RUNNING TITLE: Fluctuating selection on Monkeyflowers

TITLE: Short-term fluctuating and long-term divergent selection on sympatric Monkeyflowers: insights from repeated reciprocal transplants

Caroline M. Dong[1,2], Bolívar Aponte Rolón[1,3], Juj K. Sullivan[1], Diana Tataru[1,4], Max De Leon[1], Rachael Dennis[1], Spencer Dutton[1], Fidel J. Machado Perez[1,5], Lissette Montano[1] & Kathleen G. Ferris[1]

[1]Tulane University, Department of Ecology and Evolutionary Biology, New Orleans, LA

[2]Grinnell College, Department of Biology, Grinnell, IA

[3]Iowa State University, Department of Agricultural and Biosystems Engineering, Ames, IA

[4]Utah State University, Department of Biology, Logan, UT

[5]University of California Merced, Life and Environmental Sciences Department, Merced, CA

Corresponding author: dongca@grinnell.edu

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ABSTRACT:
Sympatric species are often locally adapted to distinct microhabitats. However, temporal variation may cause local maladaptation and species boundary breakdown, especially during extreme climatic events. Repeated reciprocal transplants can reveal the interplay between spatially and temporally varying patterns of natural selection. To examine long-term patterns of selection between sympatric Monkeyflowers occupying dramatically different niches, *Mimulus guttatus* and *M. laciniatus,* we performed three replicated transplants and combined them with previous experiments to leverage a dataset of five single-year transplants spanning a decade. We performed phenotypic selection analyses on parents and hybrids in each species' habitat in Yosemite NP, CA during years of drastically differing snowpack. If there is ecological isolation, then we predicted divergent phenotypic selection between habitats in line with species' differences and local adaptation. We found interannual fluctuations in phenotypic selection, sometimes in unpredicted directions. However, a combined-year analysis detected longer-term differences in the magnitude of selection between habitats on flowering time, a key temporally isolating and adaptative trait, suggesting that selection may reinforce species boundaries despite short-term fluctuations. Finally, we found temporal variation in local adaptation with *M. laciniatus* locally adapted in low snowpack years, while an extreme snowfall event contributed to overall local maladaptation of *M. guttatus*.

INTRODUCTION

Closely related species often occupy distinct habitats within areas of geographic overlap (Coyne and Orr 2004; Rundle and Nosil 2005; Schluter 2009). Species boundaries in sympatry can be maintained by adaptation to differing environments that generate pre- and post-zygotic isolation via selection against immigrants (e.g. habitat isolation) and intermediate hybrids (e.g. extrinsic post-zygotic isolation; Rundle & Nosil, 2005). However, identifying the individual traits contributing to reproductive isolation is difficult because as speciation progresses, multiple forms of reproductive isolation accumulate between divergent lineages which hinders the measurement of individual barriers (Coyne and Orr 2004). Once species are partially isolated, neutral processes also cause the accumulation of phenotypic divergence. Thus, experimental manipulation is necessary to determine whether habitat isolation is a key barrier, and which traits are involved in divergent adaptation (Ramsey et al. 2003; Hall and Willis 2006; Lowry et al.

2008). Measuring phenotypic selection on closely related sympatric species in a reciprocal transplant between native environments can identify whether divergent adaptation is important for reproductive isolation and speciation (Lowry et al. 2008; Anderson et al. 2015. If so, we expect each species to have higher fitness in its habitat and phenotypic selection in the direction of species' differences (Anderson et al. 2015*a*), indicating habitat isolation and local adaptation to current conditions.

Despite these predictions of local adaptation, maladaptation to native habitats is often observed in reciprocal transplants (Hereford 2009; Kooyers et al. 2019; Dittmar and Schemske 2023). This could be due to the prevalence of temporal fluctuations in selection (Siepielski et al. 2009) which can influence the strength of reproductive isolation and species boundaries (Tataru et al. 2023, 2024). Additionally, current environmental conditions may have changed from the conditions of original divergence (Coyne and Orr 2004; Rundle and Nosil 2005). If species are no longer adapted to their current niches due to climate change, then we expect to find local maladaptation (Crespi 2000) and selection for the non-local species' phenotype (Wilczek et al. 2014; Kooyers et al. 2019; Anderson and Wadgymar 2020). In this scenario, spatially varying selection may act contrary to reproductive isolation and in the absence of strong intrinsic barriers, could erode species boundaries by driving each towards the other's phenotypic optimum.

Variation in selection in longitudinal studies is usually measured on a seasonal or inter-annual timescale, which is a short-term measurement of population evolution. This leads to the question of how short-term fluctuations affect long-term evolutionary change in species and populations (Wadgymar et al. 2017; Kelly 2022; Dittmar and Schemske 2023; Oakley et al. 2023). A synthesis of phenotypic selection studies by Kingsolver & Diamond (2011) found that while temporal variation in selection is common, it does not significantly inhibit long-term directional selection. Therefore, even with fluctuations in the direction of selection, there may be an average directional or stabilizing trend over a longer timescale. For example, Wadgymar et al. (2017) found that interannual fluctuations in the direction of selection on the perennial plant *Boechera stricta* gave rise to long-term patterns consistent with stabilizing selection and local adaptation. In *Arabidopsis thaliana*, Lee et al. (2024) found long-term divergent selection on cold tolerance between populations in Italy and Sweden despite interannual fluctuations. However, due to the

arduousness of temporally replicating reciprocal transplant experiments, it is not currently well understood how short versus longer-term patterns of natural selection compare and impact species' divergence and reproductive isolation.

Another understudied agent of evolutionary change is episodic selection stemming from sudden and extreme environmental events. Long-term studies capturing the evolutionary responses to these dramatic ecological changes are rare yet critical to understand their impact on species boundaries (Coltman et al. 1999; Pemberton et al. 2022). For instance, through their long-term study of the Galapagos finches, Grant and Grant (1993) were able to illustrate how an extreme El Niño year altered selection on beak size and rates of interspecific gene flow. Strong episodes of selection such as this can impact biodiversity by affecting the evolutionary trajectory of species adaptation and reproductive isolation (Grant and Grant 1993). Studies such as this are vital because extreme climatic events are predicted to become more frequent with continuing anthropogenic climate change (Bailey and van de Pol 2016).

The *Mimulus guttatus* species complex is well-suited for studying how natural selection shapes species boundaries and reproductive isolation (Wu et al. 2008). *Mimulus guttatus* and *M. laciniatus* (syn. *Erythranthe guttata* and *E. laciniata*) occur in contrasting microhabitats throughout central and southern Sierra Nevada, CA. *Mimulus guttatus* inhabits moist meadows and seeps while *M. laciniatus* occupies rocky outcrops characterized by shallow soils, intense light, extreme temperatures, and a short growing season (Ferris et al. 2014; Ferris and Willis 2018). *Mimulus laciniatus*, an obligate summer annual, has a smaller stature, lobed leaves, self-fertilization with reduced floral size, and early rapid flowering (DeMarche et al. 2013; Ferris and Willis 2018). In contrast, *M. guttatus* populations are facultatively annual, later-flowering, predominantly outcrossing, round-leaved, and larger in size and flower morphology (Awadalla and Ritland 1997; Ferris et al. 2014). Despite ecological divergence, reproductive isolation is incomplete (Vickery 1964; Ferris et al. 2017; Tataru et al. 2024).

Previous studies show evidence of local adaptation to contrasting microhabitats, but it remains unclear how environmental variation alters the strength or direction of selection over time (Ferris and Willis 2018). Early flowering, a drought escape strategy, functions as a key pre-mating

barrier in the *Mimulus guttatus* species complex (Hall and Willis 2006; Lowry et al. 2008; Ferris et al. 2017; Mantel and Sweigart 2019). Larger plant sizes may be advantageous in meadows where herbivory is higher. Lobed leaves may improve temperature and water regulation through a reduced boundary layer (Nicotra et al. 2011*a*) and are unique to *Mimulus* species found in rocky habitat (Ferris et al. 2014; Ferris and Willis 2018; Ferris 2019). Yet how selection on these and other traits (e.g. mating system and flower morphology) fluctuates through time is unknown. Both species exhibit phenotypic plasticity with *M. guttatus* exhibiting greater plasticity in plant size and flowering time than *M. laciniatus* (Ferris & Willis 2018). Such plasticity may be adaptive in heterogenous environments like *M. laciniatus'* patchy granite outcrops (Via & Lande 1985).

Here, we investigate spatial and temporal variation in natural selection between *M. guttatus* and *M. laciniatus* using single-year reciprocal transplants repeated across five years under contrasting climatic conditions (Figure 1). In this study, we add three years of new results to two previously published years which spanned years of historically low (Ferris and Willis 2018) and high snowpack (Tataru et al., 2023). Weaker divergent selection on a key isolating barrier, flowering time, was found during the high snowpack year, potentially eroding species differentiation. We replicated transplants during low snowpack years (2021, 2022) and an exceptionally high snowpack year (2023; Figure 1a,b). We address the following questions: (1) How do environmental variables affect fitness in each species' habitat and induce phenotypic plasticity? (2) Does the strength and direction of selection on adaptive and reproductively isolating phenotypes fluctuate? (3) How do short versus long-term patterns of selection compare? (4) Are *M. guttatus* and *M. laciniatus* locally adapted to their respective microhabitats? (5) How does episodic selection affect the trajectory of species divergence? By examining both interannual variation and overarching signatures of selection, we were able to elucidate the effects of a changing climate on the maintenance of biodiversity in this system.

MATERIALS AND METHODS

Repeated reciprocal transplant design

Reciprocal transplants used hybrids created from inbred lines of *M. guttatus* (YVO 18; 37.723366, -119.746433; 5,395 ft elevation) and *M. laciniatus* (WLF 47; 37.841533, -

151 119.59385; 7993 ft elevation; Figure 1c). Advanced generation hybrids were used because
152 recombination over multiple generations breaks up parental haplotypes, increasing phenotypic
153 variation and enabling inferences about selection on individual traits (Figure S1; Nagy, 1997;
154 Hall & Willis, 2006; Groh & Coop, 2024). F_1 hybrids (WLF 47 maternal x YVO 18 paternal)
155 were self-fertilized to generate F_2 seeds used in 2021. Five hundred F_2 hybrids were propagated
156 with single-seed descent to produce F_3 seeds used in 2022 and 300 F_6 lines used in 2023, with
157 some hybrid lines lost likely due to inbreeding depression. In 2021 and 2022, seeds from 200
158 hybrid maternal families were pooled for transplants. To avoid inbreeding depression in parental
159 genotypes in 2023, inbred lines were intercrossed within each parental population, as *M. guttatus*
160 is susceptible to inbreeding depression (Willis 1999), which may impact inferences about local
161 adaptation. The 2013 and 2019 experiments used F_4 hybrids from the same parental populations
162 (see Ferris & Willis 2018; Tataru et al 2023).
163
164 Our transplants were conducted in 2021, 2022, and 2023 in Yosemite National Park, CA,
165 replicating experiments from 2013 and 2019 at four sites (Figure 1c): two granite outcrops
166 (Granite 1 [37.810700, -119.485200; 8,436 ft elevation], Granite 2 [37.843702, -119.573120;
167 8,117 ft elevation]) and two meadows (Meadow 1 [37.767781, -119.772720; 6,605 ft elevation],
168 Meadow 2 [37.755968, -119.803031; 6,163 ft elevation]). We used precisely the same
169 microhabitats within each site, experimental design, and parental source populations. Sample
170 sizes, maternal families, and hybrid generation differed annually within logistical constraints
171 (Table S1). Seedlings were transplanted in small blocks to capture fine-scale environmental
172 variation and mimic granite habitat patchiness. In 2021 and 2022, each site had 50 randomized
173 blocks (4×6 formation, 1-inch spacing) of 18 and 24 individuals, respectively. In 2021, blocks
174 contained six F_2 hybrids and six of each parent, with Granite 2 having 75 blocks, totaling 4,050
175 plants. In 2022, blocks contained 16 F_3 hybrids with four of each parent, totaling 4,800 plants. In
176 2023, local parental genotypes originating from each site were planted only in their origin site, to
177 compare fitness with the nearby source parents (WLF and YVO). We used 2–3 intrapopulation
178 parental crosses and original inbred lines, distributed evenly across blocks and sites, which did
179 not differ in mean seed count and were combined for downstream analyses (Table S2). Each site
180 had 60 blocks (5×7 formation) of 35 individuals, composed of 3–4 of parental genotypes (YVO,

181 WLF, and local), and 16–23 F_6 hybrids per block, with 1,200 of each parent and 3,000 F_6 hybrids
182 per habitat totaling 8,400 plants.
183
184 We cold-stratified parental *M. laciniatus* and hybrid seeds for 10 days and parental *M. guttatus*
185 seeds for 5 days at 4°C in the dark in plastic flats filled with soil (Sunshine Mix #4 Professional
186 Growing Mix, Sun Gro) to break dormancy and synchronize germination for one week in
187 greenhouses at the University of California (UC) Davis (2021) and UC Merced (2022–2023).
188 Following germination upon the emergence of cotyledons, individuals were planted into block
189 designs described above. Mortality within the first week was attributed to transplant shock, dead
190 germinants were replaced and not included in subsequent analyses.
191
192 *Environmental & phenotypic data collection*
193 To assess microhabitat variation, environmental measurements were taken weekly from
194 experimental blocks. We measured soil moisture (%) using the SM150T sensor (Dynamax), soil
195 surface temperature (°F) using a laser thermometer, and light intensity (µmol m-2 s-1) using a
196 MQ-200X Sunlight Quantum Meter (Apogee Instruments). Light and temperature were not
197 measured in 2013 (Ferris and Willis 2018). We recorded survival, herbivory (presence/absence),
198 and putatively adaptive phenotypes under selection: flowering time, plant height, herkogamy,
199 flower size, leaf shape (Ferris et al. 2014; Ferris and Willis 2018; Tataru et al. 2023). At first
200 flowering, we recorded the date and measured plant height (mm), stigma and anther lengths
201 (mm), and corolla width (mm). Flowering time was calculated as days from transplant to first
202 flower. Herkogamy (i.e. stigma-anther separation) was calculated by subtracting stigma length
203 from longest anther length, a metric of outcrossing ability. To assess leaf shape, the first true leaf
204 was collected one-week post-flowering. Leaves were scanned and analyzed for leaf lobing index
205 using ImageJ (Schneider et al. 2012; Ferris et al. 2015).
206
207 *Testing for effects of environmental factors on fitness*
208 To find associations between environmental variables and plant survival within each habitat, we
209 pooled data across sites and used binomial mixed models with survival as the dependent variable
210 and soil moisture, time, soil temperature and light levels with their interactions as fixed
211 independent variables, and block nested within site as a random effect. Survival was structured

212 as the number of survivors in each block at a time point relative to the number of individuals
213 originally planted in each block. We performed model selection for the best-fit model using AIC
214 selection criteria using R packages *nlme* v3.1 (Pinheiro and Bates 2000; Pinheiro et al. 2023) and
215 *MuMIn* v1.47.5 (Bartoń 2018). To test whether foliar herbivory differs between habitats, we used
216 a generalized linear model with a binomial distribution with herbivory as the dependent variable
217 and habitat as the fixed independent variable with block nested within site as a random effect. To
218 understand the effect of herbivory on plant fitness, we used generalized linear models with a
219 Poisson distribution and fitness (i.e. seed count) as the dependent variable while herbivory and
220 habitat and their interactions were fixed independent variables with block nested within site as a
221 random effect using the R package *lme4* v1.1.32 (Bates et al. 2015).
222
223 *Phenotypic plasticity analyses*
224 We used parental inbred lines to investigate each species' phenotypically plastic response to the
225 environmental variation between species' habitats within individual years. These spatial
226 contrasts provide a coarse-grained test (Levins 1968) of how genotypes may respond to differing
227 environmental conditions. Plasticity was analyzed using generalized linear mixed models with
228 phenotype as the dependent variable, habitat as a fixed effect and block nested within site as a
229 random effect. Further, we examined phenotypic plasticity between habitats and years (2013-
230 2023) using generalized linear mixed models with phenotype as the dependent variable, habitat
231 and year with their interaction as fixed effects and block nested within site as a random effect.
232 We also compared hybrid trait means between habitats which are not true measures of plasticity
233 since they represent both genetic and environmental differences.
234
235 *Phenotypic selection analyses*
236 To measure lifetime fitness for our phenotypic selection analyses, we counted fruit and seed
237 number. Plants that produced flowers but did not produce fruit or seed were indicated with a
238 value of zero. For annual plants, fruit and seed number are a good approximation of fecundity
239 which we use in our selection analyses. We calculated the correlation between fruit and seed
240 number using Kendall's correlation analysis. We found that selection gradients (β values)
241 derived from fruit number (2013) were similar to those from seed number (all other years) in
242 both strength and direction (Table S4, Table S5) likely due to a positive correlation between seed

243 and fruit number (Table S6). Therefore, we compare fruit and seed number derived selection
244 gradients across years.
245
246 To understand temporal fluctuation in the strength and direction of selection on traits in each
247 habitat, we used multivariate phenotypic selection analyses on datasets of hybrid individuals
248 across all five years of transplants. To investigate linkage between traits, we calculated
249 correlations between traits from hybrid individuals, grouped separately by habitat and year, using
250 linear mixed models with traits as dependent and fixed variables with block nested within site as
251 a random effect. We found generally weak correlations ($r < 0.50$) between traits, except between
252 plant height & leaf area and leaf area & flower width (Table S3). Therefore, leaf area was
253 removed from the following phenotypic selection analyses.
254
255 To properly compare selection gradients from all years, data published in 2013 and 2019 were
256 re-analyzed using the same multivariate linear selection model as the recent transplants (Ferris
257 and Willis, 2018; Tataru *et al*. 2023). Quantitative traits measured in each experiment (leaf
258 lobing, plant height, outcrossing, flower width, flowering time) were standardized to a normal
259 distribution with a mean of 0 and standard deviation of 1 to enable comparison of selection on
260 qualitatively different traits and with previously published studies (Lande & Arnold 1983). Traits
261 were standardized within each year for all analyses except the combined analysis (described
262 below). In our phenotypic selection model, seed count (i.e. fecundity) was the dependent variable
263 with plant height, flowering time, flower width, herkogamy, and leaf lobing as fixed independent
264 variables, with block nested in site and habitat as a random effect. We did not include quadratic
265 or correlational selection terms in our models to simplify our interpretation of the results
266 (Anderson et al. 2015*b*). We did not conduct phenotypic selection analysis of fitness combined
267 across life history stages using an ASTER model approach because our dataset did not include
268 trait data on individuals that died before flowering. To account for overdispersion of zeros in our
269 fecundity data we divided it into two components: the probability of setting any seed
270 (reproducing) vs. the number of seeds set by plants that fruited (fecundity). We used two types of
271 generalized linear mixed models using the R package *glmmTMB* v1.1.8 (Brooks et al. 2017;
272 Magnusson et al. 2017) to analyze these two fitness components separately: the probability of
273 setting seed with a binomial distribution, and a zero-truncated Poisson distribution to assess

whether trait values were associated with the number of seeds produced. Sites were pooled within habitats. To extend the comparison to the 2013 experiment which used only fruit number, we repeated all analyses using fruit number as the dependent variable.

We repeated phenotypic selection analyses on a combined dataset of hybrid genotypes pooled across all years (2013–2023) using fruit number as the dependent variable with plant height, flowering time, flower width, and leaf lobing as fixed independent variables, and block nested in site and year as random effects. Herkogamy was omitted from the combined dataset due to its absence in 2013. Raw trait data were combined across years and then standardized. To visualize the fitness-phenotype relationships, we plotted selection gradients using the R package *visreg* (Breheny and Burchett 2017). To assess whether slopes were statistically different for individual traits between meadow and granite habitats, we compared slopes of models using a bootstrap approach (1000 iterations) to derive 95% confidence intervals and *p*-values. To assess whether temporally fluctuating phenotypic selection is related to environmental fluctuation, we used the combined dataset to run generalized linear models including interactions between traits and snowpack. We used the snow water content accumulated (inches) by April 1st of each year (Figure 1a). The models included fruit as the dependent variable, phenotypic traits (flowering time, flower width, leaf lobing, plant height) and their interaction with snowpack as fixed independent variables and then block nested in site and year as random effects.

Assessing local adaptation of M. laciniatus vs. M. guttatus

To assess parental species' local adaptation, we used three metrics of fitness for parental genotypes: survival to flowering ('survival'), mean seeds per reproductive individual ('fecundity'), and mean seeds per planted individual ('total fitness'). For long term patterns, we calculated arithmetic means of each metric across years (2013, 2019, 2021, 2022, 2023) for each habitat and species. Data from 2013 was omitted from averaged fecundity and total fitness because only fruit number was counted. Because it is not known whether these species have seed banks, impacting long-term fitness, we also calculated geometric means across years (Figure S5). To test for genotype by environment (GxE) interactions, we fit linear mixed-effects models for fecundity and total fitness, and generalized linear mixed-effects models for survival, with genotype, habitat, and their interaction as fixed effects and block nested within site as a random

305 effect. Finally, to assess whether the extreme high snowpack of 2023 altered long-term patterns,
306 we compared mean parental fitness in each habitat with (Figure 5) and without data from 2023
307 (Figure S4). All models described above are summarized in Table S7.
308
309 RESULTS
310 *Environmental variation causes spatial and temporal variation in survival*
311 Fine-scale environmental variation was significantly associated with survival trends in both
312 habitats across years and fluctuated both spatially and temporally with snowpack (Figure 2,
313 Table S8). Soil moisture availability throughout the season varies significantly between *M.*
314 *laciniatus's* granite and *M. guttatus's* meadow habitat in each year with moisture in granite
315 outcrops declining rapidly after an early season plateau, while in meadows there is a gradual,
316 linear decline throughout the growing season. The amount of soil moisture available and the
317 shape of the soil moisture curve fluctuated from year to year with higher snowpack years (2019,
318 2023) showing shallower declines in soil moisture over time in each habitat (Figure 2). Light
319 intensity and temperature were higher on average in *M. laciniatus's* granite environment except
320 in the extreme high snowpack year of 2023 where temperatures were cooler than usual and
321 similar between habitats throughout the growing season (Figure 2; Table S8).
322
323 Across 2021-2023 in both meadow and granite habitats, time (days; $p < 0.0001$), soil moisture (p
324 < 0.0001), and soil surface temperature ($p < 0.0001$), were almost always significantly associated
325 with survival, with decreasing soil moisture and increasing temperature over time associated
326 with decreased survival (Table S8). Interestingly in 2023, time ($p > 0.05$) was not significant
327 associated with survival in meadow habitat. This is likely because in this exceptionally high
328 snowpack year, approximately half of meadow individuals were alive until first snowfall at the
329 end of the growing season (Figure 2a). In *M. laciniatus's* granite habitat, we found that light
330 intensity ($p < 0.0001$) also significantly affected survival in 2021-2023. Soil moisture and soil
331 surface temperature impacted survival over time in the same directions as described for *M.*
332 *guttatus's* meadow habitat in all three recent years. In 2023, soil moisture ($p > 0.05$) was not
333 significantly associated with survival in granite habitat. In summary, we found that soil moisture
334 and temperature most significantly impacted survival in both habitats and light intensity

additionally impacted survival in granite habitat. Further, 2021–2023 differed from 2019 where soil moisture was the only significant environmental factor (Tataru *et al.*, 2023).

Similar to 2013 and 2019, herbivory pressure differed significantly between habitats with greater herbivory in *M. guttatus'*s meadows in 2021 (meadow 22%, granite 1.97%; $p = 0.042$), 2022 (meadow 37.75%, granite 2.58%; $p < 0.01$), and 2023 (meadow 23.17%, granite 8.74%; $p = 0.032$). In 2021 and 2023, herbivory and the interaction between herbivory and habitat significantly affected total fitness but did not in 2022. Overall, herbivore pressure varied spatially, but its effect on fitness varied temporally.

Episodic selection: an extreme climatic event dramatically shifted the growing season

The extreme high snowpack year (2023) differed from other years in several aspects. The growing season was delayed by six weeks or more in both habitats, with surveys not beginning in granite until previous years' surveys had ended (Figure 2a,b). Soil moisture declined more gradually in both habitats in 2023 than any previous year (Figure 2c,d), while light intensity and surface temperatures were lower (Figure 2e-h). In granite, there was no characteristic temperature spike in 2023 that usually coincided with mortality (Figure 2h). Unlike previous years, many plants had not senesced in meadows at the end of the growing season: 41.7% (Meadow 1) and 50.7% (Meadow 2) alive at the last survey before snowfall (Figure 2a). Of the individuals remaining in Meadow 1, many had not flowered indicating a significant life-history delay (0% local genotype, 31.0% hybrids, 44.1% *M. guttatus*, 70.7% *M. laciniatus*). Meadow 2 was similar (0% local genotype, 47.3% hybrids, 40.4% *M. guttatus*) except most individuals of *M. laciniatus* flowered (92.0%). The 2023 growing season was 36-70 days longer than previous years in granite habitats (Granite 2013-2022: 33-87 days; 2023: 112-113 days) but comparable to other years in meadows (Meadow 2013-2022: 74-160 days; 2023: 119-146 days).

Phenotypes are adaptively plastic between habitats

Parental genotypes exhibited consistent phenotypic plasticity between habitats within years, with the non-native species generally shifting toward the phenotype of the local species. In nearly all three years, *M. laciniatus* grew more *M. guttatus*-like in meadow habitat with significantly longer flowering time, taller plant height, larger leaf area (Tables S9, S10, S11). This is similar

366 to patterns from 2013 except for flower size (Ferris & Willis 2018). Conversely, in its nonnative
367 granite habitat, *M. guttatus* shifted toward *M. laciniatus*-like traits with significantly shorter
368 flowering time and smaller plant height (2021 and 2023) and smaller leaf area and increased leaf
369 lobing (2022 and 2023; Tables S9, S10, S11). Furthermore, flowering time, plant height, flower
370 width, leaf area displayed significant habitat by year interactions (all $p < 0.000$), indicating
371 plasticity over time, whereas leaf lobing and outcrossing did not (Table S12). Hybrid means also
372 differed between habitats with shorter flowering time, smaller plant height, smaller leaf area in
373 granite habitat, in the direction of the *M. laciniatus* (Tables S9, S10, S11). In 2019, hybrids in
374 granite differed by having larger flowers and larger leaf area relative to meadow (Tataru et al.
375 2023). However, we do not interpret hybrid differences as plasticity as they may instead reflect
376 differences in habitat-dependent selection resulting in differing genetic composition.
377
378 *Interannual fluctuation versus long-term directional selection*
379 We found temporal and spatial fluctuations in the strength and direction of selection on each
380 quantitative trait (Tables 1, 2; Figure 3). Our binomial models revealed how phenotypes affected
381 whether plants reproduced whereas the zero-truncated Poisson models revealed how selection
382 acted among individuals that did reproduce (number of seeds). Based on observed trait
383 differences between species, we predicted selection in *M. laciniatus's* harsh granite habitat for
384 early flowering time, smaller flowers, increased leaf lobing, shorter plants, and decreased stigma-
385 anther distance (herkogamy), with the inverse direction of selection in *M. guttatus's* meadow
386 habitat (Figure 3a-e). We found that selection fluctuated across years in habitats and was at times
387 in the opposite direction of our expectations. Selection on the probability of reproduction
388 (binomial models) was typically stronger and more consistent in direction with predictions than
389 selection on fecundity (zero-truncated Poisson models), suggesting that selection acting early in
390 the life cycle on survival and flowering may be more vital than selection acting on fecundity
391 (Figure 3).
392
393 Across all years, selection favored earlier flowering time in both habitats; with early flowering
394 time often under stronger negative selection in the granite habitat as expected in the binomial
395 analysis (Figure 3f,k). Selection on flower width fluctuated but was often in the direction
396 expected with larger flowers more favorable in meadow than in granite in the binomial analysis

397 (Figure 3g). Zero-truncated models of fecundity selection on flowering time and flower width
398 varied but, in most years, there was still stronger selection for early flowering in granite habitats
399 and stronger selection for larger flowers in meadow as expected (Figure 3k, l). Plants with more
400 lobed leaves were more likely to reproduce in granite habitat in low snowpack years, aligning
401 with predicted species differences (Figure 3h). In high snowpack years, the selection was
402 reversed with more lobed leaves being advantageous in meadow habitat (Figure 3h). Selection on
403 leaf lobing also fluctuated temporally in fecundity selection, where there was often selection for
404 more lobed leaves in meadow, but not granite, contrary to predictions. Taller plants were
405 favorable across habitats and years but contrary to predictions there was often stronger positive
406 selection for height in granite (Figure 3i,n). For herkogamy, we found selection in the direction
407 predicted in high snowpack years (2019, 2023), with shorter stigma-anther separation associated
408 with higher fecundity in granite and greater stigma-anther separation favorable in meadow, but
409 reversed in the low snowpack year 2021 (Figure 3o). Phenotypic selection analyses where
410 models excluded herkogamy in all years were largely similar (Figure S2). We found that these
411 temporal fluctuations in phenotypic selection were statistically associated with variation in
412 snowpack. In meadow habitat, there was a significant plant height by snowpack interaction in the
413 zero-truncated Poisson model ($p < 0.0001$), and snowpack significantly interacted with both
414 plant height and leaf lobing in the binomial analysis (both $p < 0.05$). In granite habitat, flowering
415 time and flower width both had significant interactions with snowpack in the zero-truncated
416 Poisson (both $p < 0.001$) while there was a plant height by snowpack interaction in the binomial
417 model ($p < 0.0001$).
418
419 Although we found interannual fluctuations in the strength and direction of selection on all traits,
420 when we combined data across years, we saw long term patterns of directional selection (Table
421 1, Table 2; Figure 4, Figure S3). In both zero-truncated Poisson and binomial analyses, we found
422 long-term selection for earlier flowering time, smaller flowers, more lobed leaves and taller
423 plants in both habitats. Selection was significantly stronger in the granite habitat for early
424 flowering time (binomial: $p < 0.0001$), lobed leaf shape (Poisson: $p < 0.0001$), and larger plant
425 sizes (Poisson: $p < 0.0001$). Therefore, while inter-annual fluctuations in the strength and
426 direction of selection are common in this system, we still find longer-term differences in the

427 strength of selection in the direction of species' differences in both flowering time and leaf
428 shape.
429
430 *Local adaptation fluctuates temporally with long-term maladaptation of M. guttatus*
431 We found temporal fluctuation in the signature of local adaptation in both habitats. In 2013, a
432 drought year, we found a clear signature of local adaptation in total fitness, but this was not true
433 for other years in our study (Figure 5). There was also often a difference in local adaptation
434 between the individual components of fitness: survival and fecundity. *Mimulus laciniatus* had
435 higher survival to flowering than *M. guttatus* in both habitats in all years, except in 2019 when
436 there was low overall survival of parental genotypes (Figure 5a-e). With all five years combined,
437 *M. laciniatus* had higher average survival in both habitats (Figure 5f). Patterns of fecundity
438 differed between years with parental species having higher fecundity in their native habitats in
439 2021, like in 2013, indicating local adaptation and selection against immigrants (Figure 5g-k).
440 However, in 2022, *M. laciniatus* had higher fecundity in both habitats (Figure 5j), and in 2023,
441 we found reciprocal local maladaptation where *M. guttatus* had higher fecundity than *M.*
442 *laciniatus* in granite and vice versa in meadows (Figure 5k).
443
444 With all years combined, we found overall evidence of local maladaptation in mean fecundity
445 (Figure 5l); however, removing the extreme snowpack year of 2023 reveals local adaptation in
446 fecundity (Figure S4). A significant genotype by environment interaction GxE was detected for
447 total fitness in every year except 2019, and for survival and total fitness when all years were
448 combined (Table S13). Detection of GxE in survival and fecundity varied more across individual
449 years (Table S13). For total fitness, *M. laciniatus* had higher fitness and home-site advantage in
450 low snowpack years (2013, 2021, 2022; Figure 5m,o,d), but *M. laciniatus* and *M. guttatus*
451 performed equally well in granite during high snowpack years (2019, 2023; Figure 5n,q). Total
452 fitness in meadow was not as predictable based on snowpack with *M. laciniatus* having higher
453 total fitness in recent years (2021-2023) but lower fitness in 2013 and 2019. Overall, *M.*
454 *laciniatus* had higher total fitness in both habitats (Figure 5r, Figure S4). Geometric mean
455 fitness analyses reinforced these patterns. A single year of very low or zero fitness would drive
456 extinction in the granite habitat in the absence of a seed bank (Figure S5), and *M. laciniatus*

457 would still maintain higher geometric-mean total fitness than the native *M. guttatus* in meadow
458 habitat (Figure S5).
459
460 DISCUSSION
461 In this study, we investigated spatial and temporal variation in selection on two sympatric
462 Monkeyflower species, *M. guttatus* and *M. laciniatus*. We compared multiple large-scale
463 replicated reciprocal transplants conducted in low (2013, 2021, 2022) and high (2019, 2023)
464 snowpack years including one extreme year resulting in episodic selection (Figure 1a, b). We
465 found that key environmental variables such as soil moisture, temperature, and light intensity
466 fluctuated over space and time, impacting fitness and phenotypic plasticity. Using experimental
467 hybrids, we found fluctuating selection on phenotypic traits involved in reproductive isolation
468 and microhabitat adaptation. Within each year, phenotypic selection was sometimes contrary to
469 our predicted directions, but we saw a longer-term trend of differences in the magnitude of
470 selection in the direction of species' differences in both flowering time, a key reproductive
471 isolating trait, and leaf shape. Our results also indicate that local adaptation of the parental
472 species fluctuates across years but on average, *M. guttatus* is maladapted to its meadows and that
473 habitat isolation may therefore be asymmetric and temporally dependent. Finally, we find that
474 episodic selection, caused by an extreme snowfall event, may disrupt local adaptation and impact
475 species boundaries.
476
477 *Inter-annual fluctuation in natural selection does not erase signatures of long-term divergence*
478 Temporal and spatial variation in selection has been well studied for its role in maintaining
479 genetic variation within species (Keep et al. 2021; Leidinger et al. 2021; Kelly 2022; Johnson et
480 al. 2023). However, few studies have empirically tested how fluctuating selection influences the
481 strength of reproductive isolation between sympatric species (but see Campbell and Powers
482 2015). Here, we consider this by comparing the relative strengths and direction of phenotypic
483 selection on experimental hybrids between native *Mimulus* habitats and examine how these
484 patterns changed over five repeated transplant experiments.
485
486 Although there were interannual fluctuations in selection (Figure 3), we detected interesting
487 longer-term patterns aligned with species differences, particularly for leaf lobing and flowering

488 time, a key pre-zygotic isolating barrier in the *M. guttatus* species complex (Lowry et al. 2008;
489 Figure 4). Previous studies have found that later-flowering *M. guttatus* tend to exhibit higher
490 fecundity (Mojica and Kelly 2010; Mojica et al. 2012), especially in a longer, high snowpack
491 growing season with lowered desiccation risk. In our study, flowering time selection was
492 negative in both habitats, yet in three out of four years with comparable phenotypic selection
493 data between habitats, there was stronger selection for earlier flowering time in *M. laciniatus'*
494 granite habitat as predicted by species differences (Figure 3k). The high snowpack year of 2019
495 was the exception with stronger fecundity selection for early flowering in *M. guttatus'* meadows
496 than in granite habitat (Figure 3k), indicating a temporary relaxation of divergent selection.
497
498 Selection on leaf lobing also fluctuated across years, where selection favored the direction of
499 species differences in our binomial analyses in low snowpack years whereas in high snowpack
500 years the direction reversed to be opposite our predictions (Figure 3h). This pattern of the
501 direction of selection on leaf shape switching with snowpack is supported by the significant
502 interaction between leaf lobing and snowpack in our across-year model (Table S7). The precise
503 adaptive function of leaf shape variation in this system is not known but may be related to
504 temperature or drought tolerance as leaf shape affects the leaf boundary layer and the rates of
505 heat and gas exchange with the air (Nicotra et al. 2011). Two other rocky outcrop species in the
506 *M. guttatus* complex have also evolved lobed leaves, *M. filicifolius* and some populations of
507 serpentine adapted *M. guttatus* (Ferris et al. 2015). Further, repeated altitudinal clines in leaf
508 shape have been found in *M. laciniatus* populations (Love and Ferris 2023). These repeated
509 evolutionary patterns, along with evidence of selection for lobed leaves in granite in some years,
510 suggest that lobed leaf shape is indeed adaptive in these species, even though the direction of
511 selection is not stable across time.
512
513 Annual selection on flower width fluctuated unpredictably across years and our combined
514 analysis revealed weak selection for smaller flowers (Figure 3, Figure 4, Table 1, Table 2). This
515 runs counter to species differences as *M. guttatus* typically has larger flowers than *M. laciniatus*.
516 Flower size affects reproductive success and can contribute to population differentiation and
517 reproductive isolation (Bradshaw et al. 1995; Brunet 2009; Schiestl and Schluter 2009; Venail et
518 al. 2010; Krizek and Anderson 2013). Flower size is often correlated with plant size indicating

519 that early flowering, small stature, and small flowers are linked (Troth et al. 2018). Previous
520 work has demonstrated antagonistic pleiotropy in *M. guttatus* where later flowering alleles also
521 increase plant and flower size (Mojica et al. 2012; Monnahan and Kelly 2015). Although plants
522 with larger flowers have increased fecundity, they simultaneously reduce viability, resulting in
523 net selection for smaller flowers (Mojica and Kelly 2010). In contrast, our findings of selection
524 for early flowering, small flowers, and larger plants in both habitats across years suggests that in
525 our species' these traits are genetically distinct (Tables 1, 2). Although we initially predicted
526 selection for smaller plant sizes in granite based on *M. laciniatus's* short stature, our findings
527 suggest that larger plants always have higher fecundity. This is in line with broader evidence that
528 body size at reproduction is a key determinant of fecundity across taxa (Aarseen and Taylor
529 1992; Aarssen and Jordan 2001; Kingsolver and Pfennig 2004). Despite selection for larger
530 sizes, average plant height remained smaller in granite than in meadow habitats (Table S9, Table
531 S10, Table S11), likely reflecting ecological constraints imposed by limited water and nutrient
532 availability in rocky outcrops. Finally, we found weak selection on herkogamy, suggesting that
533 selection on stigma-anther separation is no longer as strong as during the earlier stages of
534 speciation (Harder and Johnson 2009).
535
536 Across these traits, our combined dataset revealed longer-term differences in patterns of
537 selection on flowering time, plant size, and leaf shape between habitats (Table 1, Table 2; Figure
538 4, Figure S3). We detected stronger selection for early flowering time in granite than meadow
539 habitat which aligns with our predictions based on species' differences, likely contributing to
540 temporal reproductive isolation as seen in other *Mimulus* species (Hall and Willis 2006; Lowry et
541 al 2008). This pattern of spatial variation in selection is consistent with findings from other
542 systems; for example, Ågren et al. (2017) demonstrated that selection on flowering time varies
543 temporally in Italian and Swedish *A. thaliana* populations but that overall, there is stronger
544 selection for earlier flowering in Italy. Further, we found a distinct signature of differential
545 selection on leaf lobing in predicted directions with positive selection for lobing in the granite
546 outcrops, but nearly no selection on leaf shape in *M. guttatus*'s meadow habitat. Lobed leaf
547 shape is thought to be involved in adaptation to dry, exposed habitats like *M. laciniatus's* rocky
548 outcrop environment (Nicotra et al. 2011; Ferris et al 2015; Ferris 2019) and therefore appears to
549 be involved in habitat isolation between these species (Ferris and Willis 2018; Tataru et al.

550 2023). Taken together, the signatures of divergent selection on flowering time and leaf shape
551 across multiple transplants suggests ongoing adaptive differentiation and that fluctuating
552 selection has not erased long-term maintenance of species boundaries (Chapurlat et al. 2020).
553
554 *M. guttatus is locally maladapted*
555 Organisms are expected to have a fitness advantage over other genotypes in their home
556 environment because spatial heterogeneity should favor the evolution of local adaptation
557 (Hastings 1983). However, temporal changes in environmental conditions are theorized to
558 constrain adaptation if there are opposing selection pressures over time (Stearns 1992) which
559 may negatively impact reproductive isolation and species boundaries. We predicted that if
560 habitat isolation is an important reproductive isolating barrier between our sympatric *Mimulus*,
561 then there would be a fitness advantage of the local species in each habitat. Instead, we found
562 that local adaptation fluctuated temporally (Figure 5m-q) with evidence of average local
563 maladaptation of *M. guttatus* (Figure 5r). Annual fluctuations in snowpack were predictive of
564 relative fitness of the parent species in granite with *M. laciniatus* and *M. gutta*tus performing
565 equally well in high snowpack years (5n,q), but in low snowpack years the drought adapted *M.*
566 *laciniatus* had the home-site advantage (Figure 5m,o,p).
567
568 Although local adaptation is thought to be ubiquitous in natural populations (Hereford 2009),
569 fitness trade-offs are not always found in reciprocal transplants (Bennett and Lenski 2007;
570 Lowry et al. 2009). For example, in his classic metanalysis Hereford (2009) found evidence of
571 weak trade-offs associated with adaptation of populations suggesting that local adaptation is
572 often not costly. It is possible that our reciprocal transplant did not detect existing trade-offs due
573 to logistical constraints or that there are weak to no fitness trade-offs associated with adaptation
574 for *M. laciniatus* across environments (Fry, 1996; Leimu & Fischer, 2008). It is also possible that
575 *M. guttatus* lines used in the transplant were negatively affected by inbreeding depression, as a
576 largely outcrossing species. However, this is unlikely as intrapopulation crosses and inbred lines
577 performed similarly in the 2023 experiment (Table S3). Alternatively, an increase in dramatic
578 interannual environmental fluctuations due to anthropogenic climate change may mean that *M.*
579 *guttatus* is no longer at its adaptive optima. Our results could indicate an adaptive lag where, due
580 to recent rapid climate change and increasing drought, the adaptive landscape of *M. guttatus's*

habitat has changed to be more *M. laciniatus*-like and *M. guttatus*'s evolutionary response has not kept pace (Lane et al. 2012; Mills et al. 2013; Kooyers et al. 2019). This pattern of adaptive lag and local maladaptation has been found in other populations of *M. guttatus* (Kooyers et al. 2019). Over time, this could erode species boundaries by allowing colonization of *M. guttatus's* meadow by *M. laciniatus* potentially increasing hybridization or lead to population extinction.

Asymmetry in local adaptation, or a lack of trade-offs, has been found in other transplant experiments (Hereford 2009; Gosden et al. 2015; Latreille and Pichot 2017; Toll and Willis 2018). In a repeated reciprocal transplant between serpentine and sandstone adapted populations of *Leptosiphon parviflorus,* Dittmar & Schemske (2023) found that while serpentine populations had a temporally consistent local fitness advantage, sandstone populations only had a local advantage in two out of four years. While stable spatial heterogeneity should favor the evolution of local adaptation, temporal fluctuation in the environment should select against local specialization and for phenotypic plasticity (Kawecki & Ebert 2004). The average fitness advantage of *M. laciniatus* across environments could be due to adaptive plasticity, specifically adaptation to a history of environmental heterogeneity in the rocky outcrop habitat (Ghalambor et al. 2015). We found that both *M. guttatus* and *M. laciniatus* exhibit plasticity in the direction of the local species' phenotype in each habitat (Table S9, Table S10, Table S11). *Mimulus laciniatus's* occupation of a harsh, highly variable environment (Figure 2) may have driven the evolution of adaptive plasticity (Via and Lande 1985) allowing it to thrive in both habitats. However, *M. guttatus* was more plastic than *M. laciniatus* in all phenotypes except fitness indicating that plasticity is unlikely to account for *M. laciniatus's* performance advantage across habitats and the lack of fitness trade-offs.

Episodic selection weakens species divergence

The high snowpack of 2023 delayed the onset of spring in mid to high elevations by 4–6 weeks and altered soil moisture, light intensity, and surface temperature regimes (Figure 2). This shift contributed to local maladaptation between parental species (Figure 5j), as signatures of local adaptation in fecundity reappeared when 2023 was excluded (Figure S2). In *M. guttatus's* meadow habitat, the delay was detrimental to hybrids and *M. guttatus* by delaying flowering phenology and reducing fitness. Additionally, no local meadow genotypes flowered before

snowfall, suggesting negative impacts on native populations. However, many individuals remained alive at the first snowfall indicating potential facultative perenniality. Delayed flowering may have resulted from shorter day lengths failing to meet critical photoperiod thresholds (Friedman and Willis 2013; Fishman et al. 2014; Kenney and Sweigart 2016), the absence of end-of-season drought stress due to persistently high soil moisture (Kooyers et al. 2015; Mantel and Sweigart 2019), and unusually low light intensity (Figure 2). In contrast, *M. laciniatus* was less affected, likely because it flowers rapidly under shorter daylengths (Friedman and Willis 2013; Ferris and Willis 2018; Love and Ferris 2024).

In granite habitats, the delayed season in 2023 fostered unusually favorable environments for the non-native *M. guttatus* with high water availability, lower light intensity and surface temperatures, and a longer growing season than is typical in granite (Figure 2). This led to higher *M. guttatus* survival in granite (12% of total planted; 24 individuals) compared to previous years (0-2% of total planted). Although *M. guttatus* still had lower survival than *M. laciniatus*, it had remarkably high fecundity (Figure 5e,k) producing total fitness comparable to *M. laciniatus* for the first time (Figure 5q). Unlike the meadow habitat, all plants had senesced and many set seed before snowfall. This suggests that drought stress, rather than photoperiod, is more important as a flowering cue in *M. lacinaitus's* habitat. High-elevation populations of *M. laciniatus* may also possess increased plasticity in critical photoperiod (Love and Ferris 2024).

Our results demonstrate how extreme climatic events may disrupt species boundaries. The atypical conditions of 2023 produced unusually strong selection opposite of predicted directions on key traits involved in adaptation and reproductive isolation: flowering time, flower size and leaf lobing (Figure 3). In the long term, such episodic selection may shift parental ranges, promote hybrid swarms or a new hybrid species (Grant and Grant 1993), or alter adaptive potential (Campbell-Staton et al. 2017). The rarity and unpredictability of extreme climatic events complicate predictions about the evolutionary response to climate change. More longitudinal field studies are needed to understand long-term evolutionary consequences of extreme climatic events and changing climatic patterns on plant species on their native ranges (Anderson 2016; Bailey and van de Pol 2016). For instance, do these events drive evolutionary change and does this outweigh selection acting during 'normal' periods? For species with limited

ranges, such as the Sierra Nevada endemic *M. laciniatus*, will these events influence extinction risk of populations?

Conclusions

Our repeated reciprocal transplants reveal how fluctuating selection influences species' boundaries. The foreign advantage of *M. laciniatus* in the non-native meadow habitat across years suggests either low adaptation costs to the granite habitat or recent maladaptation of *M. guttatus* due to environmental shifts. Furthermore, longer-term divergent selection on flowering time and leaf shape should reinforce temporal and habitat isolation between these species. However, the lack of consistent divergent selection on other key traits could lead to eventual species fusion. Finally, a bout of episodic natural selection due to extreme snowfall shifted population dynamics with potential long-term impacts on species' range, abundance, and gene flow. Our study illustrates the strength of integrating field experiments across multiple spatial and temporal scales to gain a deeper understanding of the maintenance of biodiversity under environmental change (Wadgymar et al. 2017; Dittmar and Schemske 2023; Oakley et al. 2023).

COMPETING INTERESTS

None declared.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study will be openly available in [repository name] at http://doi.org/[doi], reference number [reference number], upon acceptance of the manuscript.

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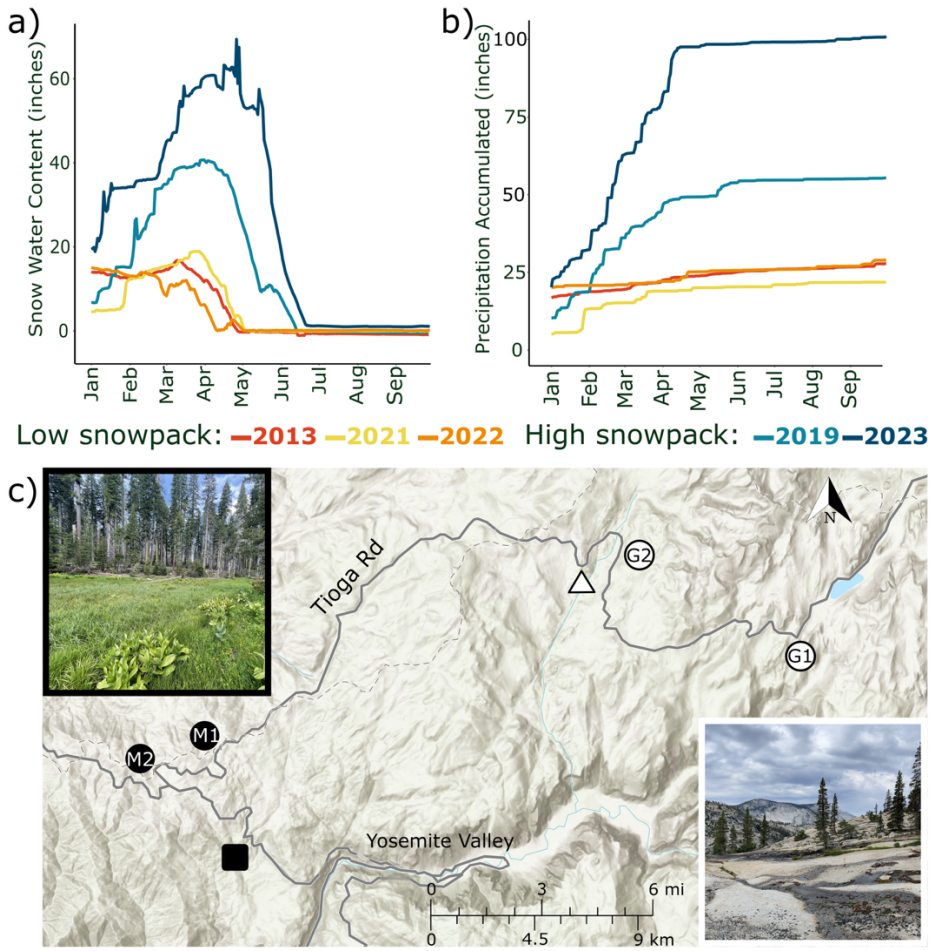


Figure 1. Temporal and spatial scale of the experimental design. Annual changes in a) snow water content and b) accumulated precipitation during experimental years of low snowpack (2013, 2021, 2022) and comparatively higher snowpack (2019 and 2023). Data are averaged from the California Department of Water Resources data stations GIN, WHW, and TUM, located nearby experimental sites along Tioga Road in Yosemite National Park (cdec.water.ca.gov). The c) spatial layout of experimental sites: meadow 1 and 2 (M1 and M2; filled circles) and granite 1 and 2 (G1 and G2; open circles). Nearby parental source populations for experimental crosses are shown: *M. guttatus* YVO (filled square) and *M. laciniatus* WLF (open triangle). Photos of representative meadow and granite habitats are shown in the insets.

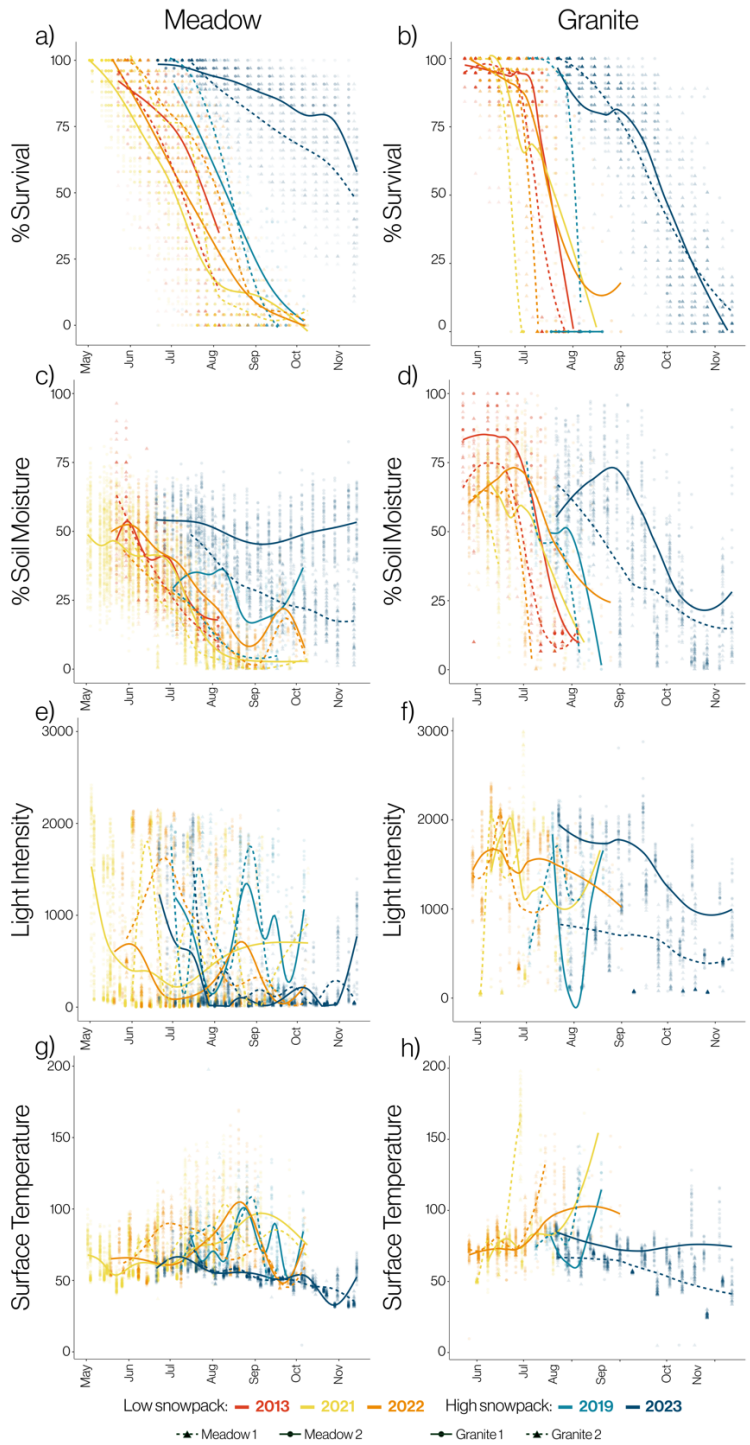


Figure 2. Seasonal changes in (a,b) survival (%), (c,d) soil moisture (%), (e,f) light intensity (µmol m-2 s-1), and (g,h) soil surface temperature (°F) in each block per site in meadow and granite habitats in low snowpack years (2013, 2021, 2022) and high snowpack years (2019, 2023). Data from 2013 and 2019 are published in Ferris and Willis 2018 and Tataru *et al*. 2023 and re-analyzed here.

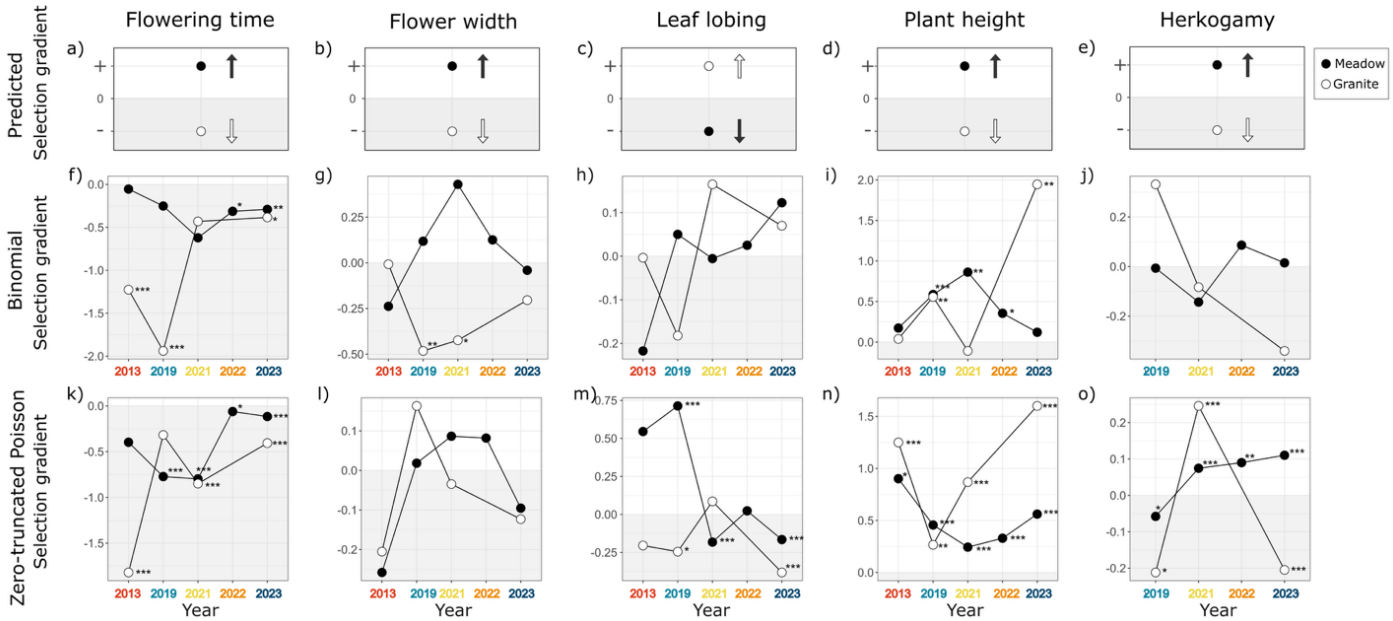


Figure 3. Visual representation of selection gradients (β) of phenotypic traits measured for hybrids during experimental years in granite (open circles) and meadow (filled circles) habitats. Shown are (a-e) predicted values in each habitat based on native species trait differences and estimated values from (f-j) binomial models and (k-o) zero-truncated Poisson models. Significance of each β value is indicated with asterisks (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$) and negative graph areas are shaded grey for clarity. All β values are based on seed number, except for values from 2013 which are based on fruit number, as seed number was not recorded. Data from 2013 and 2019 are published in Ferris and Willis 2018 and Tataru *et al*. 2023 and re-analyzed here.

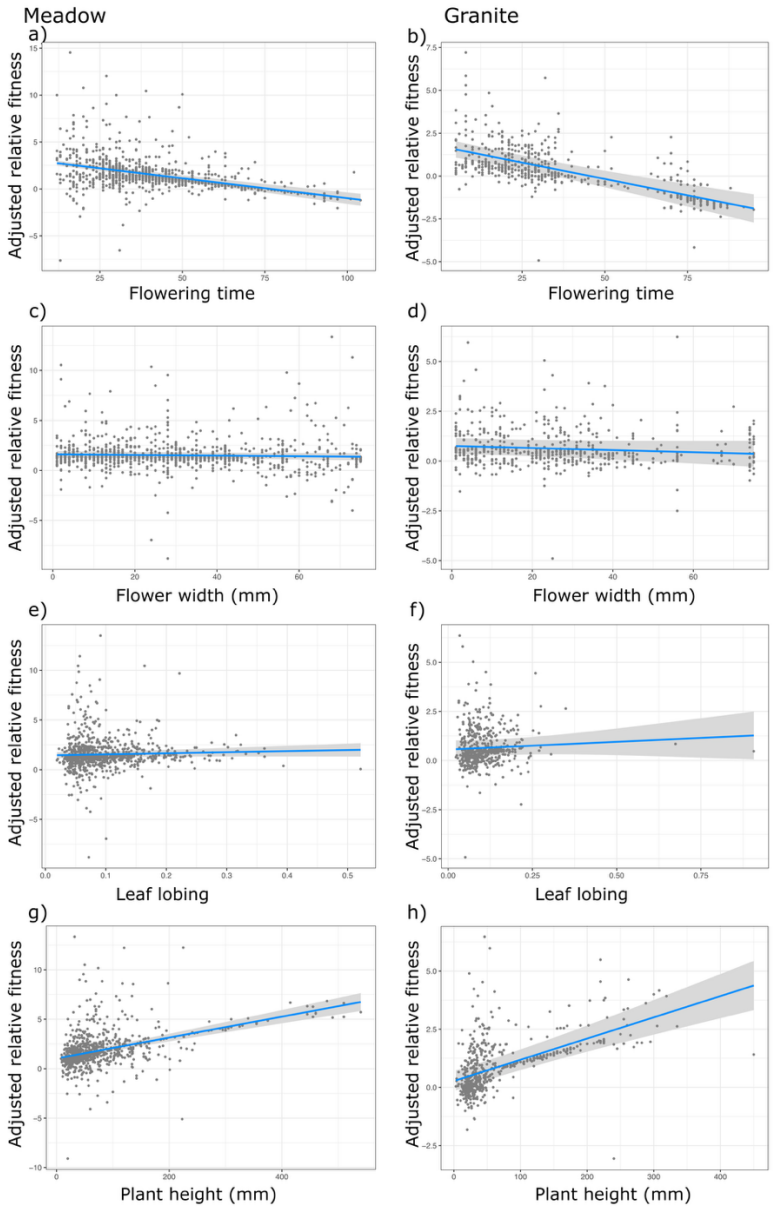


Figure 4. Patterns of cumulative selection with all years combined in meadow (left) and granite (right) habitat in a zero-truncated Poisson analysis on (a,b) flowering time (days from planting), (c,d) width of first flower (mm), (e,f) leaf lobing index, and (g,h) plant height at flowering (mm to apical meristem). Y-axes show adjusted relative fitness (fruit number), statistically corrected for other variables included in the models, and the x-axes show unstandardized trait values for biological relevance. Data from 2013 and 2019 are published in Ferris and Willis 2018 and Tataru *et al*. 2023 and re-analyzed here.

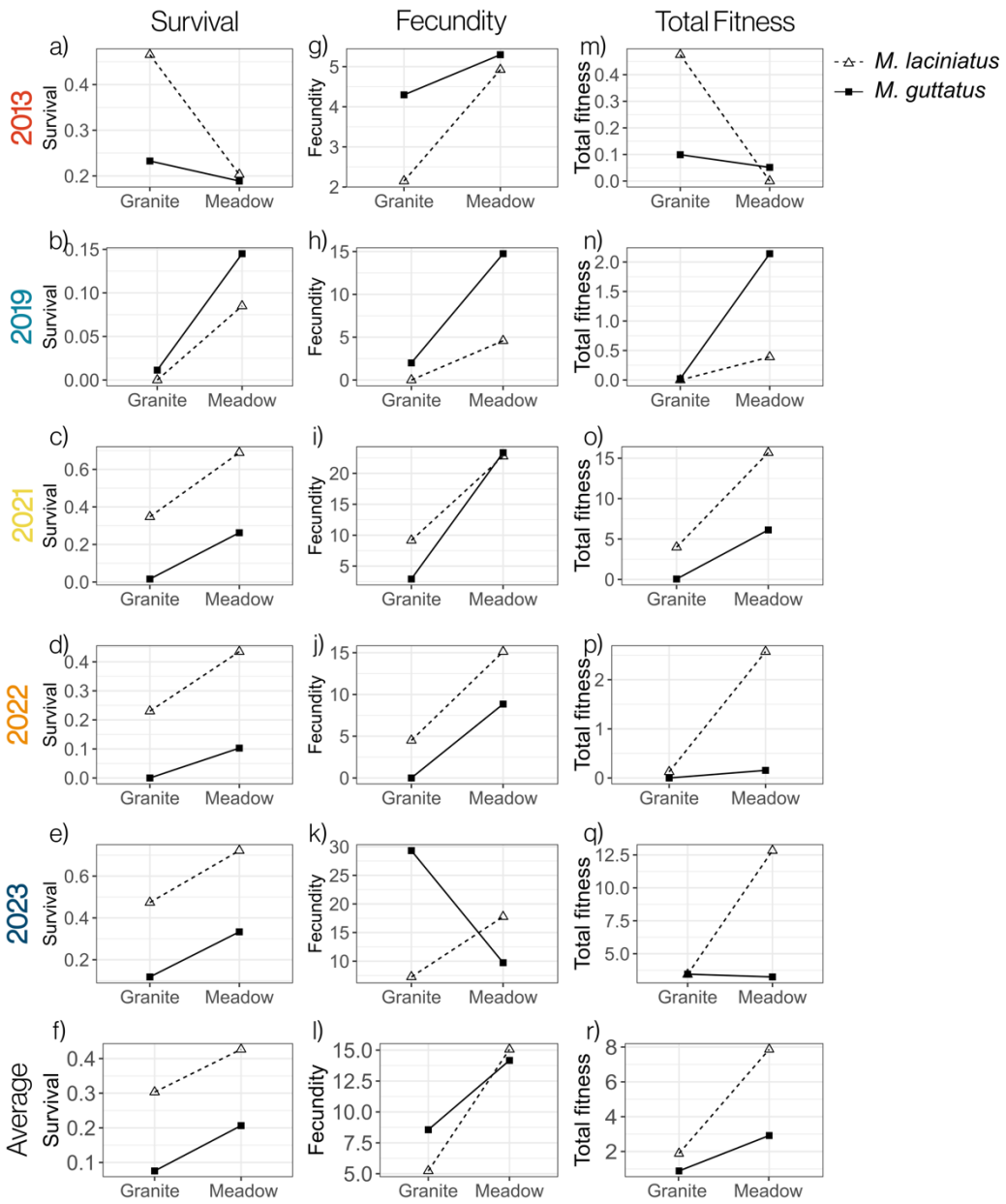


Figure 5. Survival to flowering (a-f), fecundity (mean seed number per reproductive individual; g-l), and total fitness (mean seed number per planted seed; m-r) of *Mimulus guttatus* (filled square, solid line) and *M. laciniatus* (open triangle, dashed line) in granite and meadow habitats, from each experimental year and the average (arithmetic mean) across years (f, l, r). Calculations of fecundity and total fitness for 2013 are based on fruit number because seed number was not recorded; 2013 was omitted from averaged fecundity and total fitness. Values from 2013 and 2019 are from Ferris and Willis 2018 and Tataru *et al*. 2023.

936 **Table 1**. Binomial analysis relating phenotypes to fitness, with fitness defined as whether or not
937 a plant produced fruit (2013) or seeds (2019, 2021, 2022, 2023). A combined dataset of all years
938 used fruit number for fitness. The strengths of selection for linear selection gradients are
939 represented as β values. Asterisks indicate significance of selection in a trait: * $p < 0.05$, ** $p <$
940 0.01, *** $p < 0.001$. Herkogamy was excluded from the combined analysis due to its absence
941 from the 2013 dataset. Phenotypic data from 2013 and 2019 are published in Ferris and Willis
942 2018 and Tataru *et al.* 2023 and re-analyzed here.

	Meadow					
Trait	**2013**	**2019**	**2021**	**2022**	**2023**	**Combined**
Flowering time	-0.054	-0.252	-0.622	-0.314*	-0.291**	-0.018
Flower width	-0.238	0.118	0.429	0.125	-0.041	0.044
Leaf lobing	-0.217	0.050	-0.005	0.025	0.123	-0.025
Herkogamy	NA	-0.006	-0.143	0.086	0.015	NA
Plant height	0.173	0.587***	0.863**	0.355*	0.121	0.290 ***
	Granite					
Trait	**2013**	**2019**	**2021**	**2022**	**2023**	**Combined**
Flowering time	-1.226***	-1.938***	-0.431	NA	-0.385*	-0.438 **
Flower width	-0.008	-0.482**	-0.424*	NA	-0.204	-0.223 **
Leaf lobing	-0.004	-0.182	0.165	NA	0.070	0.062
Herkogamy	NA	0.331	-0.083	NA	-0.340	NA
Plant height	0.038	0.557**	-0.109	NA	1.946**	0.144

943

Table 2. Zero-truncated Poisson analysis relating phenotypes to fitness, with fitness defined as the number of seeds produced, on individual experimental years of 2013, 2019, 2021, 2022, and 2023 and on a combined dataset of all years. The strengths of selection for linear selection gradients are represented as β values. Asterisks indicate significance of selection in a trait: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Herkogamy was excluded to from the combined analysis due to its absence from the 2013 dataset. Phenotypic data from 2013 and 2019 are published in Ferris and Willis 2018 and Tataru *et al.* 2023 and re-analyzed here.

	Meadow					
Trait	**2013**	**2019**	**2021**	**2022**	**2023**	**Combined**
Flowering time	-1.132	-1.479***	-1.333***	-0.110*	-0.168***	-1.018***
Flower width	-0.276	0.021	0.075	0.088	-0.096	-0.059
Leaf lobing	0.613	0.609***	-0.362***	0.051	-0.182***	0.058
Herkogamy		-0.053*	0.089***	0.133**	0.110***	
Plant height	0.669*	2.022***	0.708***	0.749***	0.858***	0.912***
	Granite					
Trait	**2013**	**2019**	**2021**	**2022**	**2023**	**Combined**
Flowering time	-5.183***	-0.609	-1.419***		-0.590***	-0.918***
Flower width	-0.219	0.174	-0.030		-0.120	-0.100
Leaf lobing	-0.229	-0.209*	0.170		-0.421***	0.043
Herkogamy		-0.196*	0.295***		-0.203***	
Plant height	0.927***	1.179**	2.526***		2.457***	0.786***

Supplementary Information

Fig S1 Density histograms of hybrid and parental values for phenotypic traits in 2021, 2022, and 2023.

Fig S2 Visual representation of selection gradients (β) of phenotypic traits measured for hybrids during experimental years in granite (open circles) and meadow (filled circles) habitats. The models do not include herkogamy. Shown are values from (f-j) binomial models and (k-o) zero-truncated Poisson models. Significance is indicated with asterisks (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$) and negative graph areas are shaded grey for clarity. All β values are based on seed number, except for values from 2013 which are based on fruit number, as seed number was not recorded. Data from 2013 and 2019 are published in Ferris and Willis 2018 and Tataru *et al*. 2023 and re-analyzed here.

Fig S3 Patterns of cumulative selection with all years combined in meadow and granite habitats in a binomial analysis.

Fig S4 Combined survival to flowering, fecundity, and total fitness excluding 2023.

Fig S5 The average (geometric mean) of a) survival, b) fecundity, and c) total fitness across experimental years for *Mimulus guttatus* (filled square, solid line) and *M. laciniatus* (open triangle, dashed line) in granite and meadow habitats. 2013 was omitted from averaged fecundity and total fitness. Values from 2013 and 2019 are from Ferris and Willis 2018 and Tataru *et al*. 2023.

Table S1 Hybrid genotypes and generations used each experimental year, with sample sizes of each genotype planted at each site with total experimental sample sizes.

Table S2 Intrapopulation parental crosses used in the 2023 experiment.

Table S3 Hybrid trait correlations in meadow and granite habitats for 2021-2023.

Table S4 Binomial analysis on whether or not a plant produced fruits.

Table S5 Zero-truncated Poisson analysis on number of fruit produced if any were produced.

Table S6 Strength of correlations between fruit number and seed number.

Table S7. Summary of models described in methods.

Table S8 Model selection for best fit models of plant survival and environmental variables.

Table S9 Trait means, standard error, standard deviation, and coefficient of variation from 2021.

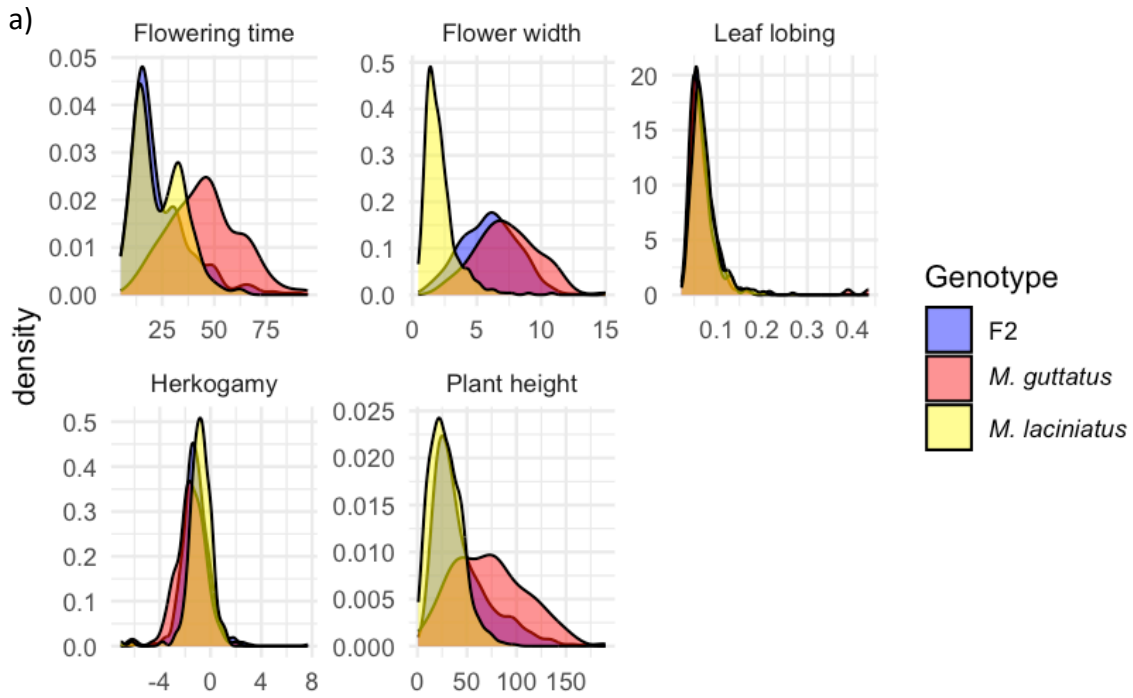
Table S10 Trait means, standard error, standard deviation, and coefficient of variation from

2022.

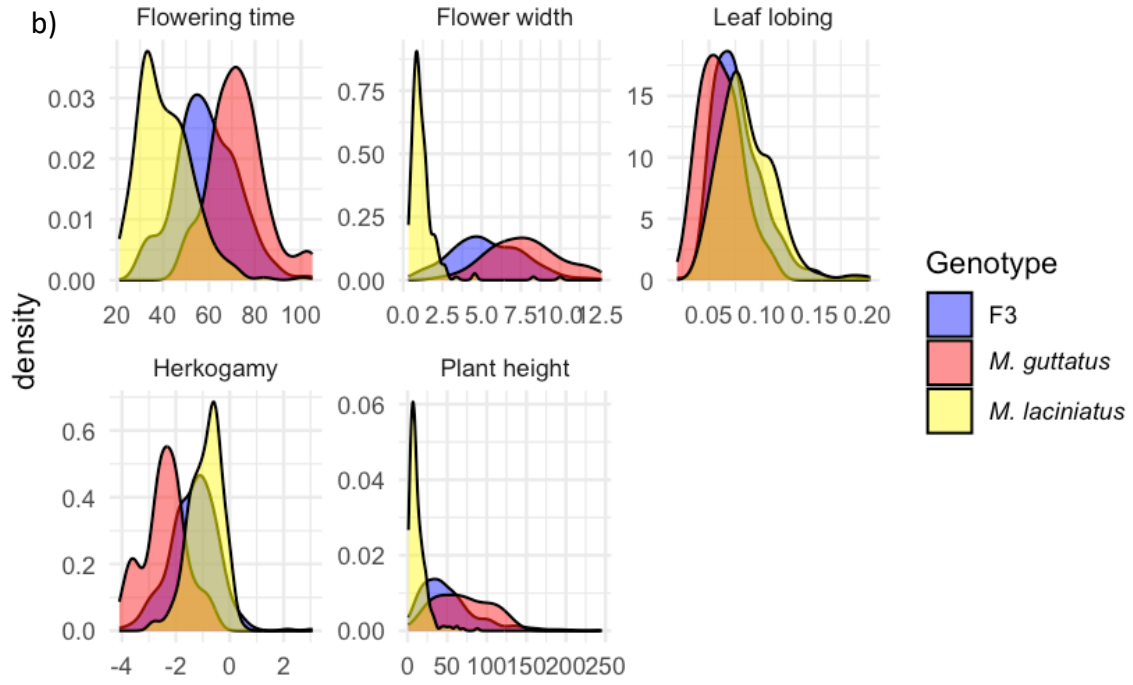
Table S11. Trait means, standard error, standard deviation, and coefficient of variation from 2023.

Table S12. Generalized linear mixed models examining phenotypic plasticity between years and habitat. Models included the phenotypic trait as the dependent variable, habitat and year with their interaction as fixed effects and block nested within site as a random effect.

Table S13. Significance of genotype (G), environment (E), and genotype by environment (GxE) interactions for each fitness term.


a)
Flowering time
Flower width
Leaf lobing
Herkogamy
Plant height
density
Genotype
F2
M. guttatus
M. laciniatus

997


b)
Flowering time
Flower width
Leaf lobing
Herkogamy
Plant height
density
Genotype
F3
M. guttatus
M. laciniatus

998
999

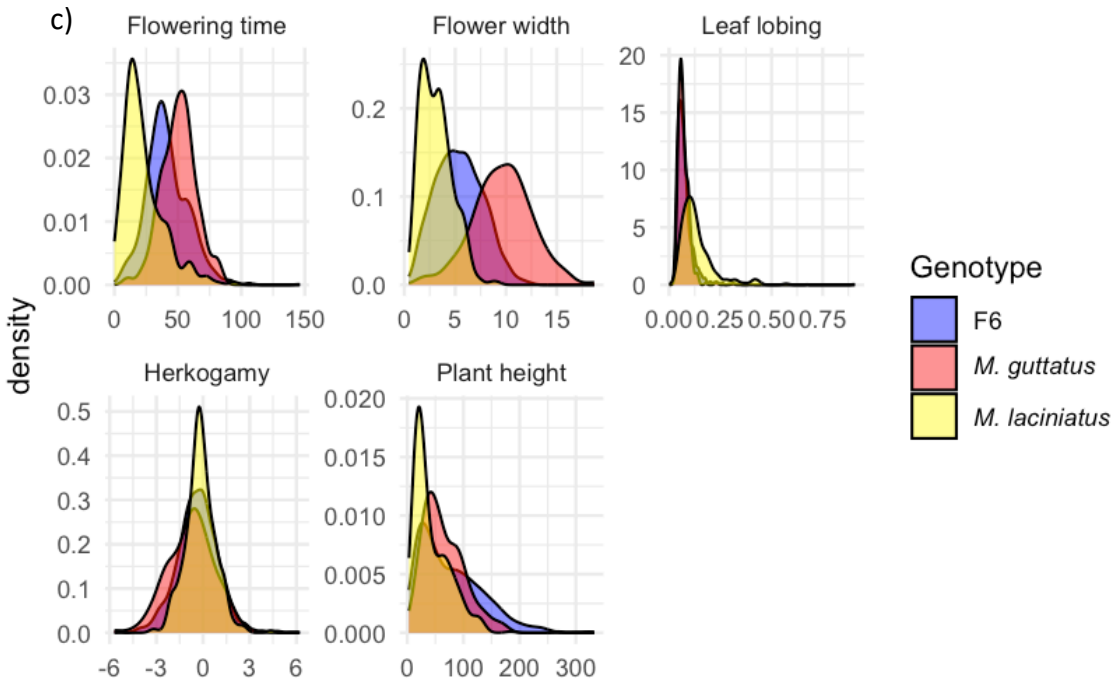


Figure S1. Density histograms of hybrid and parental values for phenotypic traits (flowering time, flower width, leaf lobing, herkogamy, plant height) in a) 2021, b) 2022, and c) 2023.

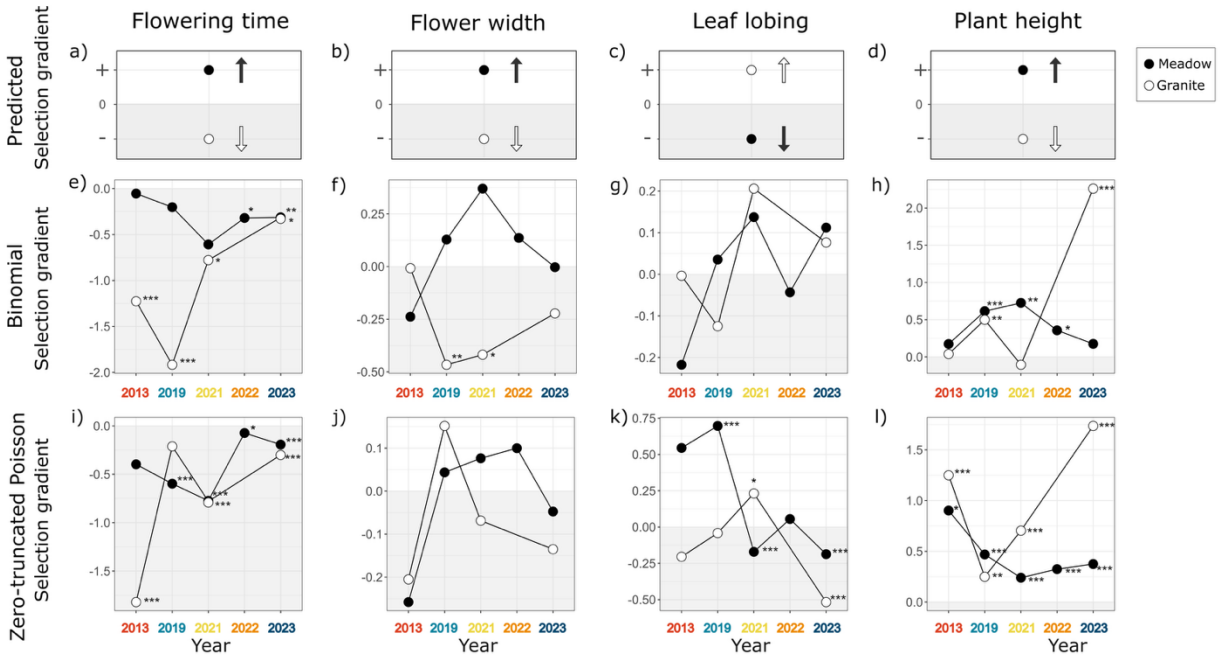


Figure S2. Visual representation of selection gradients (β) of phenotypic traits measured for hybrids during experimental years in granite (open circles) and meadow (filled circles) habitats. Models exclude herkogamy. Shown are (a-d) predicted values in each habitat based on native species trait differences and estimated values from (e-h) binomial models and (i-l) zero-truncated Poisson models. Significance of each β value is indicated with asterisks (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$) and negative graph areas are shaded grey for clarity. All β values are based on seed number, except for values from 2013 which are based on fruit number, as seed number was not recorded. Data from 2013 and 2019 are published in Ferris and Willis 2018 and Tataru et al. 2023 and re-analyzed here.

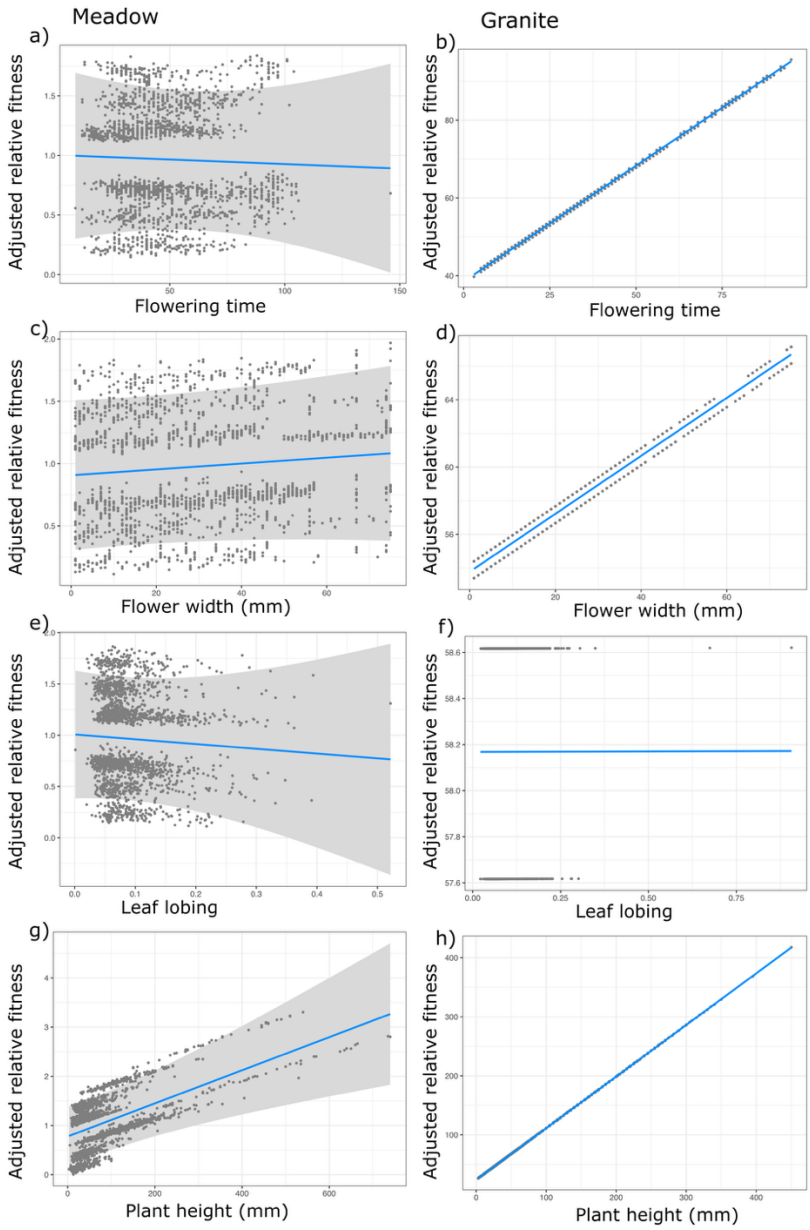


Figure S3. Patterns of cumulative selection with all years combined in meadow andgranite habitats in a binomial analysis on flowering time (days from planting), width of first flower (mm), leaf lobing index, and plant height at flowering (mm to apical meristem). Y-axes show adjusted relative fitness (fruit number), statistically corrected for other variables included in the models, and the x-axes show unstandardized trait values for biological relevance. Data from 2013 and 2019 are from Ferris and Willis 2018 and Tataru *et al.* 2023 and re-analyzed here.

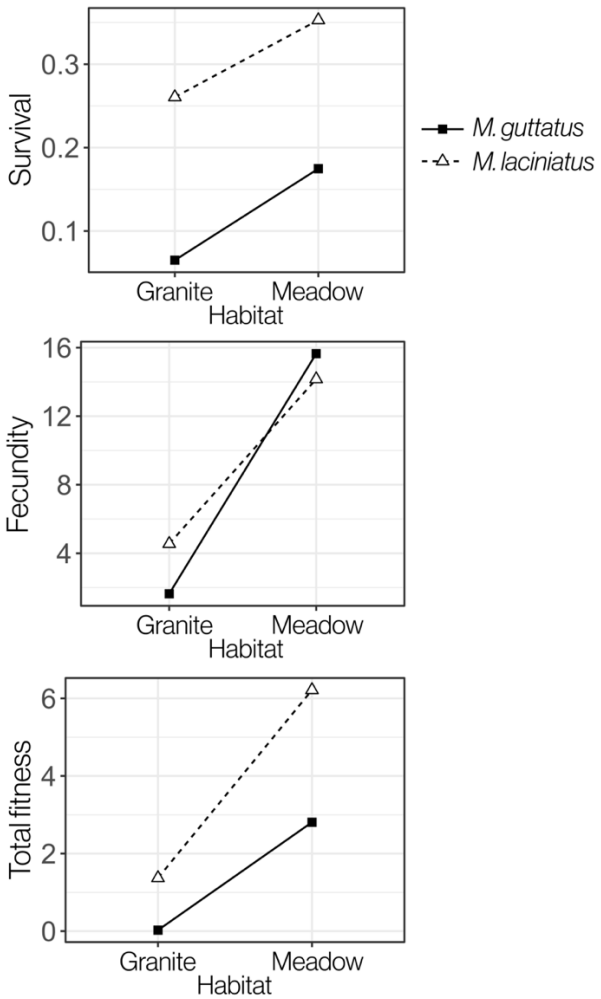


Figure S4. Combined survival to flowering, fecundity (mean seed number per reproductive individual), and total fitness (mean seed number per planted seed) of *Mimulus guttatus* (filled square, solid line) and *M. laciniatus* (open triangle, dashed line) in granite and meadow habitat from 2013-2022 excluding 2023. 2013 was omitted from fecundity and total fitness calculations because seed number was not recorded, only fruit number. Values from 2013 and 2019 are from Ferris and Willis 2018 and Tataru *et al.* 2023.

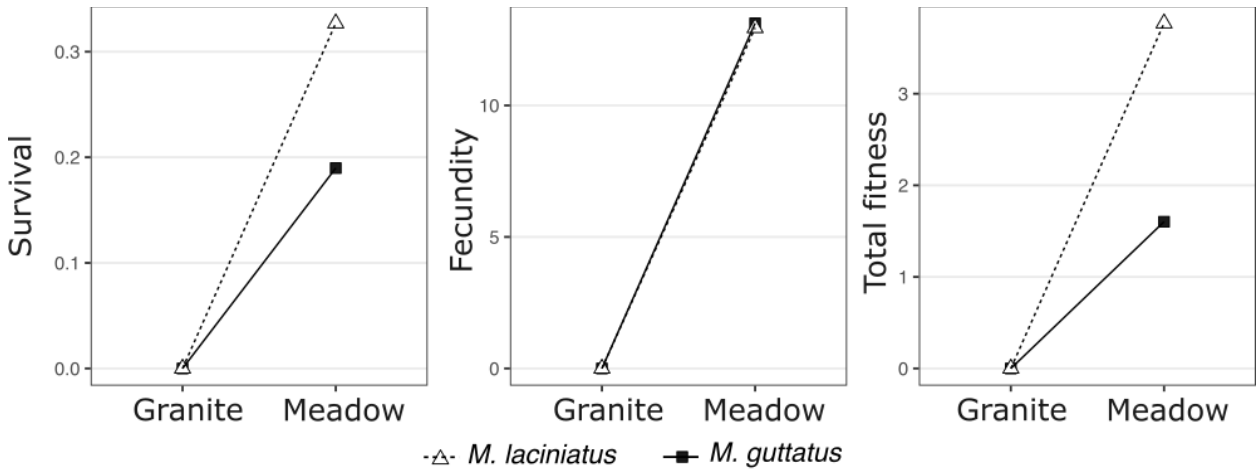


Figure S5. Combined survival to flowering, fecundity (mean seed number per reproductive individual), and total fitness (mean seed number per planted seed) of *Mimulus guttatus* (filled square, solid line) and *M. laciniatus* (open triangle, dashed line) in granite and meadow habitat from experimental years. These values represent geometric means. 2013 was omitted from fecundity and total fitness calculations because seed number was not recorded, only fruit number. Data from 2013 and 2019 are from Ferris and Willis 2018 and Tataru *et al.* 2023 and re-analyzed here.

Table S1. Hybrid genotypes and generations used each experimental year, with sample sizes of each genotype planted at each site with total experimental sample sizes. The maternal genotype (WLF 47) is *M. laciniatus*, and the paternal genotypes (YVO 6 and 18) are *M. guttatus*. Details of the 2013 and 2019 experiments are published in Ferris and Willis 2018 and Tataru *et al.* 2023.

Year	Hybrid genotype	Granite 1	Granite 2	Meadow 1	Meadow 2	Total
2013	F4 WLF 47 maternal x YVO 6 paternal	750 hybrids, 100 maternal, 100 paternal	750 hybrids, 100 maternal, 100 paternal	750 hybrids, 100 maternal, 100 paternal	750 hybrids, 100 maternal, 100 paternal	3,800
2019	F4 WLF 47 maternal x YVO 6 paternal	600 hybrids, 60 maternal, 60 paternal	660 hybrids, 44 maternal, 88 paternal	750 hybrids, 71 maternal, 100 paternal	750 hybrids, 50 maternal, 100 paternal	3,333
2021	F2 WLF 47 maternal x YVO 18 paternal	750 hybrids, 750 maternal, 750 paternal	750 hybrids, 750 maternal, 750 paternal	600 hybrids, 600 maternal, 600 paternal	600 hybrids, 600 maternal, 600 paternal	4,050
2022	F3 WLF 47 maternal x YVO 18 paternal	800 hybrids, 200 maternal, 200 paternal	800 hybrids, 200 maternal, 200 paternal	800 hybrids, 200 maternal, 200 paternal	800 hybrids, 200 maternal, 200 paternal	4,800
2023	F6 WLF 47 maternal x YVO 18 paternal	1500 hybrids, 200 maternal, 200 paternal, 200 local parent	1500 hybrids, 200 maternal, 200 paternal, 200 local parent	1500 hybrids, 200 maternal, 200 paternal, 200 local parent	1500 hybrids, 200 maternal, 200 paternal, 200 local parent	8,400

1051 **Table S2**. Intrapopulation parental crosses used in the 2023 experiment. Due to insufficient seed
1052 stock of single crosses of YVO and WLF, we used 2-3 crosses and original inbred lines,
1053 distributed evenly across blocks and sites. With habitats combined, WLF genotypes did not
1054 differ significantly in total seed count (F = 2.324, df = 2, p = 0.099). Similarly, YVO genotypes
1055 also did not differ significantly (F = 1.944, df = 3, p = 0.124).
1056

Habitat	Genotype	Survival to flowering	%Survival	Seed count	Mean Seed Count	Seed SD	N
Granite	WLF60xWLF47	81	44	585	7.31	21.27	184
	WLF61xWLF47	108	66	784	7.26	12.78	164
	WLF47 inbred	0	0	0	NA	NA	51
						Total:	**399**
	YVO18xYVO26	0	0	0	NA	NA	20
	YVO25xYVO18	12	8	417	32.08	67.69	159
	YVO26xYVO18	35	18	961	27.46	51.83	200
	YVO18 inbred	0	0	0	NA	NA	20
						Total:	**399**
Meadow	WLF60xWLF47	97	58	1760	17.25	32.41	166
	WLF61xWLF47	156	83	3201	20.13	33.95	187
	WLF47inbred	35	76	156	4.46	8.43	46
						Total:	**399**
	YVO18xYVO26	26	47	208	8	16.78	55
	YVO25xYVO18	26	23	378	14.54	47.43	114
	YVO26xYVO18	55	32	687	12.27	27.66	171
	YVO18 inbred	26	44	21	0.81	2.77	59
						Total:	**399**

1057

1058

Table S3. Hybrid phenotypic correlations in meadow (grey shaded; lower triangle) and granite (upper triangle) habitats for a) 2021, b) 2022, and c) 2023. Asterisks indicate significant (* = p < 0.05, ** = p < 0.01. *** = p < 0.001).

(a)

	Flowering Time	Leaf Area	Leaf Lobing	Flower Width	Plant Height	Herkogamy
Flowering Time		-0.21***	-0.04	-0.08*	0.04	-0.08**
Leaf Area	-0.38**		-0.04	0.30***	0.75***	0.02
Leaf Lobing	0.02	0.11**		0.15*	0.35*	0.10
Flower Width	0.15**	0.07	0.03		0.62***	0.14**
Plant Height	0.50***	0.30**	0.10	0.58***		0.01
Herkogamy	0.06	-0.08	0.07	-0.07	-0.07	

(b)

	Flowering Time	Leaf Area	Leaf Lobing	Flower Width	Plant Height	Herkogamy
Flowering Time		-0.13	-0.12	0.24	-0.14	0.03
Leaf Area	0.01		-0.04	0.01	0.02	-0.01
Leaf Lobing	0.00	-0.06		-0.38	0.36	0.44*
Flower Width	-0.01	0.27***	-0.08		-0.31	-0.06
Plant Height	0.06	0.52***	-0.05	0.65***		-0.04
Herkogamy	-0.07	-0.10	0.13	-0.10	-0.13	

(c)

	Flowering Time	Leaf Area	Leaf Lobing	Flower Width	Plant Height	Herkogamy
Flowering Time		-0.14	0.04	0.29	0.88***	-0.32
Leaf Area	-0.16		0.10***	0.24	0.58***	-0.08
Leaf Lobing	-0.02	0.13		0.11	0.44	-0.07
Flower Width	0.07*	0.17	0.03		0.69***	-0.17
Plant Height	0.15***	0.33***	0.11**	0.39***		-0.07
Herkogamy	-0.06	0.12	0.03	-0.06	-0.06	

Table S4. Binomial analysis on whether or not a plant produced fruits on individual experimental years of 2019, 2021, 2022, and 2023. The strengths of selection for linear selection gradients are represented as β values. Asterisks indicate significance of selection in a trait: ***p < 0.001; **p < 0.01; *p < 0.05. Data from 2019 are published in Tataru *et al.* 2023 and re-analyzed here.

	Meadow			
Trait	**2019**	**2021**	**2022**	**2023**
Flowering time	-0.189	-0.413	-0.180	0.019
Flower width	0.126	0.391	0.170	0.004
Leaf lobing	-0.086	-0.162	0.038	0.160
Herkogamy	0.113	-0.024	0.056	-0.059
Plant height	0.144	0.879*	0.209	0.116
	Granite			
Trait	**2019**	**2021**	**2022**	**2023**
Flowering time	-0.534	-0.304		-0.177
Flower width	-0.319	-0.497*		0.107
Leaf lobing	-0.255	0.230		0.181
Herkogamy	0.388	-0.026		-0.129
Plant height	0.255	-0.210		2.461***

Table S5. Zero-truncated Poisson analysis on number of fruit produced if any were produced on individual experimental years of 2013, 2019, 2021, 2022, and 2023. The strengths of selection for linear selection gradients are represented as β values. Asterisks indicate significance of selection in a trait: ***p < 0.001; **p < 0.01; *p < 0.05.

	Meadow			
Trait	**2019**	**2021**	**2022**	**2023**
Flowering time	-0.551***	-0.802***	-0.153	-0.691***
Flower width	-0.072	-0.020	0.060	-0.261*
Leaf lobing	0.117	-0.011	0.126	0.049
Herkogamy	-0.027	0.044	-0.146	-0.006
Plant height	0.422***	0.431***	0.521***	0.332**
	Granite			
Trait	**2019**	**2021**	**2022**	**2023**
Flowering time	-0.649***	-0.819**		-0.401*
Flower width	-0.072	0.114		-0.396*
Leaf lobing	0.135	0.009		-0.122
Herkogamy	-0.090	-0.142		0.002
Plant height	0.167***	1.333***		2.678***

Table S6. Strength of correlations between fruit number and seed number calculated using Kendall's correlation analysis.

Year	Habitat	τ	p	n
2021	Meadow	0.56	0.001	1296
	Granite	0.59	0.001	809
2022	Meadow	0.64	0.001	545
2023	Meadow	0.75	0.0001	1393
	Granite	0.69	0.0001	480

1089 **Table S7.** Summary of models described in methods.

Description of analysis	Model	Reference
plasticity	glmmTMB(trait ~ Habitat + (1|Site/Block))	Table S9, S10, S11
trait correlations	lmer(trait1 ~ trait2 + (1|Site/Block))	Table S3
survival and plant survival	glmmTMB(cbind(successes, failures) ~ soil*days*light*temp +(1|Site/Block), family = binomial)	Figure 2, Table S8
herbivory between habitats	glmer(herbivory ~ Habitat + (1|Site/Block), family = binomial)	Results text (environmental variation causes spatial and temporal variation in survival)
herbivory and fitness	glmer(seed ~ herbivory*Habitat + (1|Site/Block), family = poisson)	Results text (environmental variation causes spatial and temporal variation in survival)
phenotypic (2019-2023), with family=binomial or truncated_poisson	glmmTMB(seed ~ lobingz2 + plheightz2 + flwidthz2 + DaysToz2 + outcrossz2 + (1|Site/Block))	Figure 3, Tables 1 and 2
phenotypic (2013), with family=binomial or truncated_poisson	glmmTMB(fruit ~ lobingz2 + plheightz2 + flwidthz2 + DaysToz2 + (1|Site/Block))	Figure 3, Table 1, 2
phenotypic without outcrossing (2019-2023), with family=binomial or truncated_poisson	glmmTMB(seed ~ lobingz2 + plheightz2 + flwidthz2 + DaysToz2 + (1|Site/Block))	Figure S2
phenotypic with fruit (2019-2023), with family=binomial or truncated_poisson	glmmTMB(fruit ~ lobingz2 + plheightz2 + flwidthz2 + DaysToz2 + outcrossz2 + (1|Site/Block))	Table S4, S5
phenotypic (years combined), with family=binomial or truncated_poisson	glmmTMB(fruit ~ DaysToz + flwidthz + lobingz + plheightz + (1|Site/Block) + (1|year))	Figure 4, S3
snowpack and phenotypic traits, with family=binomial or truncated_poisson	glmmTMB(fruit ~ (DaysToz + flwidthz + lobingz + plheightz)*swc + (1|Site/Block) + (1|year))	Results text (Interannually fluctuation versus long-term directional selection)
GxE (survival)	glmer(survival ~ genotype*Habitat + (1| Site/Block), family - binomial(ink="logit"))	Figure 5
GxE (fecundity)	lmer(fecundity ~ genotype* Habitat + (1|Site/Block))	Figure 5
GxE (total fitness)	lmer(total_Fitness ~ genotype* Habitat + (1|Site/Block))	Figure 5

Table S8. Best-fit models of plant survival and environmental variables. For each best-fit model, we report the df, Log(L), the likelihood score; AIC score, and delta(i), the difference between that model and the next top model's AIC.

Year	Habitat	Model	df	Log(L)	AIC	delta(i)
2021	meadow	survival ~ days + light + soil + temp + (1 | Site/Plot) + days:light + days:soil + light:soil + light:temp + soil:temp	12	-7994.438	16013	1.17
2021	granite	survival ~ days + light + soil + temp + (1 | Site/Plot) + days:soil + days:temp + light:temp + soil:temp	11	-1231.031	2484.5	0.12
2022	meadow	survival ~ days + light + soil + temp + (1 | Site/Plot) + days:light + days:temp + light:soil + light:temp	11	-4057.269	8136.7	0.22
2022	granite	survival ~ days + light + soil + temp + (1 | Site/Plot) + days:light + days:temp + light:temp + soil:temp	11	-1708.705	3439.7	1.82
2023	meadow	survival ~ days + light + soil + temp + (1 | Site/Plot) + days:soil + days:temp + light:temp + soil:temp	11	-4467.387	8956.8	0.15
2023	granite	survival ~ days + light + temp + (1 | Site/Plot)	6	-4348.601	8709.3	0.9

Table S9. Trait means, standard error (SE), standard deviation (SD), and coefficient of variation (CV) from the 2021 experiment. Significant variation in trait means between habitat is indicated by asterisks (p-value < 0.001***; 0.01**; 0.05*).

		Meadow			Granite		
Genotype	**Trait**	**Mean**	**SE**	**CV**	**Mean**	**SE**	**CV**
F_2	Fl. time	31.58***	0.61	0.45	14.57***	0.31	0.43
	Height	57.52***	1.40	0.57	28.43***	0.63	0.45
	Fl. Width	5.89	0.11	0.37	6.09	0.12	0.36
	Leaf area	48864.77**	3838.85	1.57	33811.16**	2769.86	1.52
	Lobing	0.08	0.00	0.45	0.07	0.00	0.37
	Herkogamy	-1.34***	0.05	-0.73	-0.86***	0.07	-1.36
***M. guttatus* (YVO 18)**	Fl. time	44.59	0.99	0.34	35.08	4.23	0.42
	Height	74.65**	2.56	0.46	20.56**	3.50	0.51
	Fl. Width	7.49	0.22	0.33	5.88	0.81	0.36
	Leaf area	50215.94	6314.38	1.47	11519.75	1912.33	0.94
	Lobing	0.08	0.00	0.68	0.06	0.00	0.33
	Herkogamy	-1.63	0.10	-0.76	-0.94	0.31	-0.94
***M. laciniatus* (WLF 47)**	Fl. time	26.7	0.49	0.45	19.21	0.54	0.48
	Height	34.04**	0.75	0.49	20.41**	0.72	0.57
	Fl. Width	1.96**	0.05	0.49	2.55**	0.15	0.73
	Leaf area	16642.84	1268.08	1.46	12059.12	1095.45	1.07
	Lobing	0.08	0.00	0.47	0.07	0.03	0.40
	Herkogamy	-0.92	0.10	-1.17	-0.74	0.08	-1.01

1102 **Table S10**. Trait means, standard error (SE), standard deviation (SD), and coefficient of
1103 variation (CV) from the 2022 experiment. Significant variation in trait means between habitat is
1104 indicated by asterisks (p-value < 0.001***; 0.01**; 0.05*).
1105

		Meadow			Granite		
Genotype	**Trait**	**Mean**	**SE**	**CV**	**Mean**	**SE**	**CV**
F_3	Fl. time	59.92*	0.70	0.21	44.19*	3.10	0.32
	Height	54.89*	2.07	0.69	13.14*	1.52	0.53
	Fl. Width	5.52***	0.13	0.41	3.34***	0.30	0.41
	Leaf area	1013.85	77.72	1.31	208.62***	27.30	1.09
	Lobing	0.07***	0.00	0.33	0.09***	0.00	0.24
	Herkogamy	-1.35	0.05	-0.67	-0.92	0.17	-0.77
***M. guttatus* (YVO 18)**	Fl. time	72.66	1.89	0.17	-	-	-
	Height	69.15	5.22	0.48	-	-	-
	Fl. Width	7.73	0.36	0.29	-	-	-
	Leaf area	1788.03*	220.71	0.71	169.69*	22.08	0.47
	Lobing	0.05*	0.00	0.27	0.08*	0.00	0.22
	Herkogamy	-2.40	0.13	-0.33	-	-	-
***M. laciniatus* (WLF 47)**	Fl. time	44.53*	0.83	0.25	34.65*	1.08	0.30
	Height	15.61**	0.99	0.84	7.16**	0.42	0.57
	Fl. Width	1.25	0.08	0.74	1.22	0.14	0.97
	Leaf area	294.09*	22.64	0.97	97.56*	4.31	0.41
	Lobing	0.08*	0.00	0.30	0.09*	0.00	0.29
	Herkogamy	-0.85	0.05	-0.65	-1.01	0.11	-0.71

1106

Table S11. Trait means, standard error (SE), standard deviation (SD), and coefficient of variation (CV) from the 2023 experiment. Significant variation in trait means between habitat is indicated by asterisks (p-value < 0.001***; 0.01**; 0.05*).

		Meadow				Granite			
Genotype	**Trait**	**Mean**	**SE**	**SD**	**CV**	**Mean**	**SE**	**SD**	**CV**
F_6	Fl. time	43.04***	0.28	15.3	0.36	35.77***	0.36	19.67	0.55
	Height	91.71*	1.01	55.14	0.60	25.22*	0.27	14.81	0.59
	Fl. Width	5.62**	0.04	2.23	0.40	4.68**	0.04	2.35	0.50
	Leaf area	14342.24	287.00	15722.42	1.10	6183.81	173.97	9528.94	1.54
	Lobing	0.08	0.00	0.05	0.63	0.08	0.00	0.06	0.75
	Herkogamy	-0.34	0.03	1.4	-4.12	-0.4	0.02	1.09	-2.73
***M. guttatus* (YVO)**	Fl. time	52.94***	0.61	12.14	0.23	44.6***	0.78	15.49	0.35
	Height	76.17***	1.75	34.94	0.46	34.56***	0.84	16.78	0.49
	Fl. Width	9.92	0.13	2.68	0.27	8.69	0.16	3.1	0.36
	Leaf area	18876.1*	942.86	18833.71	1.00	11853.5*	655.40	13091.55	1.10
	Lobing	0.07***	0.00	0.03	0.43	0.08***	0.00	0.02	0.25
	Herkogamy	-0.66	0.08	1.5	-2.27	-1.11	0.07	1.41	-1.27
***M. laciniatus* (WLF)**	Fl. time	24.28	0.71	14.19	0.58	20.68	0.92	18.36	0.89
	Height	58.72*	1.72	34.45	0.59	21.16*	0.56	11.16	0.53
	Fl. Width	3.01*	0.08	1.59	0.53	3.37*	0.07	1.44	0.43
	Leaf area	17699.42	850.63	16991.34	0.96	8788.1	327.31	6537.97	0.74
	Lobing	0.15**	0.00	0.08	0.53	0.11**	0.00	0.07	0.64
	Herkogamy	-0.36**	0.05	0.98	-2.72	0.12**	0.05	0.92	7.67

Table 12. Generalized linear mixed models examining phenotypic plasticity between years and habitat. Models included the phenotypic trait as the dependent variable, habitat and year with their interaction as fixed effects and block nested within site as a random effect.

Trait	Term	Estimate	SE	t-value	p-value	
Flowering time	(Intercept)	7921.79	527.25	15.025	2.28E-48	***
Flowering time	habitat	2587.42	639.39	4.047	5.39E-05	***
Flowering time	year	-3.9	0.26	-14.955	5.81E-48	***
Flowering time	habitat*year	-1.28	0.32	-4.060	5.10E-05	***
Plant height	(Intercept)	-3433.89	809.76	-4.241	2.33E-05	***
Plant height	habitat	5925.78	978.14	6.058	1.65E-09	***
Plant height	year	1.72	0.4	4.301	1.79E-05	***
Plant height	habitat*year	-2.95	0.48	-6.087	1.38E-09	***
Flower width	(Intercept)	105.18	122.4	0.859	0.39	
Flower width	habitat	652.45	144.51	4.515	7.10E-06	***
Flower width	year	-0.05	0.06	-0.823	0.41	
Flower width	habitat*year	-0.32	0.07	-4.519	6.95E-06	***
Leaf area	(Intercept)	-3350437.73	345581.02	-9.695	1.01E-21	***
Leaf area	habitat	1923215.21	415529.75	4.628	3.93E-06	***
Leaf area	year	1663.58	170.92	9.733	7.10E-22	***
Leaf area	habitat*year	-954.01	205.58	-4.641	3.71E-06	***
Leaf lobing	(Intercept)	-370.59	81.29	-4.559	5.47E-06	***
Leaf lobing	habitat	65.65	96.23	0.682	0.495	
Leaf lobing	year	0.18	0.04	4.559	5.47E-06	***
Leaf lobing	habitat*year	-0.03	0.05	-0.682	0.495	
Herkogamy	(Intercept)	-569.84	73.52	-7.751	2.12E-14	***
Herkogamy	habitat	-102.43	164.4	-0.623	0.533	
Herkogamy	year	0.28	0.04	7.739	2.33E-14	***
Herkogamy	habitat*year	0.05	0.08	0.625	0.532	

Table S13. Significance of genotype (G), environment (E), and genotype by environment (GxE) interactions for each fitness term. Significant p-values are in bold ($p < 0.05$). Details of models are in Table S7.

Year	Fitness term	G	E	G*E
2013	**Survival**	Mean sq = 17.8400 F = 17.84 p = 0.706524	Mean sq = 2.1827 F = 2.1827 p = 0.763166	Mean sq = 10.8925 F = 10.8925 **p = 0.001112**
	Fecundity	df = 144.23 F = 0.0072 p = 0.93259	df = 106.14 F = 3.8757 p = 0.5160	df = 143.49 F = 6.6423 **p = 0.01097**
	Total Fitness	df = 595.92 F = 45.096 **p < 0.0001**	df = 196.74 F = 54.167 **p < 0.0001**	df = 595.92 F = 62.473 **p < 0.0001**
2019	**Survival**	NA NA NA	NA NA NA	NA NA NA
	Fecundity	df = 10.1845 F = 0.4372 p = 0.5232	df = 5.6865 F = 0.2081 p = 0.6652	NA NA NA
	Total Fitness	df = 572 F = 0.8102 p = 0.3685	df = 572 F = 1.6206 p = 0.2035	df = 572 F = 0.7691 p = 0.3809
2021	**Survival**	Mean sq = 259.032 F = 259.032 **p < 0.0001**	Mean sq = 121.217 F = 121.217 **p < 0.0001**	Mean sq = 22.394 F = 22.394 **p < 0.0001**
	Fecundity	df = 828.26 F = 0.0846 p = 0.771185	df = 687.43 F = 7.4232 **p < 0.001**	df = 828.26 F = 0.5004 p = 0.479517
	Total Fitness	df = 2469.72 F = 63.472 **p < 0.0001**	df = 223.04 F = 39.951 **p < 0.0001**	df = 2469.72 F = 16.277 **p < 0.0001**
2022	**Survival**	Mean sq = 118.612 F = 118.6124 **p < 0.0001**	Mean sq = 5.397 F = 5.3965 p = 0.984	Mean sq = 0 F = 0.0003 p = 0.986
	Fecundity	df = 299.16 F = 7.3132 **p < 0.001**	df = 153.12 F = 15.9022 **p < 0.0001**	NA NA NA

	Total Fitness	df = 1396.10 F = 32.493 **p < 0.0001**	df = 196.92 F = 24.333 **p < 0.0001**	df = 1396.10 F = 26.408 **p < 0.0001**
2023	**Survival**	Mean sq = 118.612 F = 246.0353 **p < 0.0001**	Mean sq = 8.625 F = 8.6250 **p < 0.0001**	Mean sq = 1.173 F = 1.1729 p = 0.281073
	Fecundity	df = 642.33 F = 4.0579 **p = 0.04438**	df = 244.77 F = 2.4746 p = 0.11699	df = 640.32 F = 26.7453 **p < 0.0001**
	Total Fitness	df = 1340.93 F = 23.236 **p < 0.0001**	df = 219.93 F = 12.279 **p < 0.0001**	df = 1340.93 F = 23.790 **p < 0.0001**
Average	**Survival**	Mean sq = 357.18 F = 357.1792 **p < 0.0001**	Mean sq = 0.14 F = 0.1353 p = 0.2814	Mean sq = 32.78 F = 32.7822 **p < 0.0001**
	Fecundity	df = 877.52 F = 0.105 p = 0.746005	df = 716.72 F = 7.0909 **p = 0.007921**	df = 883.41 F = 0.4224 p = 0.515888
	Total Fitness	df = 3034.37 F = 47.8337 **p < 0.0001**	df = 290.96 F = 46.0596 **p < 0.0001**	df = 3034.37 F = 8.1155 **p < 0.001**