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

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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 mean annual precipitation) 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 sixfold, 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.

Key words: aridity; arthropods; climate change; drought; latitude; local adaptation; plant–insect interactions; precipitation.

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. 2010, 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 (George et al. 2017, Vázquez 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 reversible 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 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 (Fig. 1). Then, over an 8-yr period oscillating between mesic (3 yr ≥ 37 cm) to extreme drought conditions (5 yr ≤ 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 multitrophic consequences of climate change.

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 yr (Sawyer et al. 2009) and relies on wind for pollination and seed dispersal. This shrub spans a 1,000-km distribution that encompasses a fivefold precipitation gradient from Northern Baja, Mexico (average annual precipitation: 20 cm) to Mendocino County, California, USA (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 on 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 S1: Table S1, Fig. 1). The site for both gardens is in Newport Beach, California (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 to 2014) of 29.9 cm and 17.6°C, respectively (Appendix S1: Table S1, Fig. 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 S1). 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
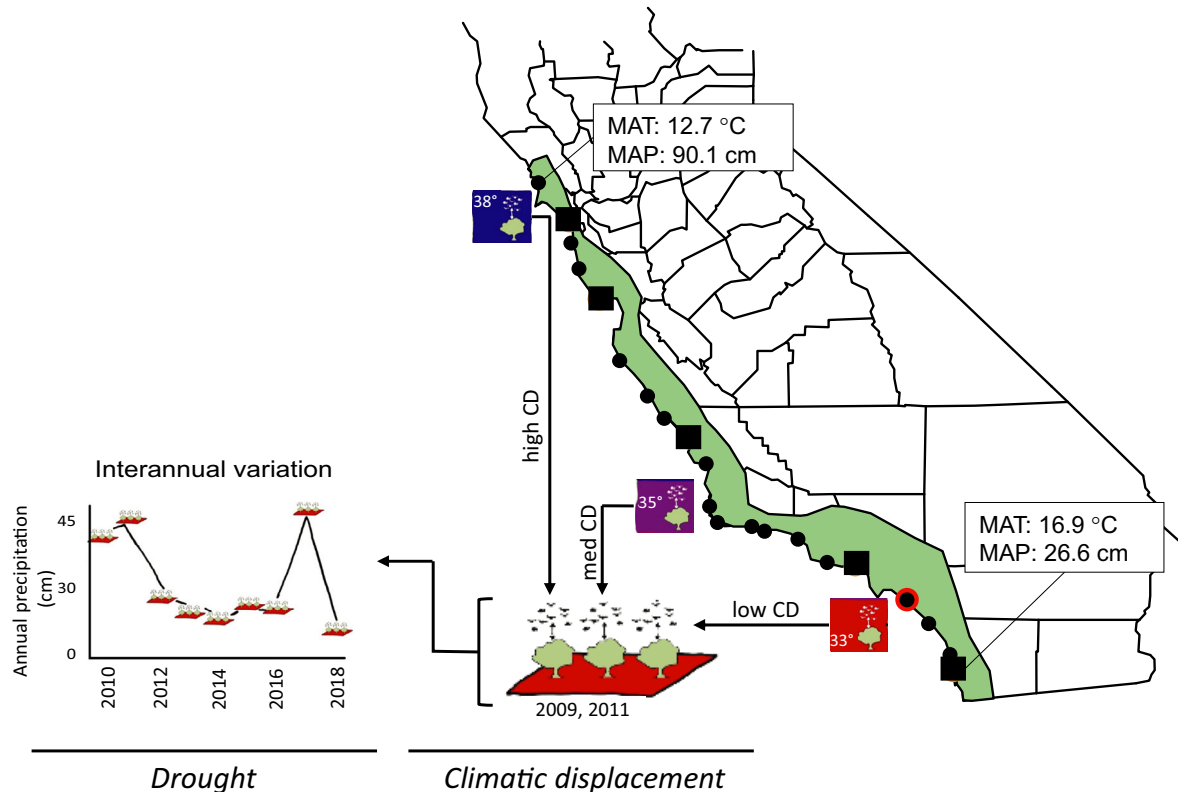
Fig. 1. Schematic of the experimental design illustrating the two axes of climate change investigated in this study: climatic displacement (CD) and drought. Points on map indicate the *Artemisia californica* populations represented in both gardens (black squares) and only in the 2011 garden (small black 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 six-fold over the duration of the study, including both severe drought and relatively mesic conditions.

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 S2, 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 10 individuals per population ($N = 210$ plants total) were transplanted into a common garden and completely randomized within a 14×15 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 yr (1964–2014) of monthly precipitation and temperature estimates for each population source site and the common garden from the PRISM database (PRISM Climate Group 2020; Appendix S1: Table S1). 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 S1: Fig. S1). 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 S1: Table S2). 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 1 October to 30 April (i.e., a hydrologic year). Precipitation between 1 May and 1 October 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 and Mooney 2013), and we subsequently converted these volume estimates to dry biomass based upon a regression formula ($F_{1,453} = 2063.9$; $P < 0.001$; $R^2 = 0.82$; $n = 455$; biomass = $7.4 \times 10^{-4} + 0.16 \times 10^{-4} \times$ 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 (K. A. Mooney, *unpublished data*). To collect arthropods, we vacuumed each shrub exhaustively with an electric vacuum (3.5 HP Ridgid model #WD0970, Ridgid Tool Company, Elyria, OH, USA) 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 and 6 yr from 2009 and 2011 gardens, respectively], $r = 0.08$, $P = 0.78$). We report the effects of plant ontogeny as a covariate in Appendix S3: Table S1.

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 S3: Table S1) and the median survival times (described in *Climate change simulations*) 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 1-yr 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 4.1.0 (R Development Core Team 2021). Linear mixed effects models, marginal effects (means $\pm$ 95% CI), sums of squares, and multivariate models were constructed and computed using the lme4 (Bates et al. 2021), ggeffects (Lüdecke et al. 2021), car (Fox et al. 2021), 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 $\pm$ SE for each plant and arthropod performance variable under four scenarios: (1) 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); (2) 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); (3) 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 (4) 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 = $\ln 0.5 / \ln S$ 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 SE 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
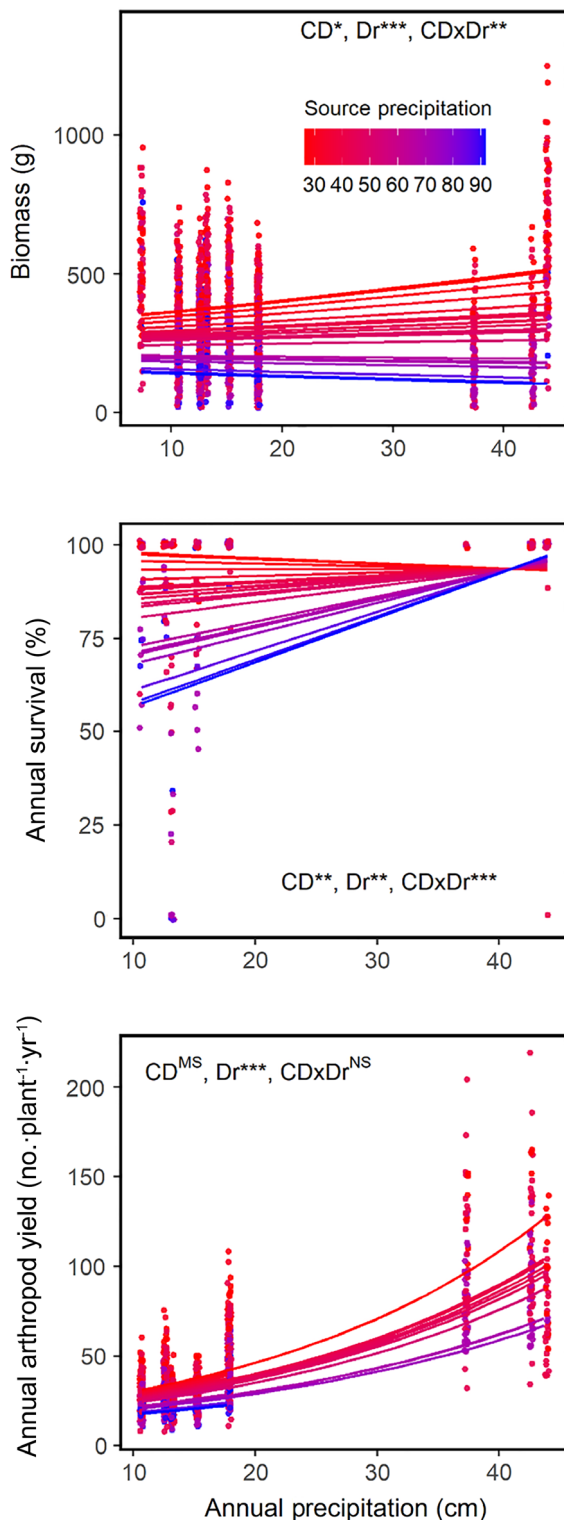
FIG. 2. Interaction plots for effects of climatic displacement (CD) and drought (Dr) on plant (top) biomass, (middle) percent survival, and (bottom) annual arthropod yield for each *Artemisia californica* population. For biomass and annual arthropod yield, the predicted linear relationships are based on marginal means (accounting for plant age, blocking, plant id, and

(FIG. 2. *Continued*)
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. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. NS and MS indicate nonsignificance and marginal significance, respectively.

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 S3: Table S1. All our analyses accounted for plant ontogenetic effects, with plant age associated with increased plant biomass ($\chi^2 = 63.8$, $P < 0.001$,) and declines in plant survival ($\chi^2 = 44.54$, $P < 0.001$) and arthropod abundance ($\chi^2 = 90.49$, $P < 0.001$).

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

Arthropod feeding guilds composition

Overall, arthropod communities were predominately comprised of sap-feeding herbivores (~72%; Fig. 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) 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).

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. 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. 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. 4c). Finally, with respect to plant lifetime arthropod yield, climatic
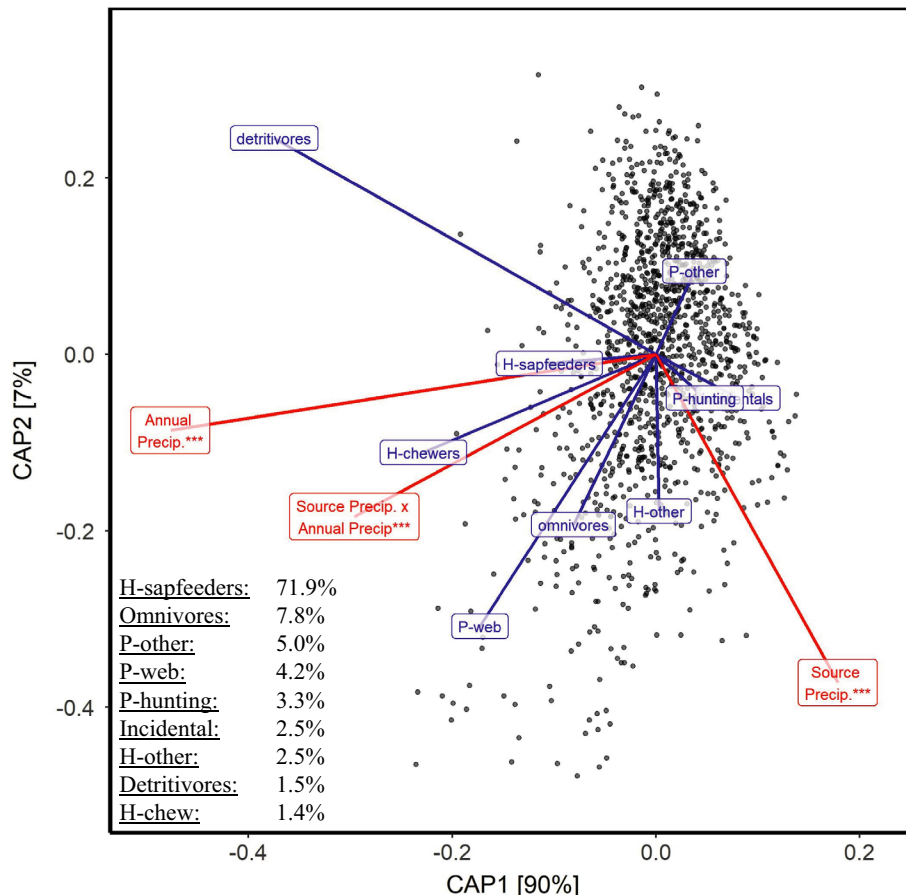

Fig. 3. Distance-based redundancy analysis (db-RDA) ordinations based on Bray-Curtis dissimilarities in ln-transformed abundance of *Artemisia californica* arthropod feeding guilds. Ordinations are constrained by climate factors (population source site precipitation, annual precipitation, and their interaction), 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.

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. 4d).

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
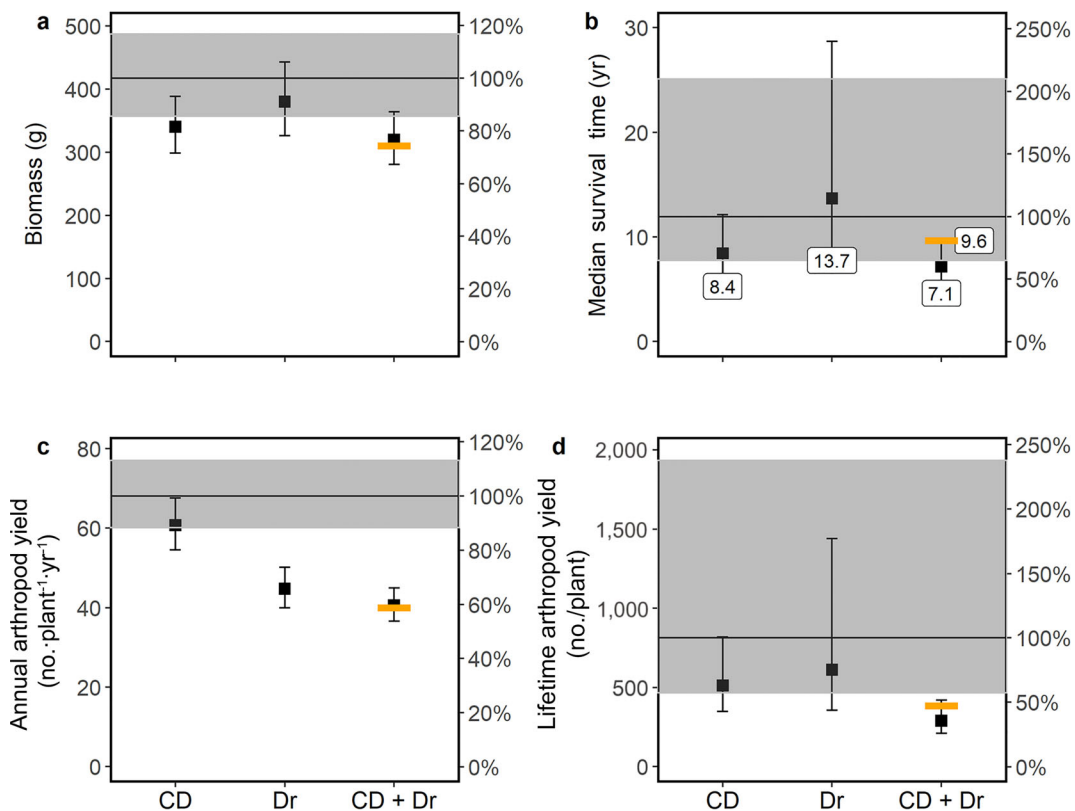

FIG. 4. The effects of 10 cm of climatic displacement, drought, and both climatic displacement and drought on (a) plant biomass, (b) plant median survival time (calculated from the annual survival rate), (c) annual arthropod yield, and (d) lifetime arthropod yield. The black horizontal line indicates 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 ± SE are plotted for each scenario. The narrow orange horizontal line indicates predicted interactive effects based upon a multiplicative risk model (Soluk and Collins, 1988; see Sih et al. [1998] for details). Asterisks indicate * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

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 percent nitrogen, specific leaf area, and percent 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 S4: Fig. S1). 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 and 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 interannual 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 intraspecific 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 bidirectional. 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 (Price 1991, Cornelissen et al. 2008). 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 and 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 percent 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 S3: Table S1), 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 S1: Fig. S2). 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 yr for a temperate forest ecosystem, whereas Lister and Garcia (2018) reported a 10-60 times reduction in arthropod biomass over 35 yr for a tropical forest. Moreover, synchronous declines in insectivorous birds and reptiles occurred over the same time period (Lister and Garcia 2018; but see Lister and Garcia 2019, 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 yr vs. additive prediction of 9.6 yr; Fig. 4b) and lifetime 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.

LITERATURE CITED

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., 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. https://doi.org/10.1002/9781118445112.stat07841

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.

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.

Bates, D., et al. 2021. lme4: linear mixed-effects models using "Eigen" and S4. https://cran.rproject.org/web/packages/lme4/index.html

Bowler, P. A. 2000. Ecological restoration of coastal sage scrub and its potential role in habitat conservation plans. Environmental Management 26:S85–S96.

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.

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.

Croy, J., J. Pratt, D. Sheng, and K. Mooney. 2021. Climatic displacement exacerbates the negative impact of drought on plant performance and associated arthropod abundance. Dryad, data set. https://doi.org/10.7280/D1CT2R

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 USA 112:3931–3936.

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.

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, The Netherlands.

Fox, J., et al. 2021. car: companion to applied regression. https://cran.r-project.org/web/packages/car/index.html

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.

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.

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.

Hallmann, C. A., et al. 2017. More than 75 percent decline over 27 years in total flying insect biomass in protected areas. PLoS ONE 12:e0185809.

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.

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.

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.

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., 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 129:271–280.

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 USA 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 USA 116:12145–12146.

Lüdecke, D., F. Aust, S. Crawley, and M. S. Ben-Shachar. 2021. ggeffects: create tidy data frames of marginal effects for "ggplot" from model outputs. https://cran.rproject.org/web/packages/ggeffects/index.html

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.

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. https://doi.org/10.1093/jue/juy003

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.

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:e0185539.

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

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., et al. 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., et al. 2014. Topic 2: Future climate changes, risks, and impacts. In R. K. Pachauri and L. Meyer, editors. 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. IPCC, Geneva, Switzerland.

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

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.

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 62:244.

PRISM Climate Group. 2020. PRISM gridded climate data. http://www.prism.oregonstate.edu/

R Development Core Team. 2021. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. www.R-project.org

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.

Rosenberg, K. V., et al. 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.

Sawyer, J. O., T. Keeler-Wolf, and J. M. Evens. 2009. A manual of California vegetation. California Native Plant Society, Sacramento, California, USA.

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 USA 115:2413–2418.

Siepielski, A. M., et al. 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.

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. American Naturalist 179:363–374.

Soluk, D. A., and N. C. Collins. 1988. Synergistic interactions between fish and stoneflies: facilitation and interference among stream predators. Oikos 52:94–100.

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

Stuart-Haëntjens, E., et al. 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.

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.

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.

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.

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. 2010. Integrating environmental and genetic effects to predict responses of tree populations to climate. Ecological Applications 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.

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 USA 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 USA 116:12143–12144.

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

Wright, I. J., et al. 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.

Supporting Information

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