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Invasive species interact with climatic variability to reduce success of natives

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Abstract

Plants have evolved resource-conservative and resource-acquisitive strategies to deal with variability in rainfall, but interactions with dominant invasive species may undermine these adaptations. To investigate the relative effect of invaders on species with these two strategies, we manipulated rainfall and invasive grass presence and measured demographic rates in three resource-acquisitive and three resource-conservative native annual forbs. We found that invasive grasses were harmful to all of the target species, but especially the resource-acquisitive ones, and that these effects were stronger under experimental drought. Invasive grass presence under drought lowered per capita population growth rates of acquisitive natives through increased mortality and decreased seed set. While invasive grasses also decreased per capita growth rates of resource conservative natives, they did so by increasing mortality under experimental watering and by limiting the production of seed under experimental drought. Invasive species can thus interact with climatic fluctuations to make bad years worse for resource-acquisitive natives and good years less good for resource-conservative natives, and they may generally tend to undermine the acquisitive strategy more than the conservative one.

Key words: invasive species, climate change, drought, drought tolerance, annual grassland, water use efficiency, relative growth rate

Introduction

Precipitation variability is expected to increase with climate change (IPCC 2013, Berg and Hall 2015, Swain et al. 2016) and although plants have evolved strategies to deal with inconsistent rainfall in variable environments, interactions with novel competitors have the ability to magnify the effects of climate and undermine the success of those strategies (Bruno 2005, Tylianakis et al. 2008). These novel interactions can make previously inhabitable environments less suitable for native plants as they try to cope with the multiple stressors of invasive dominance and climate change (Rinnan 2018). Thus invasive species may be contributing to a mounting "extinction debt" (Gilbert and Levine 2013), leading to extinction in the long term by weakening the ability of native species to deal with a changing or increasingly variable climate.

Although there is no consensus on whether changes in precipitation will favor or disfavor invasives (van Kleunen et al. 2010, Bradley et al. 2010, Sandel and Dangremond 2012), extreme events and other metrics of global change will likely exacerbate their spread (Bradley et al. 2010, Jimenez et al. 2011, Diez et al. 2012). Invasive plants, many of which display both faster resource acquisition and more efficient resource conservation than natives (Leishman et al. 2007, van Kleunen et al. 2010), can be competitively dominant under both favorable and unfavorable conditions (Suttle et al. 2007, Prevéy and Seastedt 2014). For instance, although annual invasives have been shown to respond more negatively than natives to low-resource conditions (Copeland et al. 2016, LaForgia et al. 2018, Valliere et al. 2019, Puritty et al. 2019), invaders still exhibit greater biomass than natives under these conditions (Valliere et al. 2019) and rebound more strongly following unfavorable periods (Kane et al. 2011, Puritty et al. 2019). Thus, even with more variable precipitation, they may continue to dominate over natives.

Similar to other functional groups, annual plants manifest life-history tradeoffs between the capacity for rapid growth under favorable conditions and the ability to maintain growth under unfavorable conditions (Brown and Venable 1986, Angert et al. 2007, Díaz et al. 2016). Although all annuals exhibit a fast-growing, resource-acquisitive strategy when compared to longer-lived species (Volaire 2017), there is also strong evidence that annuals exhibit an acquisitive-conservative tradeoff with respect to rainfall variability (Angert et al. 2007, Huxman et al. 2008). *Acquisitive* annuals are less drought-tolerant and can avoid seasonal drought by growing and reproducing quickly; they also avoid dry years through a high capacity for facultative seed dormancy. *Conservative* annuals are more drought-tolerant and grow more slowly to develop hardier leaves; compared with acquisitive species, they show lower facultative multiyear seed dormancy (Brown and Venable 1986, Huang et al. 2016). Acquisitive annuals typically have traits associated with faster-growing species such as high specific leaf area (SLA; leaf area/mass), low water use efficiency, and high relative growth rate, while conservative annuals tend towards the opposite trait values (Reich et al. 1997, Wright et al. 2004, Diaz et al. 2004, Angert et al. 2007). These strategies and their corresponding functional traits are clearly linked to species' relative competitive abilities (Godoy and Levine 2014, Funk and Wolf 2016) as well as climatic responses (Kimball et al. 2016, LaForgia et al. 2018). In temporally variable systems, acquisitives excel at competing for resources during wet years due to their faster growth rates, while conservatives are better at growing during dry years due to higher water use efficiency (Angert et al. 2009, Kimball et al. 2012, Gremer et al. 2013). How novel invasive species affect the abilities of native annuals with these two strategies to persist in variable environments remains uncertain, however.

Invaders can alter the benefits of the two strategies in various ways. For instance, a drying climate might generally favor conservatives (Penuelas et al. 2007, Báez et al. 2012, Hoover et al. 2014), but in wet years, competition from invaders with higher relative growth rates might reduce the benefit of additional water (Suttle et al. 2007), making this strategy less viable in wetter years due to the higher competition. Likewise, while acquisitives may be more capable than conservatives at competing with fast-growing invaders under wet conditions, they are likely to be more negatively affected by competition in general due to their sensitivity to variation in resources (Huxman et al. 2008, Angert et al. 2010). Further, when water is limiting, invaders might intensify the negative effects of drought on acquisitives (Gremer et al. 2013). In this way, interactions with invaders can make good years less good, and/or bad years even worse, with invaders being especially harmful under drought when resources are already low and even worse for species with the fast-growing, resource acquisitive strategy.

In Californian annual grasslands, native annual forbs exist at relatively low densities in a matrix of abundant and competitively dominant invasive annual grasses. At our annual grassland study site in northern California, we have observed significant changes in the plant community in response to winter rainfall. Native annual forb diversity has declined since 2000 as a result of elevated seedling mortality caused by drier winters (Harrison et al. 2015, 2017, Harrison and LaForgia 2019). This decline has been driven by the selective loss of resource-acquisitive, high-SLA forbs (Harrison et al. 2015). While similar declines also may have occurred in the past, it is alternatively possible that the arrival of invasive annual grasses since the early 19th century has reduced the resilience of native forb populations to environmental fluctuations. During the extreme drought of 2012-2014, native annual forb abundance in the seed bank increased while dominant invasive annual grasses decreased substantially both in cover aboveground and in seed abundance in the seed bank (Copeland et al. 2016, LaForgia et al. 2018), suggesting that forbs benefitted from reduced grass competition during the drought. The benefit was not distributed equally, however: while all forbs increased in abundance in the seed bank, putatively drought-tolerant low-SLA species increased more than twice as much as high-SLA species, suggesting that the strength of these interactive effects varied by resource acquisition strategy (LaForgia et al. 2018).

This study had two overarching objectives: (1) to assess whether invasive grasses affected six native annual forbs more negatively under wet or dry conditions and (2) whether the effects of invaders differed between three early-flowering acquisitive natives and three later-flowering conservative natives. We predicted that (1) the overall impact of invasive grasses would be stronger under drought conditions and that, (2) the response of acquisitives and conservatives to invaders would depend on water supply. Specifically, we expected that (2a) acquisitives would be more negatively affected than conservatives by invasive grasses, because of their dependence on abundant resources and fast growth, and that for the same reason, (2b) acquisitives would be especially affected by invasive grasses under dry conditions, which (2c) would be less true for conservatives. We tested these predictions by estimating population growth rates of the six native species in a fully factorial experiment with contrasting levels of water availability and invasive grass presence. To examine the demographic mechanism(s) responsible for changes in population growth rates, we also analyzed the treatment responses of individual vital rates.

Methods

Field Site

Our field site was the University of California McLaughlin Natural Reserve (https://naturalreserves.ucdavis.edu/mclaughlin-reserve) in the Inner North Coast Range (N 38°52’, W 122°26’). The climate is Mediterranean with cool wet winters, hot dry summers, and high interannual rainfall variability (1987-2017: mean 732 mm, range 326-1427 mm). Plant biomass in this community is dominated by Eurasian annual grasses with a smaller component of native and invasive annual forbs that germinate in the fall (Oct-Dec) shortly after rains begin, are present as seedlings during the winter (Dec-Feb), and flower in the spring (Mar-May) or summer (Jun-Sep).

Grasslands at this site are heterogeneous, including rocky serpentine outcrops with sparse grass, and nonserpentine soils with denser grass and few native species. For our experiment we selected a site with deep and fine-textured serpentine-derived soils, which support a diverse mix of native annual forbs in a matrix of invasive annual grasses (*Avena fatua, A. barbata, Bromus hordeaceus, B. madritensis, Elymus caput-medusae, Festuca perennis)*.

Watering and grass manipulations

The experiment was conducted over two growing seasons (2015-2016, 2016-2017). In spring 2015, we established 30 plots each assigned to one of three treatments: watered, drought, and control. The 10 watered plots were established along three watering lines emanating from a rainfall catchment system with each plot centered on a sprinkler that cast water over a 3-m radius (Mini Rotor Drip Emitters, Olson Irrigation, Santee, CA, USA). From 1 Dec - 1 Mar 2016 and 2017, at the end of any week in which rainfall fell below its 30-year average for the week, sprinklers operated for enough hours to bring natural plus supplemental rainfall up to the 30-year weekly average. Natural rainfall was reported by the Knoxville Creek weather station of the Western Regional Climate Center (www.wrcc.dri.edu/cgi-bin/rawMAIN.pl?caCKNO), near the center of the reserve. Supplemental rainfall was estimated by hours of watering times the measured application rate of 25 mm h^{-1}.

The 10 drought plots were set up with 3 x 3 m shelters constructed following the design of DroughtNet (wp.natsci.colostate.edu/droughtnet) except that the removable roofs intercepted 100% of rainfall. Roofs were placed on the shelters from approximately 1 Dec to 1 Mar 2016 and 2017 to reduce rainfall in winter, when roughly 60% of annual precipitation occurs. Natural rainfall during the 2015-2016 year was close to average at 701.26 mm while the 2016-2017 year was one the wettest years recorded in California, with rainfall at our site totaling 1297.87 mm. In

2015-2016, shelters reduced shallow soil moisture (3.8 cm) by 37.7% ($p = 0.004$) and reduced deep soil moisture (12 cm) by 21.0% ($p = 0.051$). In 2016-2017, shelters were not effective in reducing soil moisture due to the high rainfall, so we focus our analysis on drought effects in 2015-2016 and watering effects in both years. The remaining ten control plots were unmanipulated, allowing ambient levels of rainfall. All plots were > 4 m apart. In 2016, three plots were destroyed due to gopher burrow damage, remaining replicates were as follows: 2016 – 8 drought, 9 control, 10 watered; 2017 – 10 control, 10 watered.

Within each plot, we nested two 30 x 30 cm subplots, invasive grass removal ("no grass") and invasive grass presence ("grass"), to understand how dense invasive grasses affect the demographic responses of acquisitive and conservative native annuals to variation in water supply. Monthly throughout the growing season, the no grass subplot was weeded of all background species to estimate demographic rates of our focal forbs in the absence of grasses. In the grass subplot, only non-focal forb species were weeded, allowing the grasses to germinate and grow naturally. Mean grass cover in the grass control subplot was 60.7 +/- 3.9%; however, two of the 60 subplots had <10% grass cover and were removed from the analysis. Watering treatments had no effect on grass cover (control: 59.4 +/- 6%; drought: 59.3 +/- 9.7%; watered: 62.3 +/- 6.2%).

Demographic data collection

Within each subplot, we added six native annual forbs and measured their germination, mortality, seed set, and belowground seed survival to estimate each species' per capita population growth rates. We chose a set of prevalent forbs that spanned a wide range of SLA values and appeared to represent the range of resource acquisition strategies in the local forb community (Table 1). For the 2015-2016 year, species included *Agoseris heterophylla*, *Clarkia* *purpurea*, *Lasthenia californica*, *Plantago erecta*, and *Hemizonia congesta*. During the 2016-2017 year, we added *Calycadenia pauciflora*.

In the fall of 2015 and 2016, just before the first significant rainfall event, aboveground vegetation from both subplots was clipped to improve sowing success and 50 - 100 seeds of each species were sown into each subplot. Germination was scored in late fall prior to thinning all subplots to ≤ 20 individuals per focal species. Upon germination, individuals were marked and monitored 1-2 times per month for mortality. Unless fewer survived, flowers were counted on 5 individuals per species and seeds were counted on up to 30 flowers per species in each subplot; these means were multiplied to obtain a subplot-level estimate of seed set per individual.

To measure belowground seed survival, we buried one mesh bag per species filled with 50-100 seeds mixed with sand, 5-10 cm belowground in each plot prior to the onset of fall rains. We dug up the bags the following summer and counted the number of viable seeds by inspecting embryos under a dissecting scope. Measuring seed survival in this manner assumes that annual survival rates do not change with seed age, so that seed bank longevity is approximately exponential. To adjust the number of viable seeds in our estimates of germination rates, seed set, and belowground seed survival, seeds were tested for viability by monitoring germination in a growth chamber and inspecting embryos under a dissecting scope.

Resource Acquisition Strategy Assessment

To characterize the resource acquisition strategies of our species, we measured relative growth rate (RGR) and water use efficiency (WUE), two key performance measures that are correlated with widely studied morphological traits (SLA, seed size, and specific root length) (Reich et al. 1998, Westoby et al. 2002, Angert et al. 2009, Harrison and LaForgia 2019) and that have been strongly linked to demographic rate changes in other annual systems (Angert et al.

2007, Kimball et al. 2012). To quantify RGR, we monitored total leaf area accumulation over the 2016-2017 growing season. Two individuals per species were tagged just after germination in the field to measure RGR under natural conditions with ample rainfall, as is typical when investigating interspecific trait variation (Cornelissen et al. 2003). Leaves were counted monthly, their sizes were recorded as small, average, or large, and the length and width of a leaf representative of each size class was measured. From this we calculated total leaf area and parameterized standard models describing leaf area accumulation over time (Paine et al. 2012). Although our sample size for RGR was low, the subsequent resource acquisition strategies identified were consistent with those obtained from SLA (Table 1) and greenhouse-based measures (Appendix S1: Fig. S1). To quantify WUE, we measured leaf carbon isotope discrimination (Dawson et al. 2002). Just before peak flowering, young but fully mature leaves from five individuals per species were collected from the field, dried, ground, and analyzed at the UC Davis Stable Isotope Facility (https://stableisotopefacility.ucdavis.edu/). Carbon isotope delta values were converted to discrimination (Δ, $^{0}/_{00}$) by the equation:

$$\Delta = (\delta a - \delta p)/(1 + \delta p/1000)$$

(Farquhar et al. 1989) where δa is the carbon isotope ratio of CO2 in the atmosphere (-8 ppm, $^{0}/_{00}$) and δp is the measured relative delta value of carbon isotope found in leaf tissue. Lower Δ indicates higher integrated WUE (Farquhar et al. 1989, Seibt et al. 2008).

The six species showed the standard strong tradeoff between growth and water efficiency, with *L. californica*, *A. heterophylla*, and *P. erecta* displaying the high RGR and low WUE typical of resource acquisitives, and *C. purpurea*, *C. pauciflora*, and *H. congesta* displaying the low RGR and high WUE typical of resource conservatives (Fig. 1). The strategies identified here were used in subsequent analyses. In this system, these contrasting strategies are also associated with phenological differences, with the three acquisitives flowering in mid-spring and the three conservatives flowering in late spring to summer (i.e. they belong to the groups sometimes referred to in the Californian grassland literature as spring and summer annuals, or cold- and warm-season annuals; Dyer and Rice 1999, Hooper and Dukes 2010).

Analyses

We used per capita population growth rate (λ) as our integrative measure of native annual forb responses to watering and grass manipulations across the full life cycle. We calculated species-level λ in each subplot using the following annual plant model, adapted from Levine et al. (2008):

$$\lambda = s(1 - g) + g(1 - m)F$$

where s is the annual seed survival rate, g is the proportion of germinated seeds, m is the mortality rate, and F is the seed set, or the number of viable seeds produced per survived germinant. The first term describes the contribution of the seed bank to the annual per capita growth rate while the second term is the per-seed production of germinated individuals. With the exception of seed survival, which was measured at the plot level (i.e. watering treatment), all parameters were measured at the subplot level (i.e. grass treatment). In cases where an individual parameter value was missing in our calculation of λ, we used the species-level average value.

To test how the overall effects of invasive grass on natives varied by watering treatment (Question 1), we investigated changes in λ using linear mixed effect models with subplot-level λ for each species as the response variable, and watering treatment (watered, drought, and control), grass treatment (grass, no grass), and their interaction as predictors. This model, as well as all subsequent models, included a random intercept for species nested within plot within year. To test whether the effects of grass were stronger for acquisitives than conservatives (2a), we used grass treatment, resource acquisition strategy (acquisitive, conservative), and their interaction as predictors. Finally, to test whether the responses were stronger under drought for acquisitives (2b) and less so for conservatives (2c), we modeled λ as a function of watering treatment, grass treatment, resource acquisition strategy, and all interactions as predictors. Values of λ were log-transformed after adding a small constant to meet model assumptions.

To understand how changes in individual vital rates contributed to changes in λ, we tested how watering and grass manipulations affected mortality and seed set, the two transition rates directly affected by our grass treatments. For mortality, we used generalized linear mixed effect models with a binomial response variable reflecting success (number dead) and failures (number survived). We included watering treatment, grass treatment, resource acquisition strategy, and all interactions as predictors. For seed set, we log-transformed values after adding a small constant to meet model assumptions. These values were modeled with watering treatment, grass treatment, resource acquisition strategy, and all two-way interactions as predictors. Three-way interactions were considered but excluded through model comparison using AIC. We did not analyze treatment effects on germination because grasses were absent at the initiation of the study and watering treatments did not begin until after germination.

All data analyses were done in R version 3.4.4 (R Core Team 2018) using the lme4 package (Bates et al. 2015). For each analysis, we conducted multiple comparison tests using the glht function in the multcomp package (Hothorn et al. 2008) to test our hypotheses. We adjusted *p*-values using Benjamini–Hochberg corrections to account for multiple comparisons (Benjamini and Hochberg 1995).

Results

Overall effects of competition and water supply on λ in natives

As predicted, per capita population growth rates of native annual forbs declined the most in the presence of invasive grass under drought (Appendix S1: Fig. S2). Grass lowered λ for native forbs in controls by 42.8% ($p < 0.001$), but the interaction of drought and invasive grass had a significantly stronger effect, reducing λ by 59.7% ($p = 0.003$). There was no interactive effect of watering and grass on λ.

Differential effects of competition and water supply on λ in resource acquisitive and resource conservative natives

We found marginal support for our prediction that grass has a stronger overall effect on acquisitive λ than on conservative λ (Appendix S1: Fig. S3). While grass decreased acquisitive λ by 45.4% ($p < 0.001$), grass had a marginally smaller effect on conservative λ, causing declines of only 31.3% ($p = 0.053$).

The effects of grass on acquisitive and conservative λ also varied by watering treatment (Fig. 2; Appendix S1: Table S2). As predicted, acquisitive λ was more negatively affected by grass in the drought treatment than by grass in the increased watering treatment. Acquisitive λ declined by 68.4% in the presence of grass under drought compared to drought alone ($p < 0.001$). While acquisitive λ also declined in the presence of grass under watering compared to watering alone, this effect of smaller (-33.7%, $p < 0.001$) and did not differ from the effect of grass in the control treatment ($p = 0.586$). In contrast, as predicted, grass under the drought treatment had a smaller effect on conservative λ (-42.4%, $p = 0.002$). Grass also eliminated ($p = 0.586$) the positive effect (75%; $p = 0.030$) of the watering treatment on conservative λ. Surprisingly, the drought treatment in the absence of grass increased conservative λ (60%, $p = 0.037$).

Effects of competition and climate on individual vital rates in acquisitives and conservatives

In acquisitives, changes in both mortality (Fig. 3; Appendix S1: Table S3) and seed set

(Fig. 4; Appendix S1: Table S4) drove the response of λ to grass under drought. Acquisitive mortality increased by 34.1% ($p = 0.004$) in the presence of grass under drought compared to mortality in drought alone. Changes in seed set reinforced these negative effects, with the presence of grass in the drought treatment decreasing acquisitive seed set by 63.2% ($p < 0.001$) compared to seed set in drought alone.

In conservatives, changes in mortality (Fig. 3; Appendix S1: Table S3) drove the response of λ to grass under watering, while changes in seed set (Fig. 4; Appendix S1: Table S4) drove the response of λ to grass under drought. Under increased watering, conservative mortality decreased by 36.2% ($p = 0.001$). The presence of invasive grasses reduced but did not eliminate this effect: in plots with both increased water and grass, mortality increased (41.0%; $p < 0.001$) compared to watering without grass, but mortality in the presence of watering and grass was still significantly lower than mortality in the control treatment with grass (-17.6%; $p = 0.043$). Under drought, conservative seed set increased by 50.0% ($p = 0.014$), but grass eliminated this effect ($p = 0.795$).

For germination and belowground seed survival of conservatives and acquisitives, see Appendix S1: Figures S4 and S5. For species-level effects of treatments on vital rates, see Appendix S1: Figures S6 through S10.

Discussion

In an era of increasing climatic variability, a critical emerging question is how the effects of a more erratic water supply on natural communities may be exacerbated by competitive pressure from invasive species. This study demonstrates that invasive grass species may interact with increasing rainfall variation to diminish the success of native annuals and shift the relative success of alternative plant resource acquisition strategies. We found that the detrimental effect of invasive grasses on per capita growth rates of native annual forbs worsened under experimental drought, especially for natives with the fast-growing, resource acquisitive strategy. These findings underscore that the long-term decline in native annuals with high specific leaf area, i.e., acquisitives, that has been observed in this study system (Harrison et al. 2015, 2017) is likely neither a normal fluctuation nor strictly a consequence of a drier climate. Instead, intense competition from invasive grasses during dry conditions is likely exacerbating the decline of these drought-intolerant species. Under wetter conditions, we found conservatives but not acquisitives to be strongly affected by grass competition. Similarly, in Sonoran Desert annuals, competition from a fast-growing species under high water availability had the greatest negative effect on a slow-growing species (Gremer et al. 2013). Together, our results corroborate that although the native annuals in our study system are adapted to climate variability, competition with invasive grasses reduces their resilience, particularly by limiting the abilities of acquisitives to withstand bad years.

Vital rates driving changes in per capita growth rates varied by resource acquisition strategy and by treatment. Grass competition intensified the negative effects of drought on acquisitives by increasing mortality and lowering seed set, again consistent with results in Sonoran Desert annuals (Gremer et al. 2013). Though both drought-induced mortality (Nepstad et al. 2007, Michaelian et al. 2011, Harrison et al. 2017, Young et al. 2017) and lower seed set in the presence of competitors (Goldberg et al. 2001, MacDougall and Turkington 2005, Latimer and Jacobs 2012) are well-documented, support for competition-induced mortality is less common (Goldberg et al. 2001, Thomson et al. 2018, but see Thomson et al. 2017). For conservatives, grass competition depressed per capita population growth rates by increasing mortality under added water as well as by limiting gains in seed set under drought. Though our finding of higher conservative seed set (and thus higher per capita population growth rates) under our drought treatment is seemingly anomalous, it is in line with previous findings of an increase in abundance of low-SLA (i.e., conservative) forbs during the extreme drought of 2014 when grass cover was low (Copeland et al. 2016, LaForgia et al. 2018). Novel competition and its interaction with climate thus have detrimental effects on both strategies, but with stronger negative effects on acquisitives in dry years by driving mortality and limiting seed set.

As is often the case among annual species, our three high-RGR, low-WUE acquisitive species complete their life cycles relatively early in the season when shallow soil water availability is still high, which is one aspect of their fast-growing and resource-acquisitive strategy. Phenology may well have contributed to our findings, since the early-season acquisitive species flower at a time when invasive annual grasses are still growing, whereas the later-season conservative species flower when grasses have matured and begun to senesce. Since the invasive grasses in our system and many invasive species in other systems tend to have a resource-acquisitive strategy, this greater phenological overlap with invasives may be a general reason for resource-acquisitive species to be more vulnerable than resource-conservative ones to the combination of invasions and resource fluctuations.

The values of λ we obtained were high in absolute terms, possibly due to a number of reasons. First, we did not measure seed removal rates by granivores, which are likely to be high but also extremely variable (Hobbs 1985, Schiffman 2007) and which we assumed would be little affected by our treatments. Additionally, we avoided the complications of density dependence by keeping focal plant densities relatively low, likely also contributing to high λ values. We also did not examine the effects of grass litter on forbs, an important time-delayed factor in this system known to depress germination and seed set (Wainwright et al. 2017, Chen et al. 2018). We believe added litter would have decreased λ across species, but with stronger effects on acquisitives (LaForgia, *unpublished data*), thereby likely reinforcing our present findings. Finally, while we designed our climate manipulations to match prior observations and results in our study system (Harrison et al. 2015, 2017, LaForgia et al. 2018), we acknowledge that our results would likely differ under differently-timed climatic manipulations (Levine et al. 2008, Thomson et al. 2017). Subject to these caveats, the qualitative changes in per capita growth rates we found demonstrate that rainfall and invasive grasses exert powerful interactive effects on the success of these natives with contrasting strategies.

Changes in precipitation will certainly affect invasive populations in addition to their co-occurring natives. Various studies have found these grasses to increase under high resource conditions and decrease under low resource conditions (Prevéy and Seastedt 2014, Copeland et al. 2016, Valliere et al. 2019, Puritty et al. 2019). Our study did not find any effects of either watering treatment on grass cover, possibly because of its short duration and moderate intensity of watering treatments. Invasive annual grasses have been shown to be competitively superior over natives regardless of water availability (Leishman et al. 2007, van Kleunen et al. 2010, Valliere et al. 2019), and to maintain their dominance despite observed declines under drought (Valliere et al. 2019, Winkler et al. 2019, Puritty et al. 2019). While unexpected, this aspect of our study allowed us to examine the relative vulnerabilities of acquisitive and conservative native species without the additional influence of treatment-driven variation in invasive grass abundance.

Before the arrival of invasive grasses, the alternative resource strategies we examined here allowed native annuals to persist and coexist in a highly variable climate, with acquisitive species more dependent than conservative ones on producing abundant seed in wet years and surviving drought years through high seed dormancy. The arrival of competitively dominant invasive grasses appears to have altered the effectiveness of these life histories such that acquisitive species are now at a disadvantage compared with conservative ones. The combined effects of intermittent droughts and competition from invasives may thus be expected to produce a downward trend in the abundance of acquisitives relative to conservatives, albeit with considerable interannual variability; such a long-term trend is already evident at our study site (Harrison et al. 2015, 2017). Our findings suggest a possible mechanism for a novel form of extinction debt, similar to other mechanisms that have been identified based on climate (Dullinger et al. 2012, Urban 2015) and invasion (Seabloom et al. 2006, Sax and Gaines 2008); in this case, the combination of invasive species pressure and an increasingly erratic climate may lead to the gradual but inexorable loss of a formerly viable ecological strategy. Since the conservation-acquisition tradeoff is general among plants (Diaz et al. 2004, Reich 2014, Adler et al. 2014) and since the problems of invasion and climatic extremes are general across ecosystems (Douda et al. 2018, Rinnan 2018), our results may have significant implications beyond our study system.

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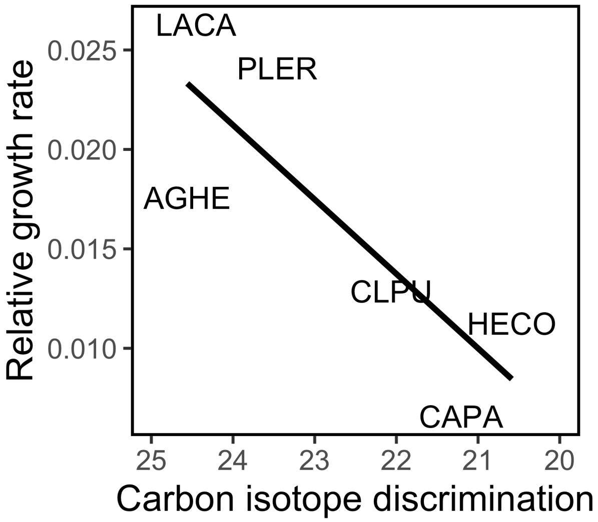
Table 1. Species used in the study along with their respective resource acquisition strategy and SLA (cm^2/g) as measured on 10 individuals in the field following standard protocols.

Species	Strategy	SLA
Agoseris heterophylla	Acquisitive	413.55
Lasthenia californica	Acquisitive	240.14
Plantago erecta	Acquisitive	130.66
Clarkia purpurea	Conservative	87.04
Hemizonia congesta	Conservative	64.05
Calycadenia pauciflora	Conservative	54.56

Figure Legends

1. Species displayed a strong negative trade-off between relative growth rate (leaf area accumulation/time; $cm \cdot cm^{-1} \cdot day^{-1}$) and intrinsic water use efficiency (carbon isotope discrimination; Δ, $^{0}/_{00}$), forming two distinct groups of acquisitives (*Agoseris heterophylla*, *Plantago erecta*, and *Lasthenia californica*) and conservatives (*Clarkia purpurea*, *Hemizonia congesta*, and *Calycadenia pauciflora*). Species abbreviations are the first two letters of the genus and specific epithet.
2. Per capita population growth rates (y-axis) of acquisitives and conservatives with and without grass (x-axis). Drought treatments are shown in red, watering treatments in blue, and control in grey. Error bars show the standard error. Treatment levels represent averages across both years of the study with the exception of drought, which was only applied in 2016.
3. Mortality rates (y-axis) of acquisitives and conservatives with and without grass (x-axis). Drought treatments are shown in red, watering treatments in blue, and control in grey. Error bars show the standard error. Treatment levels represent averages across both years of the study with the exception of drought, which was only applied in 2016.
4. Seed set (y-axis) of acquisitives and conservatives with and without grass (x-axis). Drought treatments are shown in red, watering treatments in blue, and control in grey. Error bars show the standard error. Treatment levels represent averages across both years of the study with the exception of drought, which was only applied in 2016.

Figure 1.


LACA
PLER
AGHE
CLPU
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CAPA
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Relative growth rate
25
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21
20
Carbon isotope discrimination

649 **Figure 2.**

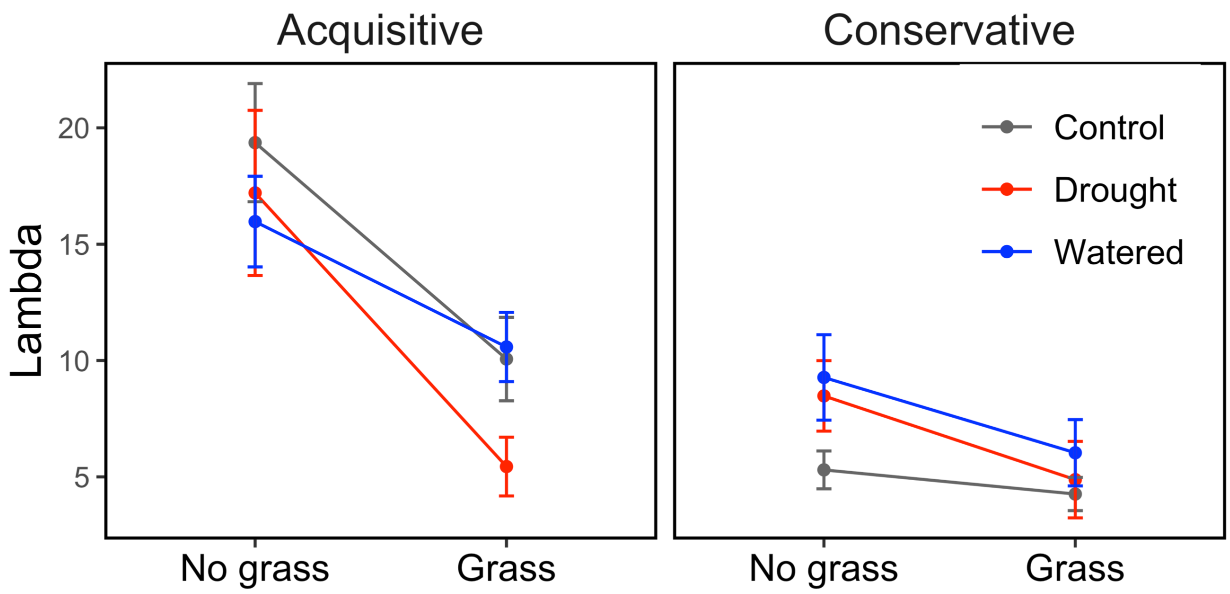

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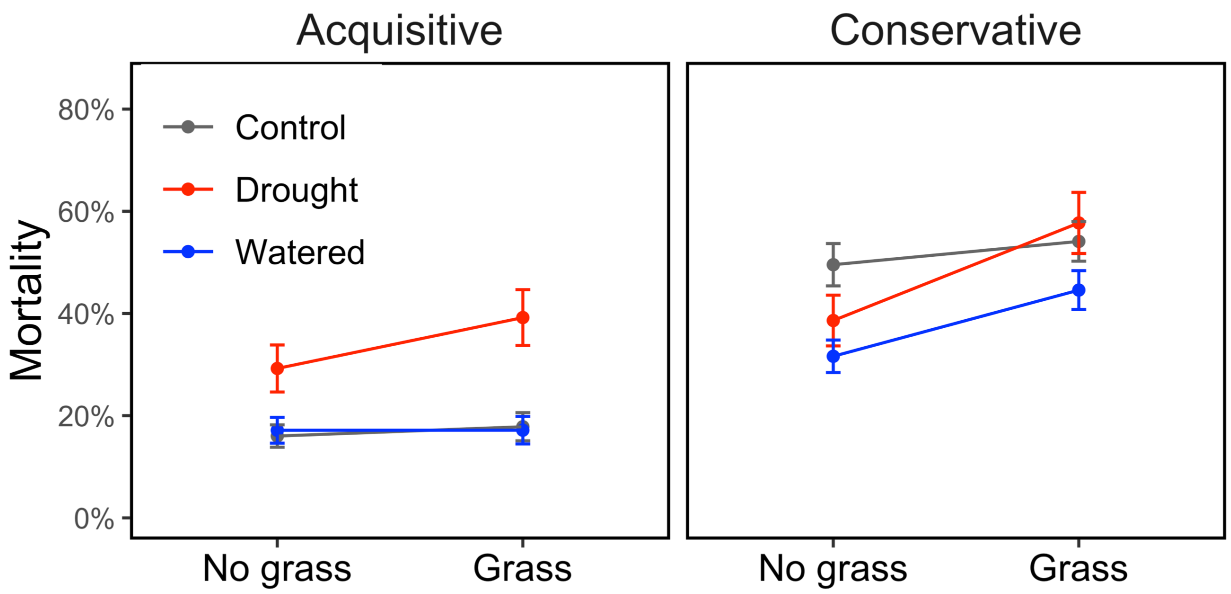
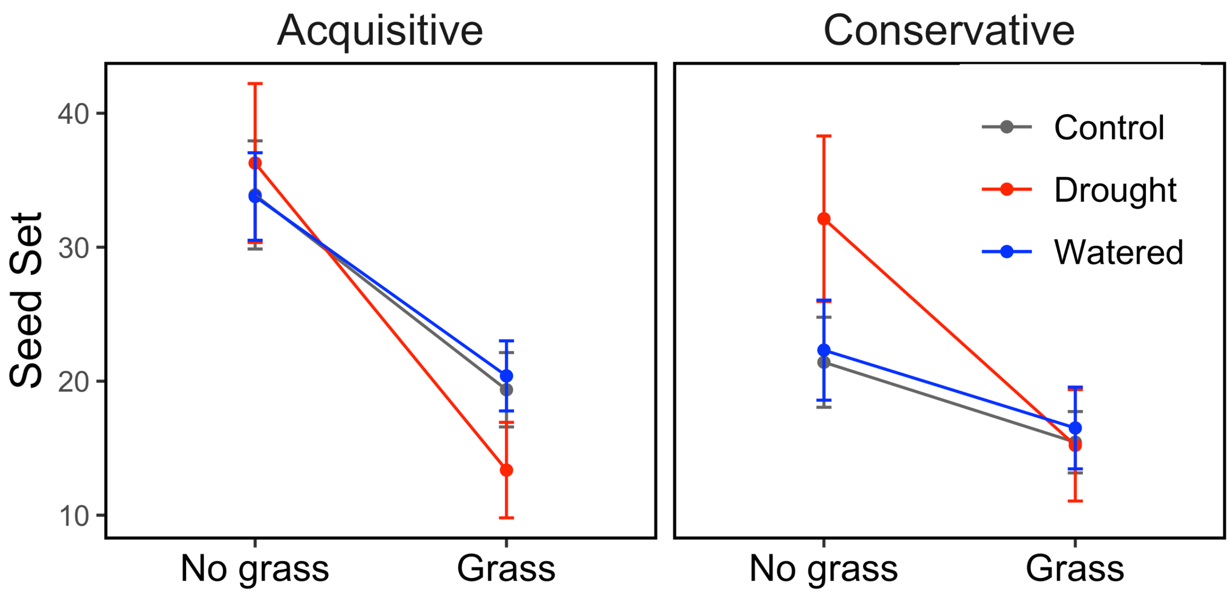
Figure 3.



Acquisitive
Conservative
Mortality
80%
60%
40%
20%
0%
Control
Drought
Watered
No grass
Grass
No grass
Grass

Figure 4.


Acquisitive
Conservative
Seed Set
40
30
20
10
No grass
Grass
No grass
Grass
Control
Drought
Watered