

LETTERS

The adaptive potential of plant populations in response to extreme climate events

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Abstract

The frequency and magnitude of extreme climate events are increasing with global change, yet we lack predictions and empirical evidence for the ability of wild populations to persist and adapt in response to these events. Here, we used Fisher's Fundamental Theorem of Natural Selection to evaluate the adaptive potential of *Lasthenia fremontii*, a herbaceous winter annual that is endemic to seasonally flooded wetlands in California, to alternative flooding regimes that occur during El Niño Southern Oscillation (ENSO) events. The results indicate that populations may exhibit greater adaptive potential in response to dry years than wet years, and that the relative performance of populations will change across climate scenarios. More generally, our findings show that extreme climate events can substantially change the potential for populations to adapt to climate change by modulating the expression of standing genetic variation and mean fitness.

Keywords

additive genetic variance, climate change, El Niño, extreme climate, Fisher's Fundamental Theorem of Natural Selection, *Lasthenia fremontii*, precipitation, vernal pools.

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INTRODUCTION

Several ecological responses of wild species to anthropogenic climate change have been documented over the last two decades (Parmesan 2006; Chen *et al.* 2011; Hoffmann & Sgro 2011; Becklin *et al.* 2016), including shifts in geographic ranges and phenology (Parmesan 2006; Fei *et al.* 2017). Substantial evidence indicates that these responses are often mediated by genetic and physiological constraints that exist within populations (Etterson & Shaw 2001; Norberg *et al.* 2012; Anderson 2016), underscoring the importance of evolutionary history in shaping species' responses to ongoing and future environmental change. Most recently, scientists have been evaluating the extent to which ongoing and future evolutionary change, such as rapid adaptation, can facilitate persistence in the face of global warming (Franks *et al.* 2007; Anderson *et al.* 2012; Gibbons *et al.* 2016). *In situ* evolution may be particularly important for organisms that cannot track their optimal climate conditions through space due to limited inherent dispersal abilities or extensive distances between habitat patches (Aitken *et al.* 2008; Angert *et al.* 2011; Schloss *et al.* 2012). While there is growing consensus that adaptive evolution can occur over very short time scales under persistent environmental change (e.g. one to several generations; Grant & Grant 2002; Hendry *et al.* 2018), the potential for adaptation to rescue populations that face an increasing frequency and magnitude of extreme climatic events, such as acute storms or drought events, has yet to be

investigated (Reyer *et al.* 2013; Grant *et al.* 2017; Kingsolver & Buckley 2017).

Genetic variation provides the raw material for evolution by natural selection, and thus the amount of genetic variation that is expressed under changing climate conditions is a key component of a population's adaptive potential (Fisher 1930; Shaw & Shaw 2014). Fisher's Fundamental Theorem of Natural Selection (hereafter FTNS) predicts that the rate of adaptation in a population is equal to the ratio of the additive genetic variance in fitness, $V_A(W)$, and mean fitness, \bar{W} , of a population while under selection (Fisher 1930; Ewens 1989; Shaw & Shaw 2014). The additive genetic variation in fitness that exists within a population is shaped by the history of gene flow, genetic drift and natural selection for traits that influence performance (Swindell & Bouzat 2005; Lopez *et al.* 2008; Shaw & Etterson 2012). However, the expression of this variation can vary with the environmental context (Hoffmann & Merila 1999; McGuigan & Sgro 2009; Sheth *et al.* 2018) and may change under stressful or novel conditions (Hoffmann & Parsons 1991; Schlichting 2008; Emery & Ackerly 2014). The denominator of the FTNS, the mean fitness of the population (\bar{W}), reflects the extent to which the environment is stressful or suitable for a population (Koehn & Bayne 1989; Imasheva *et al.* 1998). When $\bar{W} < 1$, each individual in the population is, on average, producing less than one offspring over its lifetime and population size would therefore be declining, indicating that the environmental conditions are relatively stressful (Hoffmann & Hercus 2000). On the other hand,

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when $\bar{W} > 1$, each individual is (on average) producing more than one offspring in its lifetime, and population size would be increasing (Hoffmann & Hercus 2000), suggesting that the current environment provides suitable conditions for the population. When all else is equal, the rate of adaptation will be greater when the environment is further from the population's optimum, that is, when \bar{W} is low. Thus, Fisher's theorem predicts that the increase in population mean fitness from one generation to the next will be positively associated with the amount of additive genetic variance in fitness expressed in the population, and inversely associated with the population's performance in the environment in which selection is occurring.

We evaluated the effects of extreme climatic events on the adaptive potential of populations by quantifying the effects of alternative flooding regimes on the mean and variance in post-germination reproductive success of *Lasthenia fremontii* (Madieae, Asteraceae) (Ornduff 1966), an annual herb that is endemic to vernal pool wetlands in the Central Valley of California (USA). California vernal pools are seasonal wetlands that develop in relatively shallow (~30 cm), naturally-occurring basins that are interspersed in groups throughout the valley grasslands, much like islands in archipelagoes (Holland & Jain 1981), and provide habitat for a number of endemic animals and plants (Holland & Jain 1981; Smith & Verrill 1998; Zedler 2003). The hydrological dynamics that define this habitat are driven by annual precipitation patterns, causing pools to fill with water during the rainy, cool winter season and dry during the hot, arid summers that characterise the Mediterranean climate of this region (Holland & Jain 1981; Smith & Verrill 1998; Bertassello *et al.* 2018a,b). Geographic variation in mean precipitation leads to differences in pool hydrological conditions across the geographic range of *L. fremontii* (Holland & Dains 1990; Stone 1990). Furthermore, pool hydrology varies drastically among growing seasons within a site due to inter-annual variation in the timing and amount of precipitation (Pyke 2004; Bauder 2005). This variation is particularly extreme when El Niño Southern Oscillation (ENSO) patterns develop along the Pacific Coast of North America, which cause exceptionally wet years followed by exceptionally dry years in the northern hemisphere (Cayan *et al.* 1999; Yoon *et al.* 2015; Wang *et al.* 2017). ENSO events generate drastic swings between growing seasons in the duration that vernal pools retain water, which could have strong effects on the post-germination fitness (Emery 2009; Emery & Ackerly 2014) and fine-scale distributions (Emery 2009) of *L. fremontii* and other vernal pool endemics (Javornik & Collinge 2016; Gosejohan *et al.* 2017).

We measured the effects of ENSO events on the adaptive potential of three different *L. fremontii* populations using a manipulative greenhouse experiment that incorporated a paternal half-sib (hereafter PHS) quantitative genetic crossing design (Falconer & McKay 1996; Lynch & Walsh 1998). We evaluated populations from the northern, central and southern portions of the species' geographic range (Fig. 1a). The PHS design makes it possible to estimate the amount of phenotypic variation that is due to additive genetic variation, which is the variation that is directly transferred from parents to offspring in sexually reproducing organisms (Lynch & Walsh 1998).

Quantitative genetic variance components often change with environmental context, and estimates obtained under greenhouse conditions usually differ from those that would be measured in the field (Conner *et al.* 2003; Anderson *et al.* 2013). However, conducting this experiment in the greenhouse made it possible for us to simultaneously impose three alternative annual flooding regimes across an entire generation of the focal species while standardising across other sources of environmental variation. The power of this approach is that it allows us to isolate how one specific variable – precipitation-dependent flooding regime – influences the adaptive potential of populations from geographically distant locations.

We tested the hypothesis that $V_A(W)$ would vary with environmental context without any *a priori* prediction for the direction of change (increase or decrease) under extreme vs. 'normal' conditions, as previous studies have shown that stress can either enhance (Hoffmann & Parsons 1991; Imasheva *et al.* 1998) or suppress (Blows & Sokolowski 1995; Charmantier & Garant 2005) the expression of additive genetic variation within populations. We also tested the hypothesis that geographic isolation among populations would have facilitated population differentiation and possibly local adaptation to the climate of each site. Based on these hypotheses, we predicted that $V_A(W)$ would vary among experimental hydroperiod treatments simulating extreme El Niño, Normal and La Niña conditions, and that populations would vary in their responses to hydroperiod treatments in patterns that are consistent with the historical climate regimes of their home sites.

MATERIAL AND METHODS

Generation of family-structured cohorts

We generated PHS families (see Fig. S1) from each of three *L. fremontii* populations to estimate the additive genetic variance in fitness under three experimental precipitation treatments. The three populations were collected from locations that span a latitudinal gradient in total annual precipitation that declines from north to south, which generates a corresponding gradient in the hydroperiod of vernal pools across the three sites (Fig. 1; Table S1). Our previous work described high levels of genetic differentiation at neutral loci between the northernmost and southernmost populations and moderate divergence between central and range-edge populations (Torres-Martínez & Emery 2016). Seeds were collected from the parental population at each field site in spring 2013, and an F₁ generation was raised to flower in the greenhouse. We generated 35–45 PHS families from each F₁ population, with at least nine full sibs produced per dam, by performing controlled hand pollinations in which a single sire was used to pollinate multiple unique dams (Fig. S1). Details of the greenhouse generations and crossing design are provided in the Supplemental Information (SI).

Hydroperiod experiment

We designed experimental flooding treatments using historical precipitation data to parameterise hydrological models that

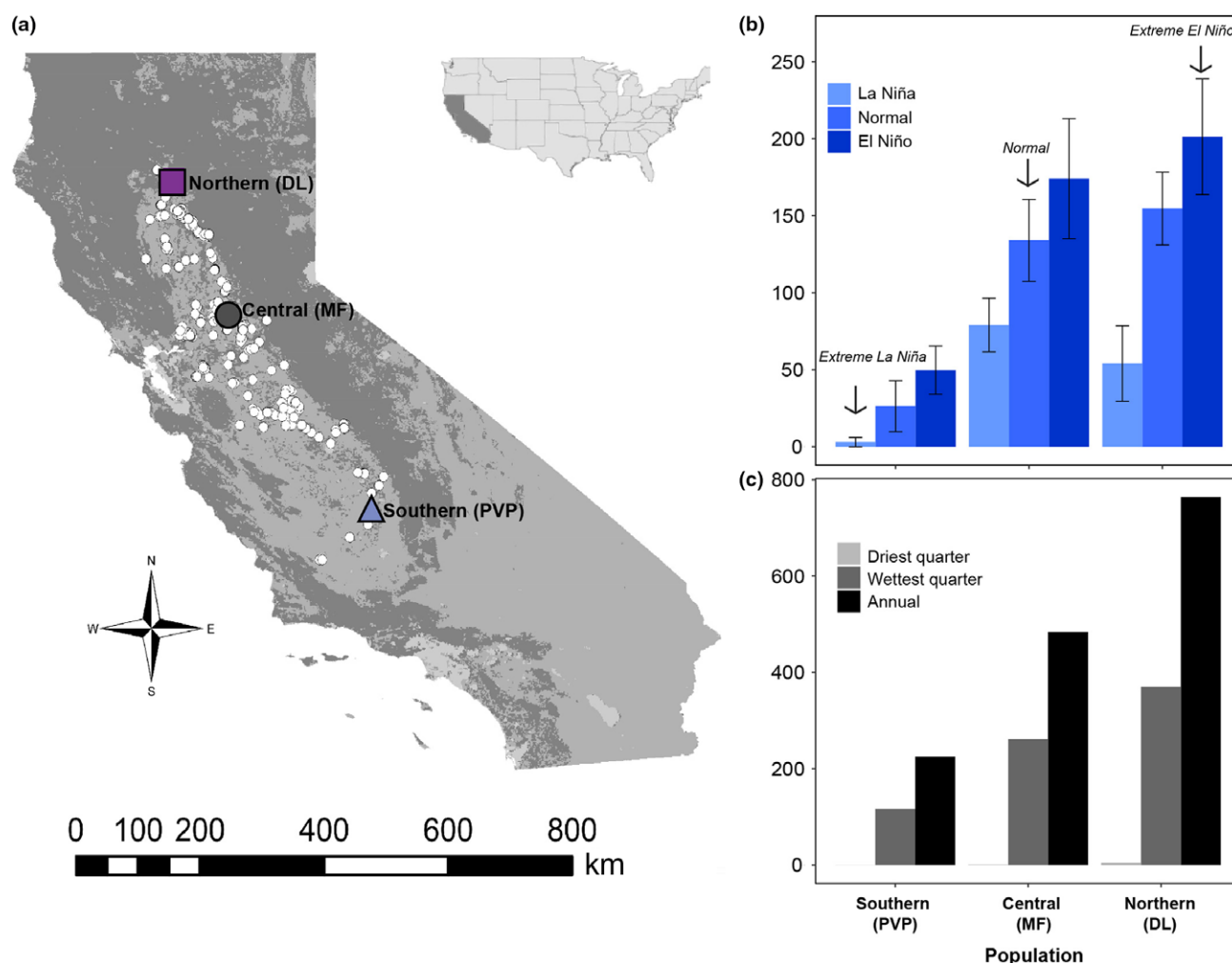


Figure 1 Experimental population source locations and historical precipitation conditions. (a) The geographic locations of the three *Lasthenia fremontii* populations in this study. The Southern population (PVP = Pixley Vernal Pool Preserve), the Central population (MF = Mather Field), the Northern population (DL = Dales Lake Ecological Reserve) in the Great Central Valley of California (USA). White circles identify other documented populations within the species' geographic range. (b) The predicted hydroperiods of vernal pools at each site under the precipitation levels of the most extreme El Niño and La Niña events recorded in the last 30 years, as well as the average of 3 years in which no ENSO was reported ('Normal'), using the NOAA MEI indices to parameterise a hydrological model for vernal pools (Supplementary Information, Tables S1 and S2). Error bars represent ± 1 SEM. Arrows identify the three flooding treatments that were simulated in the greenhouse experiment. (c) Annual historical precipitation data recorded at each site for the period 1950–2000; data extracted from Worldclim v1.4 (Hijmans *et al.* 2005).

predict vernal pool hydroperiod (Fig. 1b; see *Hydroperiod Treatment Design* in SI) (Wolter & Timlin 1998, 2011). Our treatments simulated the flooding regimes under (a) the highest precipitation event documented at any of the three sites during this time period (an El Niño season in the northernmost site), (b) the lowest precipitation event observed at any of the three sites (a La Niña event in the southernmost site) and (c) a 'Normal' wet season, estimated as the mean precipitation recorded in non-ENSO growing seasons at the central site (Fig. 1b, see Tables S3 and S4). We intentionally focused on the effects of flooding duration on post-germination reproductive success, excluding any variation that could arise due to differences in germination rates. Our previous work (Torres-Martínez *et al.* 2017) documented differences in seed dormancy and viability among *L. fremontii* populations, but this variation is expressed before plants become submerged, as

Lasthenia fremontii seeds germinate several weeks or months before pools flood each winter (Ornduff 1966; Emery *et al.* 2009). Our analysis of historical climate data found no correlation between the amount of precipitation that occurs during the germination period (November) and the amount of precipitation that occurs over the remainder of the growing season (December–April) and determines pool hydroperiod (see SI, Fig. S3), suggesting that germination variation should not have consistent effects on post-germination lifetime fitness under alternative hydroperiod conditions.

Nine full-sib seedlings from each PHS family were germinated under the same conditions as the F_1 generation (see SI, Fig. S1) and then transferred to the greenhouse and randomly assigned to a one of three hydroperiod treatments: La Niña, Normal or El Niño. This design allowed each PHS family to be represented three times in each treatment (Fig. S1).

Genotypes that did not have enough germinants to be represented at least one per experimental treatment were excluded from the experiment. Hydroperiod treatments were imposed by raising the water table 7 cm above the soil surface, completely submerging the experimental seedlings for 3, 134 or 201 days, representing the extreme La Niña, Normal or extreme El Niño treatments respectively (Table S4). At the end of the assigned flooding period, the water levels were slowly lowered over 5 weeks to simulate the gradual recession of the water table in vernal pools each spring (Table S4). Plants were hand-pollinated with randomly selected pollen donors as they flowered to generate viable seeds. Seed heads were harvested when seeds were visibly mature and nearing abscission, and then weighed to the nearest 0.001 mg using a microbalance. We used total infructescence weight as our estimate for fitness because it is significantly correlated with the total number of viable seeds produced by an individual (Table S2). Furthermore, we expect that total reproductive biomass covaries with both female (ovule) and male (pollen) potential reproductive success because *L. fremontii* has a composite inflorescence with perfect flowers.

Statistical analyses

Effects of hydroperiod on absolute and relative fitness

We evaluated the overall effects of hydroperiod treatment on plant fitness in each population using a mixed-model ANOVA with total infructescence biomass (our estimate of absolute fitness) as the response variable. Population and Hydroperiod treatment were considered fixed categorical effects, and the Population \times Hydroperiod interaction was included. The Sire of each experimental plant was included as a random effect and nested within Population, and Dam was nested within Sire. Infructescence biomass was $\log(x + 0.1)$ transformed prior to analysis to meet the assumptions of ANOVA. Upon observing a significant Population \times Hydroperiod Treatment interaction, we conducted *post hoc* comparisons among Populations within each Treatment to identify the specific pairwise comparisons that were statistically different from one another. We used the Tukey–Kramer method to control for multiple comparisons in all *post hoc* tests.

We conducted a second analysis to specifically evaluate the relative performance of each population in each hydroperiod treatment, which allowed us to more carefully test for changes in the rank order of population performance under different hydrological conditions. We first calculated the relative fitness of each individual plant by dividing its infructescence biomass by the mean infructescence biomass of all plants in the same hydroperiod treatment. We then conducted a mixed-model ANOVA with relative fitness as the response variable and Population as a fixed effect. We included Sire (nested within Population) and Dam (nested within Sire) as random effects in this analysis. All mixed models were conducted using restricted maximum likelihood (REML) in PROC MIXED in SAS v. 9.4 (SAS Institute Inc., Cary, NC, USA). We conducted *post hoc* comparisons among Populations within each Hydroperiod treatment using the Tukey–Kramer method to account for multiple comparisons.

Population- and environment-dependent short-term adaptive potential

We evaluated how the adaptive potential of *L. fremontii* varied with Hydroperiod treatment and among populations using log-likelihood tests that compared mixed-model ANOVA's with different variance structures (Shaw 1991). The primary model consisted of infructescence biomass as the response variable, Hydroperiod treatment and Population as fixed main effects, Sire (nested within Population) and Dam (nested within Sire) as random effects, and Population \times Hydroperiod and Hydroperiod \times Sire as interaction terms. We used log-likelihood tests (Shaw 1991; Saxton 2004) to evaluate if the sire variance component – that is, the additive genetic variance in fitness – varied significantly among Hydroperiod treatments, Populations and all combinations of Hydroperiod and Population (Table S6). To conduct these tests, we compared the likelihood of a model where the sire variance component was allowed to vary among the levels of the factor of interest (i.e. among Hydroperiod treatments, Populations or Hydroperiod \times Population), with a model where the sire variance component was constrained to be identical across levels. We used chi-square tests to evaluate if the heterogeneous sire variance model provided a significantly better fit to the data than the corresponding constrained model (Shaw 1991; Saxton 2004). The chi-squared statistic was calculated as the difference in the $-2\text{Res Log-Likelihood}$ scores for each model with the degrees of freedom equal to the difference in the number of estimated parameters. For visualisation purposes, we calculated the best linear unbiased predictor (BLUPs) (Liu *et al.* 2008; Piepho *et al.* 2008) for each PHS family in each Hydroperiod treatment from the model that allowed sire variances to differ for all Hydroperiod \times Population combinations. All models were conducted using PROC MIXED in SAS v. 9.4 (Copyright 2002–2010 by SAS Institute Inc., Cary, NC, USA). The annotated code is provided online as Supporting Information.

RESULTS AND DISCUSSION

We found clear support for the hypothesis that the expression of additive genetic variance in fitness is highly sensitive to extreme precipitation conditions associated with ENSO events. The additive genetic variance in reproductive success, which served as our estimate for $V_A(W)$, was almost three times greater in the La Niña treatment than in the El Niño treatment, which in turn was approximately six times greater than was measured in the Normal treatment (Fig. 2, Table 2). Furthermore, mean fitness was approximately three times lower in the La Niña treatment than in the Normal and El Niño treatments (Fig. 3; Table 2), indicating that low-rainfall years generate more stressful hydrological conditions for *L. fremontii* than years with more extended periods of flooding. Taken together, these results suggest that the rate of adaptation, estimated as $V_A(W)/(\bar{W})$ by Fisher's FTNS, for all three *L. fremontii* populations would be fastest when they experience La Niña conditions, where the additive genetic variance in fitness was highest and the mean absolute fitness was lowest, and slowest when exposed to hydroperiods that result from more typical precipitation conditions.

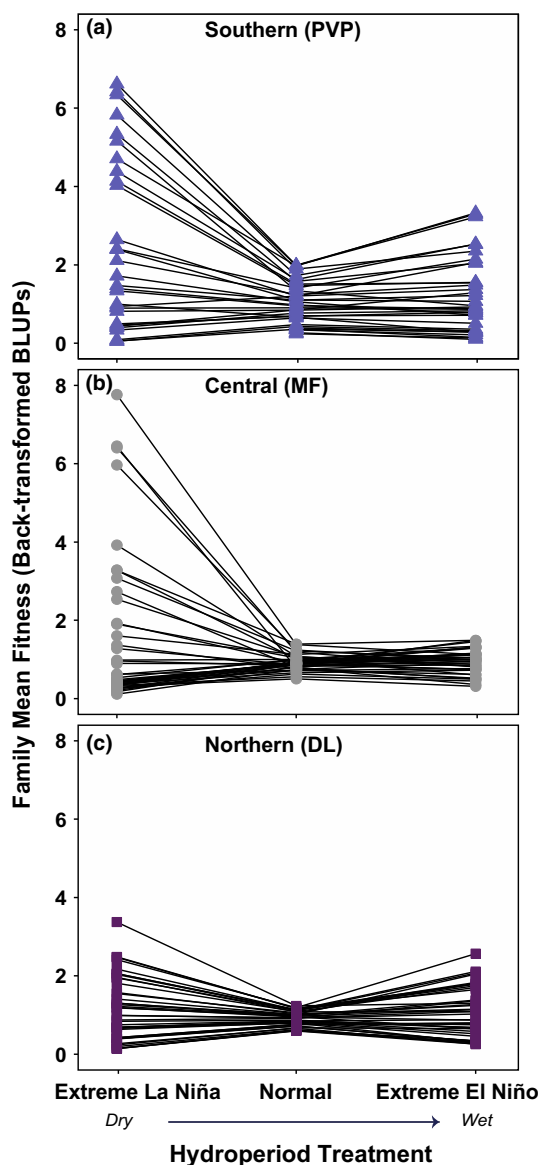


Figure 2 The expression of additive genetic variation in fitness, $V_A(W)$, under normal and extreme precipitation scenarios. Each line represents the mean fitness of a PHS family across three hydrological treatments, where mean fitness was estimated as the best least unbiased predictor (BLUP; Liu & Liu 2008; Piepho *et al.* 2008) for each PHS family in each treatment. Results are shown separately for each of the three experimental populations. The dispersion among *c.* 45 families within each Population represents the among-sire variance in fitness. To facilitate visual comparison across populations, we removed a single outlier from the Northern population so that the same y-axis could be used in each panel. A figure with the outlier included is provided in Fig. S4.

Previous studies have shown that the expression of additive genetic variance (V_A) in traits depends on the environmental context, as observed here for fitness in *L. fremontii*, though the direction of the change is not consistent among studies (see Blows & Sokolowski 1995; Imasheva *et al.* 1998; Schlichting 2008; Sheth *et al.* 2018). Various hypotheses have been proposed to explain why V_A might vary with environmental context (reviewed in Schlichting 2008; McGuigan & Sgro 2009). One hypothesis proposes that mutation rates may be greater in

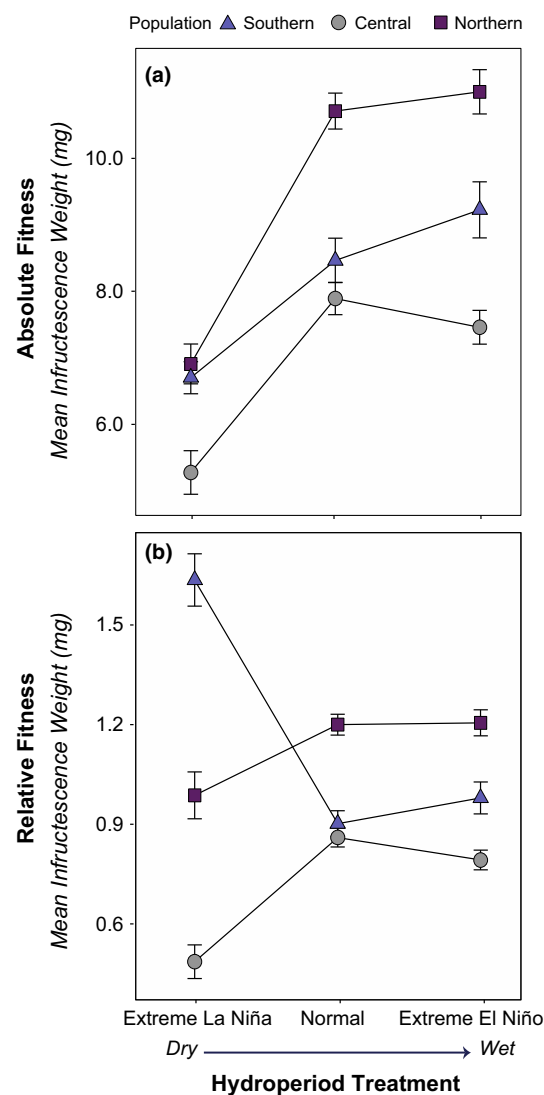


Figure 3 Mean fitness of populations within and across experimental hydroperiod treatments. Points represent (a) the mean absolute fitness and (b) mean relative fitness of each population in each hydroperiod treatment. Absolute fitness was estimated using infructescence biomass (Table S2), and relative fitness was calculated by dividing the infructescence biomass of each individual by the grand mean infructescence biomass in its treatment. Error bars represent ± 1 SEM.

stressful environments, so that over a period of time the population in a stressful environment will accumulate more mutations than one in a benign environment (Hoffmann & Merila 1999; McGuigan & Sgro 2009). This hypothesis cannot explain the results for *L. fremontii* because the differences in V_A were observed among individuals from the same cohort that had standardised genetic backgrounds across experimental treatments. Another explanation, called the ‘selection history’ hypothesis, states that standing genetic variation that is expressed under uncommon, stressful conditions, but not under typical conditions, will accumulate in populations because it is rarely exposed to selection (Hoffmann & Merila 1999; Swindell & Bouzat 2006). Our results with *L. fremontii* are consistent with the predictions of this hypothesis: the expression of genetic variation increased when populations were exposed to

environmental extremes (i.e. El Niño and La Niña hydroperiods; Fig. 2), and was highest in the treatment that was the most stressful (La Niña hydroperiods, Figs 2 and 3). The genetic variation that is expressed under relatively dry conditions could possibly be traced back to the common ancestor of the *Lasthenia* clade, which is thought to have been a strictly terrestrial lineage (Chan *et al.* 2001; Emery *et al.* 2011b). *Lasthenia fremontii*, and several other *Lasthenia* lineages, have only recently transitioned into vernal pool habitat, and thus some of the variation that was expressed in the La Niña treatment may consist of alleles that were once favourable in the terrestrial environment but are neutral in vernal pool environments.

Historical patterns of drift and selection can drive populations to diverge in their tolerances to environmental conditions (Lewontin 1974; Roff 2000; Björklund & Gustafsson 2015), particularly when gene flow is restricted. The three *L. fremontii* populations in this experiment showed similar overall responses to the three hydroperiod treatments (Fig. 3); however, their rank order within each treatment varied (Tables 1 and 2; Fig. 3). The Northern population, representing the location with the historically highest mean precipitation (Fig. 1c), outperformed the other two populations in the El Niño and Normal treatments. In contrast, the Southern population, which is from the historically driest site (Fig. 1c), had the highest relative fitness in the La Niña treatment (Tables 1 and 2; Figs. 1 and 3). These patterns are consistent with the hypothesis that the Northern and Southern populations are locally adapted to their home precipitation patterns, as they each outperform the other populations in the treatments that were designed from the historical ENSO precipitation regimes of their home sites (Fig. 1b). In contrast, we found no evidence of local adaptation in the Central population, which did not outperform the other populations in the Normal treatment, and in fact had the lowest relative fitness of the three populations in both hydrological extreme treatments (Fig. 3). Several factors likely contribute to the relatively poor overall performance of the Central population. First, molecular analyses have shown that the Central population is more highly connected by gene flow to other populations in the species' range, while the Northern and Southern populations are comparatively isolated (Torres-Martínez & Emery 2016). The variation in vernal pool size, depth, landscape position, landform and soil type generates substantial differences in species composition among pools within a contiguous site (Holland & Jain 1981). If patterns of selection vary at the same scale as patterns of species composition in vernal pools, the scale of environmental heterogeneity would be quite high relative to the scale of gene flow in the Central region of *L. fremontii*'s range. High connectivity among populations may make it relatively difficult for the Central population to specialise to its local climate regime compared to the more isolated, range-edge populations. Second, inter-annual variation in precipitation is highest at the range centre than at the northern and southern edges (Torres-Martínez *et al.* 2017), which would lead to less consistent patterns of selection in the Central population compared to those experienced in the Northern and Southern sites. This explanation is consistent with our previous work where we found that the proportion of seeds that remain dormant each year, which is an adaptation to temporally varying environments (Cohen

1966; Gremer & Venable 2014), is higher in the Central population than the Northern and Southern populations (Torres-Martínez *et al.* 2017).

All three populations expressed only marginal differences in additive genetic variation, on average, when estimated across all treatments ($P = 0.06$, Fig. 2, Fig. S4, Table S6). Given the evidence for genetic differentiation among populations (Torres-Martínez & Emery 2016), and the fact that the Northern and the Southern populations are located at edges of the species' range (Fig. 1a), it was somewhat surprising that the three populations had such similar overall levels of additive genetic variance in fitness. If anything, the southernmost population, which occupies the smallest and most isolated site, had higher levels of additive genetic variation in fitness compared to the other two populations (Table 2, Fig. 2), though this pattern was not statistically significant unless one outlying PHS family from the Northern population was excluded (Fig. S4, Table S6). Several processes likely maintain genetic variation in all *L. fremontii* populations and minimise the effects of inbreeding and drift. First, all vernal pools are highly variable environments, regardless of their geographic location within California, due to the stochasticity of the precipitation patterns that drive vernal pool hydrology (Javornik & Collinge 2016; Gosejohan *et al.* 2017). Such highly variable conditions may change the direction of selection on different alleles in different years, slowing the rate at which any specific genotype will be driven to fixation or extinction (Gillespie 1974; Lorenzi *et al.* 1989; Bell 2010; Sano *et al.* 2018). Furthermore, *L. fremontii* is an obligately outcrossing species, reducing the potential for inbreeding (Charlesworth & Charlesworth 1995). Finally, even though vernal pool habitat has shrunk substantially – up to c. 90% of its original extent since European colonisation of California (Holland 1998, 2011) – individual *L. fremontii* populations are still large (typically several hundred thousand to millions of individuals) even in relatively small, isolated vernal pool complexes (*personal observations*), and individual plants can produce tens to hundreds of seeds in the field (Emery 2009; Emery *et al.* 2009). These large population sizes likely help to maintain genetic variation in these populations by minimising the loss of alleles due to drift.

Table 1 Statistical results for the effects of hydrological treatment and population identity on absolute fitness (\bar{W}) in *Lasthenia fremontii*. The analysis was a mixed-model ANOVA with Population and Hydroperiod treatment treated as fixed main effects, and Sire (nested within Population) and Dam (nested within Sire) treated as random effects. F values are shown for fixed effects and Z values are shown for random effects

Effect	d.f.	MS	F or Z value	P
Fixed effects				
Population	2	138.29	65.52	< 0.01
Hydroperiod	2	1383.87	655.69	< 0.01
Population	4	18.41	56.1	< 0.01
× Hydroperiod				
Random effects				
Sire (Population)		0.03	2.42	< 0.01
Dam (Population × Sire)		0.03	2.61	< 0.01
Hydroperiod × Sire (Population)		0.03	3.11	< 0.01
Residual		0.05	34.21	< 0.01

Table 2 Fitness and rate of adaptation in three *Lasthenia fremontii* populations exposed to normal and extreme precipitation scenarios. The among-sire variance component, σ_s^2 , was estimated from a mixed model that allowed the sire and residual variance to vary among populations and hydrological treatments (Supporting Information, Table S6)

Site	Hydrology treatment	Mean Absolute fitness (± 1 SEM)*	Mean relative fitness (± 1 SEM)†	σ_s^2	$V_A(W)‡$	$V_A(W)/(\bar{W})$
Northern	Extreme El Niño	10.55 \pm 0.34	1.21 \pm 0.04	0.13	0.54	0.05
Northern	Normal	10.51 \pm 0.27	1.20 \pm 0.03	0.01	0.06	0.01
Northern	Extreme La Niña	3.12 \pm 0.22	0.99 \pm 0.07	0.39	1.54	0.49
Central	Extreme El Niño	6.91 \pm 0.26	0.79 \pm 0.03	0.07	0.27	0.04
Central	Normal	7.53 \pm 0.25	0.86 \pm 0.03	0.01	0.06	0.01
Central	Extreme La Niña	1.54 \pm 0.16	0.49 \pm 0.05	0.37	1.46	0.95
Southern	Extreme El Niño	8.54 \pm 0.42	0.98 \pm 0.05	0.20	0.81	0.09
Southern	Normal	7.93 \pm 0.34	0.91 \pm 0.04	0.07	0.26	0.03
Southern	Extreme La Niña	5.17 \pm 0.25	1.64 \pm 0.08	0.61	2.42	0.47

*Mean infructescence mass of plants from each population in each hydrological treatment.

†Calculated relative to the global mean fitness within each hydrological treatment.

‡The additive genetic variance in fitness, $V_A(W)$, was calculated as $4 \times \sigma_s^2$ (Falconer & McKay 1996).

Our results indicate that the short-term adaptive potential of *L. fremontii* populations will be highest in years of extreme drought, which are the conditions that are the most stressful for the species. However, Fisher's FTNS provides a single snapshot of the rate of adaptation over a single generation, and therefore the direction and rate of adaptation over multiple generations remains difficult to predict – particularly as climate becomes increasingly variable and unpredictable with climate change (Thornton *et al.* 2014; Wang *et al.* 2017). For example, if populations experience several consecutive years of drought, such as the 4-year drought in California from 2011 to 2017 (Griffin & Anchukaitis 2014; Deke 2017), the rate of adaptation would eventually decline as mean fitness (\bar{W}) increases and alleles that are beneficial under drought go to fixation (causing $V_A(W)$ to decrease). The long-term evolutionary trajectory of these populations will also depend on demographic processes that were standardised in our experiment, such as variation in the seed bank, germination fraction and population size. For example, our previous work found that germination fraction increases with moisture availability in *L. fremontii* (Torres-Martínez *et al.* 2017), which could lead to higher population sizes in particularly wet years if precipitation patterns during the germination period were correlated with vernal pool hydroperiods during the growing season. However, historical climate records at our three field sites indicate that precipitation levels during the germination period do not predict the amount of precipitation that occurs over the remainder of the growing season (see SI, Fig. S3). This suggests that the precipitation patterns that determine pool hydroperiod, and their ultimate effects on post-germination fitness in *L. fremontii*, are essentially decoupled from the climate processes that influence germination and seedling emergence. While these and other demographic processes would best be evaluated in field experiments that incorporate other ecological factors that vary among years (e.g. competing vegetation, pollinator abundance, etc; see Emery *et al.* 2011a; Emery & Ackerly 2014), we currently have no *a priori* reasons to expect that variation in early life history stages, which was minimised in our experiment, would lead to consistently different results on the adaptive potential of *L. fremontii* under different hydroperiods.

Collectively, this study shows that the potential for short-term adaptive responses of wild populations can change when extreme

climate events occur due to an inverse relationship between mean fitness and the expression of variation in fitness. Specifically, our results suggest that *L. fremontii* populations may have contrasting fitness responses to the opposing climatic extremes (high vs. low precipitation) that are projected to become increasingly common in California over the next century (e.g. Yoon *et al.* 2015). Growing seasons with unusually high levels of precipitation, such as those that accompany El Niño events, will promote high mean fitness (\bar{W}) but low evolutionary potential ($V_A(W)$); growing seasons that are particularly dry, such as those associated with La Niña events, will lead to low mean absolute fitness but high adaptive potential. The effects of hydroperiod on the expression of additive genetic variation in fitness was substantial: the differences in adaptive potential among treatments far exceeded any differences in the amount of genetic variation observed among geographically distant populations. These results indicate that extreme climate events by altering the expression of additive genetic variation in fitness-related traits are likely to play a critical, though currently underappreciated, role in determining how species will evolve in response to an increasingly variable and unpredictable climate.

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AUTHORSHIP

LTM and NCE conceived and designed the experiment, with NM leading the hydrological modelling that informed the experimental treatments. LTM implemented the experiment. LTM and NCE

analysed the data, and LTM wrote the first draft of the manuscript. All the authors contributed to editing the final manuscript.

DATA ACCESSIBILITY

All data and SAS code for statistical analyses are available on Dryad at <https://doi.org/10.5061/dryad.rt400df>.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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