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UNIVERSITY OF CALIFORNIA,
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Drivers of plant local adaptation and the consequences for multi-trophic communities in a rapidly changing world

DISSERTATION

submitted in partial satisfaction of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

in Ecology and Evolutionary Biology

by

Jordan Randall Croy

Dissertation Committee:
Professor Kailen A Mooney, Chair
Professor Diane R. Campbell
Professor Travis E Huxman

2021

Chapter 3 2021 John Wiley and Sons
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DEDICATION

To

my best bud, parents, and siblings for their iron ears, enduring warmth, and rugged pragmatism

an ode to interconnectedness

Suddenly joy stirred in his spirit. He even stood still momentarily to catch his breath. The past, he thought, is joined to the present by an unbroken chain of events, proceeding on out of the other. It seemed to him that he just seen both ends of that chain. As he shook one end of the chain he was able to touch the other.

(Anton P. Chekhov,
"The Student")

and impermanence

Dewdrops on a blade of grass,
Having so little time
Before the sun rises;
Let not the autumn wind
Blow so quickly on the field.

(Dōgen Zenji)

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ACKNOWLEDGEMENTS

I am eternally grateful to my advisor, Dr. Kailen Mooney, for his enduring support and guidance. He consistently provided the academic and financial support needed to aid my development as a young scientist, demonstrating his commitment to my success. Most importantly, Kailen taught me the art of balancing when to entertain new and exciting possibilities, and when to rest on an idea and develop it further, and his wisdom will forever be a source of inspiration both on and off the court.

I owe deep thanks to my committee members, Dr. Diane Campbell and Travis Huxman, for their sharp and prophetic insight at all stages of this dissertation. Their feedback prepared me for the déjà vu of reviewer comments and greatly improved the quality of my research. Thank you to Dr. Jessica Pratt and Dr. Claudia Czimczik for serving on my advancement committee. I have had the great pleasure of teaching under Dr. Ann Sakai and conducting undergraduate research under Dr. Jim Cronin, who each serve as models for the type of mentor I strive to be. Ann and Jim have a way of imparting their wisdom in a non-hierarchical manner, ultimately enabling growth without judgement, ensuring standards without condescension, and instilling humility without embarrassment.

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This journey would have been spiritually void if it were not for the community of friends I have had the pleasure of meeting along the way. Spontaneous bike rides with John Powers, weekly community dinners with *Phoot Phungus* (Evelyn Valdez-Ward, Chris Ward, Kendra Walters, John Powers, Annika Nelson), walks around Aldrich Park with Greg Vose, pick-up soccer with Sam Mahanes, discussions on political economy with Marwen Zorgui, Dhruba Banerjee, and Elsa Cavata, and much more with many others all served to replenish my cup of life's elixir when supply was low.

I am deeply grateful for my best bud and partner, my parents, and my siblings, who serve as the foundation on which I stand. Their iron ears, enduring warmth, unconditional love, and rugged pragmatism provided me with continuous support and perspective. My best bud has been my partner in crime for nearly a decade and her unwavering dedication to her patients, friends, and family inspire me to be a better person.

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My third dissertation chapter has been previously published. I appreciate the contributions of the following co-authors on this paper: Jessica Pratt, Daniel Sheng, and Kailen Mooney. I thank John Wiley and Sons for permission to include Chapter 3 of my dissertation, which was originally published in *Ecology*.

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(4) **Croy, JR**, Acosta NA, & KA Mooney. 2021. Regulating plant herbivore defense pathways in the face of attacker diversity. *New Phytologist.* DOI: https://doi.org/10.1111/nph.17509

(3) **Croy, JR**, Allen WJ, Meyerson LA, & JT Cronin. 2020. Lineage and latitudinal variation in *Phragmites australis* tolerance to herbivory: Implications for invasion success. *Oikos*. DOI: https://doi.org/10.1111/oik.07260

(2) Nell CS, Meza-Lopez MM, **Croy JR**, Nelson AS, Moreira X, Pratt JD, & KA Mooney. 2018. Relative effects of genetic variation *sensu lato* and sexual dimorphism on plant traits and associated arthropod communities. *Oecologia*, 187 (2), 389–400. DOI: https://doi.org/10.1007/s00442-018-4065-y

(1) Allen WJ, Young RE, Bhattarai GP, **Croy JR**, Lambert AM, Meyerson LA, & JT Cronin. 2015. Multitrophic enemy release of introduced *Phragmites australis* genotypes and gall-forming *Lipara* spp. in North America. *Biological Invasions*, 17 (12), 3419-3432. DOI: https://doi.org/10.1007/s10530-015-0968-2

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ABSTRACT OF THE DISSERTATION

Drivers of plant local adaptation and the consequences for multi-trophic communities in a rapidly changing world

By

Jordan R. Croy

Doctor of Philosophy in Ecology and Evolutionary Biology

University of California, Irvine, 2021

Professor Kailen A. Mooney, Chair

As global change disrupts historical patterns of variation in the abiotic and biotic environment, there is an urgent need to not only investigate the ecological impacts of these complex changes, but how these novel environments will affect the evolutionary trajectory of local populations. Local adaptation—the process by which populations within a species adapt to local abiotic and biotic conditions—bridges past evolutionary processes with contemporary ecological dynamics, and can serve as a vital tool for predicting how ecological communities might adapt to rapid global change. However, a gap remains in how local adaptation is shaped by the joint stressors of the abiotic and biotic environments, and climate change will impact both plants and their associated biotic communities. To fill this gap, my dissertation investigates (1) the roles of aridity, soil, and herbivore pressure in shaping plant local adaptation and (2) climate change impacts on plants and their associated biotic communities. *Artemisia californica* is a foundational shrub species of the critically endangered Coastal Sage Scrub habitat that occupies a broad range of environmental conditions and serves as a critical food source for higher-trophic levels. I leverage a series of common garden experiments comprised of populations of *A. californica* sourced along California's coast to generate ecotype by environment mixtures. I found strong evidence of plant adaptation to local aridity and soil conditions, such that plants performed worse when growing in climatic and edaphic environments that differed from their home environments. Moreover, I report evidence that plant adaptation to latitudinal variation in resource availability influenced genetic variation in multi-variate defense strategies, with plants from high- vs low-resource environments being less resistant but more tolerant to vertebrate herbivory. With respect climate change impacts, increases in mean aridity had stronger impacts on populations adapted to dry (vs wet) soils. Regarding drought, southern (arid) populations were more resilient to extreme drought compared to norther (mesic) populations, allowing southern populations support greater lifetime arthropod abundance. Altogether, these results forecast that increases in mean aridity will favor the northward migration of populations or that populations will adapt a more "southerly" defense phenotype. However, there might be heterogenous impacts of climate change, with northern populations being more vulnerable to extreme drought and populations adapted to dry soils more vulnerable to increasing mean aridity, and these reductions on plant performance can ultimately reduce arthropod abundance and alter associated arthropod community composition.

INTRODUCTION

The origins and maintenance of biological diversity lie at the heart of scientific inquiry in ecology and evolutionary biology. Such phenotypic variation across taxa drives spatial and temporal variation in ecological interactions, and these interactions then manifest in genetic change over evolutionary time. Investigation into the causes and consequences of plant diversity have long focused on species-level variation, but recent work has demonstrated that, for a variety of ecologically-relevant functional traits (e.g. secondary metabolites, nitrogen content, etc.), within-species trait variation is comparable to the magnitude of phenotypic variation across species (Siefert et al. 2015). Moreover, genotypic identity has been shown to structure multi-trophic arthropod communities (Wimp et al. 2004, 2005, Shuster et al. 2006, Crutsinger et al. 2008, Barbour et al. 2009, Koricheva and Hayes 2018, Nell et al. 2018), microbial rhizosphere communities (Bowen et al. 2017), and alter biogeochemical cycling (Schweitzer et al. 2004). Thus, as the unit of evolution and an important contributor to ecosystem processes, the population serves as a centrifugal force bridging past evolutionary processes with current ecological dynamics. However, despite the far-reaching consequences of intraspecific variation, we lack a general understanding of how evolutionary processes shape intraspecific variation in plant traits and their associated biotic communities, which is particularly pressing as climate change rapidly creates novel environments.

One important source of intraspecific trait variation is constitutive genetic variation resulting from local adaptation, in which both dispersal limitation and natural selection interact to generate patterns of locale-dependent performance. Provenance reciprocal transplant experiments are used to test for local adaptation, and they involve growing plants sourced from different geographic or climatic regions in common gardens located in each other's home environment, and evidence of local adaptation is detected when local populations out-perform non-local populations (Franks et al. 2014). This approach can be further modified to include more populations than common gardens, and plant performance can be modeled as a function of geographic transfer distance, or environmental transfer distance to identify potential drivers of adaptation (Rehfeldt et al. 1999, Wang et al. 2010a). Environmental gradients serve as powerful tools in the study of local adaptation because these gradients often result in intraspecific clinal variation or ecotypic differentiation in plant traits (Anderson et al. 2012). While clinal variation in plant traits can result from both distance-dependent gene flow and local adaptation, congruence between putative selection pressures and plant traits suggests an adaptive role of the trait under study. Thus, such genetically-based clines in functional traits provide unique opportunities for documenting co-variance among functional traits and the environment in order to decipher the selective forces underlying adaptation and responses to environmental change.

Herbivores are a powerful stressor, and thereby shape plant evolution. Plants have evolved a variety of defense strategies to either reduce the amount of herbivore damage received (i.e. resistance) or to mitigate the fitness costs of herbivore damage (i.e. tolerance; Painter 1958, Strauss and Agrawal 1999, Pilson 2000, Stamp 2003). Resistance to herbivory has been shown to be highly heritable (Simms and Rausher 1989) and under selection by herbivores (Agrawal et al. 2012, Züst et al. 2012) Herbivores also impose selection on plant tolerance to herbivory (Hakes and Cronin 2011, Puentes and Johnson 2016). Moreover, congruence between large-scale patterns of herbivory and clinal variation in defense (Salgado and Pennings 2005, Woods et al. 2012, Więski and Pennings 2014, Lehndal and Ågren 2015, Cronin et al. 2015, Bhattarai et al. 2017) suggests that herbivores can generate large-scale patterns of plant defense.

Plant adaption to aridity can shape variation in ecologically-relevant plant traits. Aridity has been linked to genetic variation in defense traits like trichome density (Agrawal et al. n.d.), resin ducts (Vázquez-González et al. 2019), and leaf terpenes (Pratt et al. 2014). Aridity can also influence variation in ecophysiological traits such as specific leaf area, leaf nitrogen content, water content, and leaf terpenes, which have been shown to enhance herbivore performance (W J Mattson 1980, Casotti and Bradley 1991, Lucas et al. 2000, Huberty and Denno 2004, Aharoni et al. 2005, Bleeker et al. 2012). These traits can in turn influence ecological community composition. For example, males in dioecious species tend to be more tolerance of drought and invest less in herbivore defense, and aridity-driven shifts in sex ratios (Hultine et al. 2016) can affect associated arthropod communities (Petry et al. 2013). As such, aridity can indirectly influence the arthropod abundance and community composition by altering the genetic composition of the plants supporting these communities.

Although there is ample evidence of plants adapting to the biotic and abiotic environment independently, we still lack an understanding of how plants adapt to multiple stressors. Given that plant defenses are costly ("Direct and ecological costs of resistance to herbivory" 2002) and trade-off with growth rate (Mooney et al. 2010), plant adaptation to the abiotic and biotic environment are likely to be deeply intertwined (Woods et al. 2012). The resource availability hypothesis (RAH; Coley et al. 1985) provides a framework for predicting variation in plant defense across resource environments, positing that low-resource environments select for slow-growing, well-defended, and intolerant plants; in contrast, high-resource environments select for fast-growing, poorly-defended, and tolerant plants. While the RAH has received considerable support across species with respect to growth and defense (Endara and Coley 2011), the RAH fails to explain intraspecific patterns of plant defense (Hahn and Maron 2016a). Hahn and Maron

(2016) attribute these shortcomings to the bottom-up effects that resource availability might have on herbivore pressure, potentially leading to increased selection for resistance as resource availability increases. However, additional study into how plants adapt to gradients in both herbivory and abiotic stress is needed to resolve these relationships.

CHAPTER 1

Plant adaptation to soil mediates climate change impacts on foundational shrub species

ABSTRACT

Rapid shifts in aridity are expected under global change, and these shifts can disrupt local adaptation and reduce population performance. However, environmental variables shaping local adaptation are changing at different rates, which can generate heterogeneous impacts of climate change. For instance, whereas we expect rapid increases in aridity, physical soil properties will remain static. We tested whether populations of a foundational plant species, *Artemisia californica*, are 1) adapted to local climates and soils and 2) if adaptation to local soils influences population response to climate change. We established five common gardens comprised of up to 55 populations of *A. californica* sourced from along California's coastal aridity gradient, totaling 838 transplants. Within each garden, we measured plant survival and reproductive output. Survival and inflorescence count decreased with displacement in aridity and soil available water capacity (difference between source site and garden aridity/soil), indicating that populations are adapted to local climates and soils. Aridity and soil displacement interactively influenced survival, such that dry soils could be compensated for with mesic climates and arid climates could be compensated for with wetter soils. Moreover, we found that increasing aridity (as projected under climate change) reduced survival (but not reproductive output) more for populations sourced from soils with low vs high available water capacity. Interestingly, even though climate change is already underway, performance peaked for local populations, indicating that populations have thus far kept up with the pace of global change. Altogether, our results provide evidence that populations of *A. californica* are adapted to both local climates and

soils, and given that global change will bring about shifts in aridity but not soils, we may expect heterogeneous impacts of climate change with sandy populations being more susceptible to increasing aridity than populations from more clayey soils.

INTRODUCTION

Climate change is altering the environmental conditions that have shaped the fitness landscapes of populations, and thus studying local adaptation—the process by which populations within a species adapt to the local abiotic and biotic conditions—is an essential tool for predicting and mitigating the consequences of these changes. For instance, even if a population experiences a new climate that falls within the species-level climate envelope, a locally-adapted population will nonetheless experience climatic displacement and possibly reduced fitness (Reed et al. 2011, Kim and Donohue 2013, Franks et al. 2014). From a mitigation perspective, the presence of local adaptation can indicate which populations or sites require triaged care, or that sources of genotypes that are pre-adapted to future climates exist elsewhere in the species' range (Hufford and Mazer 2003, Vitt et al. 2010); but see (Gibson et al. 2016)). The contemporary challenge in predicting climate change impacts remains in identifying the underlying abiotic drivers of the fitness landscape. By identifying how populations have adapted to abiotic environments past, we can predict how novel abiotic environments induced by climate change might impact local population performance, and where specifically to source potentially pre-adapted genotypes.

Water availability is a key driver of adaptive divergence among species and populations (Siepielski et al. 2017), but water derived from variation in climate vs soils will be affected differently by climate change. Aridity is expected to increase in many ecosystems under climate change, with rises in mean temperature (and potential evapotranspiration) and decreases in mean precipitation (Pachauri et al. 2014, Trenberth et al. 2014). Within the context of latitudinal and elevational climatic gradients, equatorial and low-elevation climates are shifting poleward and upslope, respectively (Lenoir et al. 2008, Chen et al. 2011, Freeman et al. 2018). For populations of species that are locally adapted to historic climates, rapid shifts in abiotic conditions can lead to ecotype by climate-environment mismatch (Wang et al. 2010b, Wilczek et al. 2014, Anderson and Wadgymar 2020) and favor poleward or upslope migration (Lenoir et al. 2008, Chen et al. 2011, Anderson and Wadgymar 2020). However, plants are also likely adapted to local soils (Macel et al. 2007), but, in contrast to climate, soils vary at much finer spatial scales (Ettema and Wardle 2002) and they are expected to remain static compared to the pace of climatic change. Thus, continental-scale shifts in climate envelopes are likely to have heterogeneous impacts on local populations due to finer-scale soil mosaics.

Adaptation to soils can interact with aridification and mediate climate change effects on plant populations. One of the clearest examples of soils mediating climate change impacts on plants comes from longitudinal surveys of plant communities on serpentine vs non-serpentine soils (Harrison et al. 2015). Harrison *et al.* (2015) report much greater consistency in understory plant community composition on serpentine soils compared to non-serpentine soils over a 57-year period. The authors attribute the high resistance of serpentine plant communities to climate change to the community-wide low specific leaf area, a plant trait linked to greater drought tolerance, and that these aboveground plant traits might be an adaptation to low soil fertility and water availability (Harrison et al. 2015). Thus, adaptation to local soils can mediate the stability of local plant populations in the face of climate change.

In this study, we investigated whether populations of a foundational plant species, *Artemisia californica*, are adapted to local climates and soils, and how adaptation to local soils might constrain population response to climate change. We grew plants sourced from 55 populations along California's coastal aridity gradient (ranging from 25.cm to 126.6 cm mean annual precipitation [MAP]) within five common gardens located in southern, central, and northern regions of the species' distribution. Within each garden, we measured plant survival and inflorescence production to address the following questions: 1) are plants populations adapted to local climate and soil available water capacity? And 2) because soil properties are static and climates are changing, how does plant adaptation to local soils that vary in available water capacity mediate the effects of increasing aridity on plant performance? Thus, our goals were not only to assess the relative and interactive roles of aridity and soil water capacity in shaping patterns of plant local adaptation, but to also provide insight on how soil might mediate heterogenous impacts of climate change for a foundational shrub species of a critically endangered ecosystem.

METHODS

Artemisia californica (Less. Asteraceae) is a dominant shrub of California's biodiverse and threatened coastal sage scrub ecosystem (Myers et al. 2000) and supports a species-rich arthropod community (Pratt et al. 2017). The species can live up to 25 years (Sawyer et al. 2009) and relies on wind for pollination and seed-dispersal. This shrub spans a 1,000 km distribution that encompasses a five-fold precipitation gradient from Northern Baja, Mexico (average annual precipitation: 20 cm) to Mendocino County, California (average annual precipitation: 103 cm). Studies have documented genetically-based trait variation across populations of *A. californica* that is suggestive of locally adapted ecotypes (Pratt and Mooney 2013). These ecotypic differences in turn influence plant response to drought (Croy et al. 2021a) and the abundance and community composition of arthropods (Pratt et al. 2017, Croy et al. 2021b) that are both a key component of biodiversity and support several endemic and endangered vertebrates that drive regional conservation efforts (Bowler 2000). Climate projections for the region include both northward shifts in aridity and an increased frequency and severity of droughts (Diffenbaugh et al. 2015, Wang et al. 2017, Swain et al. 2018); but see (Wang et al. 2017) on simultaneous projections of increased deluge), and there is evidence this change is already underway (Pratt and Mooney 2013, MacDonald et al. 2016). This current study is based upon 55 populations of *A. californica* distributed over 826 km in southern and north-central California (32.5-38.2° latitude; 25.3-126.6 cm MAP) that together represent 71% of its range and include >90% of the precipitation gradient defining its overall distribution.

Common garden design

This study is based upon the analysis of data from five common gardens initiated in separate years (2011 and 2017) and containing a total of 55 *A. californica* populations (Appendix 1A). The five common gardens span a latitudinal gradient and encompass the range of climatic and soil conditions experienced by *A. californica* (Appendix 1A; Figure 1.1).

The details regarding the construction of the two 2011 gardens can be found in (Croy et al. 2021a), but the core of the design is briefly describe here. In December 2010, we collected seed from 10 *A. californica* plants in each of 21 source populations (Table 1). Seeds were germinated in early February 2010 in a greenhouse before being transplanted into two identical common gardens. Plants were randomly assigned to locations within a 14 by 15 m grid, with each plant separated by 1.0 m from its closest neighbor. The southern garden is located at the Upper Newport Bay Ecological Preserve in Newport Beach, CA (33°39’N) and the northern garden is located at the Jenner Headlands Preserve in Jenner, California (38°27’N).

For the 2017 gardens, seeds were collected from 46 populations of *A. californica* in the

Fall of 2014. In December 2015, seeds were germinated within a greenhouse for 12 months before transplanting individuals into one of the three common gardens in the Spring of 2017. The southern garden is located in University of California, Irvine's on-campus Ecological Preserve in Irvine, CA (33°38'N); the central garden is located at the Santa Barbara Botanic Garden in Santa Barbara, CA (34°27'N); the northern garden is located at the UC-Davis Bodega Marine Lab in Bodega Bay, CA (38°18'N). The southern (N = 170) and northern gardens (N = 241) each utilize a randomized block design consisting of 18 and 13 blocks (5 x 3 m), respectively, each block containing 15 plants. To minimize variance attributed to processes dependent on community-level plant traits, we non-randomly selected plants for each block such that every block contains 15 plants spanning roughly 6.5° latitude and with a block-level mean of ~35° latitude of origin. The central garden is a single block that follow a completely randomized design (N = 76). Plants within all gardens were lightly irrigated during their first summer following transplant to increase survival.

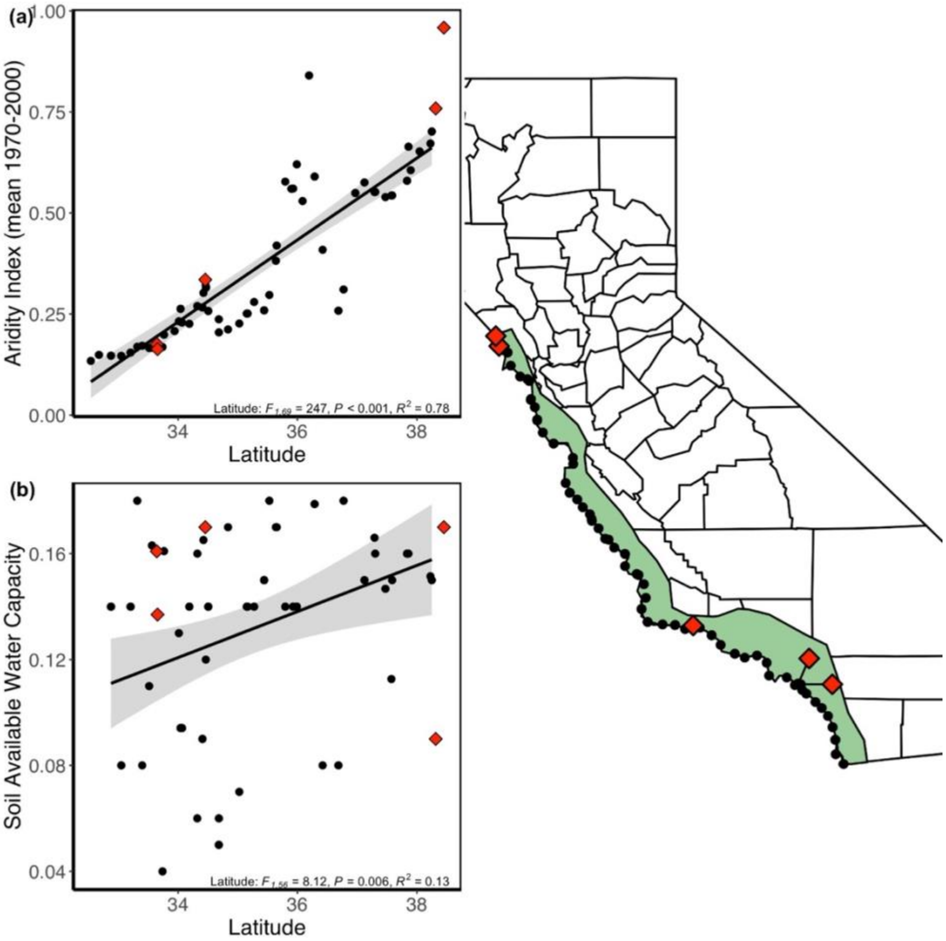

Figure 1.1. Latitudinal variation in source site (a) mean annual aridity (from 1970-2000) and (b) soil available water capacity among *Artemisia californica* populations (black circles) and common gardens (red diamonds) used in this study. The aridity index is a unitless metric that is inversely proportional to aridity, with low aridity index values corresponding to more arid sites. Soil available water capacity (AWC)—the difference in soil water content between soils at field capacity and permanent wilting point—is an indicator of a soil's capacity to hold water. Points on map indicate the *A. californica* populations used in this study, as well as the common garden locations (red diamonds). Green coastal polygon indicates the distribution of *A. californica* in California.

Climate and Soil Data

We characterized the latitudinal gradient with respect to aridity and soil available water capacity. For aridity, we extracted PRISM climate data from 1970-2000 (4km spatial resolution; PRISM Climate Group 2004) from each population source site. These climate variables were then used to calculate potential evapotranspiration (PET) using the Hargreaves equation following the protocol of the Consortium for Spatial Information (CGIARCSI) Global Aridity and PET database (https://cgiarcsi.community/2019/01/24/global-aridity-index-and-potential-evapotranspiration-climate-database-v2/). From this, we calculated a unitless Aridity Index (mean annual precipitation/ mean annual potential evapotranspiration), which is the inverse of aridity, where low values indicate more arid locations. The mean aridity index increased with latitude ($F_{1,69} = 247.1$, $P < 0.001$, $R^2 = 0.78$; Figure 1.1a), indicating a decrease in arid conditions with latitude. Full details are provided in Appendix 1A.

Using the USDA NRCS SSURGO database, we extracted the available water capacity for each population and garden site. Available water capacity is the difference between soil water content at field capacity and permanent wilting point, adjusted for salinity and soil fragments, and serves as an indicator of the amount of water in the soil available to plants (Soil Survey Staff n.d.). Each population occurs within a distinct soil type called a map unit. Each map unit is comprised of various soil components (component units), and the proportion of each component unit varies depending on the map unit. Moreover, each component unit contains unique soil horizon data. Soil properties were specifically extracted from the "chorizons" table within the SSURGO database. The chorizons table contains information on soil attributes at various soil depths, but because the majority of *A. californica* roots are concentrated within the first 50 cm of soil (Goldstein and Suding 2014), we calculated means weighted by soil depth. Soil available water capacity increased with latitude ($F_{1,56} = 8.11$, $P = 0.006$, $R^2 = 0.13$; Fig. 1.1b), although the relationship was weak. Additional details on soil characteristics across population source sites can be found in Appendix 1A.

Plant survival and reproductive output

We assessed two fundamental components of plant fitness, survival and reproductive output (Franco and Silvertown 2004). At the end of the growing season in May each year, we surveyed plants for survival. Because signatures of local adaptation can take decades to manifest (Germino et al. 2019), we used the most recent survival data available from each garden in our analyses of local adaptation, ultimately resulting in survival data of plants growing in common gardens for different periods of time. For instance, we used survival of plants in 2018 from the Irvine (one year in common garden), Newport Beach (seven years), and Jenner garden (seven years), survival of plants in 2020 from the Bodega Bay garden (three years), and survival of plants in 2021 from the Santa Barbara garden (four years).

We counted the total number of inflorescences produced by each plant as a proxy for reproductive success. To do this, we used a flowering stalk from an neighboring *A. californica* shrub or from an experimental plant and counted the total number of inflorescences on that flowering stalk. We then visually estimated the number of our sample stalks would be required to account for a shrub's total inflorescence production. We multiplied the number of flowering stalks by the number of inflorescences on the sample stalk to obtain total inflorescence production per plant. We performed this estimation twice per shrub and averaged the two estimates. For a subset of inflorescences from select populations sourced from different latitudes, we counted the total flowers per inflorescence and did not find a relationship between population latitude of origin and inflorescence flower density (Appendix 1B). Therefore, we used total inflorescences to compare relative differences in reproductive output among *A. californica* populations. For the Newport Beach garden, we estimated inflorescence production 2011-2015, whereas for the Irvine, Santa Barbara, and Bodega Bay gardens, we estimated inflorescence production in 2017 and 2018. For each plant, we summed the total number of inflorescences produced across years.

Statistical approach

Our objectives were to test if populations *A. californica* are adapted to local climates and soils, and how adaptation to soils might influence plant response to increasing aridity expected under climate change. To test for local adaptation to aridity and soils, we first calculated displacement in aridity and soil available water capacity (AWC) as the difference in aridity and soil AWC between a plant's source site environment and the common garden in which the plant was growing. An aridity displacement > 0 means that an individual was transplanted into a common garden climate more arid than its source site environment (and vice versa for displacement < 0), and a soil AWC displacement > 0 means that an individual was transplanted into a common garden with soils that retain less water than its source site environment (and vice versa for displacement < 0). If populations are adapted to local aridity and soil AWC, then plant performance would exhibit a hump-shaped relationship that peaks where aridity and soil AWC displacement = 0. For survival, this approach lends itself to a generalized linear mixed effect model treating survival as the dependent variable with a binomial link function. As fixed effects, we included the linear and quadratic terms of aridity and soil AWC displacement, as well as the interaction between linear terms and the interaction between each linear and quadratic term (no interaction between quadratic terms). For random effects, we included plant population and garden. For reproductive success, we used a linear mixed effect model with the same fixed and random effects described in the survival model, and we cube-root transformed inflorescence totals to normalize the distribution of the residuals. We only included plants that produced inflorescences in this analysis. Overall, this model structure allowed us to assess how the topography of the fitness landscape is affected by the interactive effects of displacement in aridity and soil AWC.

Our second objective sought to assess how plants adapted to soils varying in AWC might respond to increasing aridification. If plants are adapted to different soil conditions, this component of plant adaption to the abiotic environment will remain constant while aridity is predicted to increase in the future. Nevertheless, the strategies (i.e., traits) plants employ to adapt to different soil environments may mediate plant response to increasing aridity. In order to assess the evolutionary effect of soils on plant response to aridity, we added the main effect of a plant's source site AWC, as well as the interaction between a plant's source site soil AWC and the linear and quadratic terms of aridity displacement to the generalized and linear mixed effect models for survival and inflorescence production described above. Because displacement in soil AWC might affect plant performance, we retained the linear and quadratic terms for soil displacement in the model to account for these effects. An interaction between the source site soil AWC and aridity displacement would indicate that population source site soil AWC mediates the effects of aridity displacement. Note that this approach does not test for the ecological effects of soil AWC; although gardens differ dramatically in soil properties (encompassing the range of soils experienced throughout *A. californica*'s range; Fig. 1.1), gardens also vary in other environmental factors. Instead, this approach tests for how plant adaptation to different soil types (i.e. source site AWC) mediates response to aridity (i.e. aridity displacement) while controlling for garden effects (i.e. soil and other environmental factors). In this analysis, we specifically tested for the evolutionary effects of soil on aridification, and we depict the effects of aridity displacement towards more arid environments (consistent with predicted climate change), based on a range of displacement values from 0 to 0.5, corresponding to local aridity conditions (= 0; no displacement) to a magnitude of aridity increase equivalent to being transplanted from San Francisco to Los Angeles (= 0.5; displacement to more arid conditions), a magnitude of change predicted to occur by 2080 (Fitzpatrick and Dunn 2019).

Lastly, because aridity varies clinally with latitude, we tested for the effects of latitudinal displacement on plant performance as a heuristic exercise to express the fitness landscape of local adaptation in a more intuitive, spatial context. In parallel with the approach outlined above, we calculated latitudinal displacement as the difference between population source site and garden latitude, such that displacement < 0 indicates that a plant has been transplanted northward. This approach also allowed us to assess whether or not populations were already lagging behind the pace of continental shifts in climate envelopes. Given that latitudinal gradients are experiencing northward shifts in (in the northern hemisphere) in climate envelopes, if populations are lagging behind the pace of climate change, then we predict that peak performance would occur where latitudinal displacement < 0 as plants are transplanted northward into climates resembling their historic averages.

All analyses were performed in R 3.2.0 (R Core Team 2016). Linear mixed effects models and sums of squares were constructed and computed using the lme4 (Bates et al. 2015), and car (Fox and Weisberg 2011) packages in R, respectively.

RESULTS

Adaptation to local climate and soil

The linear and quadratic terms for displacement in aridity and soil AWC influenced both plant survival and inflorescence production (Table 1.1). For survival, populations exhibited peak performance in their local environments and decreasing in response to displacement in both directions for aridity (more arid/more mesic) and soil (drier/wetter). Displacement in aridity and soil AWC also interacted, such that fitness was greatest along a “ridge” occurring along a gradient of more mesic sites/drier soils to more arid sites/wetter soils, although this relationship was not completely symmetrical. Plants growing in more arid environments experienced reduced survival, but survival could be restored to peak levels if these plants were also placed into wetter soils. Plants experiencing reduced survival due to being placed into drier soils could perform better (but less than peak performance) when also placed into more mesic climates (Fig. 1.2).

For total inflorescences, production decreased with displacement in aridity in both directions (Table 1.1), but the effect of aridity displacement depended on soil displacement. Peak production occurred when populations were brought into environments that were both more climatically and edaphically mesic; however, it is worth noting that the predicted peak in inflorescence production occurred for a combination of aridity and soil displacement that we did not have data for (Fig. 1.2).

Table 1.1. Interactive effects of displacement in aridity index (AI_disp) and soil available water capacity (AWC_disp) on plant survival and inflorescence production. Displacement in aridity and soil AWC were measured as the difference in the aridity index and soil AWC between a plant's source site environment and the common garden in which the plant was growing. Because displacement is bidirectional, linear and quadratic terms and their interactions were included in the model. Reported below are χ^2 and ß estimates. Because we used *z*-transformed values (centered on 0) of aridity and soil displacement, our estimates of ß are standardized. Moreover, ß estimates are bolded where $P < 0.05$. Linear terms indicate the slope when $x = 0$ (i.e., the location of the peak when $X_1 = 0$). Quadratic terms describe a concave (-) or convex (+) relationship, and the magnitude of the quadratic term indicates the steepness of the concave/convex relationship. An interaction between linear terms means that the location of the peak when $X_1 = 0$ depends on X_2. Interactions between linear and quadratic terms mean that the steepness of X_1 depends on X_2.

Predictor Variables	*Survival*		*Inflorescences*	
	χ^2	*ß*	χ^2	*ß*
AI_disp	0.88	0.03	5.8	**-1.35**
AI_disp^2	38.16	**-1.19**	5.05	**-0.26**
AWC_disp	4.00	**-0.73**	6.44	**-0.5**
AWC_disp^2	4.33	**-0.55**	0.01	-0.39
*AI_disp*AWC_disp*	4.02	**-0.94**	0.79	0.66
*AI_disp*AWC_disp*^{2}	4.24	**-0.35**	3.39	-1.13
AI_disp^2**AWC_disp*	1.63	-0.41	5.34	**-1.47**

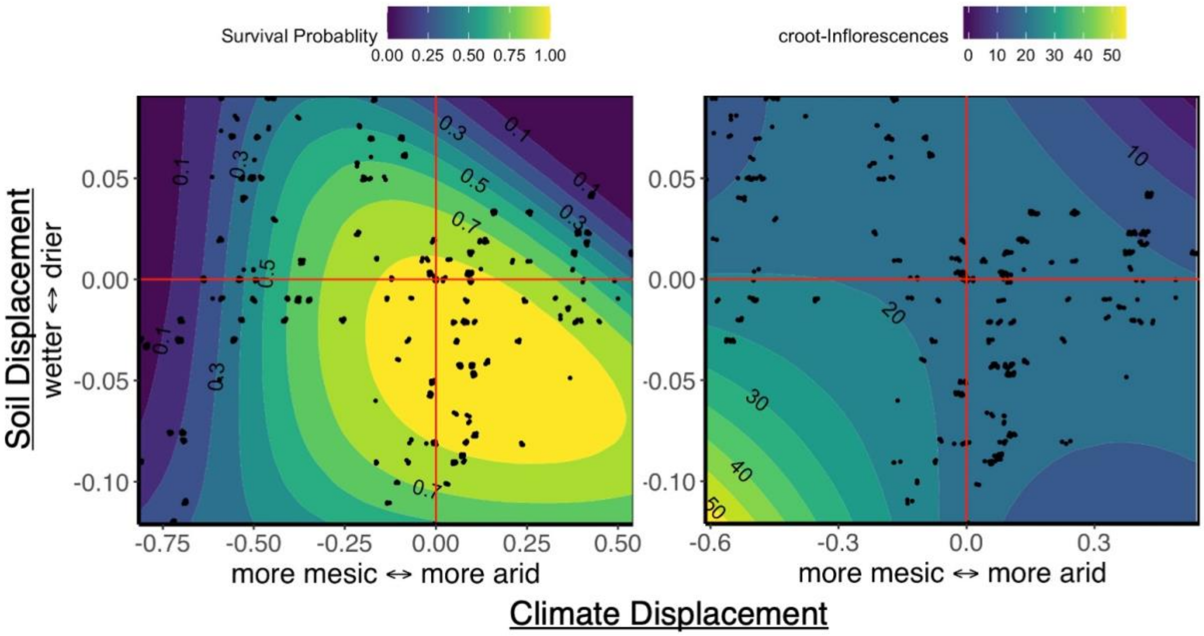

Figure 1.2. The effects of aridity displacement (x-axis) and soil displacement (y-axis) on plant survival (left) and inflorescence production (right). Yellow regions indicate performance peaks and purple regions indicate performance valleys. Vertical and horizontal red lines indicate performance for a population growing in their home aridity and soil environment, respectively. Aridity displacement > 0 represents a population that has been transferred into an environment more arid than its home climate environment, whereas aridity displacement < 0 represents a population brought into more mesic environment relative to home. Similarly, soil displacement > 0 represents a population brought into an environment with soil more clayey than its home soil environment, whereas a soil displacement < 0 represents a populations growing in soils more sandy than its home soil.

Soil-mediated effects of aridification

We found a significant main effect of source site soil AWC on plant survival (χ^2 = 5.13, P = 0.024), such that plants sourced from soils with a greater capacity to hold water tended to have greater survival than plants from soils with low AWC. Accordingly, although we found evidence of local adaptation to soil AWC with respect to survival (see above; Fig. 1.2), the maximum survival differed based on plants adapting to soils of high and low AWC.

Source site soil AWC in turn mediated plant survival response to aridification; as source site AWC interacted with both the linear (χ^2 = 100.59, P < 0.001) and quadratic term (χ^2 = 43.67, P < 0.001) of aridity displacement. Plants from high AWC soils maintained high survival as aridity increased, whereas plants from low AWC soils experienced significant reductions in survival as relative aridity increased (Fig. 1.3). In contrast, inflorescence production as not affected by home soil AWC (χ^2 = 0.70, P = 0.40), and home soil AWC interacted with neither the linear (χ^2 = 0.02, P = 0.90) nor the quadratic term (χ^2 = 0.02, P = 0.89) of aridity displacement for inflorescence production (Fig. 1.3).

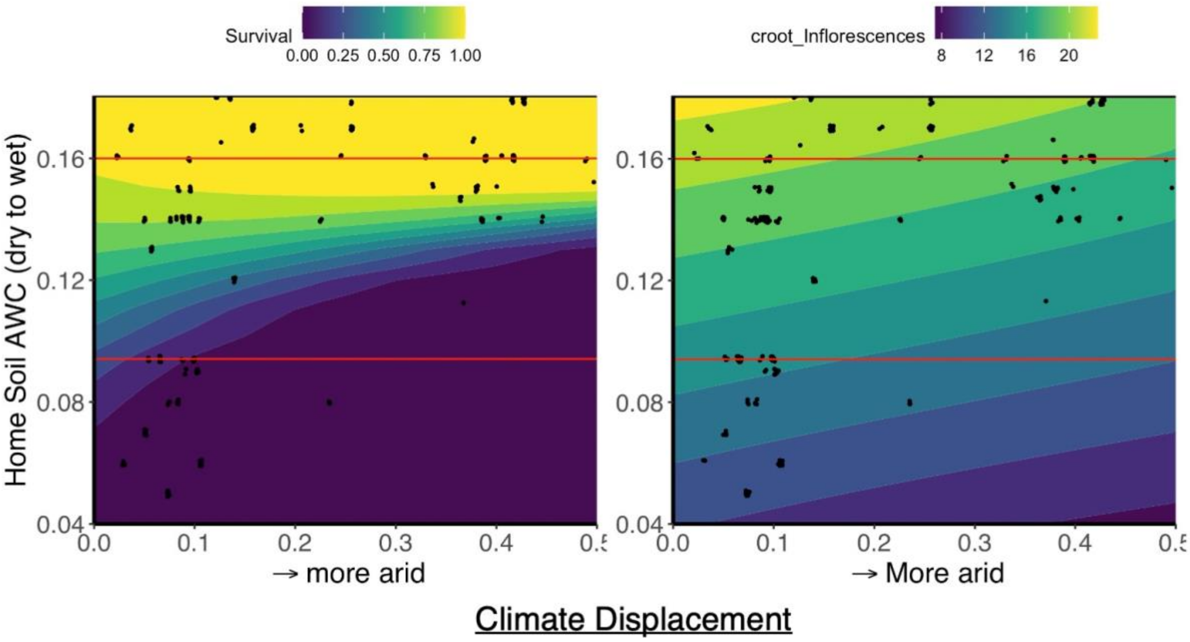

Figure 1.3. Interactive effects of population home soil available water content (AWC) and increasing relative aridity on *A. californica* survival (left) and inflorescence production (right). Yellow regions indicate high performance and purple regions indicate low performance. Because the surfaces were made using model predictions that hold soil displacement = 0, these figures illustrate how plant adaptation to soil influences the effects of increasing aridity on plant performance.

Latitudinal displacement effects

Latitudinal displacement in both directions (i.e., northward and southward transplants) reduced plant survival (χ^2 = 68.97, $P < 0.001$; Fig. 1.4) and flower production (χ^2 = 23.05, $P < 0.001$; Fig. 1.4). Survival decreased by 2.6% for one degree of latitudinal displacement (~111 km) and 11.7% for two degrees of latitudinal displacement in either direction, whereas inflorescence production declined by 3.8% and 15.2% for one and two degrees of latitudinal displacement, respectively. Peak survival is estimated to occur with a small northward displacement of -0.09° ± 0.39° (~ 10 km), while peak inflorescence production is estimated to occur with a small southward displacement of 0.09° ± 0.52°(~10 km), although in both cases these results do not provide meaningful evidence of maladaptation to local latitudes due to the variance around these estimates.

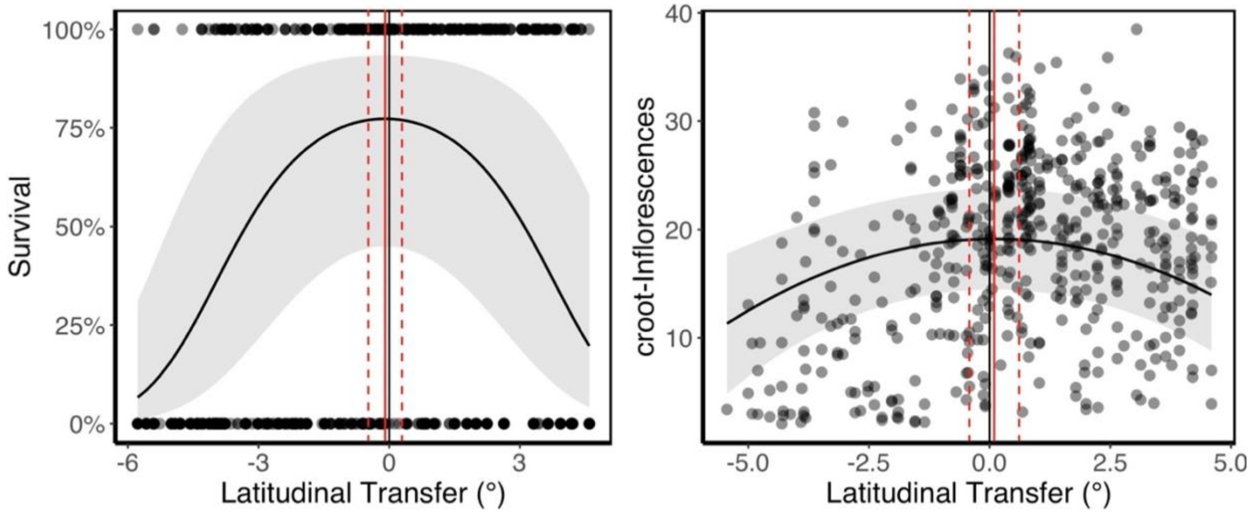

Figure 1.4. The effects of latitudinal displacement on plant survival (left) and inflorescence production (right). Latitudinal displacement < 0 indicates that plant has been transplanted northward. Estimated peak performance ± S.E. is shown with the solid red lines (dashed S.E.).

DISCUSSION

This study demonstrates that latitudinal gradients in aridity and fine-scale soil mosaics interact to shape local adaptation of *Artemisia californica* populations. Although plants flowerer more if moved to mesic environments or soils with greater water capacity, with respect to survival, plants are locally adapted to both soil water capacity and aridity. These effects interacted, such survival tended to peak along a “fitness ridge” occurring along a gradient of more mesic sites/drier soils to more arid sites/wetter soils, suggesting that climatic and edaphic variation in water availability drive local adaptation. Considering these results with respect to future climate change (aridification), plants adapted to wet soils will be less vulnerable than plants adapted to dry soils. Finally, although climate change has already occurred, there is no evidence for an evolutionary lag (i.e. plants being better adapted to sites to the north (wetter) of where they occur).

Displacement in aridity and soil water capacity influenced both plant survival and reproductive output, but signatures of local adaptation differed between the two vital rates. Plants tended to flower more under wetter soils and climates, which is consistent with the idea that flowering capacity is lagging behind the pace of climate change. However, the fact that local plants (latitudinal displacement = 0) produced the most flowers suggests rather that there is no detectable evolutionary lag, and that latitudinal variation in other environmental conditions are more important in shaping flower production (e.g., day length). In contrast, plant survival showed strong signatures of adaptation to local aridity and soil water availability, such that water loss due to displacement in one axis (e.g., more arid climates) could be partially compensated for with water gains arising from displacement in the other axis (e.g., wetter soils). The different responses of survival and reproductive output to displacement in aridity and soil water capacity can complicate predictions of population response to climate change. However, for long-lived species, population growth rates have been shown to be most sensitive to survival (Franco and Silvertown 2004), and so survival might serve as a more reliable proxy for population growth trajectories.

While studies have demonstrated plant adaptation to local climates along a latitudinal gradient (Joshi et al. 2001, Agren and Schemske 2012, Peterson et al. 2018), soils can also play a crucial role mediating plant response to varying climates, with important implications for diversity across the landscape. For instance, Eckhart et al. (2010) found that while precipitation declined towards the range border of *Clarkia xantiana* ssp. *xantiana*, reduced plant water potential on fine-grained soils at the range border suggest that soil texture can exacerbate aridity stress to define species' range limits. The nature of the interaction between climate and soil conditions reported in this study indicates that these two axes of the abiotic environment can be understood as substitutable elements of water availability that shape population range limits. Given the spatial scale at which these two axes operate, variation in soil can enhance genetic variation across plant populations (Macel et al. 2007) or species (Eckhart et al. 2017) within a given climate envelope.

Climate change involves rapid shifts in aridity alongside static abiotic soil properties, and thus soil mosaics can generate heterogenous responses to climate change. In addition to *A. californica* plants growing in wetter soils being more resilient to increasing aridity, we also found that, accounting for soil displacement, plants adapted to wetter soils were less vulnerable to increasing aridity than plants adapted to drier soils. This suggest that soils can serve as a buffer for the increasing aridity expected under climate change (Fernandez-Illescas et al. 2001, Folberth et al. 2016). Interestingly, this lies in contrast to previous studies on serpentine soils, where the resiliency to climate change of plant communities growing on resource-poor serpentine soils was attributed to plants adapting a greater capacity to tolerate drought, which was assessed via lower specific leaf area (SLA) of serpentine (vs non-serpentine) plants (Harrison et al. 2015). *Artemisia californica* plants from arid habitats tend to have leaves with lower specific leaf area compared to plants from mesic habitats (Pratt and Mooney 2013), and thus one might expect plants from drier soils to have adapted a similar trait strategy to deal low water availability. However, we found that plants adapted to wetter soils were more resilient to aridification. It is possible that soils select for different root trait strategies, and these root traits mediate plant response to increasing aridity. Further investigation into the mechanisms of drought tolerance is needed to improve our understanding of how soils might mediate plant response to increasing aridity under climate change.

Identifying drivers of local adaptation serves as a tool for predicting the impacts of climate change. Gradients in aridity are expected to shift poleward under climate change, and, in contrast to purely ecological effects, the presence of local adaptation to aridity mean that the impacts of these changes will manifest at the population vs species level. For instance, even if a population experiences a new climate that falls within the species-level climate envelope, a locally-adapted population will nonetheless experience climatic displacement and possibly reduced fitness (Reed et al. 2011, Kim and Donohue 2013, Franks et al. 2014). The evolutionary implications are that populations will experience selection towards a more southerly, arid-adapted phenotype. Southern populations of *A. californica* tend to be more tolerant of drought (Croy et al. 2021a) and they support lower densities and different communities of arthropods (Pratt et al. 2017, Croy et al. 2021a). Given that *A. californica* is a foundational shrub species of coastal sage scrub ecosystems, these evolutionary changes might ecosystem-wide consequences.

Local adaptation to aridity and soil can also be used to guide management and restoration efforts of *A. californica.* For instance, identifying aridity as a driver of population divergence means that there are potentially pre-adapted genotypes elsewhere within the species' range that can be used as source material for restoration efforts. By sourcing genotypes from more arid sites, restoration efforts can improve the chances of population success under anticipated climate change conditions (Vitt et al. 2016). By viewing population performance through the lens of latitudinal displacement, we can also determine how much further south we can source genetic material from before plants experience an appreciable reduction in survival (i.e., over what distance can we move genotypes before seeing effects of maladaptation?). Moreover, given that soils are static and populations from drier soils are more susceptible to increasing aridity, soil available water content can be used as a useful heuristic for triaging restoration efforts towards more vulnerable populations and sites. Overall, our study demonstrates latitudinal gradients in aridity and soil mosaics have shaped patterns of local adaptation in a foundational shrub species, and illustrates that adaptation to these soil mosaics can generate heterogenous impacts of increasing aridity under climate change.

SUPPLEMENTARY MATERIALS

Appendix 1A: Geographic, climatic, and edaphic information for the populations of *Artemisia californica* used in this common-garden study.

Table S1.1. Population locations and abiotic for the 55 populations of *Artemisia californica* used in this study.

Population Location		*Local Climate*		*Gardens*
Latitude (°)	*Longitude (°)*	*MAT (°C)*	*MAP (cm)*	
32.54	-117.11	252.67	16.9	2017
32.67	-117.24	260.96	17.62	2017
32.87	-117.25	276.04	17.00	2011, 2017
33.05	-117.29	281.42	16.14	2011, 2017
33.2	-117.38	305.35	16.14	2017
33.31	-117.48	334.66	16.66	2017
33.4	-117.59	343.71	16.99	2017
33.51	-117.75	321.82	16.83	2017
33.56	-117.82	300.44	16.42	2017
33.63	-117.95	308.92	16.72	2017
33.64	-117.84	348.96	17.63	Irvine Garden
33.65	-117.89	319.2	17.53	2011, Newport Back Bay Garden
33.74	-118.09	314.27	17.47	2017
33.76	-118.39	358.37	17.08	2017
33.94	-118.44	355.27	17.22	2017
34.01	-118.81	340.06	15.82	2017
34.04	-118.6	434.68	16.94	2011, 2017
34.06	-118.99	426.5	16.98	2011, 2017
34.19	-119.23	379.57	15.46	2017
34.32	-119.39	508.78	16.17	2011, 2017
34.41	-119.85	479.64	14.96	2011, 2017
34.42	-119.59	534.24	15.88	2017
34.46	-119.71	616.02	16.28	Santa Barbara Garden
34.46	-120.02	506.39	14.66	2011
34.46	-120.02	521.63	14.96	2017
34.47	-120.24	456.43	14.04	2017
34.5	-120.5	388.65	13.84	2011, 2017
34.68	-120.6	347.66	13.52	2011
34.68	-120.6	353.03	14.22	2017
34.84	-120.53	388.68	14.13	2017
35.03	-120.56	427.61	14.14	2017
35.15	-120.65	470.75	14.65	2011, 2017
35.27	-120.89	473.22	13.61	2017

35.44	-120.89	468.19	14.04	2011, 2017
35.53	-121.08	488.15	13.49	2017
35.64	-121.17	520.7	13.08	2017
35.65	-121.23	575.35	13.37	2017
35.8	-121.35	818.21	14.01	2017
35.9	-121.46	809.32	14.16	2011, 2017
35.99	-121.5	841.67	13.77	2017
36.09	-121.62	632.57	13.00	2017
36.2	-121.71	1265.76	13.63	2017
36.29	-121.84	968.23	13.99	2011, 2017
36.42	-121.91	545.88	13.09	2017
36.69	-121.78	400.82	13.56	2017
36.77	-121.79	442.67	12.43	2017
36.97	-122.12	733.55	12.12	2011, 2017
37.12	-122.31	854.01	13.07	2017
37.29	-122.4	714.28	12.01	2011, 2017
37.47	-122.45	710.21	12.12	2017
37.57	-122.52	686.36	13.43	2011, 2017
37.83	-122.54	715.81	13.41	2011, 2017
37.86	-122.57	859.38	13.76	2011, 2017
37.90	-122.7	622.76	12.30	2017
38.04	-122.86	860.22	13.35	2017
38.23	-122.92	920.91	12.76	2017
38.25	-122.96	924.00	12.79	2011
38.32	-123.07	863.39	11.43	Bodega Bay Garden
38.45	-123.12	1203.02	12.73	Jenner Garden

Table S1.2. List of nine soil properties extracted from the USDA NRCS SSURGO database, the variable name as listed in the "chorizon" table, and the descriptions provided by the USDA.

Abbreviation	*SSURGO Variable Name*	*Variable description*†
Sand	sandtotal_r‡	Mineral particles 0.05mm to 2.0mm in equivalent diameter as a weight percentage of the less than 2 mm fraction
Silt	silttotal_r	Mineral particles 0.002 to 0.05mm in equivalent diameter as a weight percentage of the less than 2.0mm fraction
Clay	claytotal_r	Mineral particles less than 0.002mm in equivalent diameter as a weight percentage of the less than 2.0mm fraction
OM	om_r	The amount by weight of decomposed plant and animal residue expressed as a weight percentage of the less than 2 mm soil material
Ksat	ksat_r	The amount of water that would move vertically through a unit area of saturated soil in unit time under unit hydraulic gradient
K	kffact	An erodibility factor which quantifies the susceptibility of soil particles to detachment by water
CEC	cec7_r	The amount of readily exchangeable cations that can be electrically adsorbed to negative charges in the soil, soil constituent, or other material, at pH 7.0, as estimated by the ammonium acetate method
pH	ph01mcacl2_r	The negative logarithm to base of 10 or the hydrogen ion activity in the soil, using the 0.01M CaCl2 method, in a 1:2 soil:solution ratio. A numerical expression of the relative acidity or alkalinity of a soil sample. (SSM)
AWC	awc_r	The amount of water that an increment of soil depth, inclusive of fragments, can store that is available to plants. AWC is expressed as a volume fraction, and is commonly estimated as the difference between the water contents at 1/10 or 1/3 bar (field capacity) and 15 bars (permanent wilting point) tension and adjusted for salinity, and fragments.

† Variable descriptions from the "chorizon" table within the USDA NRCS SSURGO database (Soil Survey Staff n.d.)

‡ r indicates that the values extracted were representative for the horizon.

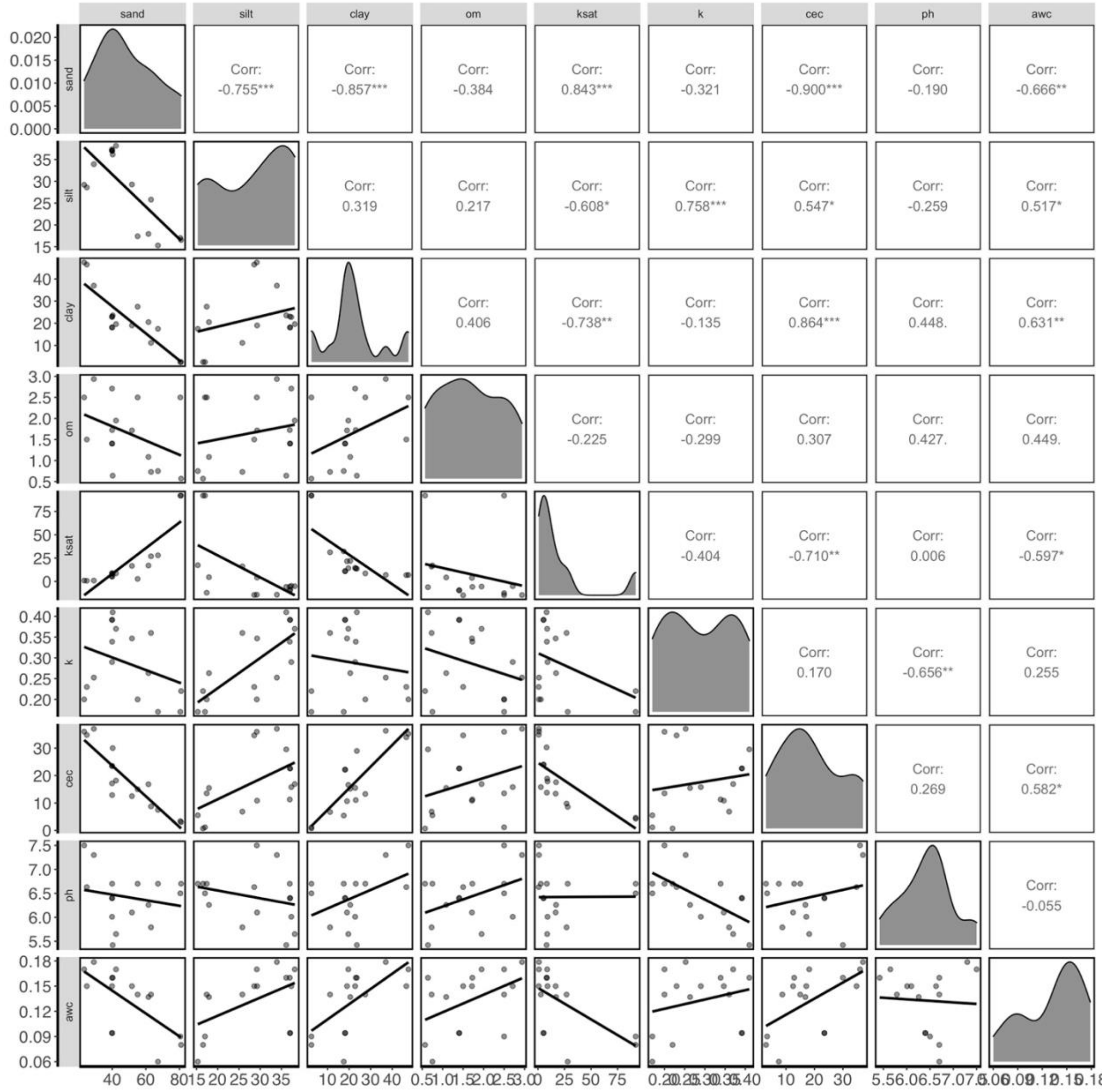

Figure S1.2. Pairwise relationships for the nine soil properties extracted from the USDA Soil SSURGO database from each *Artemisia californica* site used in this study. Histograms occupy the diagonal panels, correlation coefficients and their significance occupy the upper panels, and scatterplots for each pairwise relationship are shown in the lower panels.

Appendix 1B: Test for latitudinal clines in the number of flowers per inflorescence.

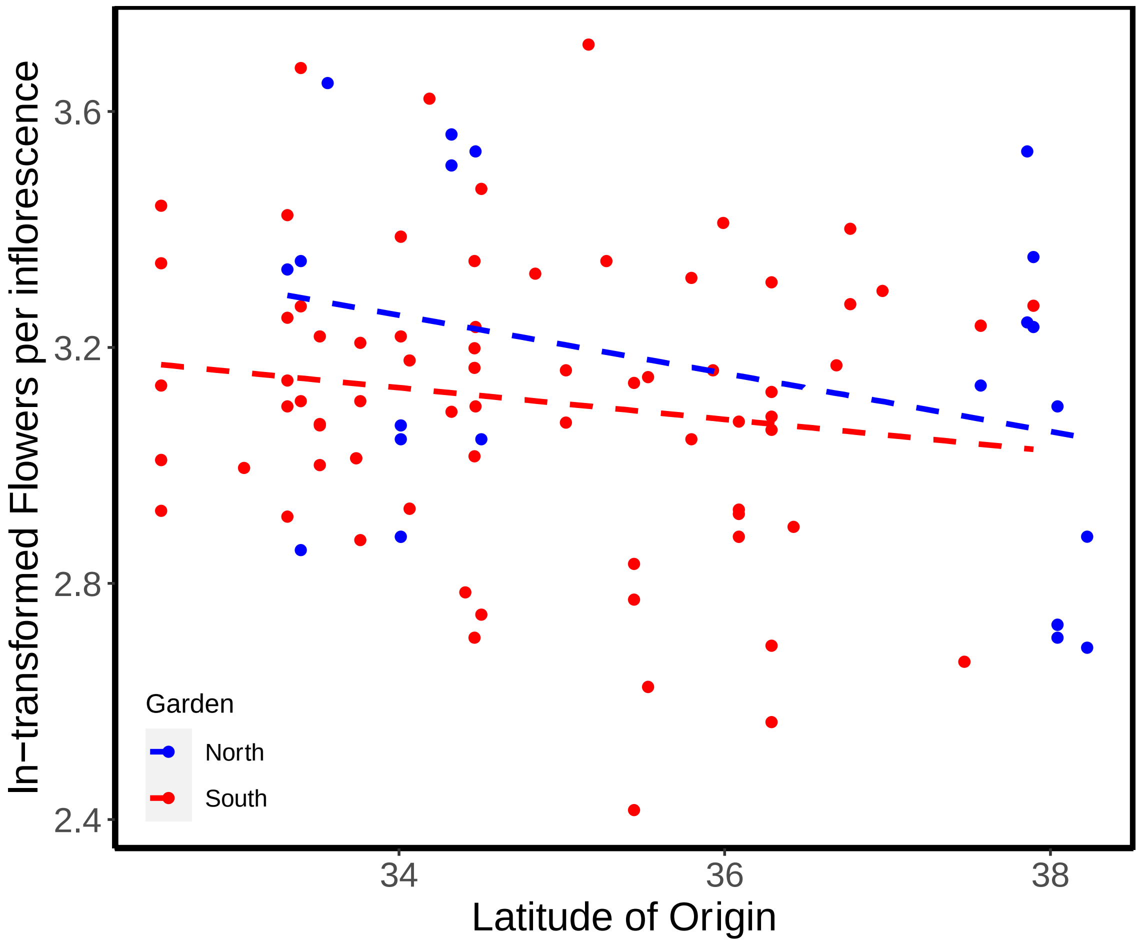

Figure S1.1. Relationship between the number of flowers per inflorescence and plant latitude of origin in a southern (Irvine) and northern (Bodega Bay) common gardens established in 2017. We collected 3-12 inflorescences per plant and averaged the number of flowers per inflorescence for each plant. Values were ln-transformed to normalize the distribution of the residuals. Dotted lines indicate a non-significant relationship between flowers per inflorescence and latitude of origin for each garden.

CHAPTER 2

Latitudinal resource gradient shapes intraspecific variation in multi-variate defense strategies in a long-lived shrub

ABSTRACT

Plant defense against herbivores is multi-dimensional, and investment into different defense traits is intertwined due to genetic, physiological, and ecological costs. This relationship is expected to generate a trade-off between direct defense and tolerance that is underlain by resource availability, with increasing resources being associated with increased investment in tolerance and decreased investment in direct resistance. We tested these predictions with respect to intraspecific variation in the shrub *Artemisia californica* by growing plants sourced from a latitudinal aridity gradient within common gardens located at the southern (xeric) and northern (mesic) portions of its distribution. We measured plant growth rate in both gardens and in the southern garden we measured putative herbivore resistance traits, resistance by quantifying naturally occurring vertebrate herbivore damage, and tolerance of herbivory by experimentally imposing simulated vertebrate damage. Plants from more mesic (northern) environments were less resistant in terms of both putative resistance traits (reduced terpenes, increased N, specific leaf area, and % water) and higher % damage by vertebrate herbivores compared to plants from more xeric environments. Mesic populations tended to be more tolerant (marginally significant) than xeric populations with respect to change in biomass measured 12 months after simulated vertebrate herbivory with 50% canopy removal by clipping. Lastly, plant growth rate did not demonstrate clear clinal patterns, as mesic populations (vs. xeric populations) grew more slowly in the southern (xeric) garden, but there was no clinal relationship detected in the northern (mesic) garden, complicating the view that growth rate within species is a constitutively

expressed trait. Overall, our findings support the prediction of lower resistance and higher tolerance in plant populations adapted to more resource-rich, mesic environments, but this tradeoff was not associated with concomitant trade-offs in growth rate.

INTRODUCTION

Plants have evolved an array of defensive strategies to cope with damage by herbivores. Plant defenses can be classified into two broad strategies, resistance and tolerance, which are the plant's ability to reduce herbivory and mitigate the fitness costs of herbivory, respectively (Strauss and Agrawal 1999). However, the costs of herbivore defense can constrain plant investment in each strategy and generate tradeoffs between tolerance and resistance (Mooney et al. 2010, Züst and Agrawal 2017, Agrawal 2020). In contrast, positive correlations among plant defense traits can arise where defense traits act synergistically, or where there is parallel selection by different selective agents on separate defense traits (Agrawal and Fishbein 2006, Hahn and Maron 2016, Agrawal 2020). Identifying the processes that shape tolerance and resistance can provide a framework for predicting plant defenses and their downstream ecological and evolutionary consequences (Tiffin 2000, Nunez-Farfan et al. 2007, Fornoni 2011, Agrawal 2020).

Resource availability has been proposed to underly patterns of genetic variation in plant tolerance and resistance through two contrasting dynamics. One long-standing hypothesis asserts that resource availability acts strictly through a bottom-up dynamic, determining genetic-based variation in growth rate, and faster growth rates are assumed to confer greater tolerance to herbivore damage. This increased tolerance in turn reduces selection for plant resistance to herbivory to generate a tolerance-resistance tradeoff(i.e., resource availability hypothesis [RAH]; Coley et al. 1985, Fine et al. 2004, Endara and Coley 2011). Alternatively, bottom-up effects of resource availability on plant growth and tolerance may be complicated by a feedback effect in which increased resource availability results in greater herbivore pressure, which in turn selects for plant resistance to herbivory to generate a positive relationship between tolerance and resistance . The bottom up dynamic has largely been applied to the study of inter-specific variation in plant growth and defense (Coley et al. 1985, Endara and Coley 2011), whereas the feedback dynamic has been proposed to underlie patterns of intra-specific variation (Hahn and Maron 2016). However, fewer studies have quantified plant growth-defense patterns within species and there is support for both the bottom-up (Pratt and Mooney 2013, Pratt et al. 2017, Hahn et al. 2021) and feedback dynamic (Hahn et al. 2018, López-Goldar et al. 2020). Therefore, more studies are needed to resolve under which conditions bottom-up vs feedback dynamics shape plant growth-defense patterns.

Essential to the RAH is that fast-growing plants from high-resource environments are less impacted by herbivory than slow-growing plants from low-resource environments, but tolerance is rarely experimentally measured. Instead, growth rates are often used as a proxy for tolerance with the assumption that fast growing plants can more easily replace tissue lost to herbivores. Although tolerance and growth may correlate positively (Gianoli and Salgado-Luarte 2017), fast relative growth rates may come at the cost of regrowth capacity (Strauss and Agrawal 1999, Rose et al. 2009), leading to tradeoffs between relative growth rate and tolerance (Croy et al. 2020) or plants may respond by increasing overall vigor (Stowe et al. 2000, Turley et al. 2013). Moreover, we know little about how adaptation to resource availability might influence tolerance to herbivory. Previous studies have documented genetic-based variation in tolerance to herbivory along latitudinal gradients (Lehndal and Ågren 2015a, Croy et al. 2020; but see Więski and

Pennings 2014, Sakata et al. 2017), suggesting that plant adaptation to the abiotic and biotic environment influences tolerance.

The objective of this study was to test whether resource availability shapes intraspecific variation in plant growth and defense through a bottom-up vs a feedback dynamic. For a latitudinal gradient in resource availability characterized by a northward decrease in aridity, we predicted that plant resistance, tolerance, and growth would increase with plant latitude or origin. To this end, we used a series of common gardens comprised of 21 populations of *A. californica* sourced along a 5° latitudinal cline that contains a northward increase in mean annual precipitation and soil conditions associated with greater resource availability. Within a single common garden located at the southern end of the species' distribution, we measured a series of resistance traits (e.g., % nitrogen, terpene concentration, SLA) and surveyed plants for damage to assess resistance, and then experimentally manipulated herbivory to quantify tolerance. Within two gardens located at the southern and northern ends of the species' distribution, we measured plant growth rate. By simultaneously quantifying plant resistance, tolerance, and growth, we sought to assess plant growth-defense relationships with the explicit consideration of plant tolerance to herbivory and resource availability.

METHODS

Artemisia californica (Less. Asteraceae) is a dominant, long-lived shrub of California's biodiverse and threatened coastal sage scrub ecosystem (Myers et al. 2000). This shrub spans a 1000 km distribution that encompasses a five-fold precipitation gradient from Northern Baja, Mexico (average annual precipitation: 20 cm) to Mendocino County, California (average annual precipitation:103 cm). Recent studies have documented genetic-based trait variation across populations of *A. californica* that is suggestive of local adaptation (Pratt and Mooney 2013).

Ecotypes vary in their ability to tolerate extreme drought (Croy et al. 2021a), and these ecotypic differences in turn influence the abundance and community composition of arthropods (Pratt et al. 2017, Croy et al. 2021a) that are both a key component of biodiversity and support several endemic and endangered vertebrates that drive regional conservation efforts (Bowler 2000).

Vertebrate herbivore communities in coastal sage scrub ecosystems are diverse, consisting of Squirrels (*S. niger* and *O. beecheyi*), Rabbits (*S. audubonii*), and Woodrats and Mice (*N. lepida* , *N. macrotis* , *P. eremicus* , and *C. californicus*) (Quon et al. 2019). Some prefer young grasses or forbs over fresh shoots of *A. californica* during the growing season, but shift their feeding onto shrubs during the summer and fall when shrubs are particularly vulnerable (Genin and Badan-Dangon 1991, Genin and Pijoan 1993). Vertebrate herbivory can substantially reduce shrub performance and alter plant community composition (Freudenberger et al. 1987, Callaway and Davis 1993). For instance, Quon et al. (2019) found that herbivores reduced the biomass of uncaged *A. californica* seedlings by 57%, which overall highlights the important, but understudied role that vertebrate herbivores play in shaping coastal sage scrub dynamics (Litle et al. 2019). Moreover, the chemical composition of *A. californica* has been invoked as a potential limiting factor of vertebrate herbivory (Halligan 1975, Duke et al. 1987, Jogia et al. 1989).

Common garden design

This study is based upon the analysis of data from three common gardens, one containing five populations and established in 2009, and the two containing 21 populations and established in 2011 (Appendix 2A). The 2009 garden is located in Newport Beach, CA (33°39’N) and within the Upper Newport Bay Ecological Preserve. Wild *A. californica* grows within 10 m of the garden perimeter. The site has a mean annual precipitation and temperature (from 1964-2014) of 29.9 cm and 17.6°C, respectively (Appendix 2A). The details regarding common garden construction are reported elsewhere (Pratt and Mooney 2013, Croy et al. 2021a), but the core design is briefly described here. For the common garden established in 2009 (hereafter the "2009 garden"), cuttings from five *A. californica* populations were collected along a coastal gradient in spring 2008 and grown within a greenhouse. In December 2009, the common garden was planted into three blocks each containing a pair of plots, one irrigated and the other unirrigated (Pratt and Mooney 2013, Pratt et al. 2014, 2017). The plants from each source population (sample sizes ranging from 7 to 21 per population) were evenly distributed among plots and randomized within each plot. To minimize non-genetic maternal effects associated with plants cloned from cuttings (Roach and Wulff 1987), rooted cuttings were grown in the greenhouse and common garden for a total of 24 months before collecting data.

In 2011, we established two identical common gardens at the northern and southern end of the *A. californica*'s distribution (hereafter the "2011 gardens"). The southern garden is located directly adjacent to the 2009 garden described above. The northern garden is located within a coastal prairie habitat at the Jenner Headlands Preserve in Jenner, California (38°27'N), and has a mean annual precipitation and temperature (from 1964-2014) 107.6 cm and 11.6°C, respectively. In December 2010, we collected seed from 10 *A. californica* plants in each of 21 source populations (Table 1). Seeds were germinated in early February 2010 in a greenhouse. In February 2011, when the plants reached a canopy volume of approximately 1,000 cm^3 (≈ 10 x 10 x 10 cm), they were transplanted to each common garden site with approximately ten individuals per population (N = 210 plants total), each from a unique seed mother. Plants were randomly assigned to locations within a 14 by 15 m grid, with each plant separated by 1.0 m from its closest neighbor. Plants within each garden were lightly irrigated during their first summer following transplant to increase survival. We conducted our tolerance experiment in the southern

2011 garden, assessed vertebrate herbivory in both the 2009 and 2011 southern common gardens, and measured plant size in each of the 2011 common gardens.

Latitudinal variation in resource availability and herbivory

We characterized the latitudinal gradient with respect to aridity, soil properties, and vertebrate and invertebrate herbivory. For aridity, we extracted PRISM climate data from 1970-2000 (4km spatial resolution; PRISM Climate Group 2004) These climate variables were then used to calculate potential evapotranspiration (PET) using the Hargreaves equation following the protocol of the Consortium for Spatial Information (CGIARCSI) Global Aridity and PET database (https://cgiarcsi.community/2019/01/24/global-aridity-index-and-potential-evapotranspiration-climate-database-v2/). From this, we calculated a unitless Aridity Index (mean annual precipitation/ mean annual potential evapotranspiration), which is the inverse of aridity, with low values indicating more arid locations. Full details are provided in Appendix 2A.

Using the USDA NRCS SSURGO database, we extracted percent sand, silt, and clay because of their relationship to water storage capacity and other indices of resource availability (Appendix 2A). Each population occurs within a distinct soil type called a map unit. Each map unit is comprised of various soil components (component units), and the proportion of each component unit varies depending on the map unit. Moreover, each component unit contains unique soil horizon data. Soil properties were specifically extracted from the "chorizons" table within the SSURGO database. The chorizons table contains information on soil attributes at various soil depths, but because the majority of *A. californica* roots are concentrated within the first 50 cm of soil (Goldstein and Suding 2014), we calculated means weighted by soil depth. Due to the multi-variate nature of soil, we used the prcomp function in R (R Core Team 2019) to perform a principal component analysis on percent sand, silt, and clay (each *z*-transformed) in order to collapse soil variables into single principal component before using in subsequent analyses.

To estimate herbivore pressure along the coast, we extracted iNaturalist (*iNaturalist*) observations within a 5 km^2 square around each population source location along the California coast using the rinat package in R (Barve et al. 2021). Because the vertebrate herbivores that feed on *Artemisia californica* are herbivorous mammalian taxa, we collected the total number of mammalian observations and filtered them by known *A. californica* herbivores (Litle et al. 2019) and potential *A. californica* herbivores (Appendix 2A). To account for substantial variation in sampling effort along the coast, we also collected the total number of observations of reptiles, birds, and insects. The total number of vertebrate herbivore observations were divided by the sum of total reptile, bird, insect, and non-herbivore mammal observations to account for variation in sampling effort across sites. Variation in arthropod herbivore pressure along the coast has previously been presented for five wild-sampled *A. californica* populations distributed along a latitudinal gradient (Pratt et al. (2017), and is presented here again (Fig. 2.1d).

Plant resistance traits

We measured a suite of leaf-level traits that are widely recognized to influence herbivory (Pérez-Harguindeguy et al. 2016) in order to characterize plant direct resistance to herbivory. In April 2014, during peak growing season, we collected 30 fully expanded leaves from five plants within each population; ten leaves were used to assess specific leaf area (SLA) and percent water content (%WC), 10 leaves were used to assess plant defensive chemistry (i.e., terpenes), and the remaining 10 leaves for nitrogen analysis. For SLA and PWC, freshly picked leaves were immediately placed on ice and kept cool until they were scanned and weighed (wet weight) later that same day. Leaves were then dried at 60 °C for 72 h and weighed again (dry weight). Leaf area (cm^2) was determined from scanned images using ImageJ software (Rasband, 2008). SLA was calculated as mm^2 per mg^{-1} dry weight and PWC as (wet weight-dry weight)/wet weight. To assess leaf nitrogen (N) content, leaves were dried at 60 °C for 72 h and then ground to a fine powder using a Wig-L-bug grinding mill (International Crystal Laboratories, Garfield, NJ). Approximately 1 mg of this homogenized powder was then packed into 5 x 9 mm tins. Elemental analysis (Fisons Instruments 1500) and mass spectrometry (Delta plus XL, Thermo Finnigan, Asheville, NC) was then performed at the UC-Irvine Stable Isotope Ratio and Mass Spectrometry Facility.

To assess terpene concentrations, which serve as important defenses against herbivores (Eisner, 1964; Whittaker & Feeny, 1971; Mabry & Gill, 1979), haphazardly collected leaves were immediately placed in 2 ml n-hexane, sonicated for 10 min and soaked at room temperature. After seven days, extracts were poured off and stored at -80 °C until analysis by gas chromatography and mass spectrometry (GC-MS) and leaf material was dried at 60 °C for 72 h and weighed. For terpene analysis, 10 µl of an internal standard solution (0.13 µl ml^{-1} m-xylene in n- hexane) was added to 90 µl of each sample extract. Samples were injected (4 µl) onto a GC-MS (Trace MS+, ThermoFisher Scientific, Asheville, NC) fitted with a 30 m x 0.25 mm x 0.25 µm film thickness DB-5 fused silica column (J&W Scientific, Folsom, CA). The GC was operated in splitless mode with helium as the carrier gas (flow rate 1 ml min^{-1}). The GC oven temperature program was as follows: 1 min hold at 50 °C, 5 °C min^{-1} ramp to 180 °C, 20 °C min^{-1} ramp to 290 °C, and 1 min hold at 290 °C. The mass spectrometer was operated in electron ionization mode and data were collected between m z^{-1} 50–650. We identified mono- and sesquiterpenes in our samples and examined relative investment in defense by calculating the normalized area per dry weight (peak area/area of internal standard/dry weight of leaf material) for all terpenoid compounds detected.

Vertebrate herbivory

Vertebrate herbivory on *A. californica* is concentrated in late summer and early fall (Litle et al. 2019). Desert cottontails (*S. audubonii*) were one of the dominant herbivores observed at our southern common garden location, and we observed that herbivores often discarded stems into stems piles underneath a shrub canopy. To quantify the relative impact of this damage on plants, we visually assessed the proportion of a plant's canopy that was damaged by herbivores in Spring of 2010 in 2009 common garden. Damage on plants was assigned to one of six bins: no damage, <10%, 10-25%, 25-50%, 50-75%, >75%. Bins were converted to estimated percent canopy damage prior to analysis. To estimate damage within the 2011 garden, we collected clippings from beneath the shrub canopy that were left behind by herbivores twice in mid- to late Summer of 2016. We weighed the clippings and summed the mass across the two time points to get a measure of total herbivore damage. Because we swept debris from beneath the plant in early June, the clippings we collected represent the total amount of damage over a three-month period. The biomass of the clippings were divided by total plant biomass to obtain a percentage of aboveground biomass removed and discarded by herbivores. Although it is not clear why herbivores discard plant tissue, this may not be relevant from a plant's perspective. Also, we were unable to relate these two measures of vertebrate herbivore damage directly due to only five overlapping populations between the two gardens. However, the parallel relationship of each herbivore damage estimate to population latitude of origin suggests that clippings can serve as a proxy for percent herbivore damage on *A. californica* plants.

Simulated folivory treatment and fitness measurements

We implemented a clipping treatment to simulate the effects of heavy folivory. We used artificial herbivory treatment (clipping) to minimize variation in herbivory levels among plants. In May of 2016, we sorted plants within each population into two groups containing approximately equal biomass to standardize the starting conditions for each treatment (χ^2 = 1.55, *P* = 0.213). We then randomly assigned each group to either a “clipped” or “unclipped” control. In the spring of 2016, we then removed 50% of the aboveground photosynthetic material with scissors to simulate patterns of vertebrate feeding damaged observed in the field.

To assess the effects of folivory on plant performance, we measured plant canopy size at the conclusion of the growing season (mid-May) in 2016 and 2017, and plant survival in 2017. To estimate aboveground dry biomass, we collected reference branches from an *A. californica* shrub outside of our garden plots and estimated the total number of such branches needed to reconstruct our experimental shrubs separately for two reference branches. These reference branches were then dried and weighed in order to estimate shrub dry biomass. We estimated the growth rate of each population using two methods. First, because plants were established at the same time, we treated the biomass estimates from 2018 in the southern and northern garden as one indicator of growth rate. Secondly, in the southern garden alone, we estimated growth rate of individuals from 2016 to 2017 using a log response ratio, where Growth = ln[biomass_{2017}/ biomass_{2016}] (Hedges et al. 1999). Growth values above, equal to, or below zero indicate plant growth, stasis, and shrinkage, respectively.

Statistical Analysis

The objective of this study was to test for (1) latitudinal clines in the biotic and abiotic environments and (2) latitudinal clines in plant resistance, tolerance and growth to shed light on how a latitudinal gradient in resource availability shapes genetically-based variation in plant growth-defense strategies. Clinal variation in resource availability and herbivore pressure were assessed by regressing source site aridity, soil texture (represented by the first principal component described above), and estimates of vertebrate and invertebrate herbivore pressure, respectively, against latitude.

To test the hypothesis that resource availability alters relative investment into tolerance and resistance, we first *z*-transformed our measures of resistance and tolerance to standardize their units. Resistance was measured as the inverse of percent clipping damage and tolerance was measured as the log response ratio of plant biomass in 2017 in the clipped vs unclipped treatments ($\ln[\text{biomass}_{2017\_clipped}/\ \text{biomass}_{2017\_unclipped}]$). We then regressed *z*-transformed defense values against latitude of origin, defense strategy (resistance vs tolerance), and a latitude by strategy interaction. A significant interaction would indicate that relative investment into resistance vs tolerance depends on a population's latitude of origin. We then followed up with independent assessments of latitudinal clines in plant defense and growth. To do this, we constructed a series of linear mixed effects models each containing, at a minimum, latitude of origin as a predictor and plant population as a nested random effect. However, to test for latitudinal variation in plant tolerance, we included a clipping and a clipping by latitude interaction as predictors of plant growth and survival one year after damage. We further modified the survival model with a generalized linear mixed effects model to specify a binomial distribution. For plant growth and survival, a significant interaction between clipping and latitude would indicate latitudinal variation in tolerance. To test for genetic-based clines in growth rate, we regressed the plant size (estimated in 2018 in the southern and northern 2011 gardens) against latitude of origin, garden location, and their interaction. A garden by latitude interaction would indicate that genetically based clines in growth are context-dependent. Biomass was cubed root transformed to normalize the distribution of the residuals.

All analyses were performed in R 3.6.0 (R Core Team 2019). Linear mixed effects models and sums of squares were constructed and computed using the lme4 (Bates et al. 2019) and car (Fox et al. 2021) packages in R, respectively.

RESULTS

Clinal variation in aridity, soil, and herbivore pressure

We found significant latitudinal variation in aridity ($F_{1,19} = 151$, $P < 0.001$, $R^2 = 0.88$; Fig. 2.1a) and soil properties ($F_{1,17} = 5.063$, P = 0.0.038, $R^2 = 0.23$; Fig. 2.1b), but not vertebrate herbivore pressure ($F_{1,18} = 2.129$, $P = 0.162$, $R^2 = 0.11$; Fig. 2.1c) across the 20 populations of *A. californica* used in this study. As reported in Pratt et al. (2017), arthropod density across five populations sampled along the coast increased significantly with latitude ($F_{1,3} = 8.458$, $P = 0.004$, $R^2 = 0.75$; Fig. 2.1d).

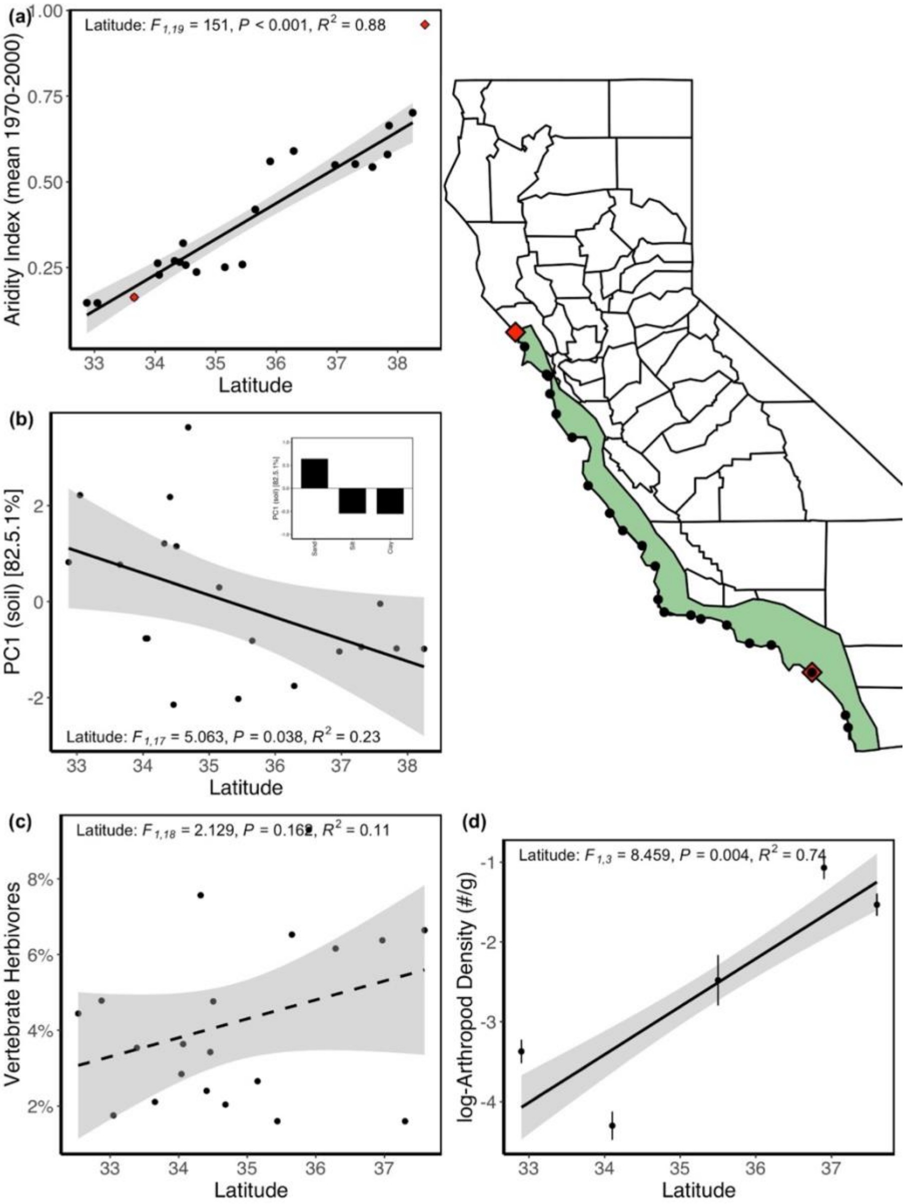

Figure 2.1. Latitudinal clines in (a) aridity (lower values indicate greater aridity), (b) soil properties, (c) estimated vertebrate herbivore pressure, and (d) arthropod density from populations of *Artemisia californica* sourced along California's coast. Soil properties were condensed via principal component, where the first principal component summarizes 82.5% of multi-variation variation in percent sand, silt, and clay. Loadings for each soil variable onto soil PC1 are displayed within panel (b). Points on map indicate the *A. californica* populations used in

this study, as well as the common garden locations (large red dots). Green coastal polygon indicates the distribution of *A. californica* in California.

Clinal variation in defense investment

Population latitude of origin and defense strategy interacted to influence defense investment ($F_{3,29}$ = 4.276, P = 0.010, R^2 = 0.31; Fig. 2.2). Populations from xeric (southern) habitats invested relatively more in resistance than tolerance to herbivory, whereas populations from mesic (northern) habitats invested more in tolerance than resistance (Fig. 2.2).

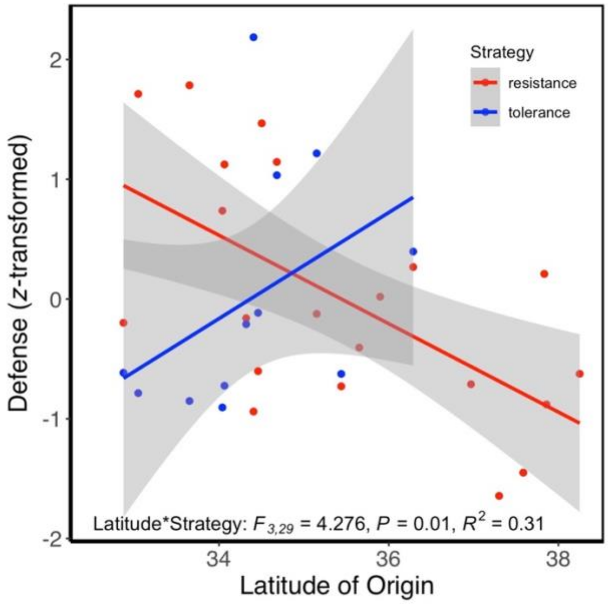

Figure 2.2. The relationship between *z*-transformed defense values for resistance (red) and tolerance (blue) vs population latitude of origin. Tolerance was calculated as $\log(\left(\frac{biomass_{2017\_clipped}}{biomass_{2017\_unclipped}}\right)$ and resistance as the inverse of percent herbivory estimated via clippings collected beneath *A. californica* canopies.

Clinal variation in leaf defense traits in the garden

We found significant latitudinal variation in four of the five traits measured. From the southern- to northern-most population, leaf percent nitrogen, specific leaf area, and percent water content increased 28% (χ^2 = 32.673, $P < 0.001$; Figure 2.3a), 17% (χ^2 = 6.492, $P = 0.011$; Fig. 2.3d) and 9% (χ^2 = 17.372, $P < 0.001$; Fig. 2.3e) with latitude, respectively, whereas total sesquiterpenes decreased 81% (χ^2 = 8.528, $P = 0.003$; Fig. 2.3c). Monoterpene concentrations did not vary with latitude (χ^2 = 0.003, $P = 0.959$; Fig. 2.3b).

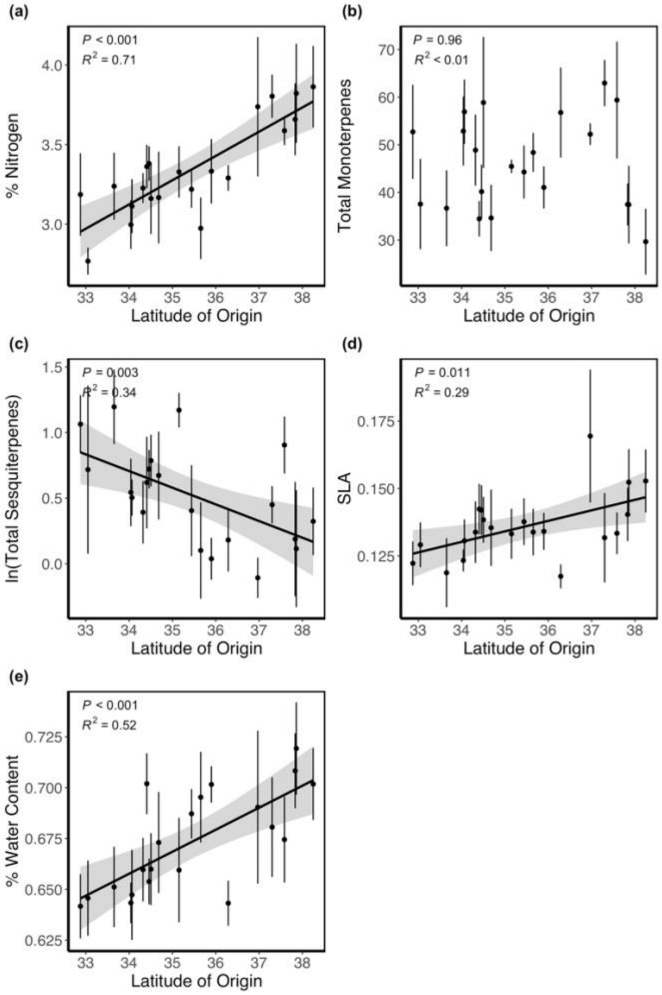

Figure 2.3. Latitudinal variation in leaf (a) % nitrogen, (b) total monoterpenes, (c) total sesquiterpenes, (d) specific leaf area, and (e) % water content, each putatively associated with plant resistance to herbivory. Least squares regression lines plotted with shaded regions indicating 95% C.I. Significant relationships indicated by solid line and non-significant relationships by dashed line

Clinal variation in vertebrate herbivory

Accounting for plant size, vertebrate herbivory in the garden increased with latitude of origin (χ^2 = 6.492, P = 0.011; Fig. 2.4a). From the southern- to northern-most population, percent herbivory increased from 2.8% to 7.2%. We corroborate this pattern within the five-population garden, where we found a significant increase in vertebrate damage on plants from south to north (χ^2 = 9.102, P = 0.003; Fig. 2.4b). In contrast, absolute herbivory declined with plant latitude of origin by 52% (χ^2 = 6.767, P = 0.009; Appendix 2B).

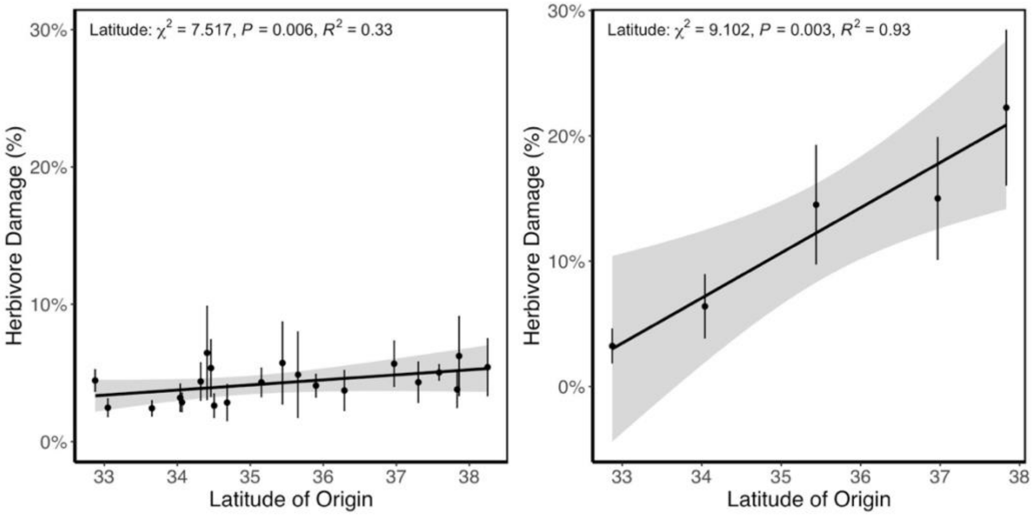

Figure 2.4. Accounting for variation in plant size, percent herbivory is plotted against plant latitude of origin for the two independent estimates. (Left) Percent herbivory was estimated in 2016 via clippings collected beneath *A. californica* canopies. (Right) Percent herbivory was estimated in 2010 via visual assessments of damage on individual plants. Least squares regression lines plotted with shaded regions indicating 95% C.I.

Clinal variation in tolerance

Results were consistent with, but somewhat equivocal for, increased tolerance in plants adapted to resource-rich environments. The clipping by latitude interaction was marginally significant for plant growth (χ^2 = 3.139, P = 0.076; Fig. 2.5) and non-significant for survival (χ^2 = 2.044, P = 0.153; Fig. 2.5). However, the patterns for both plant growth and survival were consistent with predictions for greater tolerance for plants sourced from high resource environments. With respect to the (marginally significant) result for plant growth, plants from arid (southern) environments fully compensated for clipping damage, while plants from mesic (northern) environments over-compensated. With respect to plant survival, plants from arid (southern) environments had reduced survival from clipping damage, while plants from mesic (northern) environments maintained survival. Accordingly, in both cases the patterns are suggestive of greater tolerance in plants adapted to the increased resources of mesic environments.

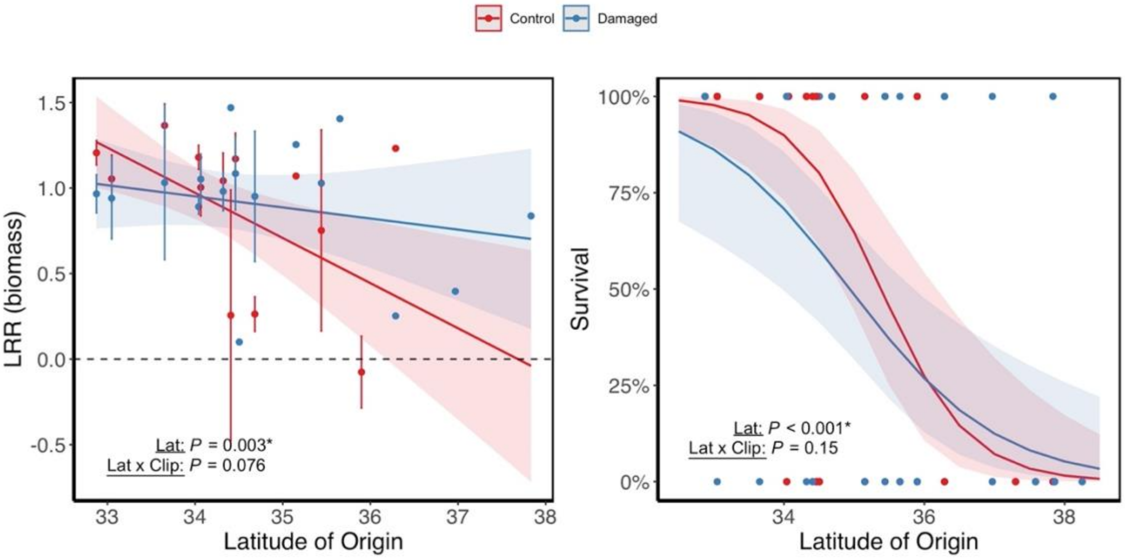

Figure 2.5. Latitudinal variation in *A. californica* growth rate (left) and survival (right) from 2016-2017 after the clipping treatment was implemented in June 2016. Growth was calculated as the log($\left(\frac{biomass_{2016}}{biomass_{2017}}\right)$, where a horizontal line at zero indicates no growth occurred. A significant interaction between latitude and our clipping treatment would indicate genetic-based variation in tolerance associated with latitude Accordingly, we report p-values for the interaction.

Clinal variation in growth

Results for growth provided no support for the prediction of increased growth rate for plants adapted to resource-rich mesic environments. Assessed across both the southern and northern gardens, growth rate was significantly affected by latitude (χ^2 = 3.882, P = 0.049) and garden (χ^2 = 23.221, P < 0.001) with higher growth from plants adapted to resource-poor (southern) environments in and the southern garden. However, the garden by latitude interaction was marginally significant (χ^2 = 3.201, P = 0.074; Fig. 2.6), suggesting that this latitudinal cline in growth rate depended on garden. Plant growth was associated with latitude of origin in the southern common garden, with plants from more mesic (northern) environments having lower growth rates (χ^2 = 6.954, P = 0.008), but there was no association observed in the northern common garden (χ^2 = 0.346, P = 0.556).

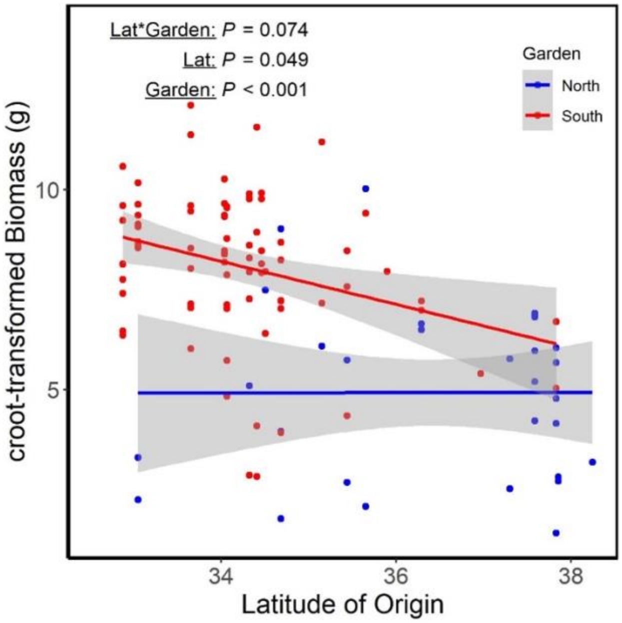

Figure 2.6. Latitudinal variation in *A. californica* size in 2018 in the northern (red) and southern (blue) gardens. Least squares regression lines plotted with shaded regions indicating 95% C.I.

DISCUSSION

We provide evidence that a latitudinal resource gradient has shaped microevolutionary patterns of plant defense strategies in *Artemisia californica*. We sampled plants from populations adapted to a coastal resource gradient characterized by mesic conditions in the north and arid conditions in the south. Within a common garden, we found that plants from mesic populations had higher quality (lower resistance) leaves for herbivores, including more nitrogen, higher water content, lower sesquiterpene concentration and, correspondingly, these plants received more damaged by vertebrate herbivores. With respect to tolerance, a results from a 50% damage suggested (marginally significance) that these same northern populations maintained fitness more than populations sourced from xeric environments. With respect to growth rate, results were equivocal, with northern populations being either indistinct or more slow growing than southern populations depending on the common garden setting (northern and southern gardens, respectively). Collectively, these results support some but not all of the theoretical predictions for the distribution of herbivore defense strategies along a resource gradient; populations from high-resource (northern) environments, exhibited lower resistance and higher tolerance (marginally significant) but not faster growth rates compared to populations from low-resource (southern) environments. Overall, the latitudinal clines in plant defense strategies uncovered here highlight the general importance of environmental gradients in shaping the evolution of plant ecological strategies within species.

Vertebrate herbivores disproportionately damaged northern vs southern plants and intraspecific variation in leaf traits suggests that northern plants are also more palatable to herbivores than southern plants. Plant traits like terpene concentration, nitrogen content, water content, and specific leaf area (as a surrogate for leaf toughness) have all been linked to herbivore performance (W J Mattson 1980, Casotti and Bradley 1991, Lucas et al. 2000, Huberty and Denno 2004, Aharoni et al. 2005, Bleeker et al. 2012), and thus these traits might underly clinal variation in resistance. Interestingly, this latitudinal cline in resistance to vertebrate herbivores parallels a previously-documented latitudinal cline in resistance against insect herbivores (Pratt et al. 2017), suggesting that plant local adaptation to a latitudinal coastal aridity gradient has generated a strategy of cross-resistance to a diverse set of herbivores. Similar patterns of cross-resistance to vertebrate and invertebrate herbivores have also been documented in species of *Eucalyptus* (Andrew et al. 2007) and *Betula* (Rousi et al. 1997). Moreover, the herbivorous insects on *A. californica* are comprised primarily of sap-feeding insects (Pratt et al. 2017), whereas the vertebrate herbivores are leaf-chewers and browsers (Litle et al. 2019). Given that sap-feeding and leaf-chewing herbivores have been shown to elicit different phytohormonal pathways (Smith et al. 2009), these results suggest that these responses may nonetheless be correlated and that latitudinal variation in environmental conditions might underly their relative co-expression.

Latitudinal and elevational clines in plant resistance have been the focus of much empirical investigation, with support for increasing resistance towards the tropics (Więski and Pennings 2014, Cronin et al. 2015, Baskett and Schemske 2018) and towards lower elevations (Rasmann et al. 2014, Dostálek et al. 2016, Moreira et al. 2017). These patterns of resistance might arise due to gradients in the strength of herbivory (Coley and Aide 1991, Schemske et al. 2009, Johnson and Rasmann 2011). However, we did not find clinal variation in vertebrate herbivore abundance, and so it is not clear that vertebrate herbivore pressure alone is responsible for driving the observed latitudinal clines in plant resistance. Aridity often varies steeply with latitude and elevation and has been linked to greater plant resistance against herbivory (Vázquez-

González et al. 2019, Kergunteuil et al. 2019, Anstett et al. n.d.). In contrast to global-scale patterns of aridity where temperate regions are more arid than tropical regions, aridity decreases with latitude within *A. californica*'s range. Therefore it is possible that heterogeneity in aridity along California's coast has influenced population response to herbivore pressure, generating genetically based latitudinal clines in plant resistance.

Contributing to a scarce but growing body of literature, we report evidence for genetically-based latitudinal clines in plant tolerance to herbivory. To our knowledge, there are only four within-species studies to date that have quantified tolerance within a common garden comprised of populations sourced along a latitudinal gradient (Więski and Pennings 2014, Lehndal and Ågren 2015, Sakata et al. 2017, Croy et al. 2020). Two of these studies found no latitudinal relationship (Więski and Pennings 2014, Sakata et al. 2017) and the other two found positive relationships latitude and tolerance (Lehndal and Ågren 2015, Croy et al. 2020). Specifically, Croy et al. (2020) found that tolerance exhibited a u-shaped relationship with latitude, illustrating that tolerance can take on non-linear relationships along environmental gradients and more studies that investigate evolutionary drivers of spatial variation in tolerance are needed. Moreover, tolerance is often assumed to be positively correlated with plant growth rate (Coley et al. 1985), and, although sometimes growth is linked to tolerance (Gianoli and Salgado-Luarte 2017), fast growth strategies may incur costs to below-ground storage or other traits related to increased tolerance (Strauss and Agrawal 1999, Rose et al. 2009). We found contrasting relationships between tolerance and growth and resource availability. However, we only measured above-ground biomass, and it is thus possible that northern populations invest more in below-ground storage. Tradeoffs between tolerance to herbivory and growth rate have been documented elsewhere (Turley et al. 2013, Croy et al. 2020), and thus growth rate may not serve as a reliable estimate of plant tolerance.

Although the patterns of inter-population variation in growth differed between the two common gardens, plants from low-resource (southern) environments were on average faster-growing than plants from high-resource (northern) environments. Intraspecific variation in *A. californica* growth (i.e., G x E) response to mesic conditions has been demonstrated with respect to both an irrigation treatment (Pratt and Mooney 2013) and over eight years of interannual variation in precipitation (Croy et al. 2021a). However, in contrast to past studies finding greater plastic increases in growth for southern vs northern populations, we found a greater reduction in growth for southern plants when growing in a mesic vs xeric common garden. One possible explanation for the differences in growth patterns is that environmental conditions across common gardens vary beyond differences in aridity solely (e.g., soil, arthropods), and these conditions in the northern common garden might impose greater stress to southern vs northern populations. We have also observed in a multi-common garden analysis that transplanting populations both northward and southward results in reduced plant size (unpublished data; JRC and KAM), suggesting that growth is a product of adaptation to particular environmental conditions. Altogether, these observations indicate that general trends between plant growth and resource availability may be difficult to detect given plant adaptation to local conditions.

Resource availability and plant growth and defense

Resource availability has been proposed to influence the evolution of plant defense strategies through both a bottom-up (Coley et al. 1985, Fine et al. 2004, Endara and Coley 2011) and feedback (Pellissier et al. 2014, Hahn and Maron 2016b, Moreira et al. 2017, Baskett and Schemske 2018) dynamic. In the bottom-up dynamic, the increased selection for plant tolerance associated with increasing resource availability reduces selection for plant resistance to herbivory, generating a tradeoff between tolerance and resistance. In contrast, a feedback dynamic is possible if resource availability increases plant productivity and, subsequently, herbivore pressure, leading to increased selection on resistance and the co-expression of plant tolerance and resistance. We find that populations from high-resource, mesic environments with relatively similar vertebrate herbivore pressure and greater invertebrate herbivore pressure were more tolerant and less resistant, suggesting that resource-driven changes in herbivore pressure do not feedback into increased selection on plant resistance. Our assessment of vertebrate herbivore pressure found that herbivore pressure did not vary with latitude, although the trend was positive. Similarly, past work on this system suggests that insect herbivory increases monotonically with latitude (higher in the north) (Pratt et al. 2017). The fact that northern populations from high-resource environments have both lower resistance and higher (insect) herbivore densities suggests that herbivore populations respond to variation in plant quality, but this variation in herbivore pressure does not in turn feedback to alter selection for resistance. We speculate that greater resource availability of northern populations results in selection for increased tolerance, and this in turn lowers selection for resistance with bottom-up consequences for associated insect communities.

Although our study provides support for a strictly bottom-up effect of resource availability on plant tolerance and resistance, there is growing empirical support for resource-driven, top-down effects of herbivory driving plant growth and defense patterns (Pellissier et al. 2012, 2014, Hahn and Maron 2016b, Hahn et al. 2018, Buckley et al. 2019, Kergunteuil et al. 2019, López-Goldar et al. 2020). These two dynamics ultimately differ in their assumption about herbivore pressure across resource environments, with the former assuming inconsequential variability in herbivory (Coley et al. 1985) and the latter assuming that favorable environmental conditions augment herbivore pressure (Janzen 1970, Coley and Aide 1991, Hahn and Maron 2016b, Moreira et al. 2017).

Concluding Remarks

Altogether, our findings provide support for a latitudinal resource gradient shaping genetically based variation in plant growth and multi-variate defense strategies among populations of a foundational shrub species. Given the evidence reported here and elsewhere for local adaptation to aridity in this system (Pratt and Mooney 2013, Pratt et al. 2014, Croy et al. 2021; unpublished data), climate-change induced shifts in the aridity landscape are likely to lead to corresponding shifts in the defensive character of local *A. californica* populations. Populations from low-resource environments have been shown to support lower densities and different communities of arthropods (Pratt et al. 2017, Croy et al. 2021a), and thus entire ecological communities might be altered as populations adapt to a changing climate. By linking environmental conditions to genetic variation in organismal traits that mediate ecological interactions, we can gain better insight into the evolutionary consequences of climate change.

SUPPLEMENTARY MATERIALS

Appendix 2A: Distribution of *Artemisia californica* populations used in this common-garden study, details on common garden design, and additional details on the methods for quantifying latitudinal variation in climate, soil, and herbivore pressure.

Table S2.1. Population locations and climate data (mean annual temperature and precipitation) for the 21 populations of *Artemisia californica* used in this study. The 21-population and 5-population gardens were established in 2011 and 2009, respectively.

Population Location		*Local Climate*		*Gardens*	*Sample Size*
Latitude (°)	Longitude (°)	MAT (°C)	MAP (cm)		
32.87	-117.25	16.9	26.6	2009, 2011	7, 10
33.05	-117.29	16.1	27.2	2011	9
33.65	-117.89	17.6	29.9	2011*	10
34.04	-118.6	16.9	42.1	2009, 2011	20, 10
34.06	-118.99	17.1	41.0	2011	10
34.32	-119.39	16.1	49.5	2011	10
34.41	-119.85	15.1	46.1	2011	10
34.46	-120.02	14.8	48.3	2011	11
34.5	-120.5	13.8	37.9	2011	10
34.68	-120.6	13.3	33.6	2011	10
35.15	-120.65	14.7	44.2	2011	10
35.44	-120.89	14.1	44.3	2009, 2011	15, 10
35.65	-121.23	13.4	54.1	2011	10
35.9	-121.46	14.3	73.6	2011	10
36.29	-121.84	14.1	91.6	2011	10
36.97	-122.12	12.1	69.3	2009, 2011	15, 10
37.3	-122.4	11.9	68.9	2011	10
37.59	-122.51	13.4	66.3	2011	10
37.83	-122.54	13.4	69.8	2009, 2011	14, 10
37.86	-122.57	13.7	84.7	2011	9
38.25	-122.96	12.7	90.1	2011	9
38.45	-123.12	11.6	107.6	2011	9

** Location of southern common garden and* A. californica *population*

†Location of northern common garden only (no A. californica *population from this site)*

Section S2.1. Common garden construction

The common garden established in 2009 (hereafter the “2009 garden”) is also described in detail elsewhere (Pratt and Mooney 2013, Pratt et al. 2014, 2017). In spring 2008, we collected 20 cuttings from 20 *A. californica* plants in each of five source populations distributed along a coastal gradient. To minimize non-genetic maternal effects associated with plants cloned from cuttings (Roach and Wulff 1987), rooted cuttings were grown in the greenhouse and common garden for a total of 24 months before collecting data. In December 2009, the common garden was planted into three blocks containing a pair of plots, one irrigated and the other unirrigated (Pratt and Mooney 2013, Pratt et al. 2014, 2017). This study focuses primarily on the unirrigated plots The plants from each source population (sample sizes ranging from 7 to 21 per population) were evenly distributed among plots and randomized within each plot.

The common garden established in 2011 (hereafter the “2011 garden”) is immediately adjacent to the 2009 garden. In December 2010, we collected seed from 10 *A. californica* plants in each of 21 source populations, including the five populations sampled for the 2009 garden. Seeds were germinated in early February 2010 in a greenhouse. In February 2011, when the plants reached a canopy volume of approximately 1,000 cm^3 (≈ 10 x 10 x 10 cm), they were transplanted to the common garden site with approximately ten individuals per population (N = 210 plants total), each from a unique seed mother. Plants were randomly assigned to locations within a 14 by 15 m grid, with each plant separated by 1.0 m from its closest neighbor. Plants within each garden were lightly irrigated during their first summer following transplant to increase survival.

Section S2.2. Methods for calculating aridity across sites.

We extracted PRISM climate data from 1970-2000 (4km spatial resolution). These climate variables were then used to calculate potential evapotranspiration (PET) using the Hargreaves equation per the protocol described by the Consortium for Spatial Information (CGIARCSI) Global Aridity and PET database (https://cgiarcsi.community/2019/01/24/global-aridity-index-and-potential-evapotranspiration-climate-database-v2/). The following equation was used to calculate monthly PET:

$$PET = 0.0023 * RA * (Tmean + 17.8) * TD^{0.5}$$

where RA is extraterrestrial radiation (on top of atmosphere), which was extracted from the R package sirad (Bojanowski 2016). RA was then converted from MJ/m-squared per day to mm/day by multiplying by 0.408 (Allen et al. 1998). As with the CGIARCSI (which is based on, Allen *et al.* 1998), we extracted RA on the 15th day of each month for each population, and then multiplied by the number of days in each month to achieve the mm/month equivalent. Tmean is monthly average temperature for each population. TD is the monthly temperature range (maximum – minimum). The unitless Aridity Index (mean annual precipitation/ mean annual potential evapotranspiration) is the inverse of aridity, with low values indicating more arid locations.

Table S2.2. List of nine soil properties extracted from the USDA NRCS SSURGO database, the variable name as listed in the "chorizon" table, and the descriptions provided by the USDA.

Abbreviation	*SSURGO Variable Name*	*Variable description*[†]
Sand	sandtotal_r[‡]	Mineral particles 0.05mm to 2.0mm in equivalent diameter as a weight percentage of the less than 2 mm fraction
Silt	silttotal_r	Mineral particles 0.002 to 0.05mm in equivalent diameter as a weight percentage of the less than 2.0mm fraction
Clay	claytotal_r	Mineral particles less than 0.002mm in equivalent diameter as a weight percentage of the less than 2.0mm fraction
OM	om_r	The amount by weight of decomposed plant and animal residue expressed as a weight percentage of the less than 2 mm soil material
Ksat	ksat_r	The amount of water that would move vertically through a unit area of saturated soil in unit time under unit hydraulic gradient
K	kffact	An erodibility factor which quantifies the susceptibility of soil particles to detachment by water
CEC	cec7_r	The amount of readily exchangeable cations that can be electrically adsorbed to negative charges in the soil, soil constituent, or other material, at pH 7.0, as estimated by the ammonium acetate method
pH	ph01mcacl2_r	The negative logarithm to base of 10 or the hydrogen ion activity in the soil, using the 0.01M CaCl2 method, in a 1:2 soil:solution ratio. A numerical expression of the relative acidity or alkalinity of a soil sample. (SSM)
AWC	awc_r	The amount of water that an increment of soil depth, inclusive of fragments, can store that is available to plants. AWC is expressed as a volume fraction, and is commonly estimated as the difference between the water contents at 1/10 or 1/3 bar (field capacity) and 15 bars (permanent wilting point) tension and adjusted for salinity, and fragments.

† Variable descriptions from the "chorizon" table within the USDA NRCS SSURGO database (Soil Survey Staff n.d.)

‡ r indicates that the values extracted were representative for the horizon.

Section S2.2. Description of the methods for extracting soil characteristics from each *Artemisia californica* site.

Methods

Using the USDA NRCS SSURGO database, we extracted nine physical attributes thought to be relevant for plant performance. These attributes are listed in Table S2.2. Each population occurs within a distinct soil type called a map unit. Each map unit is comprised of various soil components (component units), and the proportion of each component unit varies depending on the map unit. Moreover, each component unit contains unique soil horizon data. Soil properties were specifically extracted from the “chorizons” table within the SSURGO database. The chorizons table contains information on soil attributes at various soil depths, but because the majority of *A. californica* roots are concentrated within the first 50 cm of soil (Goldstein and Suding 2014), we computed weighted means for each of the nine attributes by soil depth. For instance, if the first soil layer depth was 30 cm and the second 20 cm, the attributes would be weighted accordingly. Next, to account for the varying amounts of component units within a map unit, we computed another weighted mean of the nine attributes weighted by component unit percentage. We were able to extract soil properties for 17 sites, and these results are plotted in Figure S2.1.

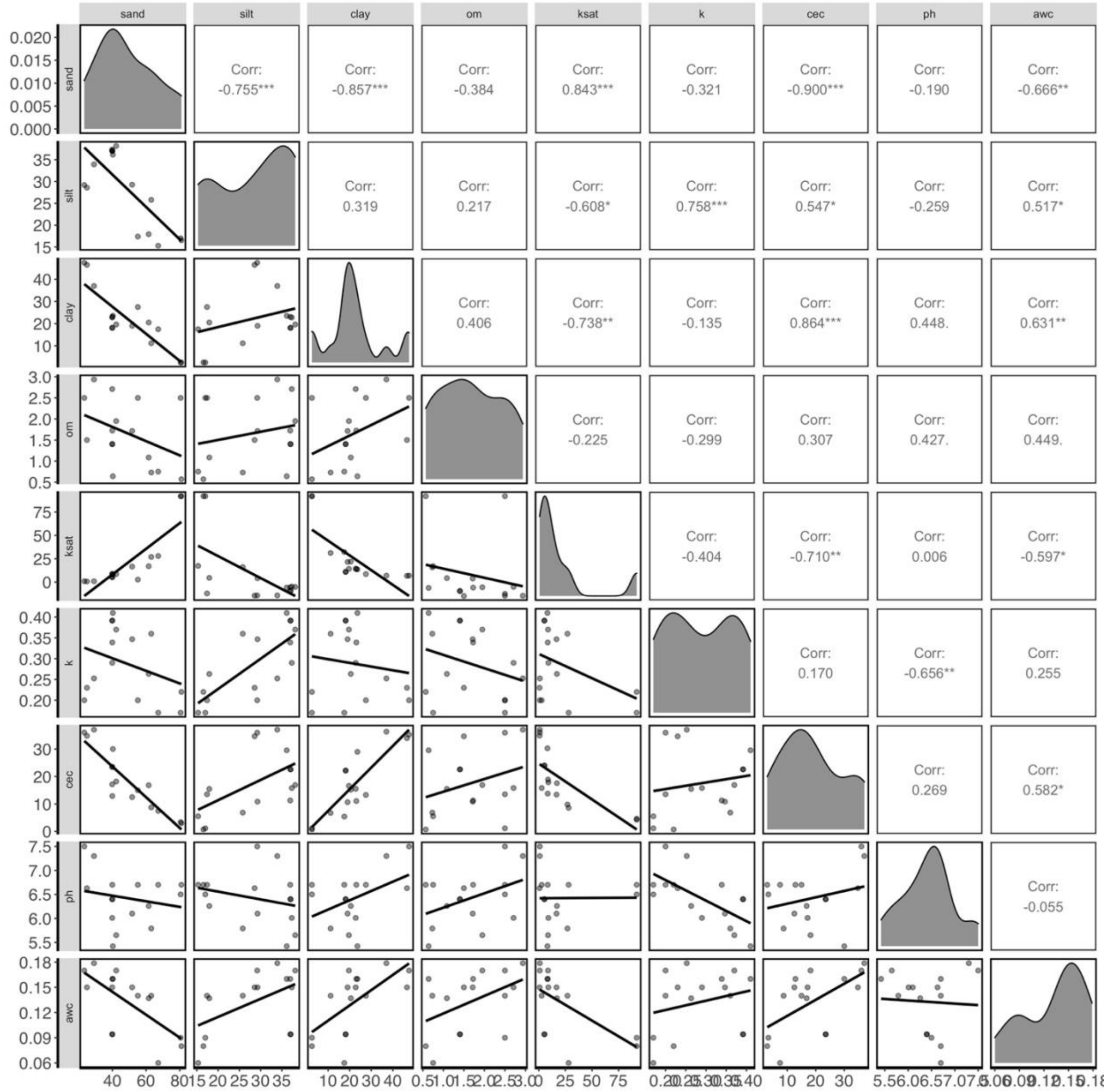

Figure S2.1. Pairwise relationships for the nine soil properties extracted from the USDA Soil SSURGO database from each *Artemisia californica* site used in this study. Histograms occupy the diagonal panels, correlation coefficients and their significance occupy the upper panels, and scatterplots for each pairwise relationship are shown in the lower panels.

Table S2.3. List of herbivorous mammalian taxa known (or likely) to feed on *Artemisia californica* that were extracted from iNaturalist to estimate herbivore pressure across *A. californica* populations.

Vertebrate herbivore taxa

Artiodactyla
Arvicolinae
Bovidae
Capra hircus
Capreolinae
Caprini
Cervidae
Cervus
Cervus canadensis
Cervus canadensis canadensis
Cervus canadensis nannodes
Cervus nippon
Chaetodipus
Chaetodipus californicus
Chaetodipus fallax
Cricetidae
Didelphimorphia
Dipodomyinae
Dipodomys
Dipodomys agilis
Dipodomys heermanni
Dipodomys merriami
Dipodomys simulans
Dipodomys stephensi
Dipodomys venustus
Geomyidae
Heteromyidae
Lagomorpha
Leporidae
Lepus
Lepus americanus
Lepus californicus
Marmota monax
Marmotini
Microtini
Microtus
Microtus californicus
Microtus californicus californicus
Microtus pennsylvanicus
Muridae
Murinae
Muroidea
Mus
Mus musculus
Myomorpha
Neotoma
Neotoma bryanti
Neotoma fuscipes
Neotoma fuscipes annectens
Neotoma lepida
Neotoma macrotis
Neotominae
Neotomini
Ochotona princeps
Odocoileus
Odocoileus hemionus
Odocoileus hemionus californicus
Odocoileus hemionus columbianus
Odocoileus hemionus fuliginatus
Odocoileus virginianus
Oryctolagus
Oryctolagus cuniculus
Oryctolagus cuniculus domesticus
Otospermophilus
Otospermophilus beecheyi
Ovis
Ovis aries
Perognathinae
Perognathus
Peromyscus
Peromyscus californicus
Peromyscus fraterculus
Peromyscus leucopus
Peromyscus maniculatus
Peromyscus maniculatus anacapae
Rattus
Rattus norvegicus
Rattus rattus
Reithrodontomyini
Reithrodontomys
Reithrodontomys megalotis
Ruminantia
Sciurus niger
Sciurus niger rufiventer
Sigmodon hispidus
Sus scrofa
Sylvilagus
Sylvilagus audubonii
Sylvilagus bachmani
Sylvilagus bachmani cinerascens
Thomomys
Thomomys bottae

Appendix 2B. Latitudinal clines in the absolute amount of herbivore damage across *Artemisia californica* populations.

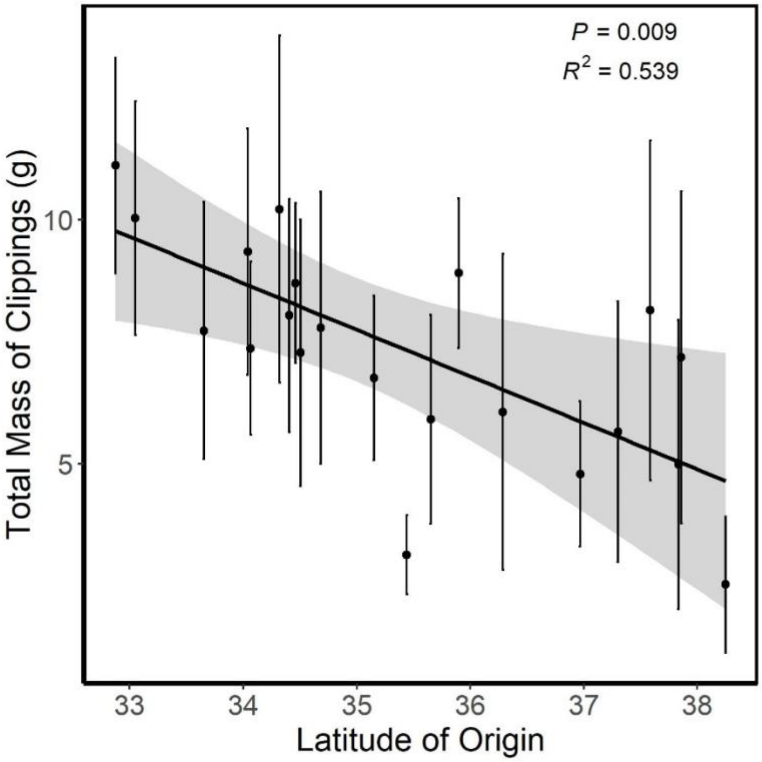

Figure S2.2 Latitudinal variation in the total mass of plant tissue removed by herbivores and collected from beneath a shrub (not accounting for plant size). Least squares regression lines plotted with shaded regions indicating 95% C.I.

CHAPTER 3

Climatic displacement exacerbates the negative impact of drought on plant performance and associated arthropod abundance

ABSTRACT

Climate change is acting on species and modifying communities and ecosystems through changes not only with respect to mean abiotic conditions, but also through increases in the frequency and severity of extreme events. Changes in mean aridity associated with climate change can generate ecotype by environment mismatch (i.e., climatic displacement). At the same time, variability around these shifting means is predicted to increase, resulting in more extreme droughts. We characterized the effects of two axes of climate change–climatic displacement and drought–on the shrub *Artemisia californica* and its arthropods. We established common gardens of plants sourced along an aridity gradient (3.5-fold variation in MAP) in an arid region of the species distribution, thus generating a gradient of climatic displacement (sustained increase in aridity) as predicted with climate change. We surveyed plants and arthropods over eight years where precipitation varied 6-fold, including both extreme drought and relatively mesic conditions. These two axes of climate change interacted to influence plant performance, such that climatically-displaced populations grew slowly regardless of drought and suffered substantial mortality during drought years. Conversely, local populations grew quickly, increased growth during wet years, and had low mortality regardless of drought. Effects on plant annual arthropod yield were negative and additive, with drought effects exceeding that of climatic displacement by 24%. However, for plant lifetime arthropod yield—incorporating effects on both plant growth and survival—climatic displacement exacerbated the negative effects of drought. Collectively these results demonstrate how climatic displacement (through increasing

aridity stress) strengthens the negative effects of drought on plants and, indirectly, on arthropods, suggesting the possibility of climate-mediated trophic collapse.

INTRODUCTION

Climate change is acting on species and modifying communities and ecosystems through changes not only in mean abiotic conditions, but also through increases in the frequency and severity of extreme events (Parmesan and Yohe 2003). Climate change is predicted to increase mean aridity in many ecosystems, with rises in mean temperature and decreases in mean precipitation (Pachauri et al. 2014, Trenberth et al. 2014). Within the context of latitudinal and elevational climatic gradients, equatorial and low-elevation climates are shifting poleward and upward in elevation, respectively (Lenoir et al. 2008, Chen et al. 2011, Freeman et al. 2018). For populations of species that are locally adapted to historic climates, shifts in abiotic conditions can lead to ecotype by climate-environment mismatch, *i.e.* climatic displacement (Wang et al. 2010b, Wilczek et al. 2014, Anderson and Wadgymar 2020). Concurrently, increased variability in precipitation associated with climate change is predicted to generate more frequent and severe droughts in many regions (Stott 2016, Wang et al. 2017). Thus, these two axes of climate change—climatic displacement and increased variability—will act simultaneously on plant performance, such that climatically-displaced plants will also be subjected to greater drought conditions. While stress from climatic displacement and drought have been studied individually, little is known how these two axes of climate change interact to influence species performance and interactions (Vázquez et al. 2017, George et al. 2017, Rudgers et al. 2018).

The effects of climatic displacement and drought on plants might interact because they operate on different time frames, and so their effects may not be substitutable (Jin and Goulden 2014, Peltier et al. 2016). Climatic displacement represents a chronic, developmental stress to which plants may plastically respond by irreversibly altering traits such as hydraulic architecture, rooting depth, root to shoot ratio, and leaf area (Vadez 2014, Barbeta et al. 2015, Tng et al. 2018). In contrast, for long-lived plants, drought may represent a discrete stress event to which plants may respond with reversable strategies involving immediate reduction in photosynthesis, respiration, and growth, and longer-term responses such as reduced leaf area (Chaves et al. 2002, Flexas et al. 2005, Xu et al. 2010). Given the potentially unique responses of plants to these two axes of climate change, it is important to understand the nature of their combined effects, and whether they operate in an additive or non-additive fashion with respect to overall plant performance.

The effects of climatic displacement and drought on plants and herbivores may cascade up to affect higher arthropod trophic levels, but, at the same time, changes in plant traits can also mediate herbivore-predator interactions (Tylianakis et al. 2008, McCluney and Sabo 2009, Barton and Ives 2014, Weldegergis et al. 2015, Barton and Schmitz 2018). Because most arthropods are herbivorous, plant-mediated effects of climate change and drought likely play a central role in arthropod population dynamics (Tylianakis et al. 2008, Jamieson et al. 2012, Rosenblatt and Schmitz 2016). Drought effects on herbivorous insects can range from positive to negative depending upon the duration of the stress and herbivore feeding guild (White 1976, Price 1991, Koricheva et al. 1998, Huberty and Denno 2004, Gely et al. 2020). Resolving the general direction of plant-mediated effects of drought on arthropods requires a holistic assessments of arthropod feeding guilds.

In this study, we investigated effects of predicted climatic displacement (sustained increase in mean aridity) and drought (discrete low-precipitation events) on the growth and survival of *A. californica* and the abundance and composition of associated arthropod feeding guilds. We grew plants sourced from populations along California’s coastal aridity gradient (ranging from 26.6 cm to 91.6 cm mean annual precipitation [MAP]) within common gardens in the south (29.9 cm MAP), thus simulating climatic displacement predicted with climate change (Figure 3.1). Then, over an eight-year period oscillating between mesic (3 years ≥ 37 cm) to extreme drought conditions (5 years ≤ 18 cm), we characterized the effects of climatic displacement and drought on *A. californica* and its associated arthropod community using the common currency of precipitation change. Our goals were not only to compare the magnitude of these two effects, but also to test whether climatic displacement amplifies or reduces the negative effects of drought. This study thus provides novel insight into the multi-trophic consequences of climate change.

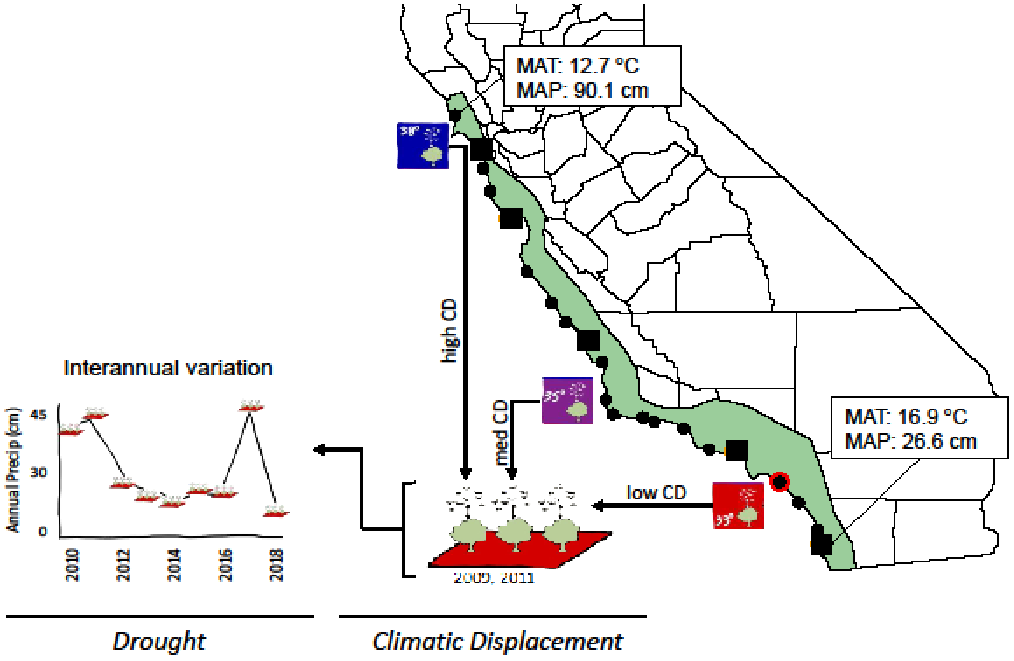

Figure 3.1. Schematic of the experimental design illustrating the two axes of climate change investigated in this study: climatic displacement (CD) and drought. Points on map indicate the *Artemisia californica* populations represented in both gardens (black squares) and only in the 2011 garden (small black dots), as well as the common garden location (large red dot). Boxes indicate climatic conditions (mean annual temperature [MAT] and precipitation [MAP]) for northern- and southern-most populations and the California distribution of *Artemisia californica* (green coastal polygon). *Climatic displacement*: By transferring populations of *Artemisia californica* sourced along a 3.5-fold latitudinal precipitation gradient into two common gardens (established in 2009 and 2011), we generated a gradient of climatic displacement predicted with climate change (sustained increased in mean aridity). *Drought*: Within the common gardens, precipitation varied 6-fold over the duration of the study, including both severe drought and relatively mesic conditions.

METHODS

Artemisia californica (Less. Asteraceae) is a dominant shrub of California's biodiverse and threatened coastal sage scrub ecosystem (Myers et al. 2000) and supports a species-rich arthropod community (Pratt et al. 2017). The species can live up to 25 years (Sawyer et al. 2009) and relies on wind for pollination and seed-dispersal. This shrub spans a 1,000 km distribution that encompasses a five-fold precipitation gradient from Northern Baja, Mexico (average annual precipitation: 20 cm) to Mendocino County, California (average annual precipitation: 103 cm). Studies have documented genetically-based trait variation across populations of *A. californica* that is suggestive of locally adapted ecotypes (Pratt and Mooney 2013). These ecotypic differences in turn influence the abundance and community composition of arthropods (Pratt et al. 2017) that are both a key component of biodiversity and support several endemic and endangered vertebrates that drive regional conservation efforts (Bowler 2000). Climate projections for the region include both northward shifts in aridity and an increased frequency and severity of droughts (Diffenbaugh et al. 2015, Wang et al. 2017, Swain et al. 2018; but see Wang et al. (2017) on simultaneous projections of increased deluge), and there is evidence this change is already underway (Pratt and Mooney 2013, MacDonald et al. 2016). This current study is based upon populations of *A. californica* distributed over 700 km in southern and north-central California (32.8-37.8° latitude; 26.6-91.6 cm precipitation) that together represent 67% of its range and include 80% of the precipitation gradient defining its overall distribution.

Common garden design

This study is based upon the analysis of data from two common gardens initiated in separate years (2009 and 2011) and containing a total of 21 *A. californica* populations (Appendix 3A). The site for both gardens is in Newport Beach, CA (33°39'N) and within the Upper Newport

Bay Ecological Preserve. Wild *A. californica* grows within 10 m of the garden perimeter. The site has a mean annual precipitation and temperature (from 1964-2014) of 29.9 cm and 17.6°C, respectively (Appendix 3A, Fig. 3.1).

Studying plants sourced from many environments within a common garden serves as a tool for documenting the consequences of environmental displacement, an approach commonly used in forestry provenance studies (O'Brien et al., 2007). Although displacement effects can be attributed to a variety of factors (e.g., climate, soil properties, biotic communities, etc.), we interpret displacement primarily through the lens of variation in aridity for several reasons. First, the coastal sites from which we sample *A. californica* vary dramatically and clinally with respect to aridity (Table A1). Second, a previous study of these populations demonstrates clinal ecotypic variation in many leaf water relations traits (Pratt and Mooney 2013, Pratt et al. 2014), consistent with local adaptation to an aridity gradient. Third, genetically-based clines in leaf functional traits parallel patterns of arthropod densities along the coast (Pratt et al. 2017), suggesting a bottom-up effect of aridity on plant-quality and associated arthropod densities. We nonetheless recognize that other factors may vary latitudinally and influence plant and arthropod performance, and we discuss the implications accordingly.

The details regarding common garden construction can be found in Appendix 3B, but the core design is briefly described here. For the common garden established in 2009 (hereafter the "2009 garden"), cuttings from five *A. californica* populations were collected along a coastal gradient in spring 2008 and grown within a greenhouse. In December 2009, the common garden was planted into three blocks each containing a pair of plots, one irrigated and the other unirrigated (Pratt and Mooney 2013, Pratt et al. 2014, 2017). While Pratt and Mooney (2013) included a precipitation manipulation that forced plants outside the precipitation that they naturally experienced in Southern California, this study focuses on the unirrigated plots experiencing an ambient Southern California climate. The plants from each source population (sample sizes ranging from 7 to 21 per population) were evenly distributed among plots and randomized within each plot. To minimize non-genetic maternal effects associated with plants cloned from cuttings (Roach and Wulff 1987), rooted cuttings were grown in the greenhouse and common garden for a total of 24 months before collecting data.

The common garden established in 2011 (hereafter the "2011 garden") is immediately adjacent to the 2009 garden. In December 2010, we collected seed from 10 *A. californica* plants in each of 21 source populations, including the five populations sampled for the 2009 garden, and germinated the seed in early February 2010 in a greenhouse. In February 2011, approximately ten individuals per population (N = 210 plants total) were transplanted into a common garden and completely randomized within a 14 by 15 m grid. Plants within each garden were lightly irrigated during their first summer following transplant to increase survival.

Climate data

We extracted and averaged 50 years (1964-2014) of monthly precipitation and temperature estimates for each population source site and the common garden from the PRISM database (PRISM Climate Group 2004; Appendix 3A). We quantify displacement specifically with respect to precipitation as a surrogate for aridity broadly because precipitation is highly correlated with both temperature (r = -0.71) and an aridity metric that incorporates temperature (e.g. Standardized Precipitation-Evapotranspiration Index [SPEI]; Thornthwaite, 1948; R^2=0.99). This also enabled us to compare spatial and temporal variation in aridity through an easily interpretable common currency of precipitation. Also, although MAP includes both wet and dry season precipitation, which may have different impacts (Michalet et al. 2021), we find that variation in dry season precipitation along the coast is negligible (Appendix 3A). In parallel, we gathered precipitation data located < 2 km away from our common garden for 2009-2018 from a local weather station (33.67°, -117.89°) maintained by Orange County Watersheds (Appendix 3A). Because *A. californica* completes most of its growth during winter and spring rains (DeSimone and Zedler 2001) and we sampled arthropods in May at peak plant biomass (see below), we computed annual precipitation from October 1 to April 30 (i.e., a hydrologic year). Precipitation between May 1 and October 1 is minimal, constituting only 5% of mean annual precipitation.

Plant performance - aboveground biomass and survival

To assess the effects of climate change on aspects of plant performance relevant to arthropods, we measured plant canopy size and survival from 2010-2018 at the conclusion of each growing season (mid-May). To estimate aboveground dry biomass, we collected reference branches from an *A. californica* shrub outside of our garden plots and visually estimated the total number of such branches needed to reconstruct our experimental shrubs separately for two reference branches. These reference branches were then dried and weighed to estimate shrub dry biomass. Data from 2010 and 2011 in the 2009 garden were based on estimations of canopy volume (Pratt & Mooney, 2013), and we subsequently converted these volume estimates to dry biomass based upon a regression formula ($F = 2063.9$; $P < 0.001$; $R^2 = 0.82$; n = 455; biomass = $7.4{*}e^{-4} + 0.16{*}e^{-4}{*}$volume). At this time, we also noted plant mortality, assuming that plants first assessed as dead in May of a given year had died during the previous summer and that this was driven by precipitation in the hydrologic year preceding that summer mortality.

Arthropod abundance and composition

Each May from 2010 to 2017 we sampled arthropods from all plants. This sampling period corresponds with the end of the growing season when plant biomass and arthropod abundance were at their peak (KAM, unpublished data). To collect arthropods, we vacuumed each shrub exhaustively with an electric vacuum (3.5 HP Ridgid model #WD0970) into a fine mesh bag that was immediately placed in a cooler and transferred to a -20° freezer later that same day. Arthropods were subsequently separated from plant chaff and stored in 70% ethanol and identified to family, and morphological species within family (Oliver and Beattie 1996). Arthropod abundance was calculated as the sum of all arthropods collected from a given plant.

Because climatic change effects might impact arthropod trophic levels and feeding guilds differently (Huberty and Denno 2004, Gely et al. 2020), cascade up from herbivores to predators, or alter herbivore-predator interactions (McCluney and Sabo 2009, Barton and Ives 2014), each morphospecies was assigned to one of nine guilds based on published accounts for the taxonomic groups. The three herbivorous guilds consisted of phloem-feeding herbivores (Hemiptera, 38 morphospecies from nine families); chewing herbivores (e.g., Orthoptera, juvenile Lepidoptera); and other herbivores (i.e., pollen and nectar feeders, and adult individuals of galling species sampled by vacuum). The three remaining guilds included omnivores (mostly Hemiptera, Miridae); detritivores (e.g., Entomobryidae); and incidentals (e.g., non-feeding, adult Diptera and Hymenoptera; see (Pratt et al. 2017) for details). The four predatory guilds consisted of: web-spinning spiders (Araneae, 17 species from five families); hunting spiders (Araneae, 28 species from six families); parasitoids (Hymenoptera, 35 species from 11 families) and other predators (e.g., larval and adult Coccinellidae beetles).

Statistical Analyses

The objective of this study was to quantify the individual and interactive effects of climatic displacement (sustained increase in mean aridity) and drought (discrete low-precipitation events) on plant performance (canopy biomass, survival) and higher trophic levels (arthropod abundance and composition). Our overall approach was to fit general linear models to test for the main and interactive effects of climatic displacement and annual precipitation. From these models, we then extracted parameters (slopes) for each factor, including how they were modified by interactive effects, and present these effects based upon a common increment of 10 cm precipitation change. We thus compared the effects of 10 cm drought, 10 cm of climatic displacement, and both combined to baseline conditions of no drought or climatic displacement for each dependent variable. These scenarios represent mild climatic displacement corresponding roughly to 0.66° of latitudinal displacement relative to predictions of 3.7° of latitudinal displacement by 2080 (Fitzpatrick and Dunn 2019). Each of our statistical models included data from the two common gardens to provide plants of two age cohorts. With this approach, annual precipitation and plant age were effectively decoupled (n = 14 [8 & 6 years from 2009 & 2011 gardens, resp.], $r = 0.08$, $P = 0.78$). We report the effects of plant ontogeny as a covariate in Appendix 3C.

For analyses of plant biomass and arthropod abundance we constructed linear mixed effects models with a repeated measures design treating annual precipitation, source site precipitation, and their interaction, as fixed effects. In addition, plant age was included as a fixed effect to account for plant ontogeny, while plant identity, source population, and planting block (n=4 ; each of the three 2009 garden blocks, the entire 2011 garden) were treated as random effects.

We modeled plant survival via a linear regression to quantify effects of drought and climatic displacement on survival transitions while accounting for plant ontogeny. We calculated the proportion of plants surviving each year for each population and within each garden and then modeled proportion survival as the dependent variable using a linear regression model with source site precipitation, annual precipitation, their interaction, and age as fixed effects. Because we pooled individuals from different blocks in order to calculate survival, we could not include planting block in the model but instead included garden as a fixed effect to account for differences between common gardens not due to plant age. We opted for this approach over others (multivariate cox regression, generalized linear mixed effect model with a binomial link function) because the model output were qualitatively identical (Appendix 3C) and the median survival times (described below) calculated from the survival rates obtained from the linear regression model most closely aligned with observed life expectancy for *A. californica* (Sawyer et al. 2009). Lastly, because annual precipitation was included with a one-year lag, and due to survival being calculated between years, the survival analysis was based on estimates for a total of seven years (2012-2018).

Lastly, to test for the effects of climatic displacement and drought on arthropod feeding guild composition, we used a permutational analysis of variance (PERMANOVA; Anderson, 2017). We used pairwise Bray-Curtis dissimilarities for arthropod community composition based upon the ln-transformed absolute abundance of each arthropod guilds (Legendre and Gallagher 2001). Moreover, we conducted permutations within plant age (strata option within the adonis function), such that distances were computed with respect to annual and source precipitation within plant cohorts of the same age, thus accounting for plant ontogenetic effects. In order to visualize these results, we performed a distance-based redundancy analysis (db-RDA), which is a generalized redundancy analysis (RDA) used to analyze non-Euclidean multivariate dissimilarities (Legendre and Anderson 1999, McArdle and Anderson 2001). The same dependent variable used in the PERMANOVA was input into a principal coordinates analysis constrained by source site precipitation and annual precipitation, and their interaction (if significant), with age included as a conditioning matrix (i.e., the effects of age are partialled out), to explain variation in arthropod community composition (partial db-RDA). We overlaid arthropod guild and explanatory variable vectors onto the first two constrained axes to illustrate how climate effects influence arthropod community composition while accounting for ontogeny.

All analyses were performed in R 3.2.0 (R Core Team 2016). Linear mixed effects models, marginal effects (means ± 95% C.I.), sums of squares, and multivariate models were constructed and computed using the lme4 (Bates et al. 2015), ggeffects (Lüdecke 2019), car (Fox and Weisberg 2011), and vegan (Oksanen et al. 2019) packages in R, respectively.

Climate change simulations

We extracted parameter means and variances from each model to describe the individual and interactive effects of climatic displacement and drought based upon the common 10 cm incremental change in precipitation (~0.66° latitude). To do so, we extracted predicted means ± S.E. for each plant and arthropod performance variable under four scenarios: (i) a “baseline” scenario based upon a population sourced from the precipitation environment of the common garden (MAP = 29.9 cm) and growing under non-drought conditions for the common garden (MAP = 29.9 cm); (ii) a “climatic displacement alone” scenario based upon a population sourced from a precipitation environment 10 cm greater than the common garden (MAP = 39.9 cm) and growing under non-drought conditions for the common garden (MAP = 29.9 cm); (iii) a "drought alone” scenario based upon a population sourced from the precipitation environment of the common garden (MAP = 29.9 cm) and growing under drought conditions of a 10 cm reduction in precipitation for the common garden (MAP = 19.9 cm); and (iv) a “combined effects” scenario. In addition to calculating separate effects for arthropod abundance per plant and plant survival, we also combined these two metrics to estimate effects on lifetime arthropod yield per plant. To do so we converted annual survival rate to plant median survival time (MST), defined here as the number of years required for a population to experience 50% mortality (MST = $\frac{\ln(0.5)}{\ln(S)}$, where S is the estimated annual survival rate). We then multiplied median survival time by plant annual arthropod abundance to obtain the plant lifetime arthropod yield under each scenario. Errors from individual arthropod abundance and survival rate estimations were propagated to obtain S.E. for lifetime arthropod yield. We also calculated predicted interactive effects. When their effects were each negative, the null prediction for additivity may be inappropriate (Sih et al. 1998). For example, if climatic displacement and drought individually each reduce plant performance by more than 50%, their combined effects cannot be more than 100%. Accordingly, in such instances we calculated expected interactive effects based upon a multiplicative risk model (Soluk and Collins 1988), in which the expected additive effect is $(Pa+Pb)-(Pa*Pb)$ where Pa and Pb are the proportional individual effects.

RESULTS

General linear models

The full model results for all statistical analyses are reported in Appendix 3C. All our analyses accounted for plant ontogenetic effects, with plant age associated with increased plant biomass (χ^2 = 63.8, $P < 0.001$,) and declines in plant survival (χ^2 = 44.54, $P < 0.001$) and arthropod abundance (χ^2 = 90.49, $P < 0.001$).

Climatic displacement and drought interacted to influence plant canopy biomass (χ^2 = 8.5, $P = 0.005$, Fig. 3.2) and plant survival ($F_{1,171} = 10.94$, $P = 0.001$, Fig. 3.2). Plants from climatically-displaced populations consistently had low biomass, whereas local populations grew well during wet years (Fig. 3.2). For plant survival, climatically-displaced populations experienced increased mortality during drought years whereas local populations maintained high survival during both drought and mesic years (Fig. 3.2). In contrast, climatic displacement and drought acted independently on annual arthropod abundance (χ^2 = 0.83, P = 0.361, Fig. 3.2), with the negative effects of drought (χ^2 = 207.04, P < 0.001) exceeding those of climatic displacement (χ^2 = 13.63, P = 0.059).

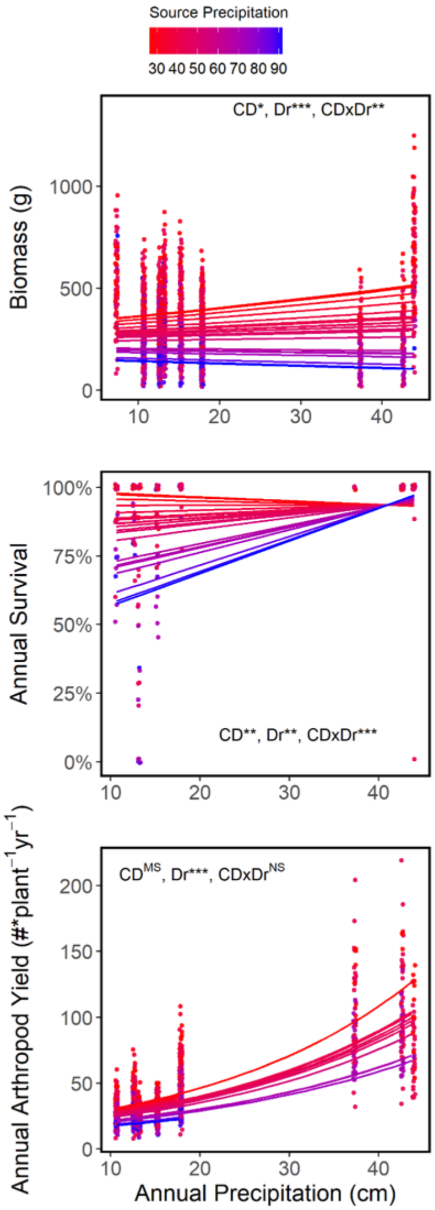

Figure 3.2. Interaction plots for effects of climatic displacement and drought on plant (top) biomass, (middle) percent survival, and (bottom) annual arthropod yield for each *Artemisia californica* population. For biomass and annual arthropod yield, the predicted linear relationships are based on marginal means (accounting for plant age, blocking, plant id, and population) and plotted over the predicted data points. Lines are truncated according to the range of available data for each population to avoid extrapolation. For survival, predicted linear relationships were

obtained similarly, but are plotted over the raw data points due to the model predicting >100% survival for some samples. Colors correspond to the population's source precipitation environment from arid (red) to mesic (blue) climates. Asterisks indicate * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. NS and MS indicate non significance and marginal significance, respectively.

Arthropod feeding guilds composition

Overall, arthropod communities were predominately comprised of sap-feeding herbivores (~72%; Fig. 3.3). Climatic displacement and drought had minimal effects on arthropod community composition as the explanatory power of the full model was low (R^2=0.062). Accounting for plant ontogeny, arthropod community composition depended on both source site precipitation (PERMANOVA, R^2=0.010; $P < 0.001$) and common garden annual precipitation (PERMANOVA, R^2=0.048; $P < 0.001$), and these effects interacted (PERMANOVA, R^2=0.003; $P = 0.026$). Similarly, the constrained axes from the distance-based redundancy analysis (db-RDA) ordination explained 7.6% of the overall variation in arthropod feeding guild composition (vs. 88% of the variation in the unconstrained ordination), with the first and second axes (displayed in Fig. 3.3) capturing 90 and 7% of this constrained variation, respectively. Broadly, climatically-displaced plants supported more of each guild except for sapfeeding and chewing herbivores, detritivores, and "other" predators (e.g., larval and adult Coccinellidae beetles). During drought years, all feeding guilds declined in abundances except for hunting spiders and "other predators" (e.g., larval and adult Coccinellidae beetles).

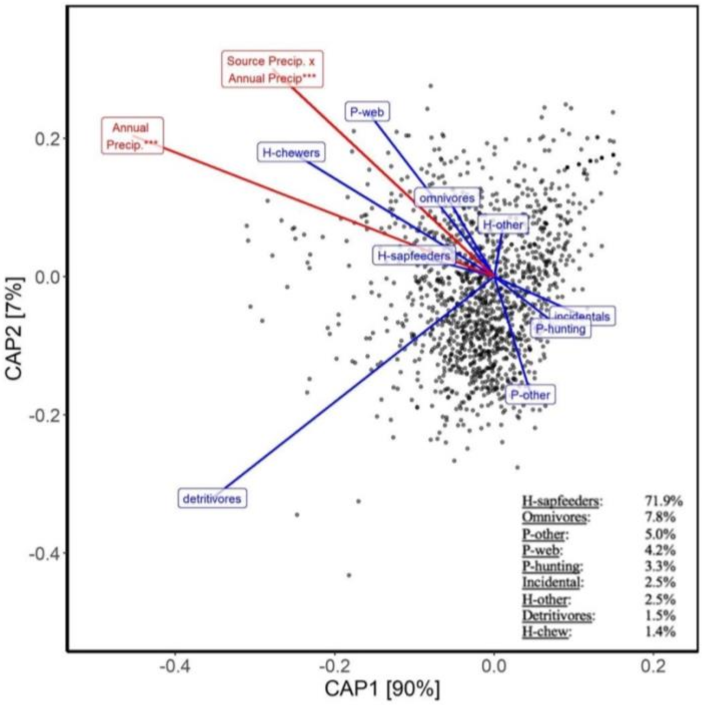

Figure 3.3. Distance-based redundancy analysis (db-RDA) ordinations based on Bray-Curtis dissimilarities in ln-transformed abundance of *Artemisia californica* arthropod feeding guilds. Ordinations are constrained by climate factors (population source site precipitation, annual precipitation, and their interaction), with the effects of ontogeny partialed out. Biplot arrows show trends with arthropod guilds (blue lines; H = herbivore, P = predator) and explanatory variables (red lines) are scaled to reflect their relative magnitude of effect based on relative variance explained. The constrained ordination explained 7.6% of the overall variation in arthropod community composition (vs. 88% of the variation in the unconstrained ordination), with the first and second axes (displayed) capturing 90 and 7% of this constrained variation, respectively. Asterisks indicate * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$ results from PERMANOVA. Relative guild abundance across all years and plants is indicated in top left corner of the left plot.

Climate change simulations

Based on parameters from the general linear models described above, we quantified the individual and combined effects of climatic displacement and drought with the common currency of a 10 cm precipitation change and compared observed and predicted interactive effects as described above. Climatic displacement and drought led to reductions in plant growth of 19.5%, and 11.9%, respectively, with observed vs. predicted combined effects of 23.4% and 25.6% reductions, respectively (Fig. 3.4a). With respect to median survival time, climatic displacement and drought led to a 29.5% reduction and a 14.5% increase, respectively, with observed vs. predicted combined effects of 40.2% and 19.3% reductions, respectively (Fig. 3.4b). Furthermore, climatic displacement and drought led to reductions in plant annual arthropod abundance of 10.8% and 34.2%, respectively, with observed vs. predicted combined effects of 40.4% and 41.3% reductions, respectively (Fig. 3.4c). Finally, with respect to plant lifetime arthropod yield, climatic displacement and drought lead to reductions of 37.1% and 24.7%, respectively, with observed vs. predicted combined effects of 64.3% and 52.6% reductions, respectively (Fig. 3.4d).

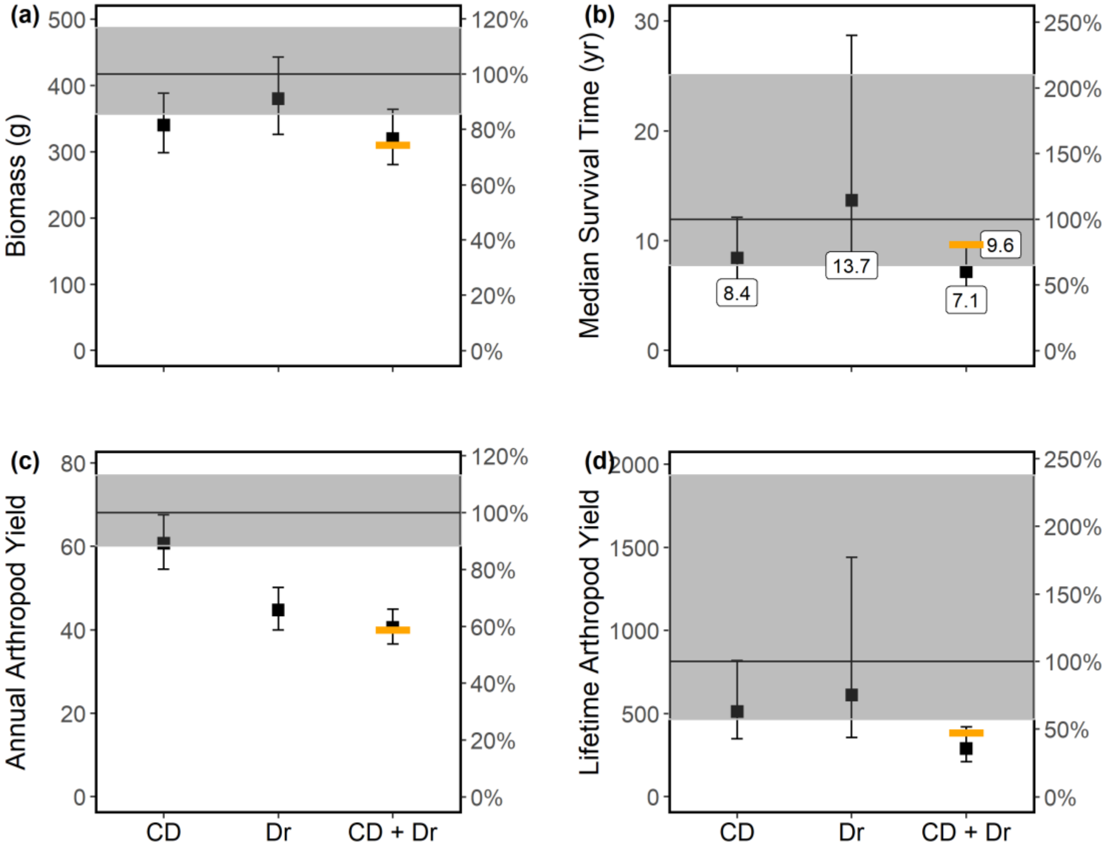

Figure 3.4. The effects of 10 cm of climatic displacement, drought, and both climatic displacement and drought on (a) plant biomass, (b) plant median survival time (calculated from the annual survival rate), (c) annual arthropod yield, and (d) lifetime arthropod yield. The black horizontal line indicates the values for a baseline scenario consisting of a population sourced from our common garden location, an environment with a historic MAP of 29.9 cm, and growing under precipitation conditions equal to the historic MAP. Means ± S.E. are plotted for each scenario. The narrow orange horizontal line indicates predicted interactive effects based upon a multiplicative risk model (Soluk & Collins, 1988; see Sih et al. (1998) for details).

DISCUSSION

We found strong effects of climatic displacement and drought on plant performance that had cascading effects on plant-associated arthropods. As compared to local genotypes, climatically displaced plants were slow growing, did not increase growth during wet years, and suffered high mortality during dry years. Climatic displacement (although marginally significant) had weaker effects on annual arthropod abundance than drought, and these two effects acted additively. In contrast, climate displacement and drought synergistically depressed lifetime arthropod yield, largely because climatic displacement increased the negative effects of drought on plant survival. Climatic displacement and drought also had weak, interactive effects on arthropod community composition with climatically-displaced populations supporting fewer sapfeeders (the most abundant herbivore feeding guild at 72%) and more hunting and web-spinning spiders. During drought years, all herbivore feeding guilds declined in abundance and hunting spiders and “other predators” (e.g., larval and adult Coccinellidae beetles) increased. Collectively, these results demonstrate how climatic displacement strengthens the negative effects of drought on both plants and arthropods and underscores the importance of evolutionary response to climate change and of management practices that may facilitate such evolutionary response.

Plant performance

We found substantial reductions in plant performance for populations that were displaced from their ecotype-environment norm, which is likely due to local adaptation to the aridity gradient. Plant performance declined with increasing climatic displacement with respect to both growth and survival, two key fitness correlates. Past work demonstrates a strong relationship between plant growth and seed production (Pratt and Mooney 2013), and we have also found superior performance of northern plants in a northern common garden (unpublished data). We argue that local adaptation within *A. californica* is likely driven by aridity for several reasons. In addition to the results reported here, ecotypic variation in leaf water-relations traits indicates that populations sourced from southern, xeric environments employ a water-conservative strategy (e.g. low % nitrogen, specific leaf area, and % water; Wright et al., 2004) relative to populations from northern, mesic environments (Pratt and Mooney 2013). Although arthropods might play a role in shaping performance patterns, previous work documented that arthropod densities across populations in the field parallel patterns found within a common garden, suggesting bottom-up effects of plants on arthropods vs top-down effects of arthropods on plants (Pratt et al. 2017). Moreover, soil properties across sites along the coast reinforce the aridity gradient. For instance, from southern to northern sites, soils transitioned from sand- to silt- and clay-dominated soils, and organic matter, erodibility, cation exchangeability, pH, and water storage capacity increased and water conductivity decreased (Appendix 3D). Interestingly, although climate and soil conditions parallel each other in terms of water availability, the processes influencing soil and climate operate on different time scales, and thus climate change may generate novel climate-soil environments that complicate predictions for plant and arthropod performance. The implication in this system is that increasing climatic aridity may negatively impact *A. californica* and associated arthropods as demonstrated here, but these effects may be attenuated by relatively unchanging soils that have a greater capacity to retain water and facilitate nutrient uptake, which tend to be concentrated towards the northern regions of the species' distribution. Indeed, further investigation is needed to uncover other potentially important drivers of adaptation (e.g., soil microbial communities) and how these factors respond to climate change. Overall, this finding contributes to the recognition of aridity as a globally-important selective force (Siepielski et al. 2017).

Climatic displacement also interacted with drought to influence plant biomass and survival. Local populations maintained high survival throughout the experiment (96.7%) and grew during wet years, whereas the most climatically-displaced population experienced a 41% reduction in survival from the wettest to the driest year and remained small throughout the duration of the experiment. Because northern populations possess a resource acquisitive strategy relative to southern populations (Pratt and Mooney 2013), it is possible that northern populations are constantly stressed in a xeric common garden, leading to compounding effects of drought on mortality. Accordingly, Pratt & Mooney (2013) demonstrated that southern populations grew more and produced more flowers in response to an irrigation treatment, whereas northern populations maintained consistent biomass and flower production. Alternatively, it is possible that northern populations of *A. californica* lack the plasticity necessary to adjust to drought conditions due to evolutionary history. For instance, the tight correlation between plasticity in biomass and flower production and inter-annual variability in precipitation of the population's source environment suggests that plasticity is adaptive (Pratt and Mooney 2013). Also, similar survival rates between northern and southern populations during mesic years suggests that northern populations are not always stressed. Our finding of increased susceptibility to drought in populations sourced from historically-mesic regions within the species' range is supported in other systems (Wolfe and Tonsor 2014, Anderegg and HilleRisLambers 2016, Stuart-Haëntjens et al. 2018).

Population local adaptation to this aridity gradient in turn suggests a fundamental distinction between species-level climatic envelopes – which assume all populations are uniform

– and population-level climatic envelopes that consider local adaptation and thus intra-specific variation in optimal climatic conditions. Because of ecotypic differentiation, plants that remain within the species climate envelope may nevertheless suffer under climate change because they are displaced from their population-level climate envelope (Sheth and Angert 2018, Anderson and Wadgymar 2020). Thus, an understanding of patterns of local adaptation can serve as a template for predicting population-level response to climate change and drought, and how these responses in aggregate then scale up to yield species-level responses. Moreover, because populations occurring at the northern edge of a species' distribution are expected to lead the latitudinal range expansion in response to climate change, our results suggest that drought may pose an additional obstacle for northern populations and hinder the species' ability to keep up with the pace of climate change. Although populations were displaced into increasingly stressful (arid) environments and it is not clear if transplanting populations into a mesic garden would yield similar results, mesic-sourced populations out-performing xeric-sourced populations in a mesic garden (unpublished) suggest that climatic displacement effects are bi-directional. We nonetheless recognize that climate change can in some cases alleviate stress and enhance plant performance, as has been shown in Arctic warming experiments (Hudson et al. 2011, Klady et al. 2011; but see Kremers et al. (2015) on diminishing returns).

Annual arthropod yield

The plant vigor and plant stress hypotheses are two non-mutually exclusive hypotheses proposed to explain how herbivorous arthropods are affected by a stressed host plant (White 1976, 2009, Price 1991). The plant vigor hypothesis predicts that herbivores prefer and perform better on healthy plant tissue, and thus a stressed host plant will support fewer herbivores. Conversely, the plant stress hypothesis predicts that stress host plants are unable to defend themselves from herbivores, and therefore herbivores benefit from a stressed host plant. Whether or not herbivores perform better on a vigorous vs stressed host plant depends on the herbivore feeding guild and the duration and type of stress (Huberty and Denno 2004). Both climatic displacement and drought reduced total arthropod yield. Moreover, each herbivore feeding guild declined in response to drought, whereas only the most dominant herbivore guild (comprising ~72%) decreased with climatic displacement. These results together lend support to the plant vigor hypothesis (Cornelissen et al., 2008; Price, 1991). Although the plant vigor hypothesis has often been studied with respect to plastic plant responses to acute stress like drought, it may apply broadly to plant stress arising from maladaptation. For example, Evans et al. (2016) found a strong signature of climate-mediated, adaptive variation in *Populus augustifolia* phenological and growth traits. Specifically, plant height was positively related to arthropod abundance, richness, and diversity, and plant height also decreased with climatic displacement. Reduced plant growth due to maladaptation may be a generalized plant response (Evans et al., 2016; Moran et al., 2017, but see Reich & Oleksyn, 2008) that overrides variability in plant defense strategies against herbivory. If so, then this suggests that displacement from the population-level climatic envelope can not only reduce plant performance, but also plant-associated arthropod yield.

The negative effects of drought on annual arthropod yield exceeded those of climatic displacement, which might be due to several factors. First, the negative effects of displacement may have been counterbalanced by northern populations being of higher quality (e.g., greater % nitrogen, lower terpene concentrations) than southern populations (Pratt and Mooney 2013, Pratt et al. 2017). Moreover, herbivore densities have been shown to correlated strongly with plant quality—$R^2 = 0.67$ (Nell and Mooney 2019) and $R^2 = 0.60$ (Singer et al. 2012)—and northern populations support greater densities of herbivores than southern populations (Pratt et al. 2017). In contrast, because biomass and plant quality—assessed through both traits (Pratt and Mooney 2013) and herbivore densities (Appendix 3C)–both decrease with increasing drought conditions, their negative combined effects might explain why drought reduced arthropod yield more so than climatic displacement. Second, it is possible that drought directly reduced arthropod yield by increasing desiccation risk (McCluney et al. 2018). However, despite the total number of precipitation events being greater in wet compared to dry years, average monthly humidity did not increase with total monthly rainfall (Appendix 3B). Thus, it is not clear that wet years provide relief to arthropods by reducing desiccation risk. Third, drought effects may also have been especially strong due to an increase in predators and top-down control, although changes in guild composition were relatively weak.

Lifetime arthropod yield

We incorporated plant survival into our assessment of climate change impacts on arthropod yield to understand how reduced habitat availability might impact associated arthropod communities. To do so, we looked at lifetime arthropod yield, finding that the cumulative effects of climatic displacement and drought on survival led to reductions in the estimated median survival time and, consequently, lifetime arthropod yield. The magnitude of these effects is concerning given recently reported global arthropod declines. For instance, Hallmann et al. (2017) reported a 75% decline in flying insect biomass over 27 years for a temperate forest ecosystem, whereas Lister and Garcia (2018) reported a 10-60 times reduction in arthropod biomass over 35 years for a tropical forest. Moreover, synchronous declines in insectivorous birds and reptiles occurred over the same time period (Lister & Garcia, 2018; but see B. Lister & Garcia, 2019 and Willig et al., 2019), and a recent analysis has suggested a 29% decline in North

American birds since 1970 (Rosenberg et al. 2019). Within our own study system, the Coastal Sage Scrub ecosystem is home to several endangered, endemic vertebrates that are mostly or entirely insectivorous, including the California gnatcatcher (*Polioptila californica*), coastal Cactus Wren (*Campylorhynchus brunneicapillus*), and the Coast Horned Lizard (*Phrynosoma coronatum*). Collectively, these findings suggest the possibility of a climate-mediated trophic collapse.

Conclusion

Because climatic displacement exacerbates the effects of drought on plants and arthropods, plant evolutionary response to such displacement (i.e. adaptation) will be critical to mitigating the effects of ongoing and future climate change. Relative to predicted values for additive effects, climatic displacement exacerbated the effects of drought on median survival time by 26% (7.1 years vs. additive prediction of 9.6 years; Fig. 4b) and life-time arthropod yield by 25% (290 lifetime arthropod total vs. additive prediction of 385; Fig. 4d). As a result, adaptation of plants to novel climates will simultaneously mitigate the negative effects of climatic displacement and drought. Analogous to evolutionary adaptation or dispersal into novel environments, plant assisted migration serves to match genotypes with their preferred environmental conditions through a manual transplant approach (McLachlan et al. 2007, Vitt et al. 2016). Assuming that precautions are taken to avoid unintended consequences, this approach should be considered where land management intentionally transplants non-local genotypes to diversify an area and facilitate an evolutionary response. Moreover, this study focuses on the ambient arthropods occurring within our common garden and it is possible that these arthropod communities are themselves arid adapted. If so, then our results might reflect conservative estimates for the impact of drought and climatic displacement on arthropods, such that arthropods in mesic environments might also be particularly susceptible to changes in aridity. Overall, our results show that assisted migration might be effective for protecting *A. californica* and associated arthropod communities, but additional measures might be required to mitigate the effects of drought on plant-associated arthropod communities.

SUPPLEMENTARY MATERIALS

Appendix 3A: Distribution of *Artemisia californica* populations used in this common-garden study and climatic variation at the garden over time.

Table S3.1 Population locations and climate data (mean annual temperature and precipitation) for the 21 populations of *Artemisia californica* used in this study.

Population Location		*Local Climate*		*Gardens*	*Sample Size*
Latitude (°)	Longitude (°)	MAT (°C)	MAP (cm)		
32.87	-117.25	16.9	26.6	2009, 2011	7, 10
33.05	-117.29	16.1	27.2	2011	9
33.65	-117.89	17.6	29.9	2011*	10
34.04	-118.6	16.9	42.1	2009, 2011	20, 10
34.06	-118.99	17.1	41.0	2011	10
34.32	-119.39	16.1	49.5	2011	10
34.41	-119.85	15.1	46.1	2011	10
34.46	-120.02	14.8	48.3	2011	11
34.5	-120.5	13.8	37.9	2011	10
34.68	-120.6	13.3	33.6	2011	10
35.15	-120.65	14.7	44.2	2011	10
35.44	-120.89	14.1	44.3	2009, 2011	15, 10
35.65	-121.23	13.4	54.1	2011	10
35.9	-121.46	14.3	73.6	2011	10
36.29	-121.84	14.1	91.6	2011	10
36.97	-122.12	12.1	69.3	2009, 2011	15, 10
37.3	-122.4	11.9	68.9	2011	10
37.59	-122.51	13.4	66.3	2011	10
37.83	-122.54	13.4	69.8	2009, 2011	14, 10
37.86	-122.57	13.7	84.7	2011	9
38.25	-122.96	12.7	90.1	2011	9

** Location of both experimental gardens*

Table S3.2. Interannual variation in climate over the duration of the experiment. Precipitation calculated on a hydrologic year (October 1st-May 1st).

Year	**Temperature (°C)**	**Precipitation (cm)**
Average (1964-2013)	17.6	29.9
2010	17.1	37.3
2011	17.5	42.6
2012	16.8	17.9
2013	17.7	12.6
2014	18.3	10.7
2015	20.3	15.2
2016	18.3	13.2
2017	17.9	43.9
2018	18.2	7.3

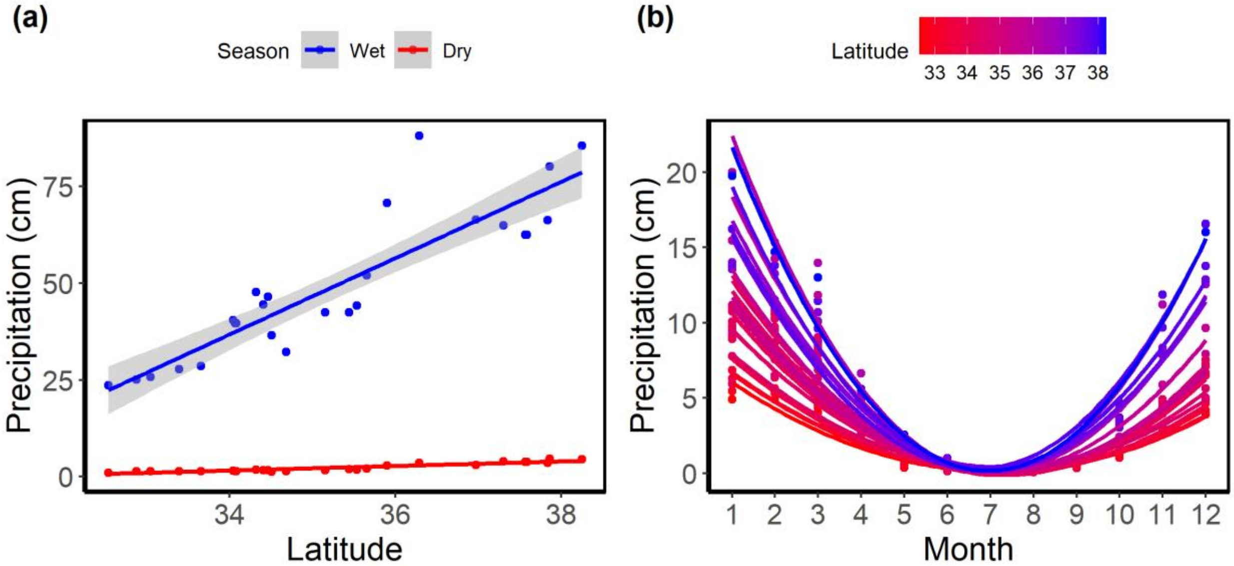

Figure S3.1. (a) Latitudinal variation in precipitation (1964-2014) for the wet (blue; October-April) and dry (red; May-September) season at the locations of each *Artemisia californica* population used in this study. (b) Average precipitation (1964-2014) for each month colored by the latitude of the *A. californica* population. Blue lines indicate more northern sites and red lines indicate more southern sites.

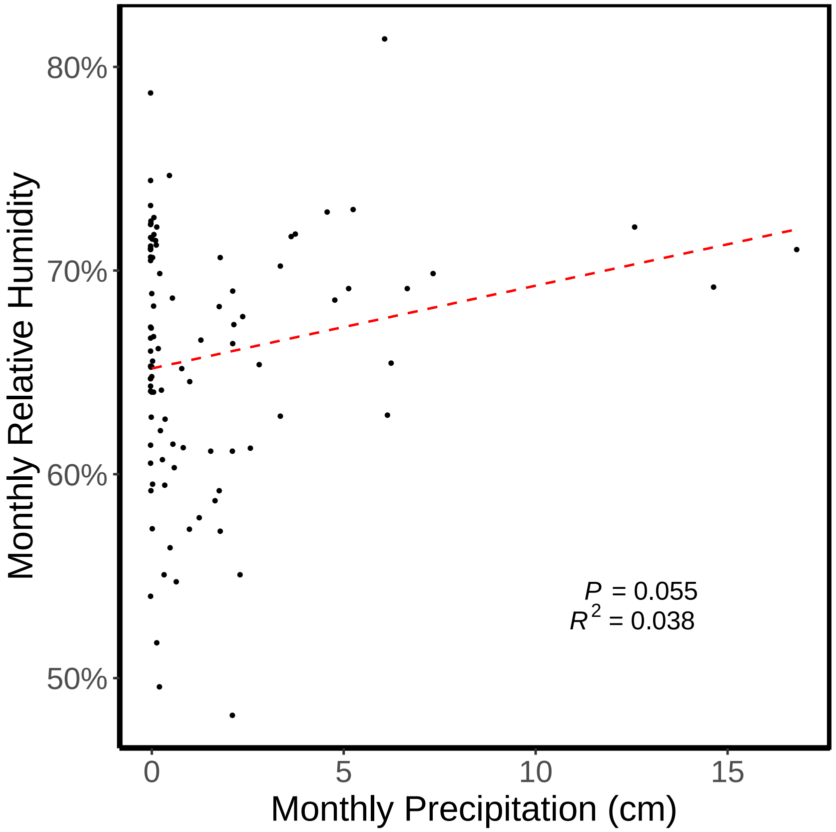

Figure S3.2. Relative humidity plotted against total monthly rainfall for each month from 2009-2017 at the common garden site. Precipitation and relative humidity was collected from the John Wayne Airport Station (33.68°, -117.87°) located < 4 km away from our common garden for 2009-2017 (from the NOAA National Centers for Environmental Information online database).

Appendix 3B. Details regarding the common garden construction.

The common garden established in 2009 (hereafter the “2009 garden”) is also described in detail elsewhere (Pratt and Mooney 2013, Pratt et al. 2014, 2017). In spring 2008, we collected 20 cuttings from 20 *A. californica* plants in each of five source populations distributed along a coastal gradient. To minimize non-genetic maternal effects associated with plants cloned from cuttings (Roach and Wulff 1987), rooted cuttings were grown in the greenhouse and common garden for a total of 24 months before collecting data. In December 2009, the common garden was planted into three blocks containing a pair of plots, one irrigated and the other unirrigated (Pratt and Mooney 2013, Pratt et al. 2014, 2017). This study focuses primarily on the unirrigated plots The plants from each source population (sample sizes ranging from 7 to 21 per population) were evenly distributed among plots and randomized within each plot.

The common garden established in 2011 (hereafter the “2011 garden”) is immediately adjacent to the 2009 garden. In December 2010, we collected seed from 10 *A. californica* plants in each of 21 source populations, including the five populations sampled for the 2009 garden. Seeds were germinated in early February 2010 in a greenhouse. In February 2011, when the plants reached a canopy volume of approximately 1,000 cm^3 (≈ 10 x 10 x 10 cm), they were transplanted to the common garden site with approximately ten individuals per population (N = 210 plants total), each from a unique seed mother. Plants were randomly assigned to locations within a 14 by 15 m grid, with each plant separated by 1.0 m from its closest neighbor. Plants within each garden were lightly irrigated during their first summer following transplant to increase survival.

Appendix 3C: Additional details on statistical models

Table S3.3. Statistical results for *A. californica* biomass, percent survival, leaf area, and associated arthropod density and abundance. Bold indicates $P < 0.05$.

Dependent Variable	Statistical model		Age		Garden		Source Precipitation		Annual Precipitation		Source Precip. * Annual Precip.	
		test statistic (TS)	TS value	ß	TS value	ß	TS value	ß	TS value	ß	TS value	ß
ln(biomass)	linear mixed effects	χ^2	**63.8**	**0.072**	--	--	**6.5**	**-0.0114**	**13.6**	**0.0182**	**8.5**	**-0.0003**
plant survival	linear regression	F	**44.5**	**-0.052**	0.05	-0.009	**30.7**	**-0.0083**	**3.9**	**-0.0068**	**10.9**	**0.0002**
plant mortality	generalized linear mixed effects (link = binomial)	χ^2	**132.1**	**1.003**	**10.1**	**-0.913**	**35.9**	**0.094**	**7.2**	**0.092**	**14.1**	**-0.003**
plant mortality	Cox proportional hazards	z	**--**	**--**	**-4.260**	**-1.125**	**5.236**	**0.060**	-0.74	-0.028	**-2.3**	**-0.0017**
ln(arthropod density)	linear mixed effects	χ^2	**110.8**	**-0.155**	--	--	**5.6**	**0.008**	**14.62**	**0.032**	1.4	-0.0002
ln(arthropod abundance)	linear mixed effects	χ^2	**90.1**	**-0.142**	--	--	3.6*	-0.008*	**30.4**	**0.046**	0.8	-0.0002

*Marginally significant ($P = 0.059$)

Appendix 3D. Extraction methods and results for physical soil properties at each *Artemisia californica* source site.

Table S3.4. List of nine soil properties extracted from the USDA NRCS SSURGO database, the variable name as listed in the "chorizon" table, and the descriptions provided by the USDA.

Abbreviation	*SSURGO Variable Name*	*Variable description*[†]
Sand	sandtotal_r[‡]	Mineral particles 0.05mm to 2.0mm in equivalent diameter as a weight percentage of the less than 2 mm fraction
Silt	silttotal_r	Mineral particles 0.002 to 0.05mm in equivalent diameter as a weight percentage of the less than 2.0mm fraction
Clay	claytotal_r	Mineral particles less than 0.002mm in equivalent diameter as a weight percentage of the less than 2.0mm fraction
OM	om_r	The amount by weight of decomposed plant and animal residue expressed as a weight percentage of the less than 2 mm soil material
Ksat	ksat_r	The amount of water that would move vertically through a unit area of saturated soil in unit time under unit hydraulic gradient
K	kffact	An erodibility factor which quantifies the susceptibility of soil particles to detachment by water
CEC	cec7_r	The amount of readily exchangeable cations that can be electrically adsorbed to negative charges in the soil, soil constituent, or other material, at pH 7.0, as estimated by the ammonium acetate method
pH	ph01mcacl2_r	The negative logarithm to base of 10 or the hydrogen ion activity in the soil, using the 0.01M CaCl2 method, in a 1:2 soil:solution ratio. A numerical expression of the relative acidity or alkalinity of a soil sample. (SSM)
AWC	awc_r	The amount of water that an increment of soil depth, inclusive of fragments, can store that is available to plants. AWC is expressed as a volume fraction, and is commonly estimated as the difference between the water contents at 1/10 or 1/3 bar (field capacity) and 15 bars (permanent wilting point) tension and adjusted for salinity, and fragments.

† Variable descriptions from the "chorizon" table within the USDA NRCS SSURGO database (Soil Survey Staff n.d.)

‡ r indicates that the values extracted were representative for the horizon.

Section S3.1. Description of the methods for extracting soil characteristics from each *Artemisia californica* site.

Using the USDA NRCS SSURGO database, we extracted nine physical attributes thought to be relevant for plant performance. These attributes are listed in Table S3.4. Each population occurs within a distinct soil type called a map unit. Each map unit is comprised of various soil components (component units), and the proportion of each component unit varies depending on the map unit. Moreover, each component unit contains unique soil horizon data. Soil properties were specifically extracted from the “chorizons” table within the SSURGO database. The chorizons table contains information on soil attributes at various soil depths, but because the majority of *A. californica* roots are concentrated within the first 50 cm of soil (Goldstein and Suding 2014), we computed weighted means for each of the nine attributes by soil depth. For instance, if the first soil layer depth was 30 cm and the second 20 cm, the attributes would be weighted accordingly. Next, to account for the varying amounts of component units within a map unit, we computed another weighted mean of the nine attributes weighted by component unit percentage. We were able to extract soil properties for 17 sites, and these results are plotted in Figure S3.3.

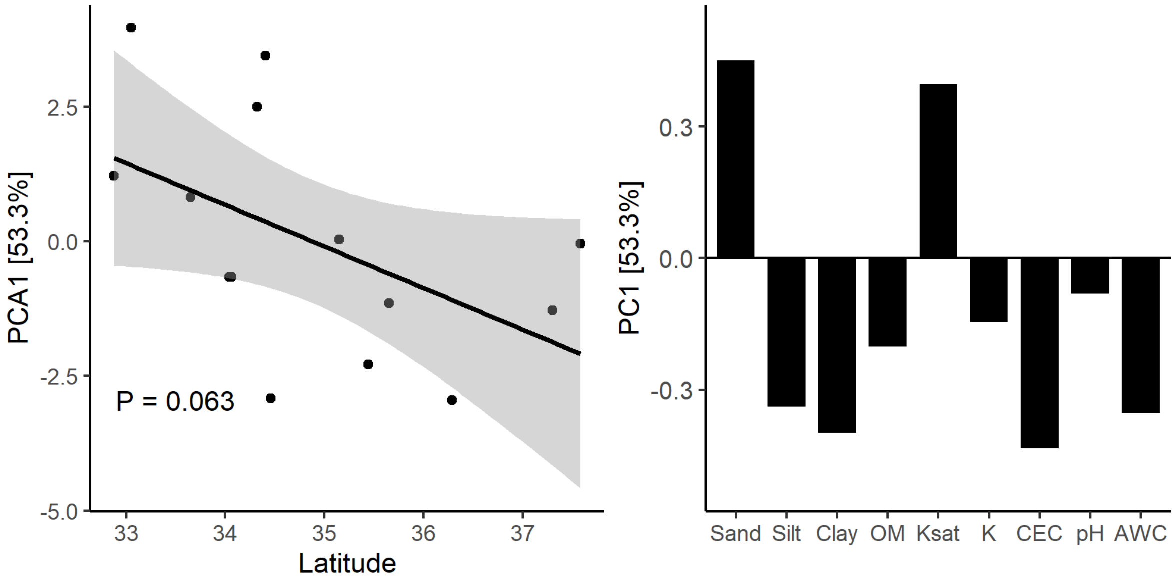

Figure S3.3. (left) Best fit line ± 95% C.I. for the relationship between the first principal component for soil properties (explaining 53.3% of total soil variation) across *Artemisia californica* population source sites and source site latitude. (right) PC loadings indicating how each of the nine individual soil properties load onto the first principal component.

REFERENCES

Agrawal, A. A. 2020. A scale-dependent framework for trade-offs, syndromes, and specialization in organismal biology. Ecology 101:e02924.

Agrawal, A. A., and M. Fishbein. 2006. Plant defense syndromes. Ecology 87:S132–S149.

Agrawal, A. A., M. Fishbein, R. Jetter, J.-P. Salminen, J. B. Goldstein, A. E. Freitag, and J. P. Sparks. (n.d.). Phylogenetic ecology of leaf surface traits in the milkweeds (Asclepias spp.): chemistry, ecophysiology, and insect behavior. New Phytologist 183:848–867.

Agrawal, A. A., A. P. Hastings, M. T. J. Johnson, J. L. Maron, and J.-P. Salminen. 2012. Insect Herbivores Drive Real-Time Ecological and Evolutionary Change in Plant Populations. Science 338:113–116.

Agren, J., and D. W. Schemske. 2012. Reciprocal transplants demonstrate strong adaptive differentiation of the model organism Arabidopsis thaliana in its native range. The New Phytologist 194:1112–1122.

Aharoni, A., M. A. Jongsma, and H. J. Bouwmeester. 2005. Volatile science? Metabolic engineering of terpenoids in plants. Trends in Plant Science 10:594–602.

Allen, R. G., L. S. Pereira, D. Raes, and M. Smith. 1998. Crop evapotranspiration: Guidelines for computing crop requirements. FAO, Rome, Italy.

Anderegg, L. D. L., and J. HilleRisLambers. 2016. Drought stress limits the geographic ranges of two tree species via different physiological mechanisms. Global Change Biology 22:1029–1045.

Anderson, J. T., A. M. Panetta, and T. Mitchell-Olds. 2012. Evolutionary and Ecological Responses to Anthropogenic Climate Change: Update on Anthropogenic Climate Change. Plant Physiology 160:1728–1740.

Anderson, J. T., and S. M. Wadgymar. 2020. Climate change disrupts local adaptation and favours upslope migration. Ecology Letters 23:181–192.

Anderson, M. J. 2017. Permutational Multivariate Analysis of Variance (PERMANOVA). Pages 1–15 Wiley StatsRef: Statistics Reference Online. American Cancer Society.

Anstett, D. N., J. R. Ahern, M. T. J. Johnson, and J.-P. Salminen. 2018. Testing for latitudinal gradients in defense at the macroevolutionary scale. Evolution 0.

Barbeta, A., M. Mejía-Chang, R. Ogaya, J. Voltas, T. E. Dawson, and J. Peñuelas. 2015. The combined effects of a long-term experimental drought and an extreme drought on the use of plant-water sources in a Mediterranean forest. Global Change Biology 21:1213–1225.

Barbour, R. C., J. M. O'Reilly-Wapstra, D. W. De Little, G. J. Jordan, D. A. Steane, J. R. Humphreys, J. K. Bailey, T. G. Whitham, and B. M. Potts. 2009. A geographic mosaic of genetic variation within a foundation tree species and its community-level consequences. Ecology 90:1762–1772.

Barton, B. T., and A. R. Ives. 2014. Species interactions and a chain of indirect effects driven by reduced precipitation. Ecology 95:486–494.

Barton, B. T., and O. J. Schmitz. 2018. Opposite effects of daytime and nighttime warming on top-down control of plant diversity. Ecology 99:13–20.

Barve, V., E. Hart, and S. Guillou. 2021. rinat: Access "iNaturalist" Data Through APIs.

Baskett, C. A., and D. W. Schemske. 2018. Latitudinal patterns of herbivore pressure in a temperate herb support the biotic interactions hypothesis. Ecology Letters 21:578–587.

Bates, D., M. Maechler, B. Bolker, S. Walker, R. H. B. Christensen, H. Singmann, B. Dai, F. Scheipl, G. Grothendieck, P. Green, and J. Fox. 2019. lme4: Linear Mixed-Effects Models using "Eigen" and S4.

Bhattarai, G. P., L. A. Meyerson, J. Anderson, D. Cummings, W. J. Allen, and J. T. Cronin. 2017. Biogeography of a plant invasion: genetic variation and plasticity in latitudinal clines for traits related to herbivory. Ecological Monographs 87:57–75.

Bleeker, P. M., R. Mirabella, P. J. Diergaarde, A. VanDoorn, A. Tissier, M. R. Kant, M. Prins, M. de Vos, M. A. Haring, and R. C. Schuurink. 2012. Improved herbivore resistance in cultivated tomato with the sesquiterpene biosynthetic pathway from a wild relative. Proceedings of the National Academy of Sciences 109:20124–20129.

Bojanowski, J. S. 2016. sirad: Functions for Calculating Daily Solar Radiation and Evapotranspiration.

Bowen, J. L., P. J. Kearns, J. E. K. Byrnes, S. Wigginton, W. J. Allen, M. Greenwood, K. Tran, J. Yu, J. T. Cronin, and L. A. Meyerson. 2017. Lineage overwhelms environmental conditions in determining rhizosphere bacterial community structure in a cosmopolitan invasive plant. Nature Communications 8:433.

Bowler, P. A. 2000. Ecological Restoration of Coastal Sage Scrub and Its Potential Role in Habitat Conservation Plans. Environmental Management 26:S85–S96.

Buckley, J., A. Widmer, M. C. Mescher, and C. M. D. Moraes. 2019. Variation in growth and defence traits among plant populations at different elevations: Implications for adaptation to climate change. Journal of Ecology 107:2478–2492.

Callaway, R. M., and F. W. Davis. 1993. Vegetation Dynamics, Fire, and the Physical Environment in Coastal Central California. Ecology 74:1567–1578.

Casotti, G., and J. S. Bradley. 1991. Leaf nitrogen and its effects on the rate of herbivory on selected eucalypts in the jarrah forest. Forest Ecology and Management 41:167–177.

Chaves, M. M., J. S. Pereira, J. Maroco, M. L. Rodrigues, C. P. P. Ricardo, M. L. OSÓRIO, I. CARVALHO, T. FARIA, and C. PINHEIRO. 2002. How Plants Cope with Water Stress in the Field? Photosynthesis and Growth. Annals of Botany 89:907–916.

Chen, I.-C., J. K. Hill, R. Ohlemueller, D. B. Roy, and C. D. Thomas. 2011. Rapid Range Shifts of Species Associated with High Levels of Climate Warming. Science 333:1024–1026.

Coley, P. D., and T. M. Aide. 1991. Comparison of herbivory and plant defenses in temperate and tropical broad-leaved forests. https://www.scienceopen.com/document?vid=8726f385-2463-4186-bd08-532bd061575e.

Coley, P. D., J. P. Bryant, and F. S. Chapin. 1985. Resource availability and plant antiherbivore defense. Science (New York, N.Y.) 230:895–899.

Cornelissen, T., G. Wilson Fernandes, and J. Vasconcellos-Neto. 2008. Size does matter: variation in herbivory between and within plants and the plant vigor hypothesis. Oikos 117:1121–1130.

Cronin, J. T., G. P. Bhattarai, W. J. Allen, and L. A. Meyerson. 2015. Biogeography of a plant invasion: plant–herbivore interactions. Ecology 96:1115–1127.

Croy, J. R., L. A. Meyerson, W. J. Allen, G. P. Bhattarai, and J. T. Cronin. 2020. Lineage and latitudinal variation in Phragmites australis tolerance to herbivory: implications for invasion success. Oikos 129:1341–1357.

Croy, J. R., J. D. Pratt, D. Sheng, and K. A. Mooney. 2021a. Climatic displacement exacerbates the negative impact of drought on plant performance and associated arthropod abundance. Ecology.

Croy, J. R., J. D. Pratt, D. Sheng, and K. A. Mooney. 2021b. Climatic displacement exacerbates the negative impact of drought on plant performance and associated arthropod abundance. Ecology 102:e03462.

Crutsinger, G. M., W. N. Reynolds, A. T. Classen, and N. J. Sanders. 2008. Disparate effects of plant genotypic diversity on foliage and litter arthropod communities. Oecologia 158:65–75.

DeSimone, S. A., and P. H. Zedler. 2001. Do Shrub Colonizers of Southern Californian Grassland Fit Generalities for Other Woody Colonizers? Ecological Applications 11:1101–1111.

Diffenbaugh, N. S., D. L. Swain, and D. Touma. 2015. Anthropogenic warming has increased drought risk in California. Proceedings of the National Academy of Sciences of the United States of America 112:3931–3936.

Direct and ecological costs of resistance to herbivory. 2002. . Trends in Ecology & Evolution 17:278–285.

Dostálek, T., M. B. Rokaya, P. Maršík, J. Rezek, J. Skuhrovec, R. Pavela, and Z. Münzbergová. 2016. Trade-off among different anti-herbivore defence strategies along an altitudinal gradient. AoB PLANTS 8.

Duke, S. O., K. C. Vaughn, E. M. Croom, and H. N. Elsohly. 1987. Artemisinin, a Constituent of Annual Wormwood (Artemisia annua), is a Selective Phytotoxin. Weed Science 35:499–505.

Eckhart, V. M., M. R. Howland, K. Jennison, B. K. Kircher, D. M. Montgomery, Y. Yuan, and M. A. Geber. 2017. Contrasting soil-texture niches facilitate coexistence of two congeneric plants that differ in competitive ability. AoB PLANTS 9.

Eckhart, V. M., I. Singh, A. M. Louthan, A. J. Keledjian, A. Chu, D. A. Moeller, and M. A. Geber. 2010. Plant-Soil Water Relations and Species Border of Clarkia xantiana ssp. xantiana (Onagraceae). International Journal of Plant Sciences 171:749–760.

Endara, M.-J., and P. D. Coley. 2011. The resource availability hypothesis revisited: a meta-analysis. Functional Ecology 25:389–398.

Ettema, C. H., and D. A. Wardle. 2002. Spatial soil ecology. Trends in Ecology & Evolution 17:177–183.

Evans, L. M., S. Kaluthota, D. W. Pearce, G. J. Allan, K. Floate, S. B. Rood, and T. G. Whitham. 2016. Bud phenology and growth are subject to divergent selection across a latitudinal gradient in Populus angustifolia and impact adaptation across the distributional range and associated arthropods. Ecology and Evolution 6:4565–4581.

Fernandez-Illescas, C. P., A. Porporato, F. Laio, and I. Rodriguez-Iturbe. 2001. The ecohydrological role of soil texture in a water-limited ecosystem. Water Resources Research 37:2863–2872.

Fine, P. V. A., I. Mesones, and P. D. Coley. 2004. Herbivores promote habitat specialization by trees in Amazonian forests. Science (New York, N.Y.) 305:663–665.

Fitzpatrick, M. C., and R. R. Dunn. 2019. Contemporary climatic analogs for 540 North American urban areas in the late 21st century. Nature Communications 10:614.

Flexas, J., J. Galmes, M. Ribas-Carbo, and H. Medrano. 2005. The Effects of Water Stress on Plant Respiration. Pages 85–94 *in* H. Lambers and M. Ribas-Carbo, editors. Plant Respiration: From Cell to Ecosystem. Springer Netherlands, Dordrecht.

Folberth, C., R. Skalský, E. Moltchanova, J. Balkovič, L. B. Azevedo, M. Obersteiner, and M. van der Velde. 2016. Uncertainty in soil data can outweigh climate impact signals in global crop yield simulations. Nature Communications 7:11872.

Fornoni, J. 2011. Ecological and evolutionary implications of plant tolerance to herbivory. Functional Ecology 25:399–407.

Fox, J., S. Weisberg, B. Price, D. Adler, D. Bates, G. Baud-Bovy, B. Bolker, S. Ellison, D. Firth, M. Friendly, G. Gorjanc, S. Graves, R. Heiberger, P. Krivitsky, R. Laboissiere, M. Maechler, G. Monette, D. Murdoch, H. Nilsson, D. Ogle, B. Ripley, W. Venables, S. Walker, D. Winsemius, A. Zeileis, and R-Core. 2021. car: Companion to Applied Regression.

Franco, M., and J. Silvertown. 2004. A Comparative Demography of Plants Based Upon Elasticities of Vital Rates. Ecology 85:531–538.

Franks, S. J., J. J. Weber, and S. N. Aitken. 2014. Evolutionary and plastic responses to climate change in terrestrial plant populations. Evolutionary Applications 7:123–139.

Freeman, B. G., J. A. Lee-Yaw, J. M. Sunday, and A. L. Hargreaves. 2018. Expanding, shifting and shrinking: The impact of global warming on species' elevational distributions. Global Ecology and Biogeography 27:1268–1276.

Freudenberger, D., B. Fish, and J. Keeley. 1987. Distribution and Stability of Grasslands in the Los Angeles Basin. Bulletin of the Southern California Academy of Sciences 86:13–26.

Gely, C., S. G. W. Laurance, and N. E. Stork. 2020. How do herbivorous insects respond to drought stress in trees? Biological Reviews 95:434–448.

Genin, D., and A. Badan-Dangon. 1991. Goat herbivory and plant phenology in a Mediterranean shrubland of northern Baja California. Journal of Arid Environments 21:113–121.

Genin, D., and A. Pijoan. 1993. Seasonality of Goat Diet and Plant Acceptabilities in the Coastal Scrub. Small Ruminant Research 10:1–11.

George, J.-P., M. Grabner, S. Karanitsch-Ackerl, K. Mayer, L. Weißenbacher, S. Schueler, and A. Mäkelä. 2017. Genetic variation, phenotypic stability, and repeatability of drought response in European larch throughout 50 years in a common garden experiment. Tree Physiology 37:33–46.

Germino, M. J., A. M. Moser, and A. R. Sands. 2019. Adaptive variation, including local adaptation, requires decades to become evident in common gardens. Ecological Applications 29:UNSP e01842.

Gianoli, E., and C. Salgado-Luarte. 2017. Tolerance to herbivory and the resource availability hypothesis. Biology Letters 13:20170120.

Gibson, A. L., E. K. Espeland, V. Wagner, and C. R. Nelson. 2016. Can local adaptation research in plants inform selection of native plant materials? An analysis of experimental methodologies. Evolutionary Applications 9:1219–1228.

Goldstein, L. J., and K. N. Suding. 2014. Applying competition theory to invasion: resource impacts indicate invasion mechanisms in California shrublands. Biological Invasions 16:191–203.

Hahn, P. G., A. A. Agrawal, K. I. Sussman, and J. L. Maron. 2018. Population Variation, Environmental Gradients, and the Evolutionary Ecology of Plant Defense against Herbivory. The American Naturalist:000–000.

Hahn, P. G., K. Keefover-Ring, L. M. N. Nguyen, and J. L. Maron. 2021. Intraspecific correlations between growth and defence vary with resource availability and differ within and among populations. Functional Ecology n/a.

Hahn, P. G., and J. L. Maron. 2016a. A Framework for Predicting Intraspecific Variation in Plant Defense. Trends in Ecology & Evolution 31:646–656.

Hahn, P. G., and J. L. Maron. 2016b. A Framework for Predicting Intraspecific Variation in Plant Defense. Trends in Ecology & Evolution 31:646–656.

Hakes, A. S., and J. T. Cronin. 2011. Resistance and tolerance to herbivory in Solidago altissima (Asteraceae): genetic variability, costs, and selection for multiple traits. American Journal of Botany 98:1446–1455.

Halligan, J. P. 1975. Toxic Terpenes from Artemisia Californica. Ecology 56:999–1003.

Harrison, S., E. Damschen, B. Fernandez-Going, A. Eskelinen, and S. Copeland. 2015. Plant communities on infertile soils are less sensitive to climate change. Annals of Botany 116:1017–1022.

Hedges, L. V., J. Gurevitch, and P. S. Curtis. 1999. The Meta-Analysis of Response Ratios in Experimental Ecology. Ecology 80:1150–1156.

Huberty, A. F., and R. F. Denno. 2004. Plant Water Stress and Its Consequences for Herbivorous Insects: A New Synthesis. Ecology 85:1383–1398.

Hudson, J. M. G., G. H. R. Henry, and W. K. Cornwell. 2011. Taller and larger: shifts in Arctic tundra leaf traits after 16 years of experimental warming. Global Change Biology 17:1013–1021.

Hufford, K. M., and S. J. Mazer. 2003. Plant ecotypes: genetic differentiation in the age of ecological restoration. Trends in Ecology & Evolution 18:147–155.

Hultine, K. R., K. C. Grady, T. E. Wood, S. M. Shuster, J. C. Stella, and T. G. Whitham. 2016. Climate change perils for dioecious plant species. Nature Plants 2:16109.

iNaturalist. Available from https://www.inaturalist.org. Accessed [Mar 2021]. (n.d.). .

Jamieson, M. A., A. M. Trowbridge, K. F. Raffa, and R. L. Lindroth. 2012. Consequences of Climate Warming and Altered Precipitation Patterns for Plant-Insect and Multitrophic Interactions. Plant Physiology 160:1719–1727.

Janzen, D. H. 1970. Herbivores and the Number of Tree Species in Tropical Forests. The American Naturalist 104:501–528.

Jin, Y., and M. L. Goulden. 2014. Ecological consequences of variation in precipitation: separating short- versus long-term effects using satellite data. Global Ecology and Biogeography 23:358–370.

Jogia, M. K., A. R. E. Sinclair, and R. J. Andersen. 1989. An antifeedant in balsam poplar inhibits browsing by snowshoe hares. Oecologia 79:189–192.

Johnson, M. T. J., and S. Rasmann. 2011. The latitudinal herbivory-defence hypothesis takes a detour on the map. The New Phytologist 191:589–592.

Joshi, J., B. Schmid, M. C. Caldeira, P. G. Dimitrakopoulos, J. Good, R. Harris, A. Hector, K. Huss-Danell, A. Jumpponen, A. Minns, C. P. H. Mulder, J. S. Pereira, A. Prinz, M. Scherer-Lorenzen, A.-S. D. Siamantziouras, A. C. Terry, A. Y. Troumbis, and J. H. Lawton. 2001. Local adaptation enhances performance of common plant species. Ecology Letters 4:536–544.

Kergunteuil, A., L. Humair, Z. Münzbergová, and S. Rasmann. 2019. Plant adaptation to different climates shapes the strengths of chemically mediated tritrophic interactions. Functional Ecology.

Kim, E., and K. Donohue. 2013. Local adaptation and plasticity of Erysimum capitatum to altitude: its implications for responses to climate change. Journal of Ecology 101:796–805.

Klady, R. A., G. H. R. Henry, and V. Lemay. 2011. Changes in high arctic tundra plant reproduction in response to long-term experimental warming. Global Change Biology 17:1611–1624.

Koricheva, J., and D. Hayes. 2018. The relative importance of plant intraspecific diversity in structuring arthropod communities: A meta-analysis. Functional Ecology 0.

Koricheva, J., S. Larsson, and E. Haukioja. 1998. Insect performance on experimentally stressed woody plants: a meta-analysis. Annual Review of Entomology 43:195–216.

Kremers, K. S., R. D. Hollister, and S. F. Oberbauer. 2015. Diminished Response of Arctic Plants to Warming over Time. PLOS ONE 10:e0116586.

Legendre, P., and M. J. Anderson. 1999. Distance-Based Redundancy Analysis: Testing Multispecies Responses in Multifactorial Ecological Experiments. Ecological Monographs 69:1–24.

Legendre, P., and E. D. Gallagher. 2001. Ecologically meaningful transformations for ordination of species data. Oecologia.

Lehndal, L., and J. Ågren. 2015. Latitudinal variation in resistance and tolerance to herbivory in the perennial herb Lythrum salicaria is related to intensity of herbivory and plant phenology. Journal of Evolutionary Biology 28:576–589.

Lenoir, J., J. C. Gegout, P. A. Marquet, P. de Ruffray, and H. Brisse. 2008. A significant upward shift in plant species optimum elevation during the 20th century. Science 320:1768–1771.

Lister, B. C., and A. Garcia. 2018. Climate-driven declines in arthropod abundance restructure a rainforest food web. Proceedings of the National Academy of Sciences 115:E10397–E10406.

Lister, B., and A. Garcia. 2019. Reply to Willig et al.: Long-term population trends in the Luquillo Rainforest. Proceedings of the National Academy of Sciences 116:12145–12146.

Litle, J., L. H. Quon, M. L. Antill, E. J. Questad, and W. M. Meyer. 2019. Vertebrate herbivory on shrub seedlings in California sage scrub: important but understudied interactions. Plant Ecology 220:523–528.

López-Goldar, X., R. Zas, and L. Sampedro. 2020. Resource availability drives microevolutionary patterns of plant defences. Functional Ecology 34:1640–1652.

Lucas, P. W., I. M. Turner, N. J. Dominy, and N. Yamashita. 2000. Mechanical Defences to Herbivory. Annals of Botany 86:913–920.

MacDonald, G. M., K. A. Moser, A. M. Bloom, A. P. Potito, D. F. Porinchu, J. R. Holmquist, J. Hughes, and K. V. Kremenetski. 2016. Prolonged California aridity linked to climate warming and Pacific sea surface temperature. Scientific Reports 6:1–8.

Macel, M., C. S. Lawson, S. R. Mortimer, M. Šmilauerova, A. Bischoff, L. Crémieux, J. Doležal, A. R. Edwards, V. Lanta, T. M. Bezemer, W. H. van der Putten, J. M. Igual, C. Rodriguez-Barrueco, H. Müller-Schärer, and T. Steinger. 2007. Climate Vs. Soil Factors in Local Adaptation of Two Common Plant Species. Ecology 88:424–433.

McArdle, B. H., and M. J. Anderson. 2001. Fitting Multivariate Models to Community Data: A Comment on Distance-Based Redundancy Analysis. Ecology 82:290–297.

McCluney, K. E., T. George, and S. D. Frank. 2018. Water availability influences arthropod water demand, hydration and community composition on urban trees. Journal of Urban Ecology 4.

McCluney, K. E., and J. L. Sabo. 2009. Water availability directly determines per capita consumption at two trophic levels. Ecology 90:1463–1469.

McLachlan, J. S., J. J. Hellmann, and M. W. Schwartz. 2007. A framework for debate of assisted migration in an era of climate change. Conservation Biology 21:297–302.

Michalet, R., P. Choler, R. M. Callaway, and T. G. Whitham. 2021. Rainfall continentality, via the winter Gams angle, provides a new dimension to biogeographical distributions in the western United States. Global Ecology and Biogeography 30:384–397.

Mooney, K. A., R. Halitschke, A. Kessler, and A. A. Agrawal. 2010. Evolutionary Trade-Offs in Plants Mediate the Strength of Trophic Cascades. Science 327:1642–1644.

Moran, E. V., A. Reid, and J. M. Levine. 2017. Population genetics and adaptation to climate along elevation gradients in invasive Solidago canadensis. PLoS ONE 12.

Moreira, X., W. K. Petry, K. A. Mooney, S. Rasmann, and L. Abdala-Roberts. 2017. Elevational gradients in plant defences and insect herbivory: recent advances in the field and prospects for future research. Ecography:n/a-n/a.

Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. B. da Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. Nature 403:853.

Nell, C. S., M. M. Meza-Lopez, J. R. Croy, A. S. Nelson, X. Moreira, J. D. Pratt, and K. A. Mooney. 2018. Relative effects of genetic variation sensu lato and sexual dimorphism on plant traits and associated arthropod communities. Oecologia 187:389–400.

Nell, C. S., and K. A. Mooney. 2019. Plant structural complexity mediates trade-off in direct and indirect plant defense by birds. Ecology 100:e02853.

Nunez-Farfan, J., J. Fornoni, and P. Luis Valverde. 2007. The evolution of resistance and tolerance to herbivores. Annual Review of Ecology Evolution and Systematics 38:541–566.

O’Brien, E. K., R. A. Mazanec, and S. L. Krauss. 2007. Provenance variation of ecologically important traits of forest trees: implications for restoration. Journal of Applied Ecology 44:583–593.

Oksanen, J., F. G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P. R. Minchin, R. B. O’Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, E. K. Szoecs, and H. Wagner. 2019. vegan package | R Documentation. https://www.rdocumentation.org/packages/vegan/versions/2.4-2.

Oliver, I., and A. J. Beattie. 1996. Designing a Cost-Effective Invertebrate Survey: A Test of Methods for Rapid Assessment of Biodiversity. Ecological Applications 6:594–607.

Pachauri, R. K., M. R. Allen, V. R. Barros, J. Broome, W. Cramer, R. Christ, J. A. Church, L. Clarke, Q. Dahe, P. Dasgupta, N. K. Dubash, O. Edenhofer, I. Elgizouli, C. B. Field, P. Forster, P. Friedlingstein, J. Fuglestvedt, L. Gomez-Echeverri, S. Hallegatte, G. Hegerl, M. Howden, K. Jiang, B. Jimenez Cisneroz, V. Kattsov, H. Lee, K. J. Mach, J. Marotzke, M. D. Mastrandrea, L. Meyer, J. Minx, Y. Mulugetta, K. O’Brien, M. Oppenheimer, J. J. Pereira, R. Pichs-Madruga, G.-K. Plattner, H.-O. Pörtner, S. B. Power, B. Preston, N. H. Ravindranath, A. Reisinger, K. Riahi, M. Rusticucci, R. Scholes, K. Seyboth, Y. Sokona, R. Stavins, T. F. Stocker, P. Tschakert, D. van Vuuren, and J.-P. van Ypserle. 2014. Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Page (R. K. Pachauri and L. Meyer, Eds.). IPCC, Geneva, Switzerland.

Painter, R. H. 1958. Resistance of Plants to Insects. Annual Review of Entomology 3:267–290.

Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37.

Pellissier, L., K. Fiedler, C. Ndribe, A. Dubuis, J.-N. Pradervand, A. Guisan, and S. Rasmann. 2012. Shifts in species richness, herbivore specialization, and plant resistance along elevation gradients. Ecology and Evolution 2:1818–1825.

Pellissier, L., A. Roger, J. Bilat, and S. Rasmann. 2014. High elevation Plantago lanceolata plants are less resistant to herbivory than their low elevation conspecifics: is it just temperature? Ecography 37:950–959.

Peltier, D. M. P., M. Fell, and K. Ogle. 2016. Legacy effects of drought in the southwestern United States: A multi-species synthesis. Ecological Monographs 86:312–326.

Pérez-Harguindeguy, N., S. Díaz, E. Garnier, S. Lavorel, H. Poorter, P. Jaureguiberry, M. S. Bret-Harte, W. K. Cornwell, J. M. Craine, D. E. Gurvich, C. Urcelay, E. J. Veneklaas, P. B. Reich, L. Poorter, I. J. Wright, P. Ray, L. Enrico, J. G. Pausas, A. C. de Vos, N. Buchmann, G. Funes, F. Quétier, J. G. Hodgson, K. Thompson, H. D. Morgan, H. ter Steege, L. Sack, B. Blonder, P. Poschlod, M. V. Vaieretti, G. Conti, A. C. Staver, S. Aquino, and J. H. C. Cornelissen. 2016. Corrigendum to: New handbook for standardised measurement of plant functional traits worldwide. Australian Journal of Botany 64:715–716.

Peterson, M. L., D. F. Doak, and W. F. Morris. 2018. Both life-history plasticity and local adaptation will shape range-wide responses to climate warming in the tundra plant Silene acaulis. Global change biology 24:1614–1625.

Petry, W. K., K. I. Perry, A. Fremgen, S. K. Rudeen, M. Lopez, J. Dryburgh, and K. A. Mooney. 2013. Mechanisms underlying plant sexual dimorphism in multi-trophic arthropod communities. Ecology 94:2055–2065.

Pilson, D. 2000. The evolution of plant response to herbivory: simultaneously considering resistance and tolerance in Brassica rapa. Evolutionary Ecology 14:457.

Pratt, J. D., A. Datu, T. Tran, D. C. Sheng, and K. A. Mooney. 2017. Genetically based latitudinal clines in Artemisia californica drive parallel clines in arthropod communities. Ecology 98:79–91.

Pratt, J. D., K. Keefover-Ring, L. Y. Liu, and K. A. Mooney. 2014. Genetically based latitudinal variation in Artemisia californica secondary chemistry. Oikos 123:953–963.

Pratt, J. D., and K. A. Mooney. 2013. Clinal adaptation and adaptive plasticity in Artemisia californica: implications for the response of a foundation species to predicted climate change. Global Change Biology 19:2454–2466.

Price, P. W. 1991. The Plant Vigor Hypothesis and Herbivore Attack. Oikos.

Puentes, A., and M. T. J. Johnson. 2016. Tolerance to deer herbivory and resistance to insect herbivores in the common evening primrose (Oenothera biennis). Journal of Evolutionary Biology 29:86–97.

Quon, L. H., E. G. Bobich, and E. J. Questad. 2019. Facilitation and herbivory during restoration of California coastal sage scrub. Restoration Ecology 27:1041–1052.

R Core Team. 2019. R: A language and environment for statistical computing. https://www.r-project.org/.

Rasmann, S., A. Buri, M. Gallot-Lavallée, J. Joaquim, J. Purcell, and L. Pellissier. 2014. Differential allocation and deployment of direct and indirect defences by Vicia sepium along elevation gradients. Journal of Ecology 102:930–938.

Reed, T. E., D. E. Schindler, and R. S. Waples. 2011. Interacting Effects of Phenotypic Plasticity and Evolution on Population Persistence in a Changing Climate. Conservation Biology 25:56–63.

Rehfeldt, G. E., C. C. Ying, D. L. Spittlehouse, and D. A. Hamilton Jr. 1999. Genetic Responses to Climate in Pinus Contorta: Niche Breadth, Climate Change, and Reforestation. Ecological Monographs 69:375–407.

Reich, P. B., and J. Oleksyn. 2008. Climate warming will reduce growth and survival of Scots pine except in the far north. Ecology Letters 11:588–597.

Roach, D. A., and R. D. Wulff. 1987. Maternal Effects in Plants. Annual Review of Ecology and Systematics 18:209–235.

Rose, K. E., R. L. Atkinson, L. A. Turnbull, and M. Rees. 2009. The costs and benefits of fast living. Ecology Letters 12:1379–1384.

Rosenberg, K. V., A. M. Dokter, P. J. Blancher, J. R. Sauer, A. C. Smith, P. A. Smith, J. C. Stanton, A. Panjabi, L. Helft, M. Parr, and P. P. Marra. 2019. Decline of the North American avifauna. Science 366:120–124.

Rosenblatt, A. E., and O. J. Schmitz. 2016. Climate Change, Nutrition, and Bottom-Up and Top-Down Food Web Processes. Trends in Ecology & Evolution 31:965–975.

Rudgers, J. A., Y. A. Chung, G. E. Maurer, D. I. Moore, E. H. Muldavin, M. E. Litvak, and S. L. Collins. 2018. Climate sensitivity functions and net primary production: A framework for incorporating climate mean and variability. Ecology 99:576–582.

Sakata, Y., T. P. Craig, J. K. Itami, M. Yamasaki, and T. Ohgushi. 2017. Parallel environmental factors drive variation in insect density and plant resistance in the native and invaded ranges. Ecology 98:2873–2884.

Salgado, C. S., and S. C. Pennings. 2005. Latitudinal Variation in Palatability of Salt-Marsh Plants: Are Differences Constitutive? Ecology 86:1571–1579.

Sawyer, J. O., T. Keeler-Wolf, and J. M. Evens. 2009. A Manual of California Vegetation. Second. Califrnia Native Plant Society, Sacramento, CA.

Schemske, D. W., G. G. Mittelbach, H. V. Cornell, J. M. Sobel, and K. Roy. 2009. Is There a Latitudinal Gradient in the Importance of Biotic Interactions? Annual Review of Ecology, Evolution, and Systematics 40:245–269.

Schweitzer, J. A., J. K. Bailey, B. J. Rehill, G. D. Martinsen, S. C. Hart, R. L. Lindroth, P. Keim, and T. G. Whitham. 2004. Genetically based trait in a dominant tree affects ecosystem processes. Ecology Letters 7:127–134.

Sheth, S. N., and A. L. Angert. 2018. Demographic compensation does not rescue populations at a trailing range edge. Proceedings of the National Academy of Sciences 115:2413–2418.

Shuster, S. M., E. V. Lonsdorf, G. M. Wimp, J. K. Bailey, and T. G. Whitham. 2006. Community heritability measures the evolutionary consequences of indirect genetic effects on community structure. Evolution 60:991–1003.

Siefert, A., C. Violle, L. Chalmandrier, C. H. Albert, A. Taudiere, A. Fajardo, L. W. Aarssen, C. Baraloto, M. B. Carlucci, M. V. Cianciaruso, V. de L. Dantas, F. de Bello, L. D. S. Duarte, C. R. Fonseca, G. T. Freschet, S. Gaucherand, N. Gross, K. Hikosaka, B. Jackson, V. Jung, C. Kamiyama, M. Katabuchi, S. W. Kembel, E. Kichenin, N. J. B. Kraft, A. Lagerström, Y. L. Bagousse-Pinguet, Y. Li, N. Mason, J. Messier, T.

Nakashizuka, J. McC. Overton, D. A. Peltzer, I. M. Pérez-Ramos, V. D. Pillar, H. C. Prentice, S. Richardson, T. Sasaki, B. S. Schamp, C. Schöb, B. Shipley, M. Sundqvist, M. T. Sykes, M. Vandewalle, and D. A. Wardle. 2015. A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. Ecology Letters 18:1406–1419.

Siepielski, A. M., M. B. Morrissey, M. Buoro, S. M. Carlson, C. M. Caruso, S. M. Clegg, T. Coulson, J. DiBattista, K. M. Gotanda, C. D. Francis, J. Hereford, J. G. Kingsolver, K. E. Augustine, L. E. B. Kruuk, R. A. Martin, B. C. Sheldon, N. Sletvold, E. I. Svensson, M. J. Wade, and A. D. C. MacColl. 2017. Precipitation drives global variation in natural selection. Science 355:959–962.

Sih, A., G. Englund, and D. Wooster. 1998. Emergent impacts of multiple predators on prey. Trends in Ecology & Evolution 13:350–355.

Simms, E. L., and M. D. Rausher. 1989. The Evolution of Resistance to Herbivory in Ipomoea Purpurea. Ii. Natural Selection by Insects and Costs of Resistance. Evolution 43:573–585.

Singer, M. S., T. E. Farkas, C. M. Skorik, and K. A. Mooney. 2012. Tritrophic Interactions at a Community Level: Effects of Host Plant Species Quality on Bird Predation of Caterpillars. The American Naturalist 179:363–374.

Smith, J. L., C. M. De Moraes, and M. C. Mescher. 2009. Jasmonate- and salicylate-mediated plant defense responses to insect herbivores, pathogens and parasitic plants. Pest Management Science 65:497–503.

Soil Survey Staff. (n.d.). Web Soil Survey. Natural Resources Conservation Service, United States Department of Agriculture.

Soil Survey Staff. (n.d.). Soil Survey Geographic (SSURGO) Database. https://sdmdataaccess.sc.egov.usda.gov/?referrer=Citation.htm-SSURGOLink.

Soluk, D. A., and N. C. Collins. 1988. Synergistic Interactions between Fish and Stoneflies: Facilitation and Interference among Stream Predators. Oikos 52:94–100.

Stamp, N. 2003. Out of the quagmire of plant defense hypotheses. Quarterly Review of Biology 78:23–55.

Stott, P. 2016. How climate change affects extreme weather events. Science 352:1517–1518.

Stowe, K. A., R. J. Marquis, C. G. Hochwender, and E. L. Simms. 2000. The evolutionary ecology of tolerance to consumer damage. Annual Review of Ecology and Systematics 31:565–595.

Strauss, S. Y., and A. A. Agrawal. 1999. The ecology and evolution of plant tolerance to herbivory. Trends in Ecology & Evolution 14:179–185.

Stuart-Haëntjens, E., H. J. De Boeck, N. P. Lemoine, P. Mänd, G. Kröel-Dulay, I. K. Schmidt, A. Jentsch, A. Stampfli, W. R. L. Anderegg, M. Bahn, J. Kreyling, T. Wohlgemuth, F. Lloret, A. T. Classen, C. M. Gough, and M. D. Smith. 2018. Mean annual precipitation predicts primary production resistance and resilience to extreme drought. Science of The Total Environment 636:360–366.

Swain, D. L., B. Langenbrunner, J. D. Neelin, and A. Hall. 2018. Increasing precipitation volatility in twenty-first-century California. Nature Climate Change 8:427.

Thornthwaite, C. W. 1948. An Approach toward a Rational Classification of Climate. Geographical Review 38:55–94.

Tiffin, P. 2000. Mechanisms of tolerance to herbivore damage:what do we know? Evolutionary Ecology 14:523–536.

Tng, D. Y. P., D. M. G. Apgaua, Y. F. Ishida, M. Mencuccini, J. Lloyd, W. F. Laurance, and S. G. W. Laurance. 2018. Rainforest trees respond to drought by modifying their hydraulic architecture. Ecology and Evolution 8:12479–12491.

Trenberth, K. E., A. Dai, G. van der Schrier, P. D. Jones, J. Barichivich, K. R. Briffa, and J. Sheffield. 2014. Global warming and changes in drought. Nature Climate Change 4:17–22.

Turley, N. E., W. C. Odell, H. Schaefer, G. Everwand, M. J. Crawley, and M. T. J. Johnson. 2013. Contemporary evolution of plant growth rate following experimental removal of herbivores. The American Naturalist 181 Suppl 1:S21-34.

Tylianakis, J. M., R. K. Didham, J. Bascompte, and D. A. Wardle. 2008. Global change and species interactions in terrestrial ecosystems. Ecology Letters 11:1351–1363.

Vadez, V. 2014. Root hydraulics: The forgotten side of roots in drought adaptation. Field Crops Research 165:15–24.

Vázquez, D. P., E. Gianoli, W. F. Morris, and F. Bozinovic. 2017. Ecological and evolutionary impacts of changing climatic variability. Biological Reviews 92:22–42.

Vázquez-González, C., X. López-Goldar, R. Zas, and L. Sampedro. 2019. Neutral and Climate-Driven Adaptive Processes Contribute to Explain Population Variation in Resin Duct Traits in a Mediterranean Pine Species. Frontiers in Plant Science 10:1613.

Vitt, P., P. N. Belmaric, R. Book, and M. Curran. 2016. Assisted migration as a climate change adaptation strategy: lessons from restoration and plant reintroductions. Israel Journal of Plant Sciences 63:250–261.

Vitt, P., K. Havens, A. T. Kramer, D. Sollenberger, and E. Yates. 2010. Assisted migration of plants: Changes in latitudes, changes in attitudes. Biological Conservation 143:18–27.

W J Mattson, J. 1980. Herbivory in Relation to Plant Nitrogen Content. Annual Review of Ecology and Systematics 11:119–161.

Wang, S.-Y. S., J.-H. Yoon, E. Becker, and R. Gillies. 2017. California from drought to deluge. Nature Climate Change 7:465–468.

Wang, T., G. A. O'Neill, and S. N. Aitken. 2010a. Integrating environmental and genetic effects to predict responses of tree populations to climate. Ecological Applications: A Publication of the Ecological Society of America 20:153–163.

Wang, T., G. A. O'Neill, and S. N. Aitken. 2010b. Integrating environmental and genetic effects to predict responses of tree populations to climate. Ecological Applications: A Publication of the Ecological Society of America 20:153–163.

Weldegergis, B. T., F. Zhu, E. H. Poelman, and M. Dicke. 2015. Drought stress affects plant metabolites and herbivore preference but not host location by its parasitoids. Oecologia 177:701–713.

White, T. C. R. 1976. Weather, food and plagues of locusts. Oecologia 22:119–134.

White, T. C. R. 2009. Plant vigour versus plant stress: a false dichotomy. Oikos 118:807–808.

Więski, K., and S. Pennings. 2014. Latitudinal variation in resistance and tolerance to herbivory of a salt marsh shrub. Ecography 37:763–769.

Wilczek, A. M., M. D. Cooper, T. M. Korves, and J. Schmitt. 2014. Lagging adaptation to warming climate in Arabidopsis thaliana. Proceedings of the National Academy of Sciences 111:7906–7913.

Willig, M. R., L. Woolbright, S. J. Presley, T. D. Schowalter, R. B. Waide, T. H. Scalley, J. K. Zimmerman, G. González, and A. E. Lugo. 2019. Populations are not declining and food webs are not collapsing at the Luquillo Experimental Forest. Proceedings of the National Academy of Sciences 116:12143–12144.

Wimp, G. M., G. D. Martinsen, K. D. Floate, R. K. Bangert, and T. G. Whitham. 2005. Plant genetic determinants of arthropod community structure and diversity. Evolution 59:61–69.

Wimp, G. M., W. P. Young, S. A. Woolbright, G. D. Martinsen, P. Keim, and T. G. Whitham. 2004. Conserving plant genetic diversity for dependent animal communities. Ecology Letters 7:776–780.

Wolfe, M. D., and S. J. Tonsor. 2014. Adaptation to spring heat and drought in northeastern Spanish Arabidopsis thaliana. New Phytologist 201:323–334.

Woods, E. C., A. P. Hastings, N. E. Turley, S. B. Heard, and A. A. Agrawal. 2012. Adaptive geographical clines in the growth and defense of a native plant. Ecological Monographs 82:149–168.

Wright, I. J., P. B. Reich, M. Westoby, D. D. Ackerly, Z. Baruch, F. Bongers, J. Cavender-Bares, T. Chapin, J. H. C. Cornelissen, M. Diemer, J. Flexas, E. Garnier, P. K. Groom, J. Gulias, K. Hikosaka, B. B. Lamont, T. Lee, W. Lee, C. Lusk, J. J. Midgley, M.-L. Navas, Ü. Niinemets, J. Oleksyn, N. Osada, H. Poorter, P. Poot, L. Prior, V. I. Pyankov, C. Roumet, S. C. Thomas, M. G. Tjoelker, E. J. Veneklaas, and R. Villar. 2004. The worldwide leaf economics spectrum. Nature 428:821–827.

Xu, Z., G. Zhou, and H. Shimizu. 2010. Plant responses to drought and rewatering. Plant Signaling & Behavior 5:649–654.

Züst, T., and A. A. Agrawal. 2017. Trade-Offs Between Plant Growth and Defense Against Insect Herbivory: An Emerging Mechanistic Synthesis. Annual Review of Plant Biology 68:513–534.

Züst, T., C. Heichinger, U. Grossniklaus, R. Harrington, D. J. Kliebenstein, and L. A. Turnbull. 2012. Natural Enemies Drive Geographic Variation in Plant Defenses. Science 338:116–119.