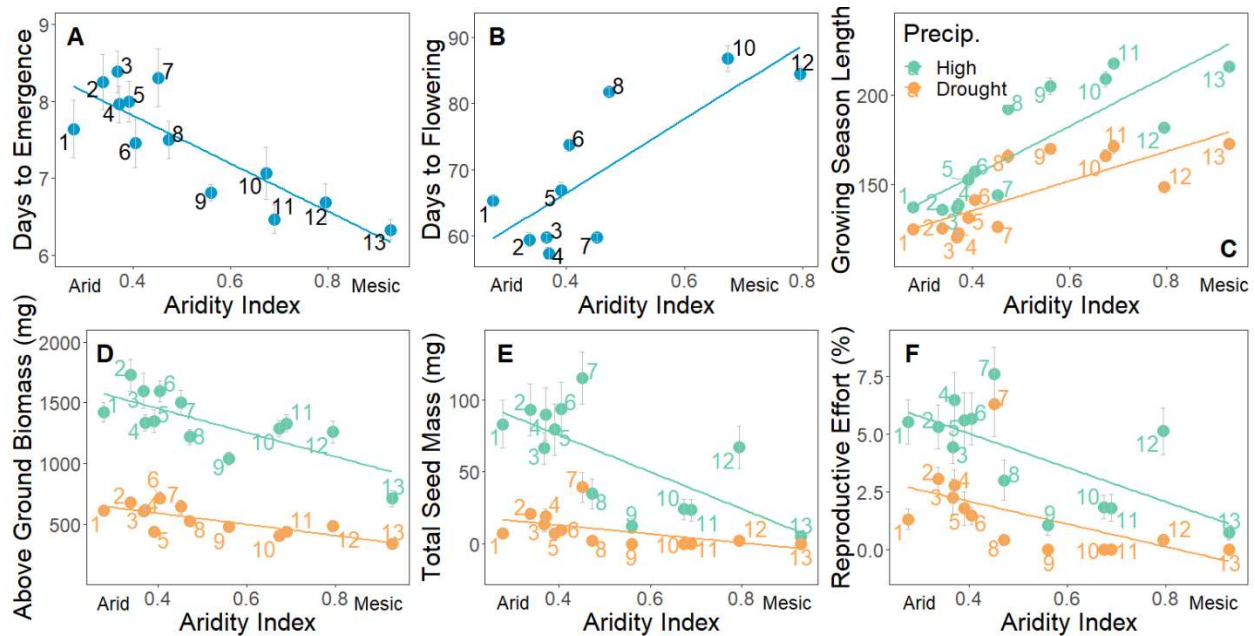
Figure 1.2 (A, B, C, D, E, F). Phenological traits of emergence, flowering and growing season length all show strong clinal variation in *E. californica* (A: Aridity, p = <0.001; B: Aridity, p = <0.001; C: Aridity, p = < 0.001). Flowering was not plastic in response to precipitation (Precip, p = 0.46; Aridity:Precip, p =0.08). Growing season length decreases under drought, especially in populations from mesic sites (Precip, p = < 0.001; Aridity:Precip, p = < 0.001). Gray bars indicated standard error for the point. In panel B the error may be smaller than the size of the point. Populations from arid sites produce more above ground biomass and seed mass, and have higher reproductive effort, under all conditions (D: Aridity, p = <0.001; E: Aridity, p = 0.002; F: Aridity, p = 0.005). All populations are less fit and have lower reproductive effort under drought conditions, especially populations from mesic sites (D, E, F: Precip, p <0.001) but populations from arid sites do relatively better when grown under high precipitation conditions (D, E: Aridity:Precip, p = <0.001).
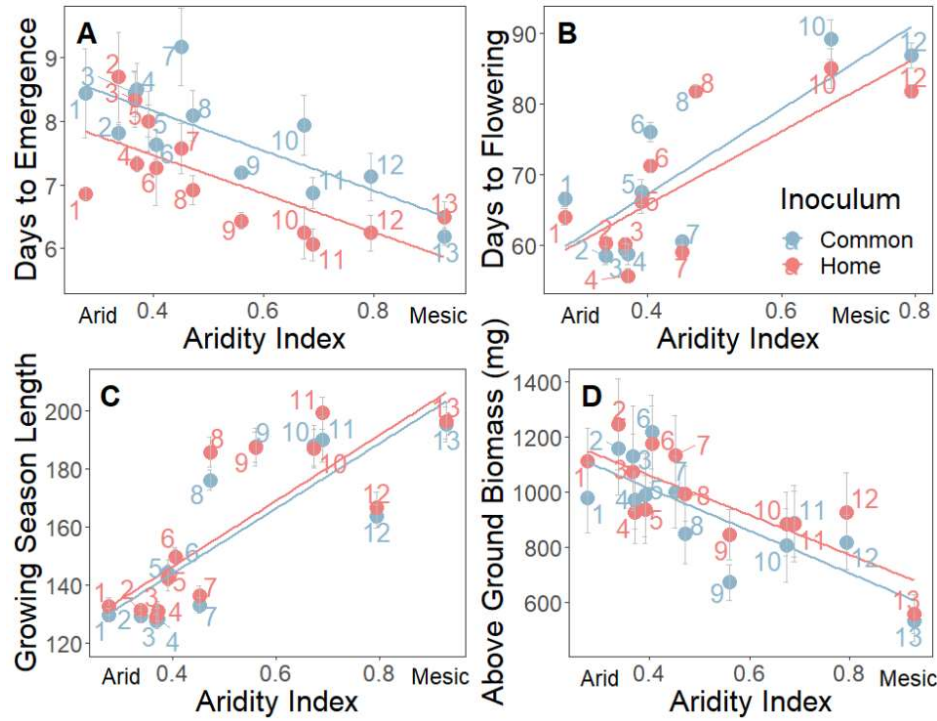
Figure 1.3 (A, B, C, D). When grown with home soil inoculum, days to emergence and flowering advance, and populations extend their growing seasons and produce more above ground biomass. A: Inoculum, p <0.001; B: Inoculum, p = 0.01; C: Inoculum, p = 0.03; D: Inoculum, p = 0.02).
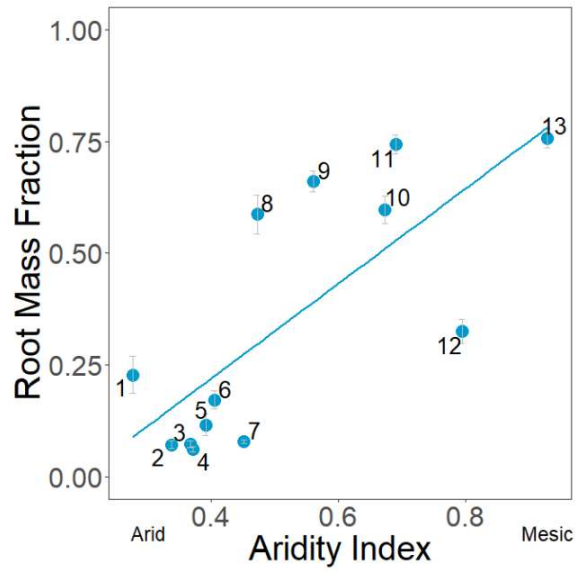
Figure 1.4. Root mass fractions shows strong clinal variation in *E. californica* (A: Aridity, p = <0.001), with increasingly mesic sites allocating a higher proportion of biomass to their roots.

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Chapter 1 Supplementary Material

1. Aridity Index Calculation Methods
PET = Mean Annual Potential Evapotranspiration

$PET = 16 \, d \, (10T / I)^a$

Where T is the mean temperature for the month (in °C), I is the annual thermal index, which is

the sum of monthly indices i:

$i = (T/5)^{1.514}$

d is a correction factor for day length, and a is $0.49 + 0.0179 \, I - 0.0000771 \, I^2 + 0.000000675 \, I^3$.

Using Precipitation and PET, we then calculated the Aridity Index (AI) for each site:

$AI = P / PET$

Where P = Mean Annual Precipitation.

Mean annual precipitation (P) values were calculated by aggregating total monthly precipitation

values from PRISM (PRISM Climate Group), for years 1987-2016. PET values were calculated

by month, for years 1987-2016, by the Thornthwaite method, and were subsequently aggregated

into a single mean annual value (PET) for 1987-2016 (Thornthwaite, 1948). An Aridity Index

was calculated for each year (1987-2016), and then subsequently averaged for the 30-year

period.

2. Linear mixed effects models

The following syntax was used for the linear mixed effects models of phenological variables and

fitness measures, with Growing Season Length as an example:

model1=lme(SeasonLength~Aridity * Water + Aridity * Inoculum + Water * Inoculum,

data=perf, random = ~1 | Site)

In one instance, we removed Water treatment from the model because all pots were subjected to the same amount of water while seedlings were emerging:

model2=lme(DaystoEmergence~Aridity * Inoculum, data=perf, random = ~1 | Site)
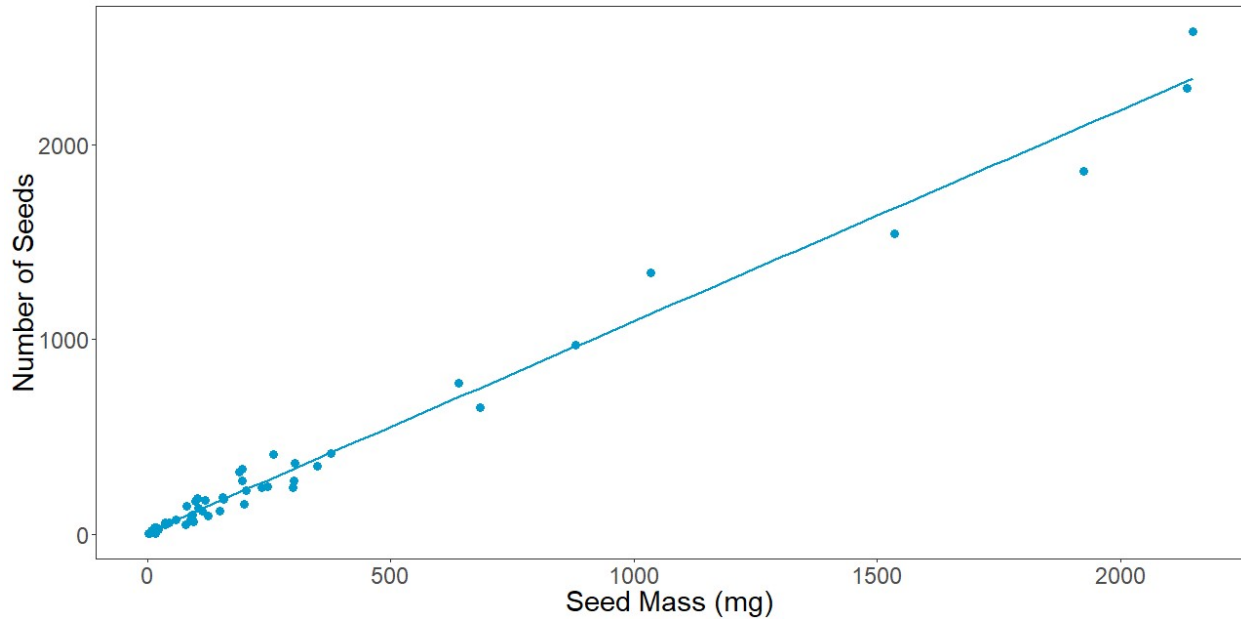
Figure S1. Seed number was strongly predicted by seed mass (p <0.001).
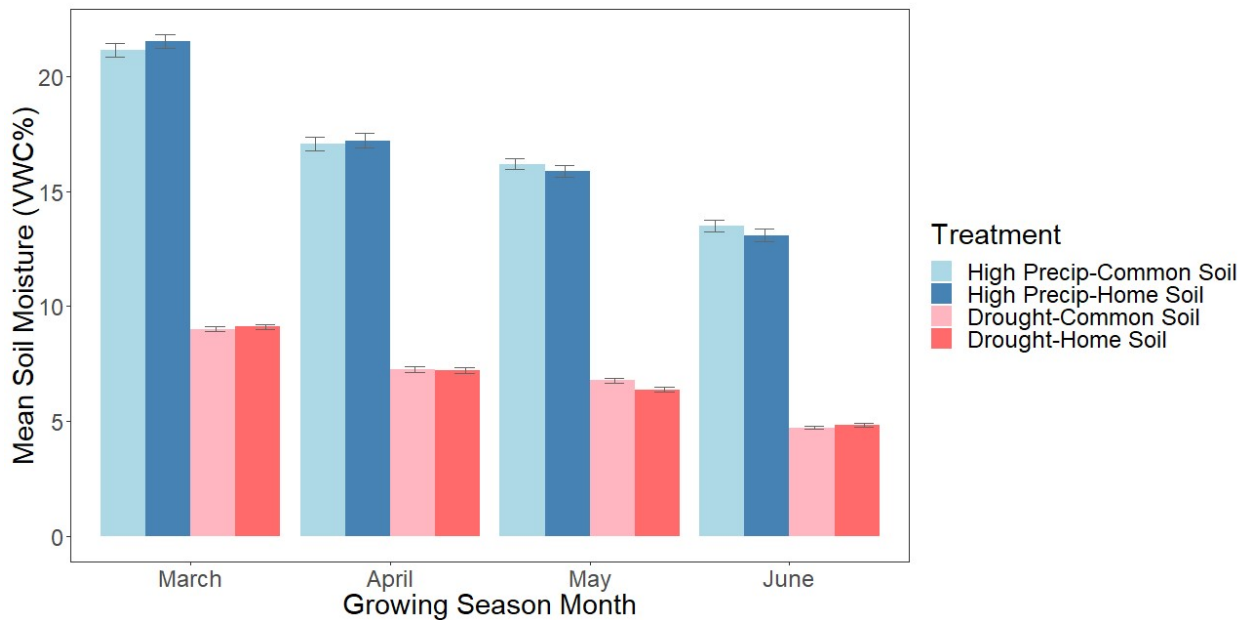
Figure S2. Mean soil moisture by treatment, over four months of the growing season. Soil moisture levels do not vary between home and common garden soil inoculum treatments (Table S3).
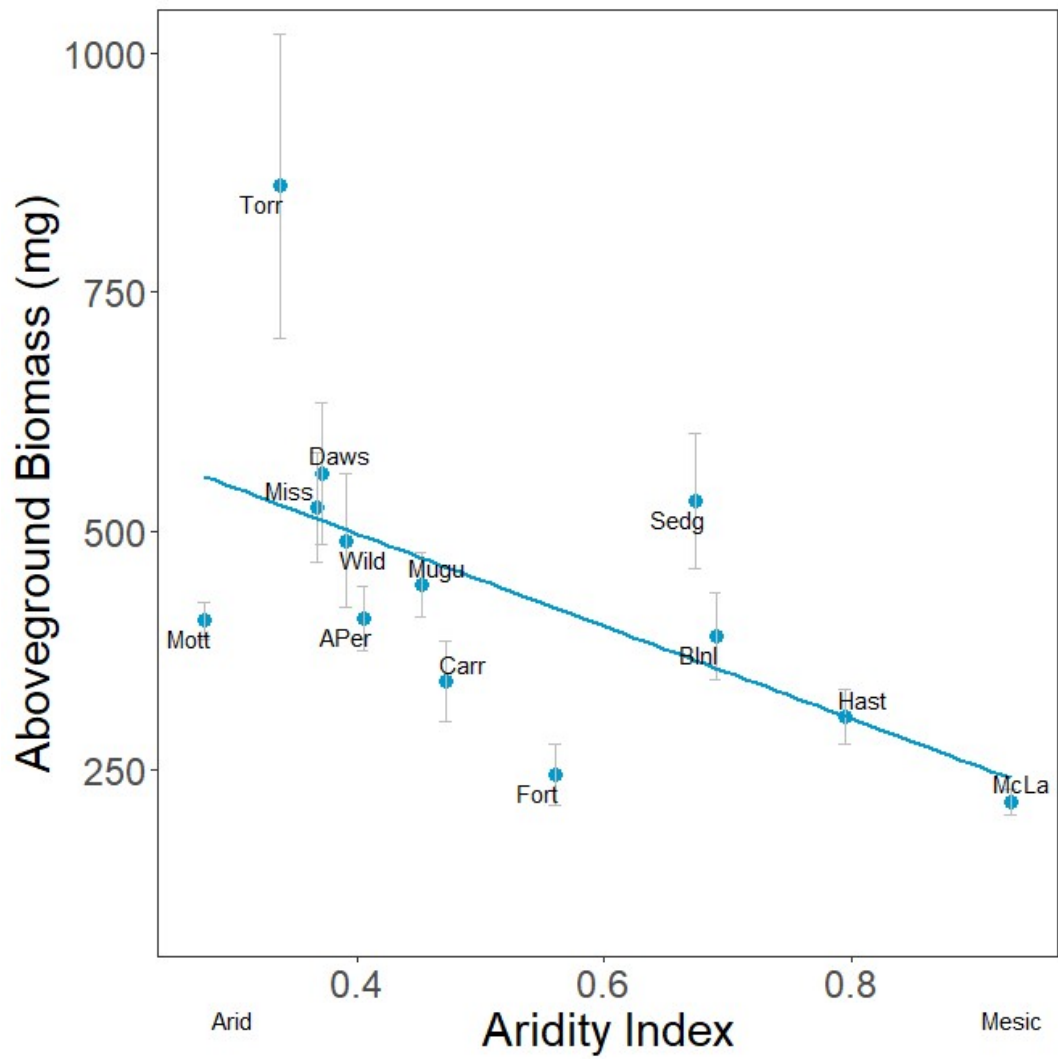
Figure S3. Aboveground biomass from our second greenhouse experiment shows strong clinal variation in *E. californica* (Aridity, p = <0.001), with arid site populations having higher aboveground biomass.
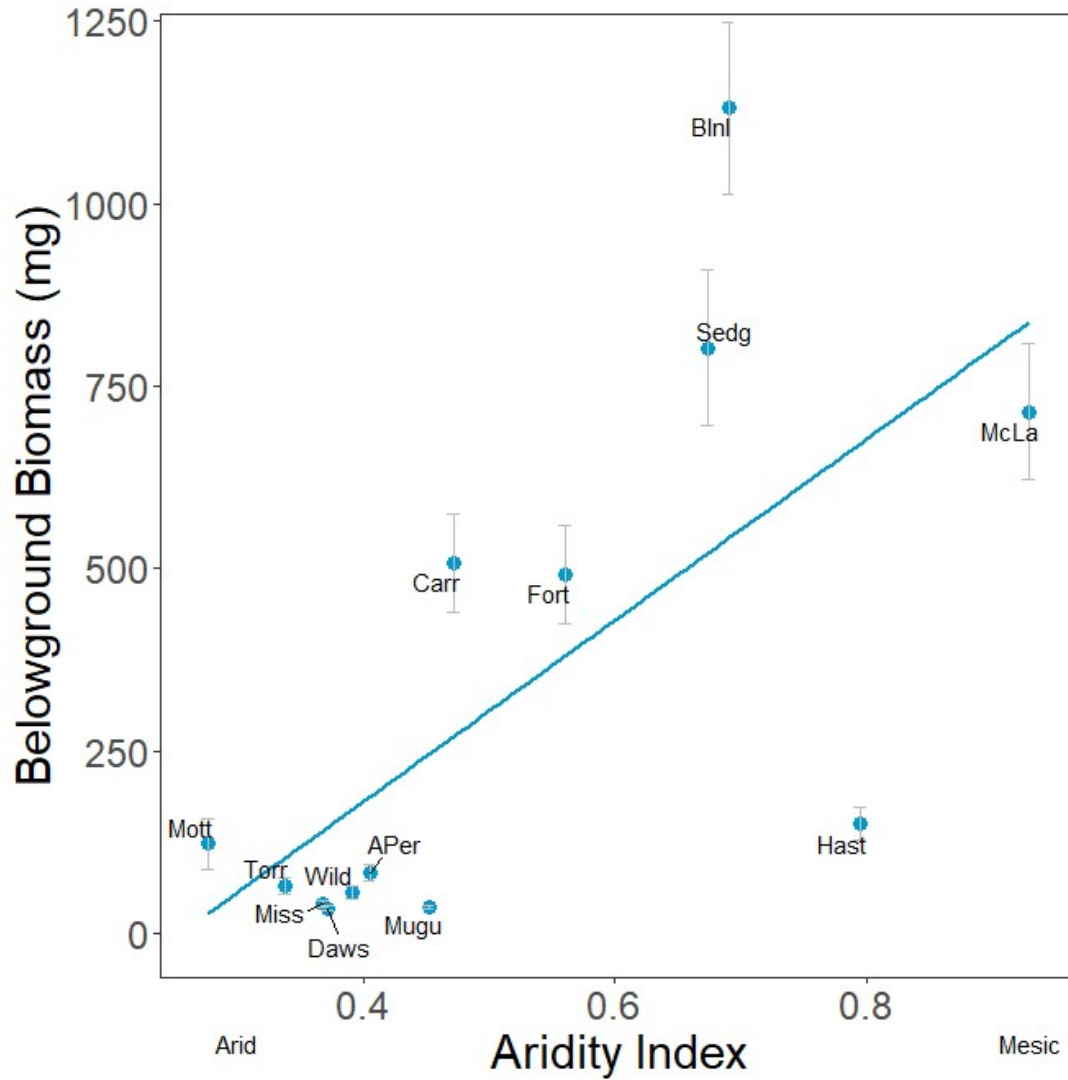
Figure S4. Below ground biomass from our second greenhouse experiment shows strong clinal variation in *E. californica* (Aridity, p = <0.001), with mesic site populations having higher belowground biomass.

Figures S5-S13. Q-Q plots for residuals of all *lme* statistical models:
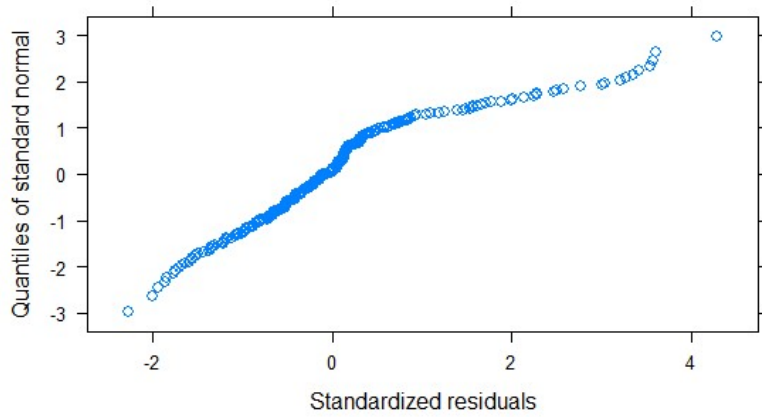
Figure S5. Seed Mass.
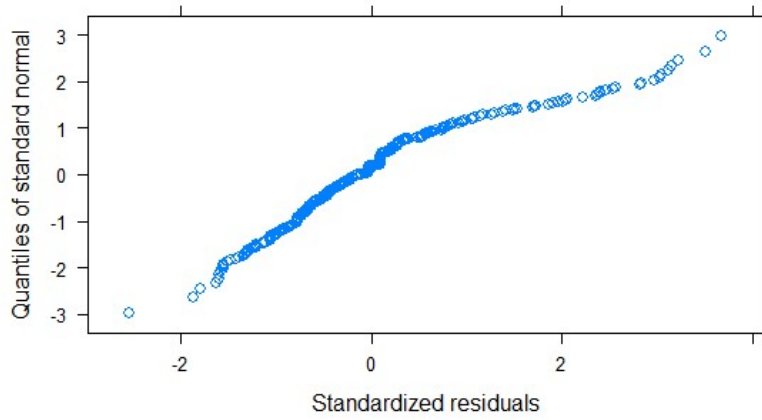
Figure S6. Reproductive Effort.
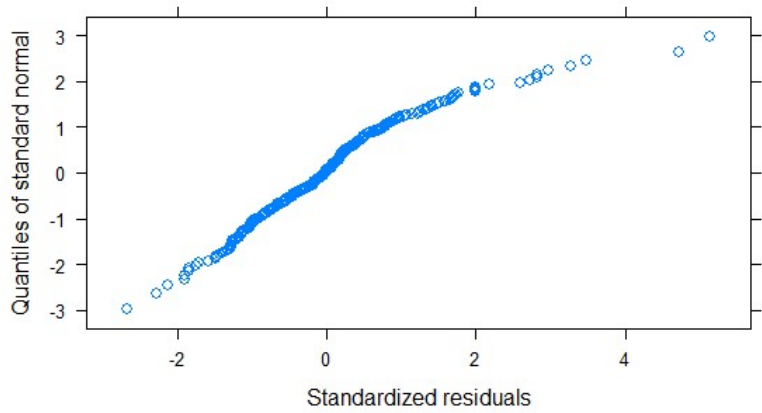
Figure S7. Aboveground Biomass**.**
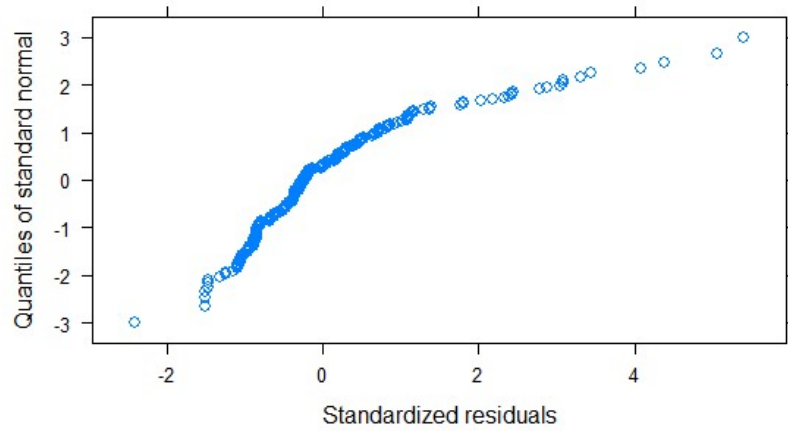
Figure S.8 Emergence.
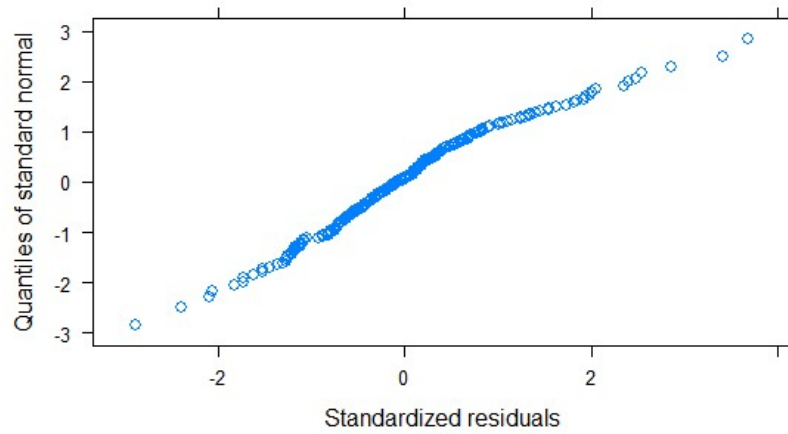
Figure S9. Flowering.
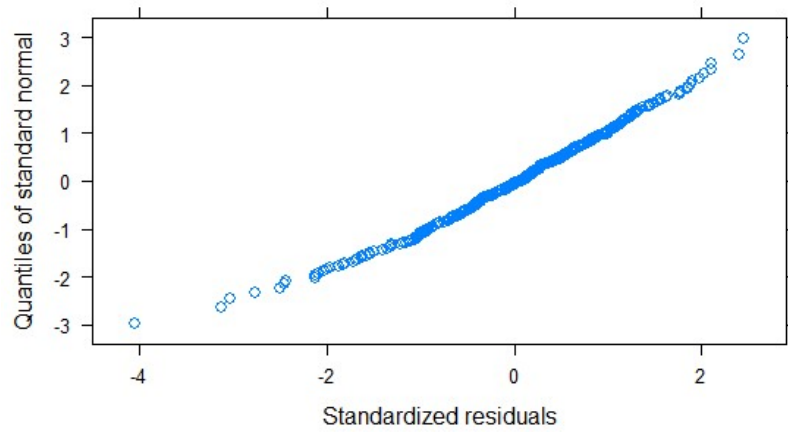
Figure S10. Growing Season.
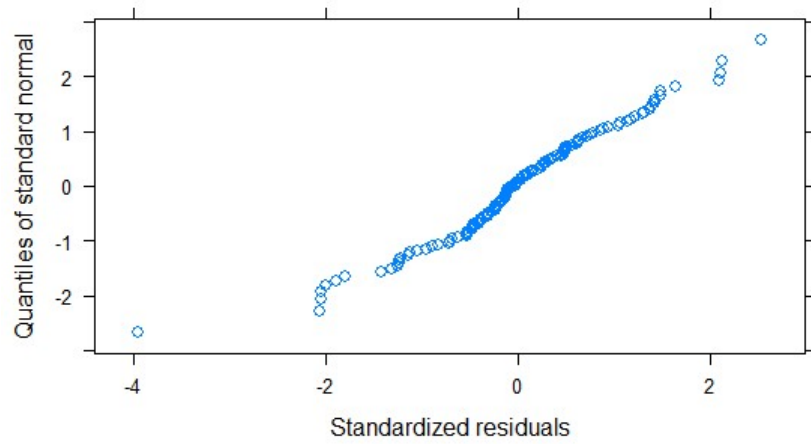
Figure S11. Root Mass Fraction.
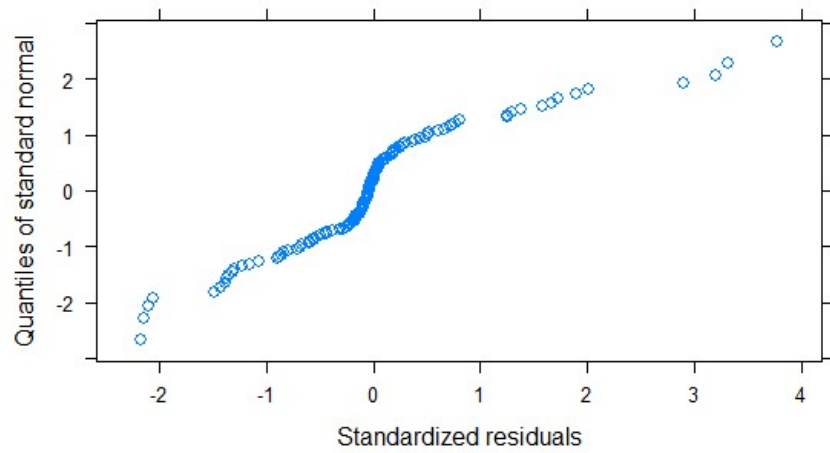
Figure S12. Belowground Biomass.

Table S1. Pearson correlations among environmental variables across the 13 population collection locations. MAP= mean annual precipitation, MAT = mean annual temperature, AI= aridity index. Values are Pearson correlation coefficients (r), with statistical significance in parentheses.

	Environmental variable				
	MAP	MAT	AI	Latitude	Longitude
MAT	-0.49 (ns)				
AI	0.91 (***)	-0.73 (**)			
Latitude	0.81 (**)	-0.87 (**)	0.89 (***)		
Longitude	-0.72 (**)	0.92 (***)	-0.89 (***)	-0.95 (***)	
Elevation	0.53 (ns)	-0.36 (ns)	0.53 (ns)	0.54 (ns)	-0.42 (ns)

P-value significance: * <0.05, ** <0.01, ***<0.001. Positive r values indicate a positive correlation. N=13 for all correlations.

Table S2. Correlation between response of phenological traits and fitness to home soil inoculation versus Organic Matter LOI in individual population's home soils. For instance, "change in emergence" is difference (in days) between emergence in the home soil inoculation treatment, versus the common soil. These findings indicate that the significant shifts observed in these phenological variables were not due to soil organic matter differences among home soils.

	Organic Matter LOI	
	R	P
Change in Emergence	0.10	0.7626
Change in Flowering	0.05	0.9135
Change in Growing Season	-0.26	0.4155
Change in Fitness	-0.19	0.5518

P-value significance: * <0.05, ** <0.01, ***<0.001 Positive R values indicate a positive correlation. N=13 for all correlations.

Table S3. Statistics from linear mixed effects models evaluating how experimental treatment (Precipitation and Inoculum) influenced soil moisture levels across 4 months of the growing season of *E. californica.*

	March		April		May		June	
	X^2	P	X^2	P	X^2	P	X^2	P
Precip.	618.89	<0.001***	353.60	<0.001***	507.69	<0.001***	402.32	<0.001***
Inoculum	0.20	0.6583	0.01	0.9617	0.81	0.3676	0.13	0.7155
Precip * Inoculum	0.14	0.7087	0.04	0.8471	0.04	0.8535	0.41	0.5232

P-value significance: * <0.05, ** <0.01, ***<0.001. N=80.

Table S4. Statistics from linear mixed effects models evaluating how Aridity Index influenced biomass allocation across 13 populations of *E. californica.*

	Aridity	
	X^2	P
Root Mass Fraction	20.01	<0.001***
Aboveground Biomass	7.54	0.0060**
Belowground Biomass	12.467	<0.001***

P-value significance: * <0.05, ** <0.01, ***<0.001. N=13.

CHAPTER 2: Functional traits predict life history variation across the native range of California poppy under drought and warming

Abstract

Predicting how species will respond to climate change can be complicated by population-level differences in demography and life history strategy. Trait variation can be a useful tool to aid these predictions if they prove 'functional', thereby influencing population demographics. While interspecific associations between functional traits and population demographics have been found, it's not known whether functional traits predict intraspecific demographic variation, nor whether these relationships are being influenced by global change. We investigated 20 populations of *Eschscholzia californica* (California poppy) distributed across a fourfold gradient in annual precipitation. In a field common garden, plants received precipitation treatments approximating the wettest and driest sites, crossed with the presence and absence of a 1.5°C warming treatment. We documented clinal variation across populations; plants from southern populations (arid sites) were more likely to survive to flower, be annuals, have higher seed set, higher population growth rates and higher elasticities to fecundity, than northern, mesic, populations. Populations, especially from arid sites, had higher growth rates, seed set and rates of survival to flowering under warm and wet conditions. Functional traits (SLA, days to flowering, seed size) predicted elasticities to fecundity for our populations. Our results suggest that conservation efforts in similar systems should focus on seeding efforts (versus plant longevity) in populations with high SLA, short time to flowering and small seed size. Assisted gene flow sourced from arid population would be most likely to allow populations to persist in the face of increasing warming and more extreme precipitation trends, due to their high fecundity and population growth rates.

Introduction

Population-level differences in demography and associated life history strategies, common among species (Clausen et al., 1948; Endler, 1977; Hall & Willis, 2006; Turesson, 1922), can complicate traditional species-level predictions of response to climate change. One way to incorporate population-level variation is through quantifying the effect of selection from past climates on population demographics (survival and fecundity) and functional traits associated with climate tolerance (Dalgleish et al., 2011; Kelly et al., 2012). Clinal variation in these demographic parameters and functional traits, and the degree of plastic response to climate, can reveal how species might respond to future climate change (Etterson et al., 2016; Kelly et al., 2012; Pearson & Dawson, 2003; Thuiller et al., 2008). When populations of the same species have different methods of persistence (i.e. regeneration by recruitment versus longevity), then conservation efforts targeting the most critical demographic stage could improve species persistence in the face of climate change (Aronne, 2017; García & Zamora, 2003).

Because quantifying this critical demographic stage (via vital rates and their subsequent population growth rates and elasticities) is time intensive, researchers often choose trait-based approaches to predict the fate of species (Laughlin, 2012; Lavorel & Garnier, 2002). If the traits in question are 'functional', thereby influencing population demographics (survival and fecundity) (Lavorel & Garnier, 2002; Violle et al., 2007), we can use them to help identify what the critical demographic stage is. For example, flowering time is a key functional trait because it impacts fitness in a variety of species (Anderson & Gezon, 2015; Franks et al., 2007; Kooyers et al., 2019; Wilczek et al., 2010). Flowering time variation within a species can also cause differences in populations demographics, through varying survival (Agren et al., 2017) and fecundity (May et al., 2017). Adler et al. (Adler et al., 2014) found that using just a few

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functional traits can predict a species' life history strategy, and could allow researchers to identify the demographic stages that are most important for predicting species persistence, without the need for population models and elasticities (Adler et al., 2014). While the significance of functional traits is apparent across many species, as a proxy for different ecological and life history strategies, their usefulness within species as a predictor of demographic variation is less clear (Adler et al., 2014; Anderegg et al., 2018; Cochrane, 2016; Wright et al., 2004). Determining if intraspecific trait variation across environmental gradients is functional and associated with life history strategies could help us more efficiently understand how plants will respond to future climate change.

The association between functional traits and life history strategies can be further categorized by strategic tradeoffs that are mediated by climatic conditions. Specifically, in mesic environments there may be fitness advantages to a "slow" life history strategy with high adult survival (perenniality) and slow vegetative growth (low SLA), while unpredictable and harsh arid environments may select for a "fast" strategy of low adult survival (annuality), fast vegetative growth (high SLA) and early phenology (Franks et al., 2007; Friedman & Rubin, 2015; Hall & Willis, 2006; Peterson et al., 2016; Westoby et al., 2002). A perennial life-history strategy may also be associated with fewer but larger seeds that provide more stored energy for the seedling, thus improving survival between growing seasons, at the expense of having high numbers of offspring (fecundity) (Adler et al., 2014; Moles & Westoby, 2006). In contrast annuals may produce smaller seeds in greater quantities, as their maternal plants are limited to only one reproductive cycle (Adler et al., 2014; Moles & Westoby, 2006). This functional trade-offs between seed size and seed number and leaf area and longevity, is well-documented at the species level, but less clear across populations within species (Westoby et al., 2002, 2003).

These relationships between functional traits and demographics can potentially be augmented by how each one responds in the short-term to climatic changes. For example, plasticity in flowering time due to drought and warming has been documented (Aronson et al., 1992; Cleland et al., 2012; Franks, 2011), and the result could significantly impact population demographics and population persistence (Miller-Rushing et al., 2010). Climate manipulation experiments are therefore needed to quantify how established trait-demographic relationships might vary in response to future climate change (Pearson & Dawson, 2003; Thuiller et al., 2008).

Driven by increased evaporative demand and global temperatures, aridity is expected to increase across the globe (except Northern Africa and high latitudes) (Berg et al., 2016; Cook et al., 2014; Dai, 2013; Feng & Fu, 2013; Scheff & Frierson, 2015). Understanding past and future selection across gradients in aridity, and its climatic components (temperature and precipitation) will be critical to predicting plant responses to future climate change. Our study was conducted in California, a Mediterranean-climate region expected to experience increasingly severe drought periods, along with warming and lower precipitation (Cayan et al., 2008; Dai, 2013). Here, we investigated clinal variation and plastic responses to drought and warming, for 20 populations of California poppy (*Eschscholzia californica*) distributed across a climate gradient characterized by a fourfold difference in precipitation. We also investigated the association between functional traits and the elasticity to fecundity. California wildflowers are at risk from future climate change due to directional selection from rapid and increasingly extreme climatic changes (Jump & Peñuelas, 2005), and an inability to migrate due to regional habitat fragmentation (Davis & Shaw, 2001; Underwood et al., 2009). In fact, climatic change has already caused decreases in the diversity of California wildflowers (Harrison et al., 2015), highlighting the need for studies in these systems.

Prior research in California poppy has found a large degree of intraspecific variation. Some of these studies showed variation along a geographic gradient, such as in perenniality and seed dormancy (Cook, 1962). While other studies showed clinal variation in phenological traits, fitness, reproductive effort, and drought tolerance, as well as local adaptation to climate (Leger & Rice, 2007; Ryan & Cleland, 2021). We built on this work with the goals of: 1. testing for clinal variation in functional traits, demographic factors, population growth rate and elasticity to fecundity, consistent with past selection in relation to aridity. 2: measuring population-level plasticity in functional traits, demographic factors, population growth rate and elasticity to fecundity in response to drought and warming. 3. testing if functional traits predict variation in life history strategies (via elasticity to fecundity).

We expected to find population level variation in functional traits, demographic parameters, elasticities to fecundity and population growth rate in response to climate. We expected populations from more arid sites would display short-lived life history characteristics associated with drought escape (Friedman & Rubin, 2015; Schaffer & Gadgil, 1975; Stearns, 1992). We chose traits which had been shown in other studies to directly impact population or species fitness across various climates, including flowering time (Aronson et al., 1992; Franks, 2011; Franks et al., 2007; Hall & Willis, 2006; Sherrard & Maherali, 2006), specific leaf area (Adler et al., 2014; Reich, 1999; Wright et al., 2004), and seed size (Adler et al., 2014; Moles & Westoby, 2006; Montalvo et al., 2002).

We also expected functional traits and demographic parameters would respond differently to climatic treatments. We expected under drought and warming, all populations would have decreased population growth rates, driven by decreases in survival to flowering and total seed set in conditions outside of their climate optima (Jump & Peñuelas, 2005; Leimu &

Fischer, 2008). Under drought, warming and ambient temperature conditions, we expected populations from southern arid sites would have higher population growth rates (λ) and survival to flowering than those from northern mesic sites, and lower rates under high precipitation conditions, consistent with documented frequent local adaptation to climate in plants (Leimu & Fischer, 2008). We expected the greatest plasticity in functional traits, demographics and population growth rates in arid site populations that have previously experienced higher levels of environmental variability (Atkin et al., 2005; Bradshaw, 1965; Chevin & Hoffmann, 2017; Gugger et al., 2015; Pratt & Mooney, 2013; Schlichting, 1986; Sultan, 1987). Finally, we expected populations with traits associated with a short lived life history strategy (small seeds, high SLA and shorter durations to flowering) would have higher elasticities to fecundity, whereby population growth rates (λ) are driven by high seed set in a single year (Adler et al., 2014).

2. Materials and Methods

2.1 Collection and preparation of seeds

This study focuses on 20 natural (non-planted) populations of *E. californica* collected between April and July, 2017. These populations encompass significant life history variation, some annual others perennial, when grown under our common garden field conditions. The collection sites were distributed over 700km in southern, central, and northern California (32.8-38.9 latitude) and span a climatic gradient that varies fourfold in precipitation (Table 1; Figure 1). Within a site, seed pods were collected from 10 maternal plants spaced at least 5 meters apart. Seeds were stored at room temperature until planting by maternal line. Prior to planting seeds were surface sterilized with a 5,000 ppm concentration of Clorox Household Bleach (8.25%

active chlorine) and treated with a 500 pm concentration of gibberellic acid to help break dormancy (Cook, 1961; Fox et al., 1995). Populations from arid sites have a higher instance of seed dormancy (Cook, 1962; Montalvo et al., 2002), even after gibberellic acid treatment (Cook, 1961). Twenty-four hours after gibberellic acid was applied, three seeds were planted in each PVC ring, 1 cm below the surface, because light inhibits germination of *E. californica* (Fox et al., 1995). The first seedling to emerge was the focal individual, and any later emerging seedlings were removed.

2.2 Common garden design and treatments

The field common garden was located at the University of California San Diego Biological Field Station in La Jolla, CA (32.8855, -117.2299). This site is coastal, and like all the collection sites has a winter growing season (average annual precipitation: 26.7cm, average annual temperature: 16.9°C; full list of sites in Table 1). Seeds for this field experiment were planted in February of 2018 and 2019, following the start of the rainy season in January. Although winter rains often start in November, the onset of the growing season has been delayed in recent years due to lower than normal fall precipitation, a trend expected to continue in the future (Pierce et al., 2018). Seeds were planted inside 3 cm diameter PVC rings to facilitate identification, inside hexagonal 1m diameter plots and grown under 4 experimental treatments (factorial combinations of +/- added rainfall, and +/- warming chambers), with eight replicates (each a separate maternal line) of each population by treatment combination (a total of 640 plants, Data S1, S2, S3). The eight replicates were arranged spatially by block. The 20 populations were divided such that representatives of ten populations were planted in an equally spaced circle in each plot, and plots were paired by treatment to group all 20 populations

spatially. Population positions were rotated in each plot to disperse the potential effects of highly competitive populations and to expose populations to variation in aspect. Plots were spaced with 0.5 m walkways between them.

Half of the plots were surrounded by passive warming chambers and the other half by window screen mesh chambers constructed to mimic the shading and herbivore-exclusion of the warming chambers (Marion, 1996). The warming chambers increased air temperature by 1.5 degrees Celsius/2.7 degrees Fahrenheit.

The high precipitation and drought treatments approximated the annual precipitation totals of the wettest (McLaughlin UC Reserve, 98.1cm annually) and driest sites (Motte Rimrock UC Natural Reserve, 26.72cm annually). Each row of plots was designated high precipitation treatment or drought treatment. Plots were watered with drip irrigation 1100 mL every day in the high precipitation treatment, and 900 mL every 3 days in the drought treatment from February through the end of May. Precipitation events were monitored and subtracted from experimental watering amounts. At the start of the experiment, plants were watered at an intermediate level, halfway between the drought and high precipitation treatments for two weeks to ensure sufficient germination.

2.3 Soil moisture data collection

Soil moisture levels were measured every two weeks from February-May with a Field Scout TDR 100 Soil Moisture Sensor, which measures volumetric water content integrating to a depth of 12cm, to assure the precipitation treatments were influencing soil moisture as expected (see supplementary figure S2).

2.4 Functional trait (seed mass of an individual, specific leaf area, days to flowering) data collection

We calculated mass of an individual seed by taking the average weight of 20 seeds from each individual plant from the 2018 growing season. We calculated specific leaf area as leaf area / leaf biomass (O'Neal et al., 2002). We sampled one young, full sun leaf per plant, measured leaf area while fresh, and then oven-dried it at 60 °C for 2 days. Dry mass was then measured using a fine balance and leaf area was calculated using imageJ (vers. 1.52) (Schneider et al., 2012).

We conducted daily phenology surveys on emergence and day to first flower. Flowering was calculated as the number of days between emergence and day to first flower, to represent time to reproduction.

2.5 Demographic parameters (plant fecundity, germination rate, survival to flowering, survival) data collection

We estimated seed number, our measure of fecundity, by multiplying total seed mass of a plant x seed mass of a single seed. *E. californica* are insect or wind pollinated, and are self-incompatible (Cook, 1961; Darwin, 1876). To calculate the number of juveniles in subsequent growing seasons, needed for matrix modelling, we tracked germination rates in 2018 by site and treatment. We defined number of juveniles as plant fecundity x site and treatment specific germination rate (Caswell, 2001).

We conducted daily senescence surveys. After a plant senesced, it was harvested, and the root was examined to confirm that the root was dead, and hence the plant was not dormant. Survival to flowering and survival to the subsequent growing season were both tracked. A plant

did not survive to the following growing season if it senesced before January of the following growing season. Survival to flower was measured as a fitness component which influences fecundity. We continued to monitor the survival of perennial individuals until September 2020.

2.6 Matrix models

Matrix models were constructed with our demographic parameters using the *popbio* package in in R version 3.6.2 (R Core Team, 2021; Stubben & Milligan, 2007). Population growth rate (λ) values were calculated via the *pop.projection* function on projection matrices constructed for each site and treatment (n=80). Elasticities to fecundity and survival for each site and treatment were obtained using the *eigen.analysis* function (n=80). Matrix population models allow us to transform demographic parameters and measures of fitness across a species life cycle into predictions of how populations will grow or shrink in the future (Caswell, 2001; Morris & Doak, 2002).

2.7 Aridity Calculations

To examine patterns in mean annual Aridity we used the Thornthwaite function in SPEI v1.7 to calculate monthly evapotranspiration (PET) (R Core Team, 2021). The Thornthwaite formula is a standard calculation that uses temperature and day length (via latitude and month) to estimate the water needs of plants in a specific environment (Thornthwaite, 1948). Aridity index values that are low indicate arid environments, while high values indicate mesic environments (Data S4). As expected, the environment becomes more mesic, colder, and wetter across our sites going from south to north (Table 1). See Supplemental Material for detailed methods of the Aridity index calculation.

2.8 Statistical analysis

All analyses were conducted in R version 3.6.2 (R Core Team, 2021). Analysis of total seed number in relation to aridity, precipitation and warming treatments was conducted with linear mixed effect models using the *lme* call in the package *nlme* (Pinheiro et al., 2013), where population was included as a random factor. Analysis of population growth rate, demographic parameters and elasticities in relation to aridity, precipitation and warming treatments, and functional traits were conducted with linear models using the *lm* call in R. Significance for each factor was evaluated with type-II tests using the *Anova* function in the *car* package (Fox & Weisberg, 2019). Significant effects of aridity indicated clinal variation in the response variables, significant main effects of precipitation and warming treatment indicated plasticity in response to these treatments, and significant aridity by precipitation or warming treatments indicated clinal variation in plasticity in response to these factors. We evaluated whether the elasticity to fecundity was affected by changes in functional traits by correlating these variables, where each population was an observation in the analysis (i.e. N=20 for the correlations).

6. Results

3.1 Clinal variation and plasticity in functional traits

Across all treatments we documented clinal variation in response to aridity in functional traits (seed size, SLA, days to flowering) (Figure 3A, B, C, Table 2). Southern, arid, populations had smaller seeds, higher SLA and shorter time to flowering. High precipitation increases SLA, especially in arid populations, while warming also increases SLA and advances flowering time across all populations.

3.2 Clinal variation and plasticity in demographic parameters and population growth rates

Across all treatments we documented clinal variation in response to aridity in population growth rate and demographic parameters (i.e. survival to flowering, perenniality, and total seed number) (Figure 4, Figure 5A, B, C, D, Table 2). Southern, arid, populations were more likely to survive to flower, be annuals, have higher seed set, and higher population growth rates than northern, mesic, populations (Table 2).

Populations, especially from arid sites, had higher growth rates and seed numbers under warm and wet conditions (Figure 4, Figure 5D, Table 2). Germination and perenniality rates did not change in response to the experimental treatments (Figure 5A, C). While all sites had higher survival to flowering under warming and high precipitation, mesic site populations had more plasticity in survival to flower, in that it increased under warming and decreased under drought conditions (Figure 5B).

Across all treatments we documented clinal variation in elasticity to fecundity (Figure 6, Table 3). Southern, arid, populations were more likely to have high elasticities to fecundity (Table 3).

3.3 *Association between functional traits and elasticity to fecundity and plasticity in elasticity to fecundity*

Functional traits (seed size, SLA, days to flowering) were associated with elasticities to fecundity for our populations (Figure 7A, B, C, Table 3). Populations with smaller seeds, higher SLA and shorter time to flowering had higher elasticities to fecundity. We found no evidence of

plasticity in elasticity to fecundity, or climate-induced changes to its association with functional traits in our system (Figure 5, 7A, B, C).

Discussion

4.1 Summary

We found significant clinal variation across populations in functional traits, demographic parameters, population growth and elasticities to fecundity. Plants from southern, arid site populations were more likely to survive to flower, be annuals, have higher seed set, higher population growth rates and higher elasticities to fecundity, than northern, mesic, populations. Populations, especially from arid sites, had higher growth rates and seed set under warm and wet conditions. Functional traits (SLA, days to flowering, seed size) were associated with elasticities to fecundity for our populations. And while experimental treatments affected functional traits, they did not affect the association between traits and elasticities to fecundity.

4.2 Clinal variation in Functional Traits

Functional traits can be the result of adaptations to the environment and often exhibit significant clinal variation (Reich et al., 2003). The functional trait variation we observed along an aridity gradient in California poppy is consistent with clinal variation found in other widespread species in California (Clausen et al., 1948; Peterson et al., 2016; Pratt & Mooney, 2013). We predicted populations from more arid sites that tend to be short-lived would have high SLA to maximize photosynthesis during a shorter life cycle, while mesic site plants would have lower SLA (i.e., sturdier yet costly leaves) to withstand growing over multiple seasons (Reich, 1999; Wright et al., 2004). We found this relationship in *E. californica*, which is contrary to

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species-level studies where plants exhibit lower SLA when growing in harsher environments (i.e. arid conditions) due to the need to limit water loss through evapotranspiration surfaces (Castro-Díez et al., 2021; Liu et al., 2017; Wright et al., 2004). We also found populations from more arid sites flowered earlier, potentially to reproduce before the summer drought (Aronson et al., 1992; Franks, 2011; Franks et al., 2007; Hall & Willis, 2006; Sherrard & Maherali, 2006). We documented a tradeoff in seed size versus seed number, whereby arid populations had smaller seeds in larger quantities compared to mesic populations, spending less energy on provisioning for individual seeds, given the opportunistic qualities of these seeds (i.e., high rates of dormancy) (Adler et al., 2014; Cook, 1962; Montalvo et al., 2002).

4.3 Clinal variation in demographic parameters and population growth rates (λ)

Demographic parameters also varied along an aridity gradient in California poppy. As predicted, populations from more arid sites exhibited lower perenniality, as a drought escape strategy (Friedman & Rubin, 2015; Schaffer & Gadgil, 1975; Stearns, 1992). We did not observe a discreet switch from the annual to perennial life history strategy as traditionally expected (Charnov & Schaffer, 1973; Cole, 1954), but high variability of perenniality rates in our mesic populations, as well as an overlap in climate space of annuals and perennials, suggesting more labile changes in life history strategy (Friedman & Rubin, 2015).

We expected higher elasticity to fecundity in our more arid site populations, where population growth rates (λ) are presumably driven by high seed set in a single year and not survival to subsequent reproductive seasons. We observed higher elasticity to fecundity in our arid site populations, where high seed set, often in a single growing season drives population growth rates. Leger & Rice (Leger & Rice, 2007), while studying perennial populations of *E.*

californica in Northern California and Chile, also documented higher seed set in more arid sites. Overall, fecundity had the greatest effect on population growth rate across all populations and contributed to the highest population growth rates in arid site populations. Conservation strategies that focus on regeneration through seeding efforts (encouraging pollination, seed dispersal and reducing seed predation) will have the largest effect on persistence for populations whose growth is determined by fecundity (García & Zamora, 2003).

4.4 Association between functional traits and life history strategies

Quantifying traits that are both 'functional' (Lavorel & Garnier, 2002; Violle et al., 2007), and associated with life history strategies, can be a powerful tool to help identify what a populations critical demographic stage is. Furthermore, they can be used to help predict species responses to climate change (Soudzilovskaia et al., 2013).

Some of the intraspecific relationships we observed between functional traits and life history variation confirms associations seen across species. One meta-analysis of 222 perennial plants showed that traits associated with a short lived life history strategy, such as small seeds and high SLA, have higher elasticities to fecundity and lower elasticity to survival, whereby population growth rates (λ) are driven by high seed set in a single year (Adler et al., 2014). Based on this study, we predicted that within a species whose populations exhibit various life history strategies, populations with functional traits indicative of a short life history strategy (small seeds, high SLA, shorter days to flowering) would have higher elasticities to fecundity. Similar to Adler et al. (Adler et al., 2014), we found SLA predicted elasticities to fecundity, in that higher SLA populations had higher elasticities to fecundity. Like Adler et al. (2014), we also

found that seed size predicted elasticities, in that populations with larger seeds had higher elasticities to survival.

However, we observed instances were associations between functional traits and life history strategy were the opposite of those observed across species. Adler et al. (2014), found that lower SLA plants had higher survival rates. This relationship is commonly expected when comparing species, where thicker leaves are associated with increased survival. However, within our species, we found shorter-lived high SLA plants had higher rates of survival to flower. This could indicate a bet hedging strategy for variable environments (Rees, 1994; Venable & Brown, 1988), as short-lived arid site populations had delayed germination and greater potential for seed dormancy [Ryan, unpublished data], but higher survival to flower once germinated. We likewise did not find that larger seeds improved seedling survival to flowering, as expected based on the seed mass and number trade-off (Adler et al., 2014; Moles & Westoby, 2006), as arid site populations had higher rates of seedlings surviving to flower but smaller seeds than our mesic sites. This may be because our common garden was in the southern portion of the species range, was warmer than the collection locations for the northern populations, and hence none of our treatment combinations captured ideal growth conditions for those populations.

Like other intraspecific studies, we found a strong relationship between flowering time and fitness in our populations. Populations from the more arid collection locations, with fast growth and flowering, had the highest seed set and population growth rates under all conditions. Consistent with our results, Kooyers et al. (Kooyers et al., 2019) found that the timing of flowering allowed the fitness benefits of drought escape in *Erythranthe guttata,* a widespread species found in California and Oregon. And like May et al. found in *Arabidopsis thaliana* (May et al., 2017), we found an association between flowering time and fecundity.

The association between functional traits and our demographic parameters and elasticity to fecundity indicate that functional traits can be used to predict a species life history strategy at the population-level, and thus the demographic stage that best predicts population persistence (i.e. regeneration by recruitment or longevity). In our study, populations with smaller seeds, higher SLA and shorter durations to flowering had higher elasticities to fecundity, indicative of a short-lived life history strategy. Past studies have shown that functional variation across many species is predictive of life history variation (Adler et al., 2014). Here, across many populations of one species, we observe largely the same associations, with some exceptions potentially due to bet hedging in our more arid, variable environments.

4.5 Experimental treatments affect population growth rates, demographics, and functional traits

We observed select demographic parameters that responded to experimental treatments, resulting in plasticity in population growth rates under different climate conditions. As expected, population growth rates decreased under drought, while contrary to expectations, population growth rates increased in response to warming. Consistent with our results, others have found warming increased population growth rates, while drought decreased them (Dalgleish et al., 2011). This plasticity in population growth rates was especially strong in arid site populations, driven by high levels of climate-induced changes in seed set. This may be a product of southern arid populations experiencing historically higher levels of environmental variability, namely greater interannual rainfall and climatic variability (Dettinger et al., 2011a), which would favor plasticity that allows persistence in various conditions (Atkin et al., 2005; Bradshaw, 1965; Chevin & Hoffmann, 2017; Gugger et al., 2015; Pratt & Mooney, 2013; Schlichting, 1986; Sultan, 1987). In one experimental study, the strongest fitness decrease due to drought was

observed in arid plant populations from Southern California (Pratt & Mooney, 2013). These findings highlight how a population-level approach could change predictions of how species will respond to climate change.

We also found that under both warming and high precipitation, populations from southern arid sites had higher population growth rates (λ) and survival to flowering than those from northern mesic sites. This is contrary to expectations based on frequent local adaptation to climate in plants (Leimu & Fischer, 2008), in that mesic site populations would have higher λ under the high precipitation treatment. Also contrary to expectations that our populations would be adapted to local climates, survival to flowering increased under warming for our most mesic site populations (Leimu & Fischer, 2008). Further investigation is needed to determine the mechanism by which warming increased survival for our more mesic sites. As expected, survival to flower decreased under drought for our most mesic site populations. We documented greater plasticity in survival to flowering in populations from mesic sites because survival to flowering in arid site populations was near 100% under all treatments.

We likewise found functional traits of SLA and Flowering time responded to climatic treatments, without affecting the association between traits and elasticities to fecundity. As expected, our arid site populations had the highest levels of plasticity in SLA, which could be the result of our arid sites being located in the most climatically variable part of the U.S. (Dettinger et al., 2011a). Such environments should favor plasticity, due to the need to possess traits and strategies that provide a fitness advantage in variable climates (Atkin et al., 2005; Bradshaw, 1965; Chevin & Hoffmann, 2017; Gugger et al., 2015; Pratt & Mooney, 2013; Schlichting, 1986; Sultan, 1987). SLA decreased under drought, most likely due to an increased need for water use efficiency (Wellstein et al., 2017). Although we would expect warming to trigger a similar water

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use efficiency response (Wellstein et al., 2017), we observed SLA increased under warming, similar to what was found in a meta-analysis by Poorter et al. (Poorter, 2009). Consistent with species across the globe (Stuble et al., 2021), *E. californica* plants flowered earlier under warming. However, this plasticity was not consistent across latitudes as found in other species (Stuble et al., 2021), but mostly observed in our lower latitude, arid populations. And consistent with previous experiments in *E. californica* (Ryan & Cleland, 2021), flowering time did not respond to drought. Seed size, expected to decrease under drought (Pichancourt & van Klinken, 2012), did not respond to any experimental climate treatments. Although we observed plasticity in functional traits in response to the experimental treatments, this plasticity did not change the association established between traits and elasticities to fecundity.

4.6 Caveats of our Study

We implemented high precipitation levels for all experimental treatments during the first two weeks of our study to germinate adequate numbers of plants for our study. Germination rates did not change in response to climatic conditions, potentially due to the consistent high watering during this period, as well as our pre-treatment with gibberellic acid which led to high germination rates under all conditions. Another caveat is that our field experiment was conducted in the absence of competitors, which contributed to the unrealistically high λ values we calculated. However, because competition is thought to be higher in more productive habitats (Grime, 1979), it is likely there is less competition in our arid site locations and thus we would find an even stronger degree of clinal variation in population growth rates if we incorporated realistic levels of competition in our experiment. Additionally, Adler et al.'s (2014) study of functional traits and elasticities in perennials calculated elasticity to growth, which is not a

parameter in our model. Because our study included annual populations, we also calculated a survival to flowering demographic parameter to document senescence in these populations and allow a comparison to studies of solely perennials.

4.7 Implications for conservations efforts

The significant clinal variation we found here and in previous work in *E. californica* annuals (Ryan & Cleland, 2021) highlights the importance of incorporating population variation in predictions of future species ranges (Hamann & Aitken, 2013; Hällfors et al., 2016; Marcer et al., 2016; Oney et al., 2013; Pearman et al., 2010). The trailing southern edges of species ranges have long been expected and found to be most at risk under future climate change (Jump et al., 2006; Jump & Peñuelas, 2005). Surprisingly, our southern populations responded well to experimental treatments warmer than their typical climatic conditions. This suggests these populations, while located at the southern edge of the species range, are not at the edge of *E. californica's* temperature niche. These populations could even expand under future warming if other limiting conditions, such as water-availability, are sufficiently met. Taking a population-level approach enables the observations that some populations can do just as well, or better, outside of the climatic conditions of their home locations, and may be ideal candidates for restoration efforts in the face of future climate change.

Assisted gene flow (AGF), in which advantageous alleles are moved from one population to another (Aitken & Whitlock, 2013), could improve species persistence in the face of increased warming and drought. Our study suggests moving alleles from southern to northern populations would be most beneficial, due to their relatively high population growth rates under drought and warming. The high elasticity to fecundity found in *E. californica*, especially in southern, arid site

populations also suggests that restoration efforts in similar systems should focus on seeding efforts when restoring short-lived populations exhibiting traits such as small seeds, high SLA and early flowering. Methods to encourage pollination, seed dispersal and reducing seed predation could be useful (García & Zamora, 2003).

Conclusion

Efforts to quantify population level variation in demographics have the potential to improve predictions of how species will persist under climate change (Merow et al., 2014; Metcalf & Pavard, 2007). While parameterizing population models with demographic data is not feasible for all species at risk, a trait-based approached may improve predictions of the fate of species (Laughlin, 2012; Lavorel & Garnier, 2002). When functional traits are able to predict life history strategies both across various species (Adler et al., 2014) and across populations within the same species, and are consistent in the face of climatic variation, then researchers can use them to identify the most critical demographic stage for species persistence, potentially improving predictive and conservation outcomes.

Acknowledgements

Table 2.1. Collection locations, climate means, and elevations for the 20 focal populations of *E. californica* in California, USA. Field location and environmental conditions for the four climate treatments are provided for comparison. Abbreviation is the number used to label points in Figures in this manuscript, which correspond to a given population.

Site Name	Abbreviation	Mean Annual Precip. (cm)	Mean Annual Temp. (C)	Aridity Index	Latitude	Longitude	Elevation (m)
Motte Rimrock UC Reserve	1	26.72	17.8	0.2765	33.7985	-117.2545	502
Torrey Pines State Park	2	27.25	16.9	0.3377	32.9233	-117.2586	42
Mission Trails Regional Park	3	33.55	18.1	0.3672	32.8449	-117.0467	181
Dawson UC Reserve	4	32.18	17.2	0.3710	33.1490	-117.2578	130
Wildomar (Clinton Keith Rd.)	5	40.41	18.4	0.3911	33.6017	-117.2312	387
Antelope Valley State Nat. Reserve	6	36.30	16.4	0.4048	34.7338	-118.3786	828
Montaña de Oro State Park	7	43.18	14.1	0.4474	35.3022	-120.8732	74
Coal Oil Point UC Reserve	8	48.67	14.3	0.4498	34.0486	-119.8786	8
Point Mugu State Park	9	41.66	17.2	0.4515	34.0880	-119.0343	91
Carrizo Plains National Monument	10	37.99	15.2	0.4721	35.2125	-119.8765	597
Fort Ord UC Reserve	11	37.72	13.8	0.5603	36.6868	-121.7784	46
Sedgwick UC Reserve	12	57.61	16.3	0.6738	34.7054	-120.0560	425
Kenneth S. Norris UC Reserve	13	46.17	13.6	0.6832	35.5227	-121.0725	61
Blue Oak Ranch UC Reserve	14	58.87	14.6	0.6901	37.3808	-121.7384	542
San Luis Obispo Inland	15	59.54	14.9	0.7699	35.4094	-120.5483	433
Hastings UC Reserve	16	53.80	14.5	0.7947	36.3855	-121.5551	659
Landels-Hill Big Creek UC Reserve	17	89.13	14.4	0.8155	36.1832	-121.6938	20
McLaughlin UC Reserve	18	98.10	14.6	0.9292	38.8602	-122.4166	701
Younger Lagoon UC Reserve	19	80.78	12.4	1.1485	36.9493	-122.0671	28
Bodega Bay UC Reserve	20	86.18	11.6	1.2708	38.3171	-123.0698	2
Field – High Precipitation, Ambient		98.10	18.17				
Field – Drought, Ambient		26.72	18.22				
Field – High Precipitation, Warming		98.10	19.71				
Field – Drought, Warming		26.72	19.64				

Table 2.2. Summary statistics from linear mixed effect models evaluating how Aridity of collection site and experimental treatment (Precipitation and Warming) influenced functional traits, in 20 populations of *E. californica.*

	Seed Size		SLA		Days to Flowering	
	X^2	P	X^2	P	X^2	P
Aridity	23.18	<0.001***	40.14	<0.001***	35.13	<0.001***
Precip.	0.07	0.7885	38.00	<0.001***	1.40	0.2363
Warming	0.02	0.8954	10.05	0.0015**	11.22	<0.001***
Aridity*Precip.	2.65	0.1032	6.66	0.0098**	0.08	0.7747
Aridity*Warming	0.63	0.4275	0.56	0.4547	1.66	0.1975
Precip*Warming	0.83	0.43622	0.60	0.4403	1.57	0.2106

P-value significance: * <0.05, ** <0.01, ***<0.001.

Table 2.3. Summary statistics from linear mixed effect models (Total Seed Number) and linear models evaluating how Aridity of collection site and experimental treatment (Precipitation and Warming) influenced demographic parameters, population growth and elasticities to fecundity in 20 populations of *E. californica*.

	Germination Rate		Survival to Flowering		Total Seed Number		Perenniality		Population growth rate (λ)		Elasticity to Fecundity	
	F	P	F	P	X²	P	F	P	F	P	F	P
Aridity	0.00	0.8472	54.77	<0.001***	10.94	<0.001***	19.09	<0.001***	66.36	<0.001***	37.37	<0.001***
Precip.	N/A	N/A	11.7	<0.001***	72.85	<0.001***	0.11	0.7371	32.20	<0.001***	2.28	0.1358
Warming	0.00	0.8430	5.64	0.0202*	21.33	<0.001***	0.06	0.8094	10.95	0.0015**	0.01	0.9121
Aridity*Precip.	N/A	N/A	3.99	0.0464*	12.53	<0.001***	0.32	0.5710	10.89	0.0015**	1.03	0.3132
Aridity*Warming	0.00	0.8766	5.32	0.0239*	4.88	0.0272*	0.38	0.5375	4.51	0.0370*	0.33	0.5701
Precip*Warming	N/A	N/A	0.90	0.3466	0.54	0.4611	2.42	0.1242	1.28	0.2618	0.26	0.6140

P-value significance: * <0.05, ** <0.01, ***<0.001.

Table 2.4. Statistics from linear models evaluating how functional traits (Seed Mass, SLA, Days to Flowering) effect the elasticity to the fecundity vital rate in 20 populations of *E. californica* grown under drought and warming conditions.

Functional Trait			Precip.		Warming		Trait:Precip.		Trait:Warming		Precip.:Warming	
Elasticity to Fecundity	F	P	F	P	F	P	F	P	F	P	F	P
Seed Mass	10.58	0.0017**	2.00	0.1478	0.00	0.9642	0.41	0.5252	0.01	0.9053	0.21	0.6514
SLA	11.89	<0.001***	0.23	0.6336	1.21	0.6445	1.86	0.1764	0.34	0.5607	0.31	0.5767
Days to Flowering	12.04	<0.001***	2.36	0.1289	0.11	0.7446	0.98	0.3252	0.30	0.5833	0.12	0.7291

P-value significance: * <0.05, ** <0.01, ***<0.001.
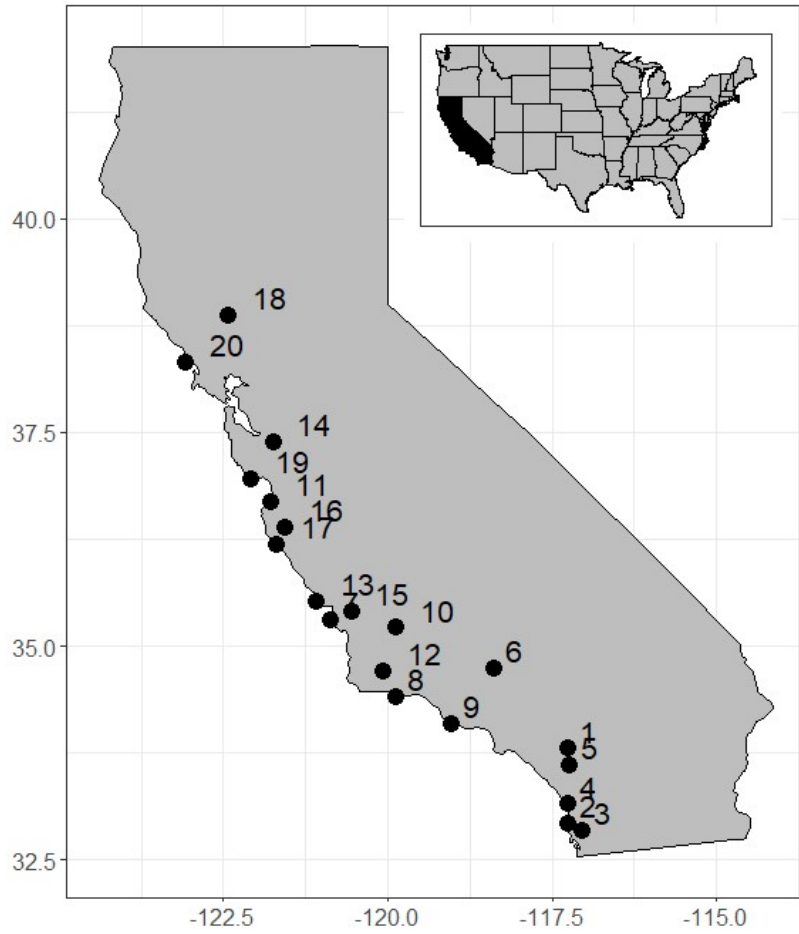
Figure 2.1. Black dots indicate our 20 seed collection sites for *E. californica*, numbered 1-20, from most arid to most mesic home climate conditions. The species range extends north to southern Washington state, and south to Baja Sur, Mexico.
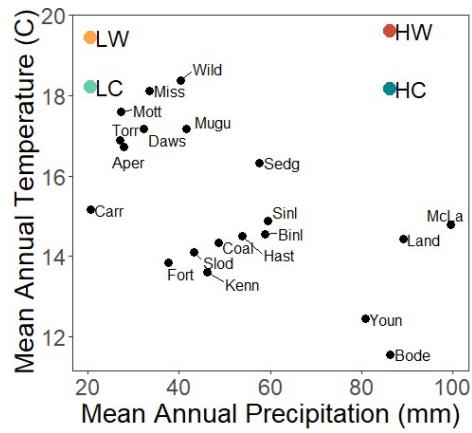
Figure 2.2. The climate space occupied by our 20 seed collection sites for E. Californica (black dots), and the four experimental climate treatments (LC – Low Precip, Ambient Temp; LW – Low Precip, Warm Temp; HC – High Precip, Ambient Temp; HW – High Precip, Warm Temp).
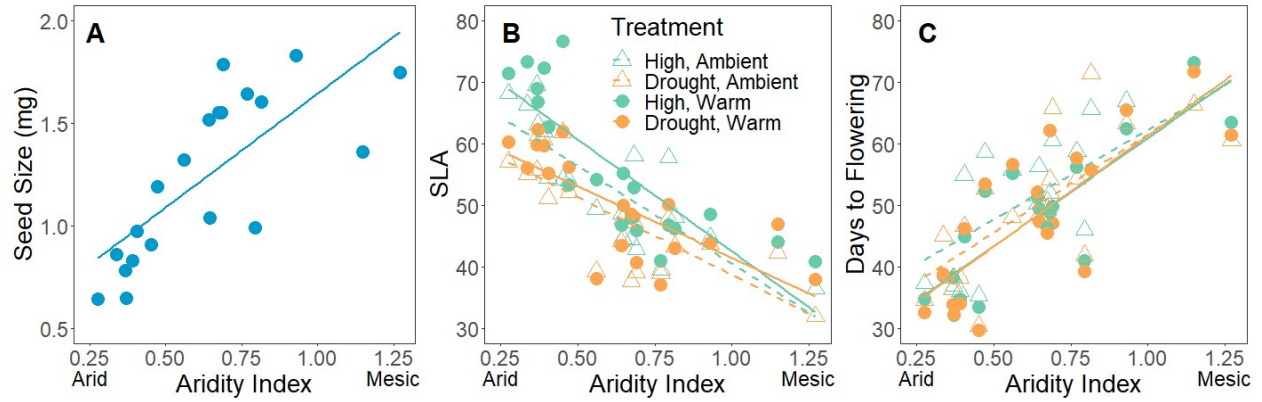
Figure 2.3 (A, B, C). Functional traits of seed size, SLA and days to flowering all show strong clinal variation in *E. californica* (A: Aridity, p = <0.001; B: Aridity, p = <0.001; C: Aridity, p = < 0.001). Seed size was not plastic in response to warming or precipitation (Precip, p = 0.79; Warming, p = 0.90). SLA decreases under drought, especially in populations from arid collection sites (Precip, p = <0.001; Aridity:Precip, p = <0.001) and increases under warming across all populations (Warming, p = 0.0015). Flowering advanced under warming (Warming, p = <0.001), and did not respond to drought (Precip, p = 0.24).
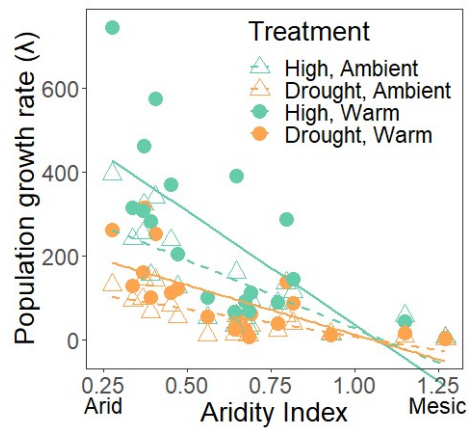
Figure 2.4. Populations from arid collection sites have higher population growth rates (λ) than populations from mesic sites under all conditions in *E. californica* (Aridity, p = <0.001). All populations have higher population growth rates under high precipitation and warming, especially populations from arid sites (Precip, p <0.001; Warming, p = 0.0015; Aridity:Precip, p = 0.0015; Aridity:Warming, p = 0.037).
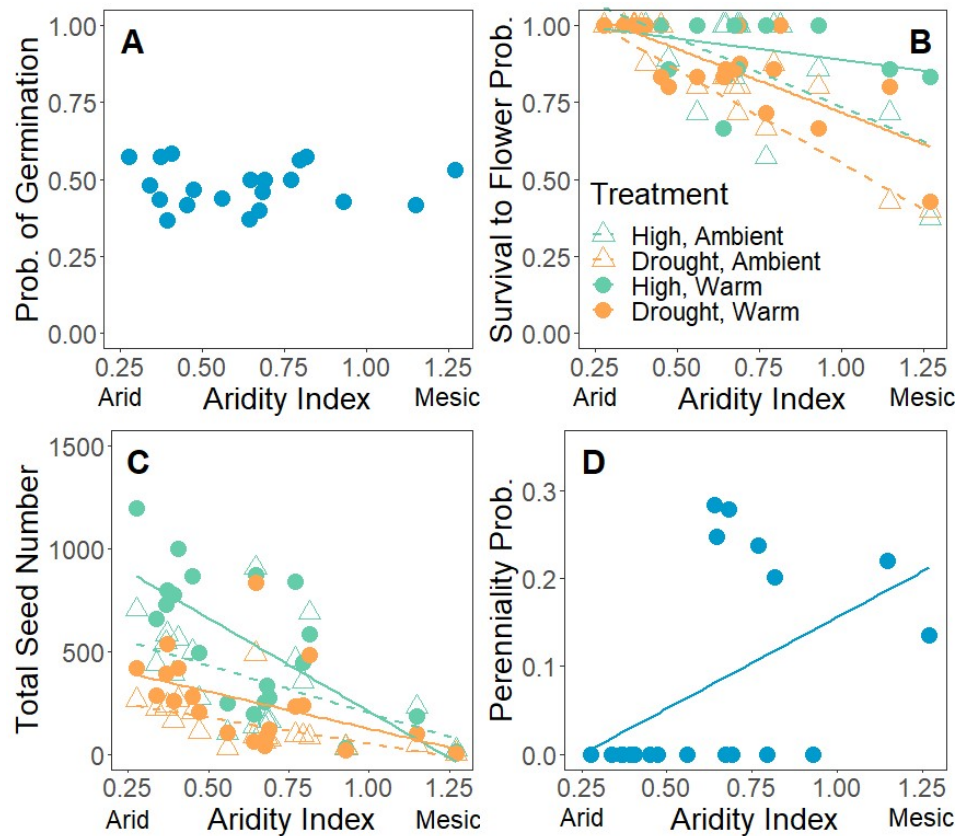
Figure 2.5 (A, B, C, D). Demographic factors of survival to flower probability, total seed mass and perenniality probability show strong clinal variation in *E. californica* (B: Aridity, p = <0.001; C: Aridity, p = <0.001; D: Aridity, p = < 0.001), while germination probability does not (A: Aridity, p =0.85). Survival to flower probability decreases under drought and increases under warming, especially in populations from mesic collection sites (Precip, p = <0.001; Warming, p = 0.02; Aridity:Precip, p = 0.046; Aridity:Warming, p = 0.024). Total Seed number decreases under drought and increases under warming, especially in populations from arid sites (Precip, p = <0.001; Warming, p = <0.001; Aridity:Precip, p = <0.001; Aridity:Warming, p = 0.027). Germination probability was not plastic in response to warming (Warming, p = 0.85) and perenniality probability was not plastic in response to either drought or warming (Precip, p = 0.74; Warming, p = 0.81).
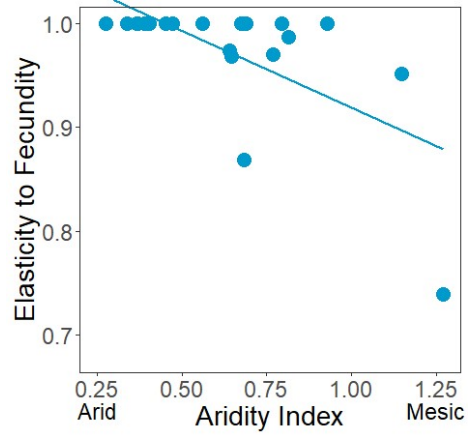
Figure 2.6. Populations from arid collection sites have higher elasticities to fecundity than populations from mesic sites under all conditions in *E. californica* (Aridity, p = <0.001). Drought and warming did not affect elasticities to fecundity (Precip, p = 0.14; Warming, p = 0.91).
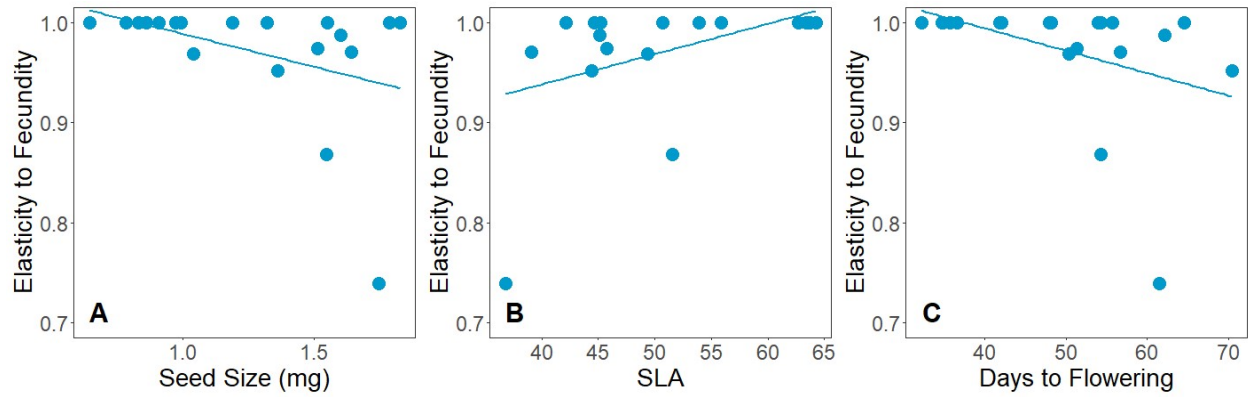
Figure 2.7 (A, B, C). Functional traits of seed size, SLA and days to flowering were all associated with elasticity to fecundity in *E. californica* (A: Seed Size, p = <0.001; B: SLA, p = <0.001; C: Days to Flowering, p = < 0.001). Drought and warming did not affect the relationship between functional traits and elasticities to fecundity (A: Seed Size:Water, p = 0.53; B: SLA:Water, p = 0.18; C: Days to Flowering, p = 0.33).

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Chapter 2 Supplementary Material

1. Aridity Index Calculation Methods
PET = Mean Annual Potential Evapotranspiration

$PET = 16 \ d \ (10T \ / \ I)^{a}$

Where *T* is the mean temperature for the month (in °C), *I* is the annual thermal index, which is

the sum of monthly indices *i*:

$i = (T/5)^{1.514}$

d is a correction factor for day length, and a is $0.49 + 0.0179 \ I - 0.0000771 \ I^2 + 0.000000675 \ I^3$.

Using Precipitation and *PET*, we then calculated the Aridity Index (*AI*) for each site:

$AI = P \ / \ PET$

Where *P* = Mean Annual Precipitation.

Mean annual precipitation (*P*) values were calculated by aggregating total monthly precipitation

values from PRISM (PRISM Climate Group), for years 1987-2016. *PET* values were calculated

by month, for years 1987-2016, by the Thornthwaite method, and were subsequently aggregated

into a single mean annual value (*PET*) for 1987-2016 (Thornthwaite, 1948). An Aridity Index

was calculated for each year (1987-2016), and then subsequently averaged for the 30-year

period.

2. Linear models

The following syntax was used for the linear mixed effects models of functional traits and total

seed number's relationship with aridity and treatment, with SLA as an example:

model=lme(SLA~Aridity * Water + Aridity * Warming + Water * Warming,

data=traitelastpoptreat, random = ~1 | Site)

The following syntax was used for the linear models of demographics parameters and elasticity to fecundity's relationship with aridity and treatment, with elasticity to fecundity as an example:

model=lm(elf~Aridity * Water + Aridity * Warming + Water * Warming, data=elasticitiesarid)

Finally, the following syntax was used for the linear models describing the association of elasticity to fecundity and functional traits, with elasticity to fecundity ~ SLA as an example:

model=lm(elf~SLA* Water + SLA * Warming + Water * Warming, data=traitelastpoptreat)
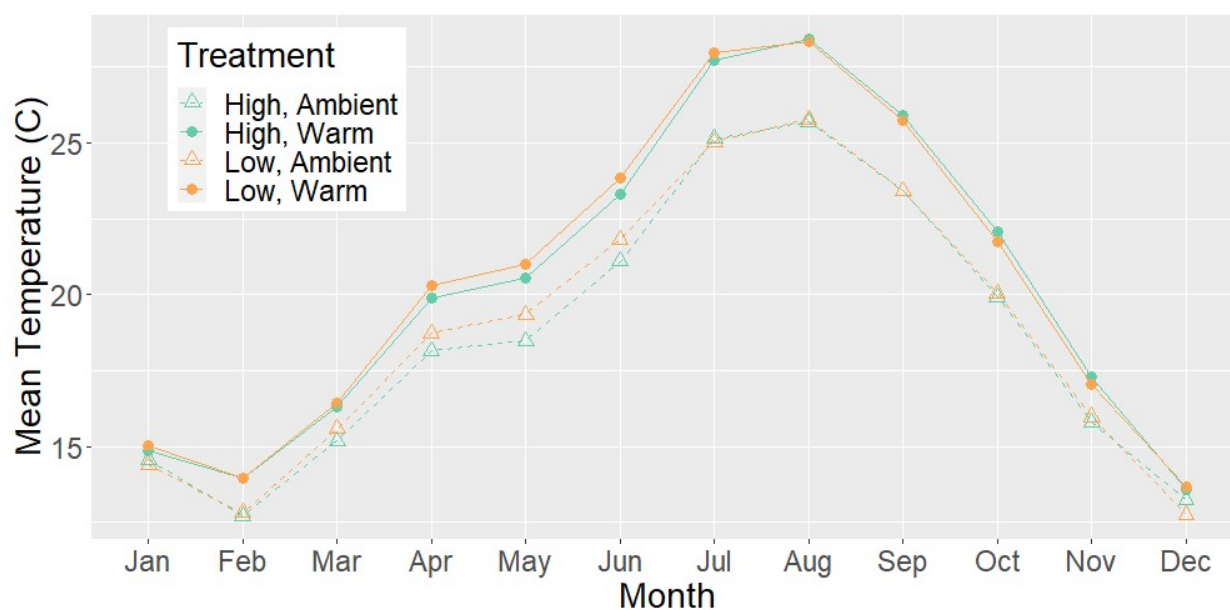
Figure S1. Monthly mean temperature for each treatment, averaged over 2018, 2019 and 2020 growing seasons. The warming treatments logged an average of 1.5 degree Celsius warmer temperatures than the ambient treatments over the course of the experiment.

CHAPTER 3: Phenotypic change in response to 60 years of climate change across the native range of California poppy

Abstract

Rapid evolution may be necessary for species that cannot move or respond plastically to accelerating climate change. However, it is unclear which specific climatic changes may drive adaptations in fitness-related traits. We investigated clinal variation, and phenotypic change, over a 60-year period of climate change by comparing data sets from a 1958-1960 common garden and field collection by Stanton A. Cook with a 2017 re-survey. This data set included 74 populations of *Eschscholzia californica* (California poppy) distributed across a sixfold gradient in annual precipitation. Aridity was the most important climate variable for predicting seed diameter, while mean annual temperature was most important for percent germination and stamen number. Seed diameter and percent germination both exhibited clinal variation, while stamen number showed marginal clinal variation. Seed diameter decreased over time, consistent with expectations based on increasing aridity over the past 60 years. However, the change was greater than expected based on changes in aridity and suggests factors other than aridity are driving this phenomenon. While percent germination and stamen number did not change significantly over time, observed present stamen numbers were lower than expected, based on predictions from past data and the last 60 years of warming in California. Our results suggest that plant traits may be responding to a complex suite of climatic and non-climatic changes over the past 60 years.

Introduction

Under accelerating rates of climate change, species that cannot move or respond plastically to challenging climatic conditions must adapt (Anderson et al., 2012; Hoffmann &

Sgrò, 2011; Parmesan, 2006; Reed et al., 2011; Shaw & Etterson, 2012). There is now growing evidence of contemporary evolution on decade long timescales due to rapid climate change presumably causing shifts in selection (Etterson, 2004; Hoffmann & Sgrò, 2011). Specifically in plants, where rapid natural dispersal is challenging (Davis & Shaw, 2001; Huntley, 1991; Loarie et al., 2009), climate change has already caused recent evolution in plant phenology and morphology (Dickman et al., 2019; Franks, 2011; Franks et al., 2007; Franks et al., 2014; Miller-Rushing & Primack, 2008; Parmesan & Hanley, 2015; Peñuelas & Filella, 2001). However, while climate change is impacting some aspects of the environment, such as temperature and precipitation, other key factors that influence plants, such as daylength, are not changing. Hence, it is not yet clear which aspects of climate change are most likely to exert strong selection on plant fitness, nor which fitness-related traits are most likely to show evidence of adaptive change.

Understanding population-level variation in traits due to varying climatic conditions across a species range (i.e. clinal variation) can be critical to accurately predicting how plants might respond to future climate change. Clinal variation can provide evidence of the effects of past climatic selection, thus revealing the potential future response to climate change (Etterson et al., 2016; Pearson & Dawson, 2003; Thuiller et al., 2008). While there is extensive evidence of clinal variation in plants (Clausen et al., 1948; Endler, 1977; Hall & Willis, 2006; Turesson, 1922), we lack a full understanding of how climate change might results in different evolutionary outcomes across a species range (Kingsolver & Buckley, 2017).

Evolution and intraspecific variation are often ignored in models that predict species responses to climate change, while often having a direct impact on species' futures (Atkins & Travis, 2010; Oney et al., 2013; Pearman et al., 2010; Peterson et al., 2019). If evolution is not keeping pace with climate change, and plants cannot disperse to newly suitable habitat, then we

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might need to explore conservation interventions, such as assisted gene flow (AGF) from warmer and drier populations, in the face of rapid climate change (Aitken & Whitlock, 2013; Hufford & Mazer, 2003; Rehfeldt et al., 1999).

In the future, both aridity and temperature are expected to increase globally (except in North Africa and high latitudes) (Berg et al., 2016; Cook et al., 2014; Dai, 2013; Feng & Fu, 2013; Scheff & Frierson, 2015), potentially altering the direction of selection on plants. By comparing experiments and surveys from the past and present, we can determine if changes in climate in recent decades drove significant changes in selection and traits. This can improve our understanding of the future effects of climate change on plants. Here, we investigated clinal variation and climate-induced evolution of traits over a 60-year period by comparing trait data sets from a 1958-1960 collection by Stanton A. Cook with a 2017 re-survey, that included 74 populations of California poppy (*Eschscholzia californica*) distributed across a climate gradient including a sixfold difference in precipitation.

Our re-survey and experiment were conducted in California, a Mediterranean-climate region that has experienced significant drought events and warming since the 1950s (Dai, 2011; Feng & Fu, 2013). In California, more of these climatic changes are expected in the future (Cayan et al., 2008; Dai, 2013). California wildflower diversity has already decreased due to climate change (Harrison et al., 2015), and is at risk of future declines due to rapid and increasingly extreme climatic changes (Jump & Peñuelas, 2005), exacerbated by regional habitat fragmentation that can inhibit migration (Davis & Shaw, 2001; Underwood et al., 2009). Re-visiting an extensive study of intraspecific variation in *E. californica* in 1958-1960 affords the opportunity to investigate evolutionary changes over the past 60 years that may help predict the future effects of climate induced selection on wildflowers.

Previous studies in *E. californica*, including those of Cook, found evidence of extensive intraspecific variation. Cook found traits such as seed diameter and dormancy varied along a geographic gradient (Cook, 1961, 1962). Other studies have showed clinal variation in phenological traits, functional traits, fitness, reproductive effort, population growth rates, demographic parameters (survival and perenniality), drought tolerance, elasticity to fecundity, and local adaptation to climate (Leger & Rice, 2007; Ryan & Cleland, 2021). Our goal in this study was to: 1. determine the most important climate variables for predicting intraspecific trait variation in *E. californica* in data sets from 1958-1960 and 2017, 2. test for clinal variation and evolution in seed diameter, germination rates and number of stamens in response to recent climate change over the past 60 years, 3. evaluate if predictions of present trait values, based on past clinal relationships in 1958-1960, differ from observed present trait values from 2017, and if differences in predicted and observed traits values vary across the climatic gradient.

We expected to find clinal variation in seed diameter as seed size has been shown by others to impact population or species fitness across various climates (Adler et al., 2014; Moles & Westoby, 2006), and previous work in *E. californica* has shown individuals seeds tend to have a smaller mass, an expected correlated trait, in arid populations (Ryan & Cleland, in prep). We also expect to find clinal variation in percent germination and stamen number, because Cook found rough correlations between higher aridity and both lower percent germination and lower stamen numbers in his studies from 1958-1960 (Cook, 1962), and other studies have documented lower percent germination in arid sites populations (Montalvo et al., 2002). Percent germination is also correlated with dormancy (Huang et al., 2010), a trait which exhibits clinal variation (Gremer et al., 2020). We also expected that traits would change over time, consistent with adaptive selection, whereby traits would shift in the direction of clinal variation. Specifically, we

expected traits to shift towards the means of southern populations (that occupy the warmer, drier portion of the species range), because California has experienced significant drought and warming since the 1950s (Dai, 2011; Feng & Fu, 2013). Furthermore, we expected a greater degree of trait change over time in arid site populations, that historically experienced higher levels of environmental variability and plasticity (Atkin et al., 2005; Bradshaw, 1965; Chevin & Hoffmann, 2017; Gugger et al., 2015; Pratt & Mooney, 2013; Schlichting, 1986; Sultan, 1987), which has been shown to correlate positively with genetic diversity and adaptation (Lande, 2009; Nicotra et al., 2010).

2. Materials and Methods

2.1 Collection sites for seed diameter, percent germination, and stamen number observations

This study focuses on 20 natural "present" populations of *E. californica* studied and collected between April and July, 2017 and 64 natural "past" populations studied and collected by Stanton A. Cook from 1958-1960 (Cook, 1961). Ten of these collection locations overlap and exist in both the present and past data sets. These 74 distinct populations exhibit significant life history variation, some annual others perennial, when grown under both past and present common garden conditions (Cook, 1962; Ryan & Cleland, 2021). Our present collection sites were distributed over 700km in southern, central, and northern California (32.8-38.9 latitude), while Cook's past collection sites were distributed over 850km in an overlapping range in California (33.1-40.9 latitude) (Figure 1, Table S1). The present collection sites were chosen to avoid restoration or garden planting, hence representing "natural" populations.

2.2 Seed Diameter

To produce seeds for diameter measurements, 8 maternal lines of each population were planted in our greenhouse common garden at the University of California San Diego (n=20). During flowering, individuals of the same populations were crossed to produce seeds. Cook's collection for seed diameter measurements similarly involved seeds collected from crosses made between individuals of the same population. These individuals had been transplanted from the field to a common garden at the Berkeley Botanical Garden. Cook measured up to 40 seeds per population (3-10 seeds from 1-4 plants) using a Spencer binocular dissecting microscope and an ocular micrometer (n= 14) (Cook, 1961). We likewise measured seed diameter lengthwise on up to 40 seeds per population (4-5 seeds from 1-8 plants) using digital calipers. A population average was obtained to compare to Cook's findings.

2.3 Collection and preparation of seeds for percent germination observations

Within a site, present seed pods were collected from 10 maternal plants spaced at least 5 meters apart. Seeds were stored at room temperature until used in germination observations. Cook's past collections of seeds for the germination observations were in bulk, in that seeds from different maternal plants were not kept separate (n=44). The present germination observations were carried out in November, 2017 at the University of California San Diego following Cook's protocol: seeds were placed on DI moistened filter paper inside of closed petri dishes in the dark at 20 degrees C (Cook, 1962). The covers of the petri dishes were secured with parafilm, to limit evaporation of the distilled water. Following Cook, we calculated germination percentages based on germinations up to day 6. We used 50 seeds for each population, from up to 10 maternal lines

(a total of 1,000 seeds from 20 populations, Data S2). The seeds were inspected daily and those that had germinated were immediately removed from the petri dish to prevent fungal overgrowth.

2.4 Stamen Number

Following Cook, we counted the number of stamens on one flower from 20 individuals by locating the first individual at the edge of the population and surveying the remaining individuals in a straight line across the population (n=19) (Cook, 1962). Past mean stamen number values came from Figure 4 from Cook's Evolution paper (n=30) (Cook, 1962). The closest round number to the mean tick mark was transcribed. We excluded Cook site "887" to avoid bias, because it exists in climate space beyond the climate of the present collection sites.

2.5 Climate variable calculations

To examine patterns in mean annual aridity we used the Thornthwaite function in SPEI v1.7 to calculate monthly evapotranspiration (PET) (R Core Team, 2021). The Thornthwaite formula is a standard calculation that uses temperature and day length (via latitude and month) to estimate the water needs of plants in a specific environment (Thornthwaite, 1948). Aridity index values that are low indicate arid environments, while high values indicate mesic environments (Data S1). As expected, the environment becomes more mesic, colder, and wetter across both present and past sites going from south to north (Table 1). See Supplemental Material for detailed methods of the aridity and mean annual temperature calculations.

2.8 Statistical analysis

All analyses were conducted in R version 4.1.2 (R Core Team, 2021). We used model averaging to determine which climate variables were most important to trait variation across the native Californian range of *E. californica*, in both the past and present (Grueber et al., 2011). Model averaging allows us to calculate a relative importance of variables, based on the weight of each of the 'top models', which is particularly useful when variables are highly correlated. Separate model averaging was conducted on past and present data sets for a more robust analysis of the most important climate variables. The climate variables included: 1) aridity 2) mean annual temperature 3) mean annual precipitation. Latitude was also included, reflecting aspects of the environment that are not changing with climate change, such as daylength.

To generate a model set, we first fit a global linear model using the lm call in R (See supplement for all model averaging code). Following Grueber et al., 2011, we then standardized the input variables using the arm package (Gelman et al., 2021). We then generated a submodel set by considering all combinations of the variables in the global model, using the dredge function in the MuMIn package (Bartoń, 2020). We next obtained the 'top models', which were the top 4AICc of models using the get.models function in the MUMIn package (Bartoń, 2020). We then averaged the top model set. We reported relative importance of each variable which was calculated by summing the weights of all the models in the top model set in which the variable occurs (Burnham & Anderson, 2002).

Analyses of seed diameter in relation to aridity and time period, and percent germination and stamen number in relation to mean annual temperature and time period were conducted with linear models using the *lm* call in R. Significance for each factor was evaluated with type-II tests using the *Anova* function in the *car* package (Fox & Weisberg, 2019). Significant main effects of

climate (aridity or mean annual temperature) indicated clinal variation in the response traits, significant main effects of time period indicated a change in trait values between 1958-1960 and 2017, and significant climate by time period interaction indicated clinal variation in the degree of trait change over time.

Analyses of past seed diameter in relation to aridity, and percent germination and stamen number in relation to mean annual temperature and were conducted with linear models using the *lm* call in R. Slope and intercept values were obtained using the *summary* function from the past data. These values were used to make predictions of trait values for each present site using the equation:

Predicted present trait value = present climate variable x past slope + past intercept

Then we analyzed the relationship of the observed versus predicted values with the *lm* call in R. Significance for each factor was evaluated with type-II tests using the *Anova* function in the *car* package (Fox & Weisberg, 2019). Significant main effects of climate (aridity or mean annual temperature) indicated clinal variation in predicted and observed trait values, significant main effects of category indicated a difference in predicted and observed trait values, and significant climate by category interaction indicated clinal variation in the degree of difference in predicted and observed trait values.

7. Results

3.1 Importance of climate variables, clinal variation and change over time in traits

Using model averaging, we found aridity was the most predictive climate variable for seed diameter in the past and present (Table 1). While aridity was not a statistically important predictor in the past, it was in the present, justifying it's use in subsequent analyses (Table 1).

We documented clinal variation in response to aridity in seed diameter (Figure 2A, Table 2), in that arid, present populations had smaller diameter seeds. Seed diameter also has decreased over time; present populations have smaller diameter seeds than past populations (Figure 2A, Table 2).

Mean Annual Temperature was the most predictive climate variable for germination rates in the past and present (Table 1). Germination rates showed clinal variation in response to mean annual temperature (Figure 2B, Table 2), in that warmer populations had lower germination rates. Germination rates did not change over time (Table 2).

Mean Annual Temperature was the most predictive climate variable for number of stamens in the past and present (Table 1). While mean annual temperature was not a statistically important predictor in the past or present, its high relative importance justified its use in subsequent analyses (Table 1). We documented marginally significant clinal variation in response to mean annual temperature, in that warmer populations had lower numbers of stamens (Figure 2C, Table 2). Stamen number did not change over time (Table 2). We found no evidence of the clinal relationships in all traits changing over time, as indicated by a lack of climate by time interactions (Figure 2A, B, C; Table 2).

3.2 Observed vs. predicted present traits

Observed present seed diameter was lower than predicted for all populations, but especially populations from the southern, arid part of the range (Figure 3A, Table 3). Observed present percent germination was not different than predicted for all populations (Figure 3B, Table 3). Observed present stamen number was lower than predicted for all populations (Figure 3A, Table 3). There was no difference in the clinal relationships of observed and predicted

percent germination and stamen number (Figure 3 B, C; Table 3).

4.0 Discussion

4.1 Clinal variation

The clinal variation we observed in *E. californica* is consistent with variation seen in California in other widespread species (Clausen et al., 1948; Peterson et al., 2016; Pratt & Mooney, 2013). We expected to find clinal variation in seed diameter because seed size is tightly linked to fitness, in analyses with wide geographic and taxonomic scope (Adler et al., 2014; Moles & Westoby, 2006). Furthermore, we expected arid site populations would have smaller seed diameters, because previous work has found smaller individual seed mass in *E. californica* in many of these same arid site populations (Ryan & Cleland, in prep) and arid plant populations tend to have smaller seeds in larger quantities compared to mesic populations, due to their higher rates of dormancy (Adler et al., 2014; Cook, 1962; Montalvo et al., 2002). We did find this relationship in seed diameter. We also found arid site populations had lower percent germination and stamen number, consistent with rough correlations between aridity and these traits in studies from 1958-1960 (Cook, 1962). Similarly, other studies have documented arid site populations having lower percent germination than mesic site populations (Montalvo et al., 2002). This lower percent germination can be correlated with higher rates of dormancy, seen in *E.californica* (Cook, 1961; Montalvo et al., 2002) and other species like *Arabidopsis thaliana* (Huang et al., 2010). Annual plants and those found in highly variable environments, such as our most arid sites, are also more likely to have higher rates of dormancy (Rees, 1994). Hence the clinal variation observed in these three traits follows our expectations for *E. californica*.

4.2 Change over time in traits, observed vs. predicted present traits, and importance of climate

variables

       Because California has experienced significant drought and warming over the last 60

years (Dai, 2011; Feng & Fu, 2013), we expected to see seed size, percent germination and

stamen number shifting over time towards the trait values of the southern, warm and arid site

populations of the past. There is extensive evidence from herbarium studies of phenotypic

change over the 20th and 21st century in response to climate change, predominantly in

phenological traits (Calinger et al., 2013; Miller-Rushing & Primack, 2008; Park et al., 2018).

Flowering time advancement in response to climate change was also found using the herbarium

record of *E. californica* (Pearson et al., 2021). While rare, studies have shown phenotypic change

in morphological traits in response to climate change as well (Buswell et al., 2011; Guerin et al.,

2012). As expected, seed diameters did get smaller, shifting over time in the direction of

southern, arid, warm populations. This shift happened across all populations. However, this shift

was greater than expected, based on predictions from past data and shifting climatic conditions in

California, especially among our arid sites. There may be non-climatic variables driving these

significant changes in seed diameter. While aridity proved to be the most important climate

variable for predicting seed diameter, there was not a particularly strong association between

aridity and seed diameter in the past, suggesting other factors may be more important for seed

diameter variation. Other studies of plant phenotypic change in response to climate change using

herbarium specimens have found similarly unexpected results in plant size and leaf traits (Leger,

2013; Sritharan et al., 2021). In one study, Leger documented a positive relationship between

plant size and temperature over 120 years in several annual plants in the Great Basin, but then

found plant sizes generally decreased as temperatures increased, counter to expectations (Leger,

2013). We could also be observing plasticity in response to the conditions of the two past and present common gardens, located in different times and decades. Although, we have not found plasticity to warming or drought in individual seed mass in *E. californica* in a field common garden (Ryan & Cleland, in prep).

Contrary to expectations, germination rates and numbers of stamens did not change significantly over time. There is limited evidence from the herbarium record that plant morphological traits that exhibit clinal variation have changed as climate has changed over the last century, especially among native species (but see (Buswell et al., 2011; Guerin et al., 2012). For stamen number, 60 years may not be enough time for meaningful evolution to occur or genetic variation may be too low to result in phenotypic change via selection. Observed present stamen numbers were lower than expected, based on predictions from past data and climatic shifts in California. Again, there could be a complex set of environmental factors or non-climatic variables driving the variation we see in stamen number. Stamen number was found to be highly heritable, but possibly under relaxed selection in the annual *Scleranthus annuus* (Svensson & Persson, 1994). Mean annual temperature was the most important climate variable for predicting stamen number, but this climate variable did not have a strong relationship with past stamen number. In addition, negative correlations among various traits can constrain phenotypic change (Lynch & Walsh, 1998). The association of percent germination and mean annual temperature was the trait-climate pair that was significant in both the past and present, which may be reflected in the overlapping observed and expected present germination rates. Germination rates such as these, collected relatively early at day 6, are highly correlated with germination speed, at trait which can evolve quickly in response to changing climate (Dickman et al., 2019).

4.3 Caveats

There are inherent challenges to studies where re-surveys are conducted in increasingly populated areas. Many of the sites surveyed by Cook have been developed over the last 60 years. Only 22% of the past sites we visited to sample remained undeveloped, accessible, or within close proximity to an accessible population. In the Central Valley in particular, almost all of the past sites are now ranchland or farmland. Furthermore, these experiments and re-surveys cannot parse out plasticity and adaptive processes. The common gardens from 1958-1960 and 2017 may have different climatic or non-climatic aspects contributing to the differences we see in seed size. There is also marked variation in seed size within individual plants (Ryan, unpublished data). Cook did not describe in his methods how he selected seeds to measure. A challenge of these types of re-surveys is they necessitate different people taking fine-scale trait measurements. In many ways this study shares similar challenges with phenology studies using historical museum specimens.

Acknowledgements

Table 3.1. The relative importance of latitude and climate variables for predicting traits (mean seed diameter, percent germination, mean stamen number), in past (1958-1960) and present (2017) populations of *E. californica*. N/A parameters did not appear in any of the top models for that trait. The most important climate variable is in bold.

Trait	Parameter	Past					Present				
		Est.	SE	z-value	p value	RI	Est.	SE	z-value	p value	RI
Seed Diameter (Past, n=14; Present n=20)	Latitude	0.328	0.118	2.492	0.0127*	0.89	0.138	0.083	1.585	0.1130	0.34
	Aridity	**-0.096**	**0.126**	**0.674**	**0.5001**	**0.12**	**0.197**	**0.073**	**2.535**	**0.0113***	**0.58**
	Mean Annual Temp	N/A	N/A	N/A	N/A	N/A	-0.135	0.078	1.657	0.0974	0.38
	Precipitation	-0.05	0.127	0.379	0.7048	0.10	0.953	0.073	1.239	0.2155	0.28
Percent Germination (Past, n=44; Present, n=20)	Latitude	-12.652	14.528	0.846	0.3978	0.31	-19.750	16.011	1.146	0.2518	0.21
	Aridity	23.205	16.183	1.401	0.1614	0.33	-34.109	30.872	1.049	0.2944	0.27
	Mean Annual Temp	**-26.061**	**12.245**	**2.063**	**0.0391***	**0.72**	**-49.056**	**18.441**	**2.535**	**0.0112***	**1.00**
	Precipitation	21.797	16.159	1.317	0.1877	0.32	11.445	24.502	0.447	0.6547	0.17
Stamen Number (Past, n=29; Present, n =19)	Latitude	4.132	1.966	2.010	0.0444*	0.72	1.650	3.049	0.513	0.608	0.19
	Aridity	0.486	2.418	0.194	0.8461	0.17	0.834	3.782	0.211	0.833	0.19
	Mean Annual Temp	**-1.183**	**2.096**	**0.543**	**0.5875**	**0.17**	**-4.347**	**2.558**	**1.580**	**0.114**	**0.48**
	Precipitation	0.756	2.429	0.301	0.7636	0.16	0.648	2.668	0.229	0.818	0.14

P-value significance: * <0.05, ** <0.01, ***<0.001.

Table 3.2. Summary statistics from linear models evaluating how climate (aridity for seed diameter and mean annual temperature for percent germination and stamen number) of collection site and time period (past and present) influence traits and if the effect of time period varies across a climatic gradient in populations of *E. californica*. See methods for number of populations included in each analysis.

	Seed Diameter		Percent Germination		Stamen Number	
	F	P	F	P	F	P
Climate	20.28	<0.001***	19.13	<0.001***	3.85	0.0560.
Time	23.67	<0.001***	0.27	0.6069	1.64	0.2068
Climate:Time	1.55	0.2229	0.19	0.6625	0.17	0.6799

P-value significance: * <0.05, ** <0.01, ***<0.001.

Table 3.3. Summary statistics from linear models evaluating how observed and predicted values of traits relate to one another, respond to climate (aridity for seed diameter and mean annual temperature for percent germination and stamen number) of collection site and if the relationship of observed and predicted traits varies across the climatic gradient, in 20 populations of *E. californica*.

	Seed Diameter		Percent Germination		Stamen Number	
	F	P	F	P	F	P
Climate	52.59	<0.001***	60.55	<0.001***	13.27	<0.001***
Category (obs. vs. predict.)	210.34	<0.001***	1.41	0.2435	5.59	0.0395*
Climate*Category	15.02	<0.001***	0.61	0.4408	0.31	0.5824

P-value significance: * <0.05, ** <0.01, ***<0.001.
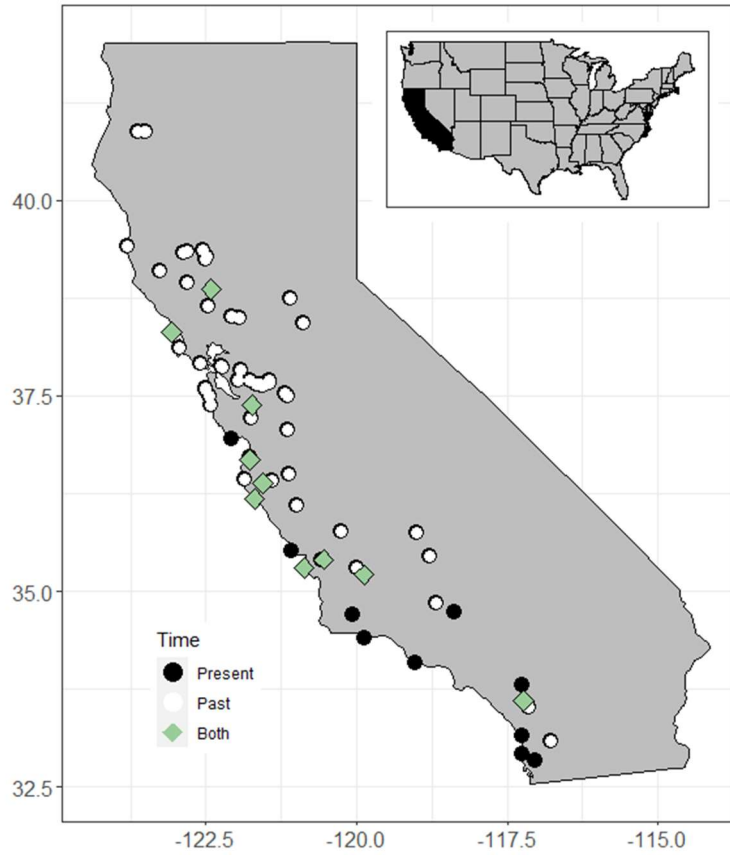
Figure 3.1. Present (n=10), past (n=54) and overlapping (n=10) Collection sites for *E. californica*. The species range extends north to southern Washington state, and south to Baja Sur, Mexico.
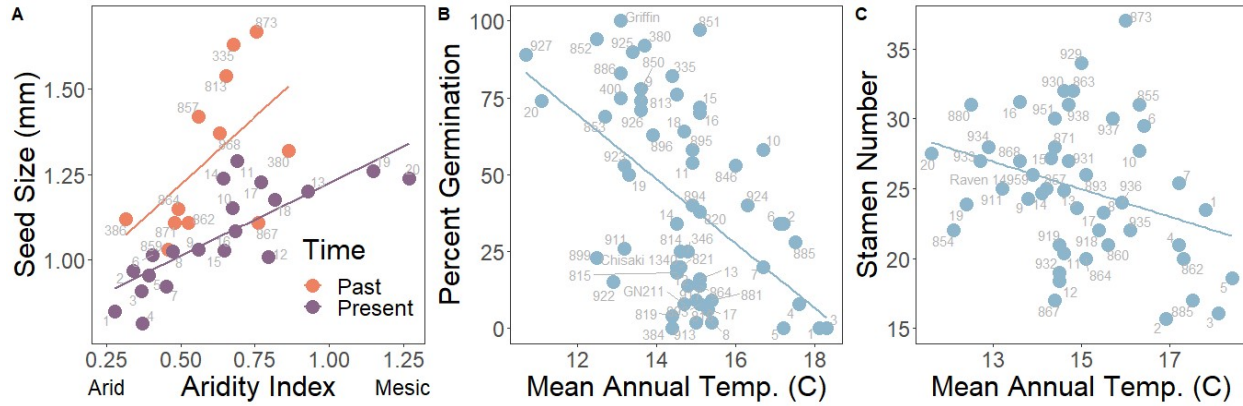
Figure 3.2 (A, B, C). Traits of seed diameter, percent germination and stamen number show significant or marginally significant clinal variation in *E. californica* in present collections (A: Climate, p = <0.001; B: Climate, p = <0.001; C: Climate, p = 0.056). Seed diameter was the only trait that changed between our two time periods, decreasing over time (Time, p <0.001). Time did not change the relationship between traits and climate (A: Climate:Time, p = 0.22; B: Climate:Time, p = 0.66; C: Climate:Time, p = 0.68).

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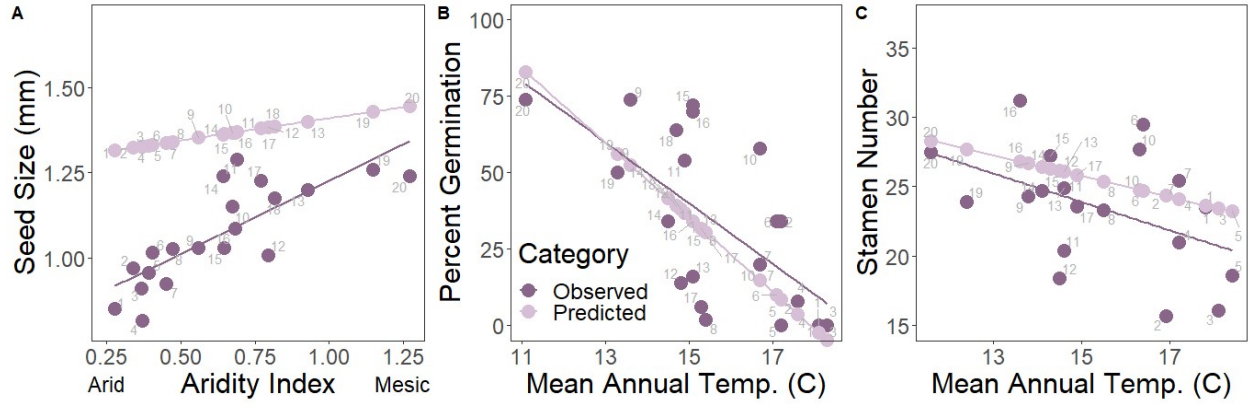
Figure 3.3 (A, B, C). Observed present seed diameter and stamen number were lower than predicted for all populations (A: Category, p = <0.001; C: Category, p = 0.039), while observed present percent germination was not different than predicted (B: Category, p = 0.24). Populations in the arid part of the range exhibited a larger difference in observed and predicted seed diameter (A: Climate:Category, p = <0.001). There was no difference in the clinal relationships of observed and predicted percent germination and stamen number (B: Climate:Category, p = 0.44; C: Climate:Category, p = 0.58).

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Chapter 3 Supplementary Material

1. Aridity Index Calculation Methods

PET = Mean Annual Potential Evapotranspiration

$$PET = 16\ d\ (10T\ /\ I)^a$$

Where *T* is the mean temperature for the month (in °C), *I* is the annual thermal index, which is

the sum of monthly indices *i*:

$$i = (T/5)^{1.514}$$

d is a correction factor for day length, and a is $0.49 + 0.0179\ I - 0.0000771\ I^2 + 0.000000675\ I^3$.

Using Precipitation and *PET*, we then calculated the Aridity Index (*AI*) for each site:

$$AI = P\ /\ PET$$

Where *P* = Mean Annual Precipitation.

Mean annual precipitation (*P*) values were calculated by aggregating total monthly precipitation

values from PRISM (PRISM Climate Group), for years 1987-2016 (modern collections) and

1929-1958 (historic collections. *PET* values were calculated by month, for years 1987-2016

(modern collections) and 1929-1958 (historic collections), by the Thornthwaite method, and

were subsequently aggregated into a single mean annual value (*PET*) for 1987-2016 (modern

collections) and a single mean annual value (PET) for 1929-1958 (historic collections)

(Thornthwaite, 1948). An Aridity Index was calculated for each year (1929-1958; 1987-2016),

and then subsequently averaged for the 30-year periods.

2. Mean Annual Temperature

To examine patterns in mean annual temperature we averaged mean annual temperatures from PRISM (PRISM Climate Group) across the 30-years preceding the collections (1929-1958 and 1987-2016).

3. Linear models

The following syntax was used in model averaging, to determine the most important climate variable for each trait, with see diameter as an example:

global.model=lm(SeedDiameter~Aridity + MeanAnnualTemp + AnnualPrecip + Lat, data=seed)

stdz.model = standardize(global.model,standardize.y = FALSE)

model.set = dredge (stdz.model)

top.models = get.models(model.set, subset = delta <4)

x=model.avg(top.models)

summary(x)

The following syntax was used for the linear models describing the relationship of traits, climate (Aridity or Mean Annual Temperature), and time period, with seed diameter as an example:

model1=lm(SeedDiameter~Aridity * Time, data=seedboth)

The following syntax was used for the linear models describing the relationship of traits and climate in the past, in order to obtain slope and intercept to make predictions for the present, with seed diameter as an example:

model1=lm(SeedDiameter~Aridity, data=seedpast)

Finally, the following syntax was used for the linear models describing the association of

observed and predicted traits ("Cat") and climate, with seed diameter as an example:

model=lm(SeedDiameter~Aridity * Cat, data=predict)

Table S1. Collection locations, climate means, and elevations for the 20 present (2017) focal populations and 67 past (1958-1960) focal populations of *E. californica* in California, USA. Abbreviation is the number used to label points in Figures in this manuscript, which correspond to a given present population. Sites 1-13 are the same as sites 1-13 in Ryan & Cleland, 2021.

Site Name	Abbreviations	Mean Annual Precip. (cm)	Mean Annual Temp. (C)	Aridity Index	Latitude	Longitude	Elevation (m)
Present Sites							
Motte Rimrock UC Reserve	1	26.72	17.8	0.2765	33.7985	-117.2545	502
Torrey Pines State Park	2	27.25	16.9	0.3377	32.9233	-117.2586	42
Mission Trails Regional Park	3	33.55	18.1	0.3672	32.8449	-117.0467	181
Dawson UC Reserve	4	32.18	17.2	0.3710	33.1490	-117.2578	130
Wildomar (Clinton Keith Rd.)	5	40.41	18.4	0.3911	33.6017	-117.2312	387
Antelope Valley State Nat. Reserve	6	36.30	16.4	0.4048	34.7338	-118.3786	828
Point Mugu State Park	7	41.66	17.2	0.4515	34.0880	-119.0343	91
Carrizo Plains National Monument	8	37.99	15.2	0.4721	35.2125	-119.8765	597
Fort Ord UC Reserve	9	37.72	13.8	0.5603	36.6868	-121.7784	46
Sedgwick UC Reserve	10	57.61	16.3	0.6738	34.7054	-120.0560	425
Blue Oak Ranch UC Reserve	11	58.87	14.6	0.6901	37.3808	-121.7384	542
Hastings UC Reserve	12	53.80	14.5	0.7947	36.3855	-121.5551	659
McLaughlin UC Reserve	13	98.10	14.6	0.9292	38.8602	-122.4166	701
Montaña de Oro State Park	14	43.18	14.1	0.6416	35.3022	-120.8732	74
Coal Oil Point UC Reserve	15	48.67	14.3	0.6467	34.4086	-119.8786	8
Kenneth S. Norris UC Reserve	16	46.17	13.6	0.6832	35.5227	-121.0725	61
San Luis Obispo Inland	17	59.54	14.9	0.7699	35.4094	-120.5485	433
Landels-Hill Big Creek UC Reserve	18	89.13	14.4	0.8155	36.0817	-121.5935	20
Younger Lagoon UC Reserve	19	80.78	12.4	1.1485	36.9493	-122.0671	28
Bodega Bay UC Reserve	20	86.18	11.6	1.2708	38.3171	-123.0698	2
Past Sites							

335	49.08	14.4	0.6759	37.23333	-121.717	375
346	34.68	14.8	0.4591	36.5	-121.133	391
380	73.08	13.7	0.8636	36.33333	-121.883	5
384	24.24	14.4	0.3229	35.3	-120	617
386	26.52	16.5	0.313	35.45	-118.783	281
400	61.80	13.1	0.9225	37.6	-122.5	16
813	48.24	14.5	0.6517	37.83333	-121.933	406
814	34.80	14.6	0.4719	37.65	-121.667	281
815	33.96	14.5	0.4578	37.63333	-121.567	219
818	31.44	15.1	0.4006	35.76667	-120.25	469
819	54.00	14.4	0.7255	35.48333	-120.45	484
820	27.36	15.1	0.3623	36.1	-121	141
821	42.96	14.6	0.7878	36.28333	-121.317	141
846	66.72	16.0	0.8051	38.75	-121.1	63
850	60.36	13.6	0.8718	37.86667	-122.233	250
851	45.12	15.1	0.5985	37.21667	-121.75	94
852	79.08	12.5	1.2043	38.11667	-122.933	25
853	65.52	12.7	0.9946	37.5	-122.45	19
854	63.96	12.1	0.9907	37.38333	-122.433	625
855	30.36	16.3	0.363	37.06667	-121.15	281
857	40.92	14.2	0.5584	36.6	-121.333	938
859	38.76	17.3	0.4567	33.51667	-117.15	322
860	59.16	15.6	0.7687	33.08333	-116.783	781
862	44.88	17.3	0.5262	33.6	-117.3	409
863	28.08	14.8	0.3598	34.85	-118.683	1031
864	21.24	15.1	0.4923	35.16667	-119.867	625
867	54.00	14.4	0.7601	35.4	-120.583	313
868	42.72	13.6	0.6305	35.28333	-120.867	5
871	34.44	14.4	0.479	36.41667	-121.4	78
873	62.28	16.0	0.7564	38.43333	-120.883	156
880	79.08	12.5	1.2043	38.11667	-122.933	25
881	22.8	15.4	0.2904	37.66667	-121.45	86
885	26.28	17.5	0.2847	35.75	-119	219
886	61.8	13.1	0.9225	37.58333	-122.517	94
893	66.72	15.1	0.8609	38.51667	-122.067	56
894	92.16	14.9	1.2014	38.65	-122.467	219
895	97.92	14.9	1.2645	38.73333	-122.517	313
896	72.84	13.9	0.9819	38.95	-122.817	516
899	111.0	12.5	1.5956	39.33333	-122.867	625
911	113.52	13.2	1.5814	39.35	-122.817	1016
913	50.28	15.0	0.6343	39.36667	-122.55	375
917	50.28	15.0	0.6343	39.36667	-122.55	375
918	22.80	15.4	0.2904	37.66667	-121.45	86
919	33.96	14.5	0.4578	37.63333	-121.567	219
922	130.32	12.9	1.8339	40.88333	-123.5	781

|						
923	127.08	13.2	1.7629	40.88333	-123.533	250
924	53.16	16.3	0.636	38.5	-121.95	39
925	141.96	13.4	2.0594	37.91667	-122.6	547
926	60.36	13.6	0.8718	37.88333	-122.25	94
927	94.80	10.7	1.5449	39.41667	-123.817	16
929	34.80	15.0	0.4575	37.7	-121.783	141
930	34.80	14.6	0.4719	37.65	-121.667	281
931	32.52	14.7	0.4333	37.65	-121.6	375
932	33.96	14.5	0.4578	37.63333	-121.583	234
933	35.52	12.7	0.5357	36.71667	-121.783	16
934	102.24	12.9	1.5248	36.43333	-121.867	8
935	26.76	16.1	0.3232	37.5	-121.15	32
936	27.12	15.9	0.3316	37.53333	-121.183	30
937	21.84	15.7	0.2735	37.7	-121.45	53
938	58.32	14.7	0.7809	37.7	-121.967	250
951	105.72	14.4	1.4166	39.1	-123.267	313
Chisaki 1340	60.00	14.5	0.781	39.25	-122.517	453
GN211	53.64	14.7	0.6901	39.28333	-122.483	380
Griffin	137.40	13.1	1.9095	40.88333	-123.633	625
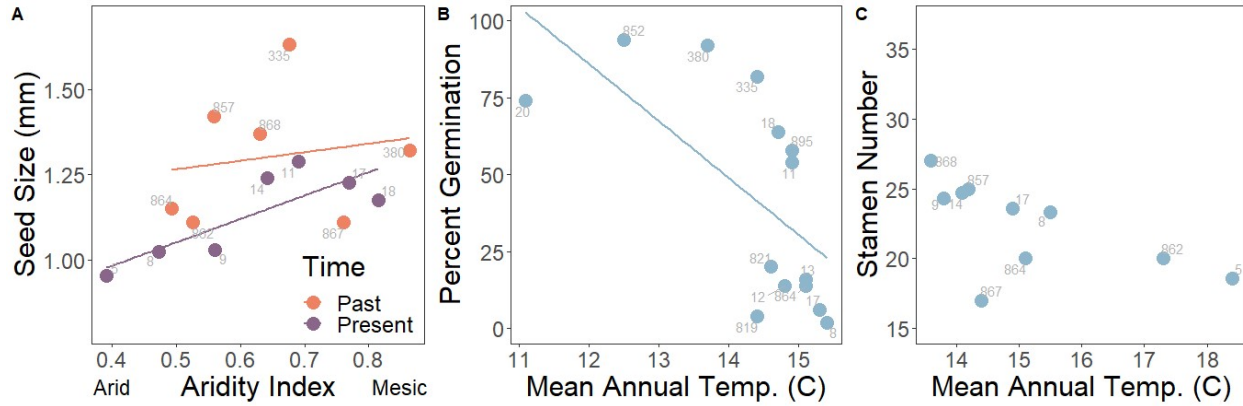
Figure S1. Linear models evaluating how climate of collection site and time period (past and present) influence traits, in overlapping past (1958-1960) and present (2017) populations of *E. californica.* Traits of seed diameter, percent germination and stamen number do not show clinal variation in *E. californica* in past and present collections, although there is marginally significant clinal variation in percent germination. Seed diameter exhibited a marginally significant difference between our two time periods, decreasing over time, but percent germination and stamen number did not. Time did not change the relationship between traits and climate. Statistics in Table S2.

Table S2. Summary statistics from linear models evaluating how climate (Aridity for seed diameter and Mean Annual Temperature for Percent Germination and Stamen Number) of collection site and time period (past and present) influence traits and if the effect of time period varies across a climatic gradient, in overlapping past (1958-1960) and present (2017) populations of *E. californica.*

	Seed Diameter		Percent Germination		Stamen Number	
	F	P	F	P	F	P
Climate	2.51	0.1442	4.39	0.0625	0.19	0.6755
Time	3.34	0.0974	0.92	0.3603	0.28	0.6115
Climate:Time	0.47	0.5098	0.00	0.9792	0.99	0.3575

P-value significance: * <0.05, ** <0.01, ***<0.001. Seed diameter, n = 7; Percent Germination, n = 7; Stamen Number, n = 5.
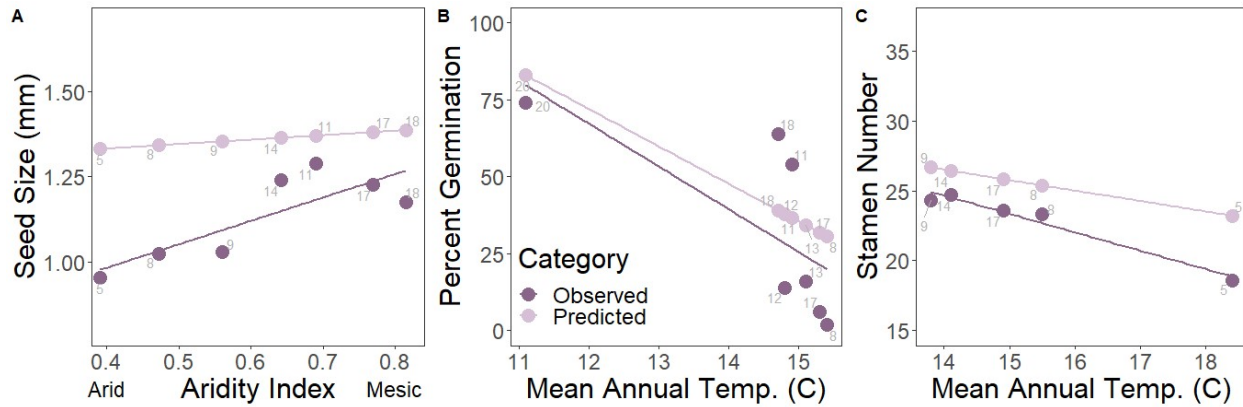
Figure S2. Present collection observed and predicted trait data in overlapping past (1958-1960) and present (2017) populations of *E. californica*. Predicted values for the present are based on the past trait data collected by Cook. Observed present seed diameter and stamen number were lower than predicted for all populations, while observed present percent germination was not different than predicted. Populations in the arid part of the range exhibited a larger difference in observed and predicted seed diameter and stamen number. There was no difference in the clinal relationships of observed and predicted percent germination. Statistics in Table S3.

Table S3. Summary statistics from linear models evaluating how observed and predicted values of traits relate to one another, respond to climate (Aridity for seed diameter and Mean Annual Temperature for Percent Germination and Stamen Number) of collection site and if the relationship of observed and predicted traits varies across the climatic gradient, in overlapping past (1958-1960) and present (2017) populations of *E. californica*.

	Seed Diameter		Percent Germination		Stamen Number	
	F	P	F	P	F	P
Climate	14.57	0.0034**	16.80	0.0021**	196.18	<0.001***
Category (obs. vs. predict.)	54.47	<0.001***	1.04	0.3314	115.30	<0.001***
Climate*Category	6.76	0.0265*	0.07	0.7902	14.82	0.0085**

P-value significance: * <0.05, ** <0.01, ***<0.001. Seed diameter, n = 7; Percent Germination, n = 7; Stamen Number, n = 5.

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