

Gene flow improves fitness at a range edge under climate change

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1 Abstract

2 Populations at the margins of a species' geographic range are often thought to be poorly adapted
3 to their environment. According to theoretical predictions, gene flow can inhibit these range edge
4 populations if it disrupts adaptation to local conditions. Alternatively, if range edge populations are
5 small or isolated, gene flow can provide beneficial genetic variation, and may facilitate adaptation
6 to environmental change. We tested these competing predictions in the annual wildflower *Clarkia*
7 *pulchella* using greenhouse crosses to simulate gene flow from sources across the geographic range
8 into two populations at the northern range margin. We planted these between-population hybrids in
9 common gardens at the range edge, and evaluated how genetic differentiation and climatic differences
10 between edge populations and gene flow sources affected lifetime fitness. During an anomalously
11 warm study year, gene flow from populations occupying historically warm sites improved fitness at
12 the range edge, and plants with one or both parents from warm populations outperformed local
13 plants. The effects of the temperature provenance of gene flow sources were most apparent at early
14 life history stages, but precipitation provenance also affected reproduction. We also found benefits
15 of gene flow that were independent of climate: after climate was controlled for, plants with parents
16 from different populations performed better at later lifestages than those with parents from the
17 same population, indicating that gene flow may improve fitness via relieving homozygosity. Further
18 supporting this result, we found that increasing genetic differentiation of parental populations had
19 positive effects on fitness of hybrid seeds. Gene flow from warmer populations, when it occurs,
20 is likely to contribute adaptive genetic variation to populations at the northern range edge as the
21 climate warms. On heterogeneous landscapes, climate of origin may be a better predictor of gene
22 flow effects than geographic origin.

23 **Impact summary**

24 What limits species geographic ranges on the landscape? One process of interest when trying to
25 answer this question is gene flow, which is the movement of genetic material between populations,
26 as might occur in plants when seeds or pollen move across the landscape. One hypothesis that has
27 been proposed is that gene flow from populations in other environments prevents populations at
28 range edges from adapting to their local habitats. Alternatively, it has been suggested that these
29 populations might benefit from gene flow, as it would provide more genetic material for natural
30 selection to act upon.

31 We tested these predictions in an annual wildflower, *Clarkia pulchella*. We simulated gene flow
32 by pollinating plants from the range edge with pollen from other populations. Then we planted
33 the resulting seeds into common gardens in the home sites of the range edge populations and
34 recorded their germination, survival, and reproduction. The weather during our experiment was
35 much warmer than historic averages in our garden sites, and perhaps because of this, we found that
36 gene flow from warm locations improved the performance of range edge populations. This result
37 highlights the potential role of gene flow and dispersal in aiding adaptation to warming climates.
38 We also found some positive effects of gene flow that were independent of climate. Even after we
39 statistically controlled for adaptation to temperature and precipitation, plants that were the result
40 of gene flow pollinations produced more seeds and fruits than plants with both parents from the
41 same population. Rather than preventing adaptation, in our experiment, gene flow generally had
42 positive effects on fitness.

43 Introduction

44 Species are limited in their geographic extents on the landscape. In many cases, the limits of species'
45 geographic distributions are the result of niche limitation, rather than simply an inability to disperse
46 to suitable areas beyond their current distribution (Lee-Yaw et al., 2016). This raises the question
47 of what prevents populations on the range periphery from adapting to sites beyond the range edge
48 (Antonovics, 1976; Bridle and Vines, 2007), particularly when boundaries are not co-incident with
49 an abrupt shift in the abiotic environment. The putative causes of limits to adaptation at the range
50 edge hinge upon demographic and genetic features of metapopulations (Sexton et al., 2009).

51 If range limits represent limits to adaptation, this could be the result of insufficient genetic
52 variation in range edge populations. Limited genetic variation at range edges is predicted because
53 range edge populations are often characterized as small, with more frequent or severe changes in
54 population size and elevated rates of turnover relative to central populations (Vucetich and Waite,
55 2003). Populations that are on the leading edge of range expansions may also exhibit patterns of
56 low genetic variation as a result of successive founder events (Pujol and Pannell, 2008). Significant
57 declines in neutral genetic variation near range edges is a common (though not ubiquitous) pattern
58 (Eckert et al., 2008; Pironon et al., 2017), indicating that some of these processes are likely to
59 affect some range edges in some species. If the observed declines in neutral variation also reflect
60 reduced adaptive genetic variation, this might result in marginal populations being less locally
61 adapted when compared to central populations, as they have less capacity to respond to local
62 selection pressures. Maladaptation is expected to lead to poor demographic performance, reducing
63 colonization opportunities in sites beyond the range, and potentially creating (or reinforcing) a
64 range edge at equilibrium along an environmental gradient (Kirkpatrick and Barton, 1997).

65 Swamping gene flow is another often-invoked hypothesis for how equilibrial range limits might
66 form and persist (Lenormand, 2002; Sexton et al., 2009). Under swamping gene flow, peripheral
67 populations are unable to adapt to their local conditions because they experience maladaptive gene
68 flow from central populations (Kirkpatrick and Barton, 1997). This process is predicted to occur
69 when populations are arranged along an environmental gradient where individuals are well-adapted
70 and abundant in the center of that gradient. Because of this asymmetry in abundance, net gene

71 flow is asymmetric and brings alleles that are adaptive in central environments to edge popula-
72 tions, disrupting local adaptation to edge environments. This causes edge populations to become
73 demographic sinks, where death rates exceed birth rates, and prevents further range expansion.
74 According to this model, the fitness of edge populations will depend upon the rate of gene flow
75 from center to edge as well as the steepness of the environmental gradient (i.e., the magnitude of
76 environmental differences between the sources of the gene flow and the recipient populations).

77 Comprehensive empirical tests of the swamping gene flow hypothesis are difficult to conduct
78 because they require demonstrating both the negative effects of gene flow on edge populations
79 as well as the occurrence of asymmetric gene flow on the landscape. Evidence to-date indicates
80 that swamping gene flow might limit adaptation along geographic gradients in some systems (Paul
81 et al., 2011) and sometimes limit the geographic range (Fedorka et al., 2012; Holliday et al., 2012).
82 However, in other systems there are no detectable fitness costs of gene flow across environmental
83 gradients (Emery, 2009; Moore and Hendry, 2009; Samis et al., 2016) and strong local adaptation
84 persists despite gene flow (Yeaman and Jarvis, 2006; Gould et al., 2014). Outbreeding depression
85 may generate patterns similar to those resulting from the disruption of local adaptation, but the
86 effects of genetic incompatibilities can be discerned from those of swamping by experimental designs
87 that allow for decoupling of environmental and genetic differentiation.

88 Most theory about swamping gene flow at range edges has been developed with the assumption
89 of smooth environmental gradients underlying the range, however, this assumption is unrealistic
90 for most species. Topography, continentality, and other landscape features make transects from
91 range centers to edges heterogeneous with regards to climate. Other habitat variables, such as soil
92 type or the biotic community (which may mediate responses to climate in addition to imposing
93 selection on their own), are also likely to be spatially heterogeneous. This complicates predictions
94 of the swamping gene flow hypothesis: range edge populations may experience gene flow from
95 environmentally divergent neighboring populations, or environmentally similar central populations,
96 as well as combinations falling anywhere in between. In this case, geography cannot be used as
97 a proxy for predictions about the effects of gene flow, rather, these predictions must be informed
98 by the environmental differences between populations. Gene flow between populations in similar

99 environments may be beneficial, even when populations are geographically disparate, because gene
100 flow can allow for the spread of environment-specific beneficial alleles that arise in a single population
101 (Sexton et al., 2011). Abundant-center distribution patterns and asymmetric gene flow have been
102 documented in some species, but are not ubiquitous (Sagarin and Gaines, 2002), perhaps at least
103 in part as a result of complex environmental gradients.

104 In addition to contributing alleles that are adaptive or maladaptive in a given environment, gene
105 flow may provide relief from homozygosity caused by drift or inbreeding. Gene flow is expected to
106 increase heterozygosity and reintroduce variation that can allow for masking or purging of fixed
107 deleterious alleles. As a result, gene flow can improve fitness in peripheral populations (Sexton
108 et al., 2011). The extent to which gene flow causes heterosis depends upon the genetic divergence of
109 populations (Ingvarsson and Whitlock, 2000), but not explicitly on the magnitude of the environ-
110 mental differences between the source and recipient of gene flow, though environmental differences
111 are correlated with genetic differentiation in some species (Sexton et al., 2014).

112 Gene flow may also be beneficial when maladaptation arises due to disequilibrium between a
113 populations' optimal conditions and the environment. This could occur when a species is undergoing
114 a range expansion, or when the environmental landscape is moving out from under individuals, as is
115 occurring under climate change (Aitken and Whitlock, 2013). If a population is locally adapted to
116 historic conditions in a site, and the environment changes rapidly, then gene flow from populations
117 with historic conditions that are more similar to these new local conditions is expected to improve
118 population performance.

119 To investigate how gene flow affects peripheral populations, we simulated gene flow among
120 populations spanning the northern half of the range of an annual wildflower, *Clarkia pulchella*,
121 and measured lifetime fitness of individuals in two common gardens at the species' northern range
122 edge. We asked 1) Are range edge populations of *C. pulchella* locally adapted? 2) What climatic
123 factors predict fitness at the northern range edge? 3) Does gene flow positively or negatively affect
124 edge populations? and 4) How does the effect of gene flow from other populations depend upon
125 the genetic differentiation and climatic distances of these populations? Under conditions where
126 the range edge is not at equilibrium with climate, we expect that gene flow from sites that are

historically similar to the experimental conditions will improve performance. Under conditions in which this species' range is at equilibrium with climate, and if this edge is limited by adaptation, we expect that gene flow from populations in similar climates will have a positive effect on fitness via heterosis or the contribution of adaptive alleles, but that gene flow from strongly contrasting climates will be detrimental. If populations have genetic incompatibilities (which need not be the result of divergent selection, but could simply be the result of drift under prolonged separation) then we expect the offspring of crosses between populations that are more genetically divergent to perform worse, regardless of the conditions of the test environment. However, if heterozygosity is positively related to fitness we expect a greater benefit from gene flow between more genetically divergent populations.

Methods

Study system, seed collection, and site selection

Clarkia pulchella Pursh (Onagraceae) is a winter annual that grows on sparsely vegetated, south-facing slopes with low canopy cover throughout eastern Washington and Oregon, Idaho, and western Montana (United States) and southeastern British Columbia (Canada). This species germinates in fall and overwinters as a seedling before flowering in late May, June, and early July. It has no observed seed dormancy, but seeds will not germinate immediately upon dehiscing and require an after-ripening period of several weeks. It has showy pink flowers and is visited by a diverse array of pollinators though it has some capacity to self-pollinate in the absence of pollinators or mates (MacSwain et al., 1973; Bontrager et al., 2018). Individual plants typically produce fewer than 10 flowers, though some larger individuals may produce up to *c.* 100 on occasion.

Seeds of *C. pulchella* were collected from 15 populations in July 2014 (Figure 1A; Table S1). We used the two northwestern-most populations of the continuous distribution of *C. pulchella* as common garden sites (hereafter referred to as focal populations). Other populations (hereafter, donor populations) were selected with the goal of sampling representative variation in major climatic axes (temperature, precipitation, and seasonality of these variables; Figure 1B) across the northern

153 half of the species' range. In each of these populations, seeds were collected haphazardly from plants
154 spaced >0.5 m apart.

155 **Greenhouse generation and crossing design**

156 We grew field-collected seeds in the greenhouse and implemented a controlled crossing design to
157 generate seeds for the field transplant. We planted maternal families from each population into
158 22 randomized blocks, with each block containing one family from each population. Two types
159 of crosses were performed: "within-population" crosses and "between-population" crosses. For
160 within-population crosses, dams were pollinated using pollen from the plant of the same population
161 in the subsequent block (Figure S1A). Each plant from each population was therefore used as both
162 a sire and a dam with other plants from the same population. For between-population crosses,
163 flowers on plants from the two focal populations within each block were pollinated using each of
164 the donor plants in that block (Figure S1B). These crosses simulate an early stage of gene flow:
165 the progeny of a mating event that is the result of long distance pollen dispersal (or the progeny of
166 a cross between a native individual and a recent immigrant). We collected the seeds from crosses
167 as fruits ripened. Further details about our greenhouse conditions and crossing design are in the
168 Supplementary Methods.

169 **Common garden design and installation**

170 For the transplant, we used seeds from 15 of our greenhouse blocks, and substituted seeds from the
171 same type of cross from other greenhouse blocks when they were unavailable from our primary 15.
172 Seeds were glued to toothpicks to expedite planting and monitoring in the field. Two seeds were
173 glued to each toothpick with a tiny dab of water-soluble glue (when seeds were limited, just one
174 seed was glued to each toothpick). At each of the two sites, toothpicks were planted into 10 fully
175 randomized plots. Each plot contained two toothpicks from each cross type from each of the 15
176 replicates. We only planted between-population crosses with local dams at each of the two focal sites
177 (i.e., Blue Lake plots only contained between-population crosses performed on Blue Lake plants,
178 and Rock Creek plots only contained between-population crosses performed on Rock Creek plants).

179 Within-population crosses from all populations were planted out at both sites. Therefore, each plot
180 contained two replicates of each of 15 crosses from 29 cross types (14 between-population groups
181 and 15 within-population groups). For some cross types, less than 15 families had sufficient seeds
182 for the full design, therefore each plot contained 832 toothpicks at Rock Creek and 836 toothpicks
183 at Blue Lake. In total, our design included 16,680 toothpicks and 32,755 seeds. Seeds were planted
184 in September 2015. Details of transplant installation are in the Supplementary Methods.

185 **Monitoring and measuring**

186 Germination was censused 16-20 November 2015. We documented the emergence of either 0, 1, or 2
187 germinants at each toothpick. If two germinants were present, these were randomly thinned so that
188 just one remained. Overwinter survival was assessed 17-21 March 2016. During both germination
189 and overwinter survival censuses, plant size was measured as the distance in mm from the tip of
190 one leaf to the tip of the other (most plants had just one pair of leaves). In early June 2016
191 we censused the spring survival of all plants and began measuring reproduction every 2-3 days.
192 As a proxy for seed production, we measured the ovary length of each flower produced on each
193 plant. Pollinators were excluded from our plots to prevent the escape of non-native genotypes,
194 so we calibrated a conversion from ovary length to seed production using hand pollinations (see
195 Supplementary Methods). We continued reproductive censuses until all plants had senesced, but
196 reduced census frequency when flowering slowed in July.

197 **Climatic and genetic differentiation**

198 We compiled monthly temperature and precipitation data from 1951-1980 for all seed sources, as
199 well as the gardens during the months of the experiment (September 2015-July 2016) from PRISM
200 (PRISM Climate Group, 2017). We calculated historic (pre-warming, 1951-1980) climate averages
201 for each site, which we compared to conditions experienced by plants during the transplant in our
202 analyses. Inter-annual climate variability was very similar in each of the seed collection sites (data
203 not shown) so we do not further consider variability in climate, and focus on averages only. Pairwise
204 population genetic differentiation (F_{ST}) was calculated from 2982 SNPs that were genotyped in up

205 to 12 parental individuals from each population. F_{ST} was calculated using the implementation of
206 Weir and Cockerham (1984) in the R package hierfstat (Goudet and Jombart, 2015). These methods
207 are described in full in Bontrager and Angert (2018).

208 **Statistical analyses**

209 **Did local populations outperform foreign populations?**

210 We tested whether local populations were, on average, superior to foreign populations using within-
211 population crosses only. We compared lifetime fitness of local vs. foreign individuals in a generalized
212 linear mixed model (GLMM) with a zero-inflated negative binomial distribution using the package
213 glmmTMB (Brooks et al., 2017). These zero-inflated models allow specification of fixed effects
214 for both the zero-inflation part of the model (the probability of a non-zero value) as well as the
215 conditional part of the model (the effect on the response after accounting for zero-inflation). Gen-
216 erally, we consider the zero-inflation part of the model to reflect early lifestages, as the majority of
217 plants that produced zero seeds did so as a result of failing to germinate or survive winter. The
218 conditional part of the model may reflect both differences during reproduction as well as differences
219 among individuals accumulated across all lifestages. In addition to testing for local adaptation
220 represented by lifetime fitness, we tested whether local populations performed better than foreign
221 populations at any component lifestage: germination, size after germination, overwinter survival,
222 size after winter, fruit count, and estimated seed production. Plant size was modeled with a Gaus-
223 sian response distribution, germination and survival with binomial response distributions and logit
224 link functions, and fruit counts and seed production with zero-inflated negative binomial response
225 distributions and log link functions. For component lifestage analyses, we included only individuals
226 that had survived to the preceding census, and always included plant size at the previous census
227 to account for differences that had accumulated at earlier lifestages. For all of these models we
228 initially included a random effect structure of block within site, dam within dam population, and
229 sire within sire population. However, models of later lifestages and lifetime fitness frequently failed
230 to converge with this parameterization. When convergence failed, we reduced random effects to
231 only block within site and sire population. Predictions and confidence intervals were visualized

232 with ggeffects (Lüdecke, 2018).

233 **Does climate of origin explain performance in common gardens?**

234 We built GLMMs using the methods described above to evaluate the effects of mismatch between
235 the experiment conditions and population’s historic climates on lifetime fitness and all fitness com-
236 ponents, again using only within-population crosses. We calculated the absolute difference between
237 the garden conditions and the historic temperature and precipitation of each source population. We
238 use absolute differences because we expect that mismatch in either direction along a climate axis
239 will negatively impact fitness. Very few source populations were from sites drier or hotter than con-
240 ditions during the experiment, so absolute differences mostly result from source populations being
241 historically cooler or wetter than the experiment. Our lifetime fitness model included absolute dif-
242 ferences in temperature (for the experiment duration, September-July) in both the conditional and
243 zero-inflation parts of the model, as well as absolute differences in spring and summer precipitation
244 (April-July) in the conditional part of the model only. We isolated the specific lifestages affected by
245 each of these climatic predictors using the methods described above. In lifestage-specific analyses,
246 we calculated climate differences using only the months in each census window. In all analyses, all
247 continuous predictors were scaled and centered.

248 **Does gene flow help or hurt edge populations?**

249 Based on the results of the analyses above, we expected that gene flow from some populations was
250 likely to confer benefits by contributing adaptive genetic variation to focal populations experiencing
251 an anomalous climate. To evaluate whether there were benefits of gene flow that were independent
252 of these climate effects, we calculated the midparent historic temperature average for all individuals
253 (that is, the average temperature of dam and sire sites) and then calculated the absolute difference
254 between this temperature and the experimental temperature (Figure S2). We calculated a metric
255 of absolute midparent precipitation difference (averaged over April-July) in the same manner. We
256 used GLMMs as described above to test for an effect of gene flow in addition to an anticipated effect
257 of midparent climate differences on lifetime fitness and each component lifestage. In these models,

gene flow was included as a categorical fixed effect (within-population cross vs. between-population cross) along with midparent temperature and precipitation differences. We included gene flow and temperature differences in both the conditional and zero-inflation parts of the lifetime fitness model, and precipitation differences in only the conditional part. We had difficulty disentangling effects of precipitation differences and gene flow (see Results), so we ran these models with and without precipitation differences.

Do the effects of gene flow depend upon the genetic differentiation between focal and donor populations?

We examined whether the genetic differentiation (F_{ST}) between the two parental populations of the between-population crosses positively or negatively affected offspring fitness. We could only estimate genetic differentiation between parental populations for individuals with parents from different populations, so in these analyses we use between-population crosses only. We built zero-inflated GLMMs as described above using lifetime fitness and included predictors of absolute midparent temperature and precipitation differences as well as F_{ST} . We also tested the effects of these parameters on each component lifestage. Our ability to detect significant effects of climate in full models was limited, likely due to the narrow range of midparent climatic variability across between-population crosses, so we also built separate models of each of our three predictors on lifetime fitness and each lifestage. All statistical analyses were implemented in R version 3.4.3 (R Core Team, 2017).

Results

Climate of origin explains performance in common gardens

Local populations were not superior to the average foreign population in their cumulative fitness across all lifestages, or in any component lifestage (Figure S3, Table S2). Populations that were best matched to experimental temperatures performed best in our gardens; lifetime fitness declined with increasing absolute temperature differences between the source and the experimental conditions (Figure 2A). This occurred via effects on both the probability of producing any seeds (the zero-inflation part of the model; $\beta = -0.341$, $SE = 0.033$, $P < 0.001$; Figure 2B), and the number of

seeds produced (the conditional part of the model; $\beta = -0.114$, $SE = 0.050$, $P = 0.022$; Figure 2C). Local populations, which are historically intermediate in temperature (Figure 1B), were mismatched from the experiment conditions and performed worse than populations from warmer sites that were more climatically similar to the garden conditions.

Analyses of component lifestages support these inferences (Figure 2D, Table S3): being poorly matched to experimental temperatures had negative effects on germination proportion, overwinter survival, and the size of plants after winter. While precipitation differences were not significant in the model of lifetime fitness ($\beta = -0.067$, $SE = 0.049$, $P = 0.177$, Figure 2C), they did have a negative effect on seed production among plants surviving the winter (Figure 2D, Table S3).

Gene flow may confer some benefits to edge populations

As in the analyses of within-population plants only, both midparent temperature differences and midparent precipitation differences had negative effects on lifetime fitness in our common gardens (Table S4A; Figure 3AB). Gene flow (i.e., being a between-population rather than a within-population cross) did not have a significant effect in the lifetime fitness model that also included climate differences.

It is difficult to disentangle the effects of precipitation differences from the effects of gene flow in these analyses. This is because our focal populations are already among the driest provenances in our experiment. Therefore, the average between-population plant is better matched to the experimental conditions than the average within-population plant, because the midparent precipitation of between-population plants is always calculated with at least one very dry focal parent (Figure S2B). This was not an issue with temperature differences, because our focal populations are intermediate to other provenances in terms of temperature (Figure S2A). When lifetime fitness was analyzed without precipitation differences in the model, we found that gene flow (being a between-population cross, rather than a within-population cross), had a positive effect on lifetime fitness in addition to effects of temperature (Table S4B).

A small positive effect of gene flow, independent of climatic differences, is supported by analyses of some lifestage components (Figure 3C; Table S4C). Negative effects of precipitation and tem-

311 perature differences were similar to those found in the analyses of climatic drivers of performance,
312 while gene flow (i.e., being from a between-population vs. a within-population cross) had a positive
313 effect on fruit production and a marginal positive effect on seed production.

314 **Genetic differentiation between parental populations positively affects fitness**

315 Both midparent temperature difference from the garden conditions and genetic differentiation be-
316 tween parental populations had significant effects on fitness (Figure 4, Table S5AB, Table S6A).
317 Genetic differentiation between parental populations had a positive effect on lifetime fitness via
318 increasing the probability of producing seeds (the zero-inflation part of the model). The effects
319 of genetic differentiation on lifetime fitness were mirrored in the analyses of single lifestages: F_{ST}
320 had a positive effect on germination, size after winter, fruit count, and seed production (Figure 4C,
321 Table S5A, Table S6A).

322 The negative effect of midparent temperature differences in between-population crosses is gen-
323 erally consistent with our analyses of climatic drivers of performance in within-population crosses.
324 Between-population plants with donor parents that were well-matched to temperatures during the
325 experiment were more likely to produce seeds, as indicated by the significant negative effect of
326 midparent temperature differences in the zero-inflation part of that model (Table S5B, Table S6A).
327 Midparent temperature differences did not significantly affect any single lifestage, but had marginal
328 negative effects on size after germination, size after winter, and fruit number (Figure 4C, Table S5B).
329 Midparent precipitation differences did not significantly affect lifetime fitness or component lifestages
330 (Table S5C).

331 It is important to note that genetic differentiation is not especially correlated with temperature
332 differences ($r = -0.25$), though genetic differentiation and precipitation differences are correlated (r
333 $= 0.64$), with plants whose parents are more genetically differentiated also having larger differences
334 between their historic midparent precipitation and conditions during the experiment. We think
335 it is unlikely that the apparent positive effects of genetic differentiation are actually driven by
336 precipitation differences, because we would expect high precipitation differences to negatively affect
337 fitness. The overall weak or absent effects of temperature and precipitation differences in these

models may be due to a narrower range of variation in midparent climate for the between-population crosses relative to the within-population crosses (Figure S2).

Discussion

We conducted a common garden experiment at the northern range margin of *Clarkia pulchella* to examine how the effects of gene flow on peripheral populations vary with climatic and genetic differentiation between focal and source populations. We examined predictors of fitness of within-population crosses, in which both parents originated from the same source population, as well as between-population crosses, in which one parent was local to the common gardens and the other was from another population from across the northern half of the range of *C. pulchella*. In our experiment, provenances of *C. pulchella* from climates that most closely matched the conditions during the experiment performed best, even better than local populations. Populations of *C. pulchella* at the northern range margin benefited from gene flow from warm source locations during the warm year of our experiment. Gene flow also conferred some benefits independent of climate, as evidenced by the positive effect of gene flow on later lifestages when controlling for temperature differences and the positive effect of increasing genetic differentiation between the parental populations.

Climate of origin predicts performance

Populations of *Clarkia pulchella* are adapted to their historic climate regimes, a pattern consistent with findings in many other species (Anderson et al., 2015; Wilczek et al., 2014). When grown in common sites, the performance of individuals was determined by the degree to which conditions during the experiment deviated from historic temperature and precipitation averages of each provenance (Figure 2). Because of this local adaptation to climate, gene flow from sites that deviate from local conditions (in our experiment, sites that are cooler than the focal populations) had the potential to disrupt local adaptation, as indicated by the somewhat negative effects of midparent temperature differences on between-population plants (Figure 4, Table S5). Although simulated gene flow from divergent environments had the potential to reduce fitness in this experiment, it is unlikely that gene flow occurs at a high enough rate among natural populations to swamp local

364 adaptation. However, our results highlight that gene flow and dispersal need not be from popula-
365 tions that are geographically distant (or from the center of the range) to be climatically divergent
366 from historic or current conditions. Rather, two of the most temperature-mismatched populations
367 used in the experiment are from sites nearest to our common gardens (populations D1 and D3;
368 Figure 1).

369 Under climate change, local adaptation to historic climate regimes may generate local maladapt-
370 ation in field trials. We see this in our results, where populations from warmer locations performed
371 best in our gardens (Figure 2, Table S3), and gene flow from warmer locations had positive effects
372 on some lifestages (Figure 4, Table S5). This lagging adaptation to climate has been documented
373 in other recent common garden studies. In a reciprocal transplant experiment of a long-lived sedge,
374 McGraw et al. (2015) found that populations were displaced 140 km south of their optimal climate
375 conditions. Wilczek et al. (2014) found that local genotypes of *Arabidopsis thaliana* from across
376 Europe were consistently outperformed in common gardens by accessions from historically warmer
377 locations. These results indicate that dispersal and gene flow are important processes promoting
378 range stasis as climate warms, as they allow alleles that are beneficial in warm environments to
379 spread from historically warm populations to recently warming sites. However, climate is multi-
380 variate, and as the climate changes it may generate combinations of conditions that no population
381 has historically experienced (Williams and Jackson, 2007; Mahony et al., 2017). The particular
382 combination of hot and dry conditions in our common gardens was unlike any of our populations’
383 historic temperature and precipitation combinations (Figure 1), though they are similar to normals
384 from some populations not included in our experiment, primarily from the southern half of the
385 species range (data not shown). While precipitation conditions were similar to those historically
386 experienced by the focal populations, temperature conditions favored another set of populations.
387 Whether the optimal traits for different climatic axes are antagonistic and whether segregation and
388 recombination will allow adaptation to novel climates are important considerations in predicting
389 climate change responses.

390 **Gene flow confers benefits independent of climate**

391 We saw some additional positive effects of gene flow once the effects of climate are controlled for
392 (Figure 3, Table S4). These positive effects may be the result of increased heterozygosity when
393 parental plants come from two different populations; this inference is supported by the positive
394 effect of genetic differentiation between parental populations on performance (Figure 4, Table S5).
395 These results are also generally consistent with previous work in which experimental populations
396 of *Clarkia pulchella* with higher genetic effective population sizes had lower extinction probabil-
397 ities (Newman and Pilson, 1997). An interesting direction for future models of swamping gene
398 flow along environmental gradients might be to explore whether incorporating heterosis-dependent
399 increases in the effective migration rate (Ingvarsson and Whitlock, 2000) alters predictions (this
400 could be done with various dispersal distances, under scenarios of various magnitudes of isolation-
401 by-distance). However, an important question is whether the benefits of reduced homozygosity (or
402 increased heterozygosity) are transient effects among F₁s, how long they would persist in future
403 generations if our between-population plants backcrossed into the focal populations, and whether
404 these benefits may be counteracted by outbreeding depression as recombination disrupts co-adapted
405 gene complexes. The answers to these questions are likely to depend on many factors, including
406 the genetic architecture of local adaptation and population size (Willi et al., 2007), but fitness de-
407 clines in subsequent generations are not uncommon after between-population crosses (Fenster and
408 Galloway, 2000; Johansen-Morris and Latta, 2006). Novel environments may alter the costs and
409 benefits of outbreeding: increases in variation among individuals might help populations adapt,
410 despite temporary decreases in mean fitness due to outbreeding depression.

411 During this study, the effects of being well-matched to the experimental conditions seemed
412 to dominate over potential benefits of being from a local population (for example, the benefits
413 of being adapted to local soil conditions or herbivores). This inference is supported by the fact
414 that lifetime fitness of local populations did not differ from that of foreign populations even once
415 climate differences were controlled for (results not shown) though our experiment was not especially
416 well-suited to test this because we have only two local populations.

417 **Limited inference about population persistence**

418 Our ability to make inferences from our results about the longer-term effects of gene flow on the
419 persistence and adaptive potential of range edge populations is limited. While it seems clear that
420 gene flow from warm sites is likely to accelerate adaptation to warming conditions, we do not know
421 whether these populations were historically limited by adaptation, and whether the additional
422 genetic variation introduced by gene flow would permit better adaptation to local conditions and
423 range expansion on an evolutionary time scale. These types of questions are difficult to test in
424 field systems (but see Etterson and Shaw 2001), but inferences can be made by examining genetic
425 variance of wild populations in the lab (Kellermann et al., 2006; Hoffmann et al., 2003). The
426 development of experimental evolution systems to test equilibrial range dynamics is an exciting
427 avenue for future work—this would be a natural extension of recent studies of range expansion
428 dynamics using experimental evolution in the lab (Ochocki and Miller, 2017; Williams et al., 2016).

429 It is also important to note that all populations in our experiment had reproductive rates
430 that were well above replacement (one seed produced per seed planted, see y-axis on Figure 2A,
431 Figure 4A), so we have no evidence that gene flow has the potential to drive populations extinct,
432 or to rescue them from extinction. The high lifetime fitness we observed during our experiment
433 could be due to several factors. First, perhaps warm conditions over the entire season are favorable
434 for all sources, but are more favorable for warm-adapted populations. Alternatively, we could have
435 increased fitness by limiting antagonistic biotic interactions. Finally, and perhaps most plausibly,
436 our plot placement may have upwardly biased our germination and reproductive estimates. We
437 placed plots in patches that appeared favorable to *C. pulchella*, but naturally dispersing seeds are
438 likely to land in a mix of favorable and unfavorable patches. We do not know whether any of these
439 factors might interact with provenance, in which case they might change the relative performances
440 of populations in our experiment.

441 **Conclusions and future directions**

442 On heterogeneous landscapes, the effects of gene flow are likely to depend strongly on climate
443 of origin, which may be decoupled from geography. Although gene flow from divergent climates

may result in reduced fitness, gene flow can also confer benefits to range edge populations via both preadapted alleles and reduced homozygosity. As a result, moderate rates of gene flow likely represent a net benefit to edge populations, particularly as the environment is changing. This study highlights the challenges of testing hypotheses about equilibrial range limits in the field, where climate change is a persistent reality. Even if populations were once locally adapted, they are likely no longer at equilibrium with climate. The signal of climate anomalies disrupting local adaptation can be detected in published literature to date (Bontrager et al., in prep.). In light of this, future studies of local adaptation at range edges should be designed in such a way that the results will be informative even in non-equilibrial conditions.

Author contributions

MB and ALA conceived of the project. MB performed greenhouse crosses, garden installation, and data collection. MB analysed the data in consultation with ALA. MB wrote the manuscript with advice and edits from ALA.

Data deposition

All data and code required to recreate these analyses is publicly available at github.com/meganbontrager/clarkia-pulchella-transplant. Upon publication, all data and code will be archived in an appropriate repository (e.g., Dryad).

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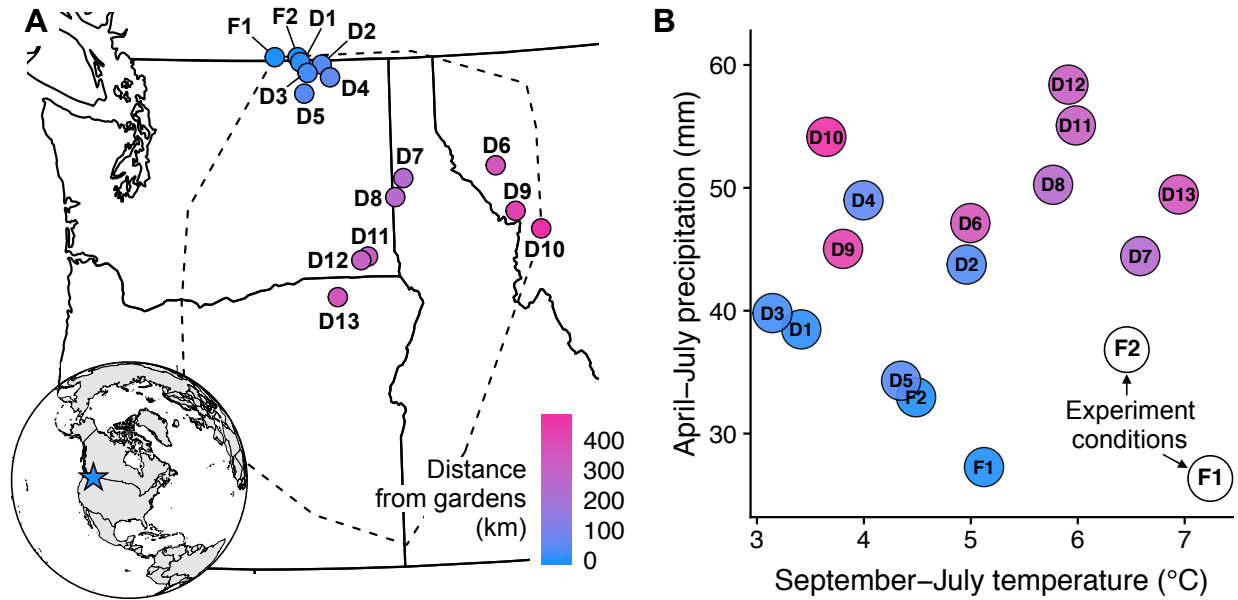


Figure 1 Geographic locations and climate averages of populations used in this experiment. **(A)** Populations span the northern half of the geographic range of *Clarkia pulchella* (indicated by the dashed line). Focal population sites (where common gardens were installed) are indicated by “F” and donor population sites are indicated by “D”. Identifying codes for each population correspond to the Map ID column in Table S1. **(B)** Temperature and precipitation conditions of common gardens and source provenances. Colored circles represent the 1951-1980 average temperature and precipitation in the home site of each population. Open circles represent weather conditions during the experiment. Focal populations are historically intermediate relative to donor populations in average historic temperature (x-axis), but are the from the driest sites of any population used in the experiment (y-axis). Conditions in common gardens during the experiment were hot relative to normal conditions at those sites, and hot and dry relative to average conditions of all populations in the experiment.

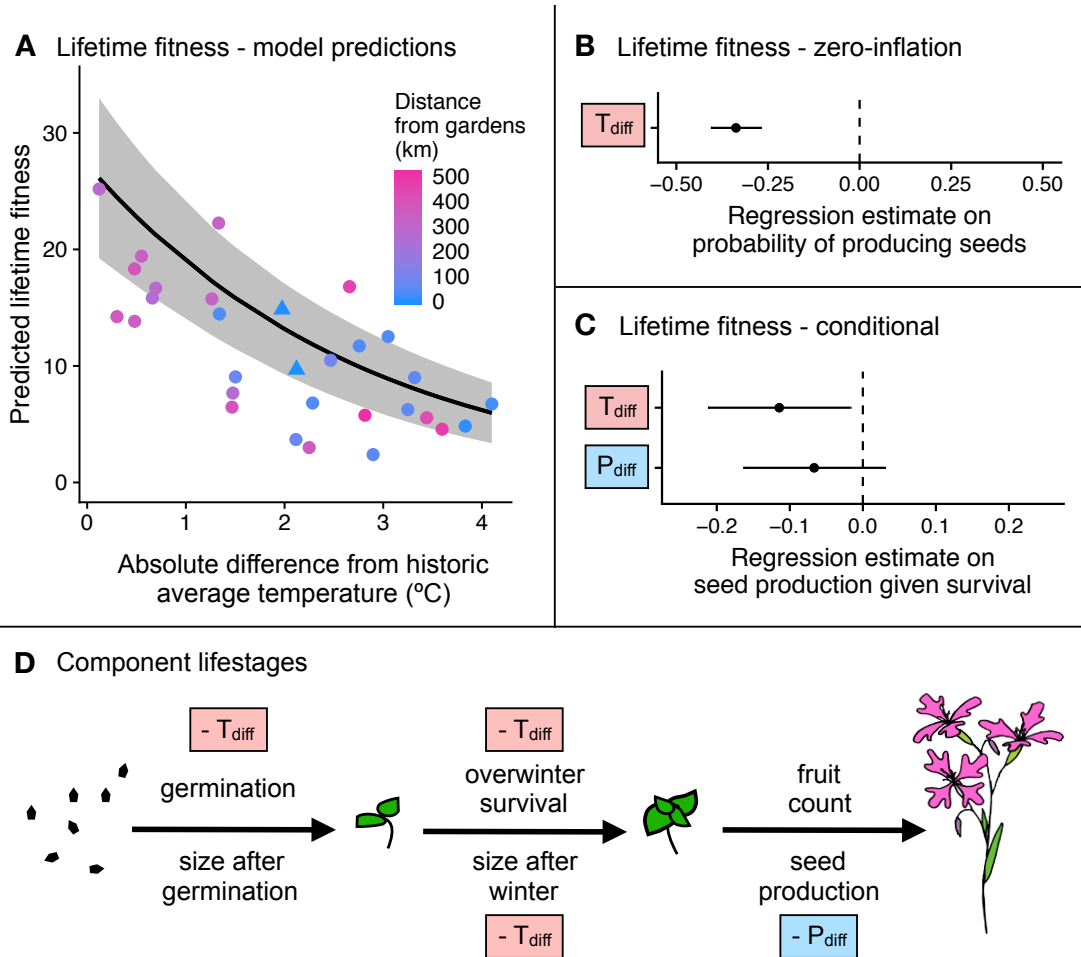


Figure 2 Effects of absolute temperature difference (September-July; T_{diff}) and absolute precipitation difference (April-July; P_{diff}) on performance of *Clarkia pulchella* in common gardens. These analyses include within-population plants only (no gene flow). **(A)** Lifetime fitness declines with increasing differences in temperature between the historic average of the source population and the experimental conditions in the transplant gardens. The shaded area represents the 95% confidence interval of the model estimate conditioned on fixed effects only. Though these temperature differences are expressed as absolute, almost all populations were from sources that are historically cooler than the transplant sites were during the experiment. Points are raw averages for each source population in each garden, colored by the distance between the source population and the transplant garden. Triangles are focal populations in their home sites. **(B)** Regression estimates and standard errors from the zero-inflation part of a model of lifetime fitness. **(C)** Regression estimates and standard errors from the conditional part of a model of lifetime fitness. **(D)** Schematic of effects of absolute temperature differences (T_{diff}) and absolute precipitation difference (P_{diff}) on component lifestages of *Clarkia pulchella*. Directionality of effects is illustrated with “-”; in these analyses all significant effects were negative. Predictors in boxes are significant ($P < 0.05$). Size in the previous lifestage is not shown here, but has a significant positive effect on overwinter and reproductive lifestages. This summarizes the significant results of separate models for each lifestage; full statistical results of these tests are in Table S3.

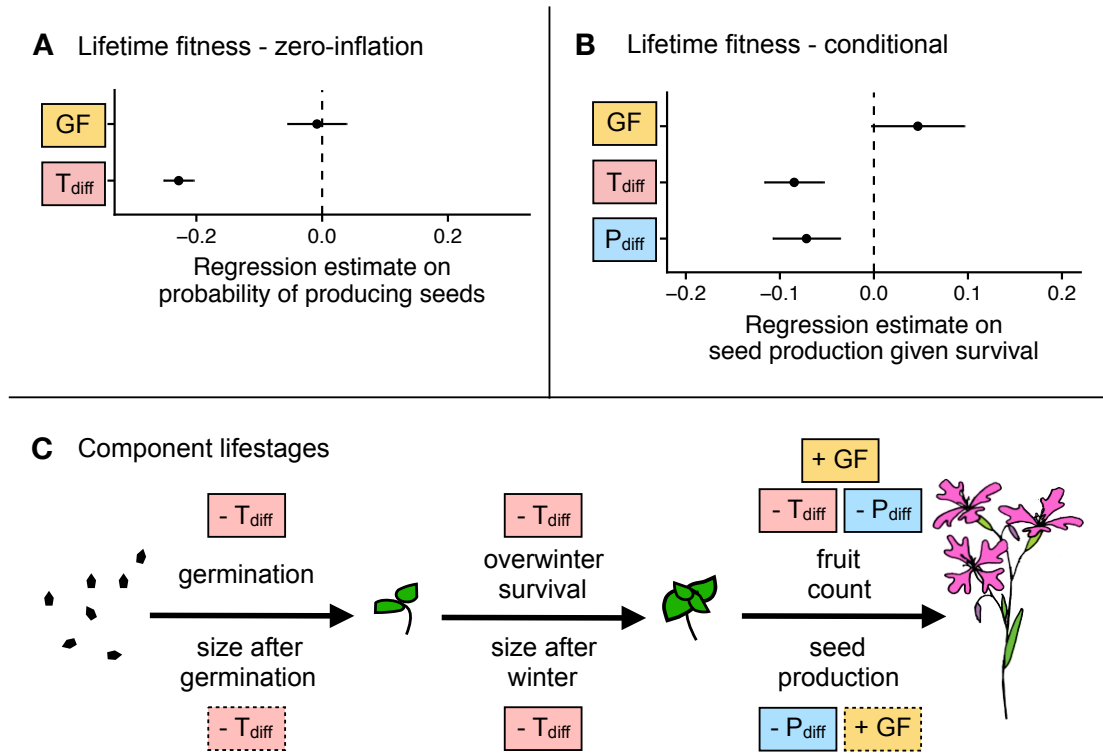


Figure 3 Effects of gene flow (differences between between-population and within-population crosses) on performance of *Clarkia pulchella*, accounting for midparent temperature and precipitation. **(A)** Regression estimates and standard errors from the zero-inflation part of a model of lifetime fitness. **(B)** Regression estimates and standard errors from the conditional part of a model of lifetime fitness. **(C)** Effects of gene flow (GF), absolute midparent temperature differences (T_{diff}), and absolute midparent precipitation differences (P_{diff}) on component lifestages of *Clarkia pulchella*. Directionality of effects is illustrated with “+” and “-”. Marginally significant parameters ($0.05 < P < 0.10$) are shown in boxes with dashed margins, predictors in solid boxes are significant ($P < 0.05$). Size in the previous lifestage is not shown here, but has a significant positive effect on overwinter and reproductive lifestages. This summarizes the significant results of separate models for each lifestage; full statistical results of these tests are in Table S4.

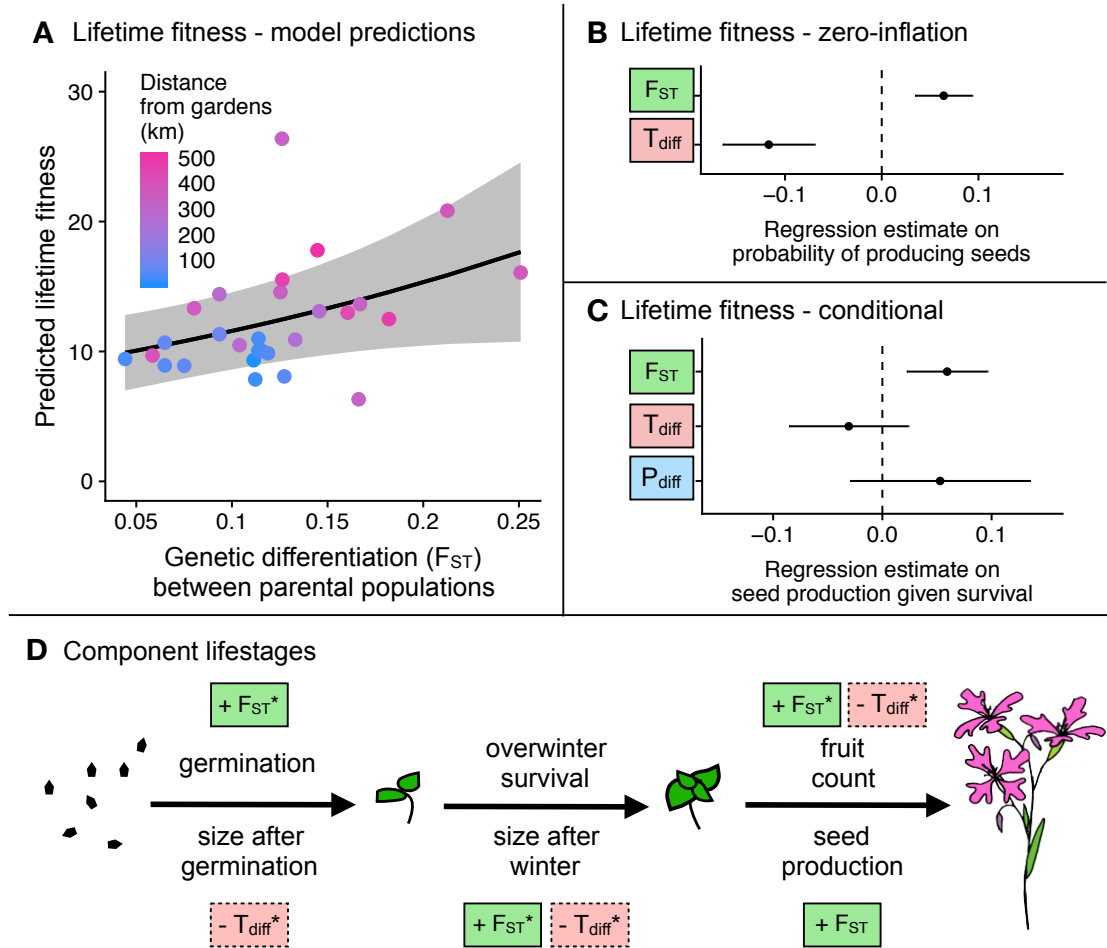


Figure 4 Effects of genetic differentiation between parental populations, as well as midparent temperature and precipitation on performance of *Clarkia pulchella*. **(A)** Among between-population crosses, increased genetic divergence between parental populations had a positive effect on lifetime fitness. Points are raw averages for each gene flow source in each garden, colored by the distance between the source population and the garden (the home of the recipient population). **(B)** Regression estimates and standard errors of genetic differentiation (F_{ST}) and absolute midparent temperature differences (T_{diff}) on the probability of producing seeds. **(C)** Effects of genetic differentiation, temperature differences, and absolute precipitation differences (P_{diff}) on conditional seed production. **(D)** Effects of T_{diff} and F_{ST} on component lifestages of *Clarkia pulchella*. Precipitation differences were not significant when tested for component lifestages. Directionality of effects is illustrated with “+” and “-”. Marginally significant parameters (0.05 < P < 0.10) are shown in boxes with dashed margins, predictors in solid boxes are significant (P < 0.05). Size in the previous lifestage is not shown here, but has a significant positive effect on overwinter and reproductive lifestages. * indicates predictors that are only significant in separate models, not in full models with all predictors. Complete statistical results of these tests are in Table S5 and Table S6.

583 **Supplementary methods**

584 **Greenhouse conditions and crossing design**

585 Seeds were planted in the greenhouse 9-11 December, 2014 in conetainers (Stuewe and Sons, Tan-
586 gent, Oregon, USA) filled with Sunshine Mix No. 4 (Sun Gro Horticulture, Agawam, MA, USA).
587 For each of 22 maternal families per population, 3-5 seeds were planted on the soil surface in each
588 pot. For families from each of the two focal populations, three replicate pots were planted per
589 family because larger quantities of flowers would be needed from these families; other populations
590 were represented by one replicate per family. Pots were arranged into randomized blocks, with each
591 block containing one family from each population (one pot from each donor population and three
592 replicate pots from each of the two focal populations). The soil was kept moist until germination,
593 then plants were hand watered every 1-3 days as needed to prevent wilting. After germination,
594 plants were thinned randomly to one per cone and pumice was added to the soil surface to prevent
595 fungal growth. Plants began to flower in March 2015. Plants were bagged to prevent unintentional
596 pollination, and flowers were emasculated upon opening to prevent self-pollination. For the crosses,
597 20 of the 22 blocks were used, the other two were maintained in the same growing conditions to
598 provide alternate plants in case of mortality or sterility. We performed as many crosses as possible
599 using a single focal plant, but if flower production was too low on that plant we also used one of
600 the replicate focal plants from the same family. Most crosses had to be performed 2-3 times to
601 obtain adequate numbers of seeds for the experiment. Some crosses could not be performed due
602 to mortality, sterility, or limited flower production. As ripening progressed, the ends of fruits were
603 taped shut to prevent seed loss. Upon ripening, fruits were collected and stored in coin envelopes
604 in the lab. Crosses were performed March-May 2015 and we collected fruits March-June 2015.

605 **Transplant installation**

606 Seeds attached to toothpicks were planted in the ground 18-21 September 2015. Plots were prepared
607 by removing litter, large rocks, and dried remains of herbaceous perennial plants. The ground surface
608 was minimally leveled to allow for placement of planting grids that aided in consistently spacing
609 the plants. Each toothpick was inserted into the ground gently so that seeds were not dislodged or

610 damaged until seeds were ~ 3 mm below the soil surface. Toothpicks were inserted at 5 cm spacing
611 into ~ 1 m by 2 m blocks. Block shape was varied to accommodate rocks and shrubs surrounding
612 the planting area. After planting, each block was protected with 20 cm high hardware cloth cages
613 supported by rebar. These cages were intended to prevent trampling by larger animals but did
614 not prevent entry of rodents and other small animals. The area surrounding the plots at each
615 site was sprayed with deer repellent several times during the course of the experiment. To ensure
616 germination, plots were watered at a rate of ~ 10 L per plot 27-29 October 2015, though at that
617 time most seeds that were checked already had radicles emerging. In May 2016 cattle fencing was
618 put around the plots at the Blue Lake site before cattle were released into the area for grazing; this
619 fencing succeeded in keeping the cows off the plots. No cattle were present at the Rock Creek site.

620 **Details of monitoring and measuring**

621 Our transplant gardens were installed in areas where *C. pulchella* occurs naturally, and because of
622 this we wanted to evaluate how frequently we might have mistaken naturally occurring plants for
623 experimental plants. During germination surveys we censused one more germinant than the number
624 of seeds that we planted at 23 out of 16,680 grid points (0.14%). This gives an estimate of the
625 minimum rate at which naturally occurring seeds were indistinguishable from our planted seedlings.
626 So, while it is probable that some naturally occurring plants were mistaken for experimental plants,
627 we consider the frequency of possible misidentification to be acceptably low.

628 During winter, some plots were affected by frost-heave and seedlings were uprooted from their
629 planting locations when their toothpick was forced out of the ground (1901/16680 grid points,
630 11.4%). In lightly affected areas, toothpicks and seedlings were gently settled back into the soil.
631 In more heavily affected areas, individual identity could no longer be determined confidently and
632 individuals were excluded from further measurements and analyses (95/16680 grid points, 0.57%).

633 Censuses of reproduction began on 2 June 2016. On 12-13 June 2016 we censused spring survival
634 of all plants. Once flowering began, we placed bridal-veil nets over the hardware cloth on each plot
635 to prevent pollen escape into local populations. In June we censused each plot every 2-3 days. We
636 recorded the date of first flowering of each plant at this temporal resolution. During each census,

the immature ovary length of each new flower was recorded to be used as a proxy for maximum seed set. Flowers were marked as they were measured with a permanent marker and a running flower count was kept for each plant to avoid double-counting as flowers senesced. We continued these assessments as flowering slowed in July, but reduced the census interval to once a week. Damage to plants, such as rodent activity or herbivory, was noted during monitoring. Any plants with uncertain identities (due to frost damage as mentioned above, being far from their toothpick, or the toothpick disappearing; $n = 201/16680$ toothpicks, 1.2%) were excluded from all analyses. Plants that were killed by gophers, browsers, or galling insects were excluded from analyses that involved lifestages downstream from these events ($n = 525/16479$ plants, 3.2%) because we do not think that this mortality is related to population origin but rather to block-specific factors.

Ovary length as a fitness proxy

Pollinations were performed on a subset of plants to calibrate a conversion from immature ovary lengths to seed production. On 596 flowers (mean = 29.8 per plot, range = 0–126) stigmas were dusted with an ample pollen load using all four anthers from another plant in the plot. These flowers were marked with strings around the pedicles and fruits were collected when ripe. Seeds in each of these pollinated fruits were later counted in the lab. Total seed production per individual was estimated by multiplying the total ovary length of each plant by the average number of seeds per mm of immature ovary, as determined from the pollinated fruits. This resulted in an estimate of 4.75 seeds per mm based on a linear regression of number of seeds predicted by ovary length with the intercept set to 0 ($R_0^2 = 0.87$). We pollinated only a maximum of one flower per plant, so these may be overestimates because they do not account for potential resource limitation of seed set. However, we checked whether variation in seeds per mm of fruit was associated with individual fitness (the overall fruit production per individual) or block quality (estimated based on the average fruit production of a block), and we could not attribute variation in seeds per mm of fruit to either of these factors. Therefore, while our conversion from fruit length to seeds may not be exact, we do not expect it to be systematically biased.

663 Supplementary tables and figures

Table S1 Geographic information for the populations of *Clarkia pulchella* used in this experiment.

Population name	Map ID	Type	Latitude	Longitude	Elevation (m)
Blue Lake	F1	Focal	49.05	-119.56	842
Johnstone Creek	F2	Focal	49.04	-119.05	866
Border	D1	Donor	48.98	-118.99	1211
Day Creek Road	D2	Donor	48.94	-118.51	911
Bodie Mountain	D3	Donor	48.83	-118.83	1603
Boulder Creek Road	D4	Donor	48.76	-118.33	1115
Aeneas Valley	D5	Donor	48.54	-118.91	1126
Henry Creek Road	D6	Donor	47.45	-114.77	1103
Heyburn State Park	D7	Donor	47.34	-116.79	801
McCrosky State Park	D8	Donor	47.09	-116.98	1186
Graves Creek Road	D9	Donor	46.80	-114.41	1201
Bitterroot	D10	Donor	46.54	-113.89	1424
Abel's Ridge	D11	Donor	46.28	-117.60	1457
Tucannon	D12	Donor	46.24	-117.74	1022
Pendleton	D13	Donor	45.74	-118.25	649

Table S2 Results of generalized linear mixed effects models for the effect of local vs. foreign origin on performance of *Clarkia pulchella* in common gardens. There are no significant differences between populations of local vs. foreign origin in fitness components or lifetime fitness. Size during the previous census (November for overwinter survival and size, March for fruit counts and estimated seed production) is always a significant predictor of performance in subsequent lifestages.

Response	Foreign vs. local origin			Size during previous census		
	Estimate	SE	<i>P</i> -value	Estimate	SE	<i>P</i> -value
Germination	-0.034	0.088	0.702	-	-	-
Size after germination	0.027	0.073	0.708	-	-	-
Overwinter survival	0.176	0.126	0.161	0.377	0.033	< 0.001
Size after winter	-0.068	0.182	0.708	0.750	0.042	< 0.001
Fruit count	0.089	0.146	0.544	0.544	0.041	< 0.001
Seed production	-0.005	0.128	0.966	0.388	0.032	< 0.001
Lifetime fitness - zero inflation	-0.032	0.123	0.798	-	-	-
Lifetime fitness - conditional	-0.093	0.128	0.469	-	-	-

Table S3 Results of generalized linear mixed effects models of the effects of absolute precipitation and temperature differences on component lifestages of *Clarkia pulchella*. Temperature and precipitation differences refer to absolute differences between the historic conditions that a population experienced and the conditions in the common gardens during the experiment. These differences were calculated using climate data from only the months of that census period (i.e., September-November for germination and size after germination, December-March for overwinter survival and size after winter, and April-July for fruit counts and seed production). Analyses were conducted using only plants surviving the previous census window. Whenever applicable, size in the previous census was included as a covariate to account for differences accumulated during earlier lifestages. Significant parameters are indicated with bold text.

Response	Absolute temperature difference			Absolute precipitation difference			Size in previous census		
	Estimate	SE	<i>P</i> -value	Estimate	SE	<i>P</i> -value	Estimate	SE	<i>P</i> -value
Germination	-0.094	0.035	0.007	-	-	-	-	-	-
Size after germination	-0.027	0.026	0.293	-	-	-	-	-	-
Overwinter survival	-0.078	0.032	0.015	-	-	-	0.366	0.033	< 0.001
Size after winter	-0.518	0.095	< 0.001	-	-	-	0.748	0.042	< 0.001
Fruit count	-0.114	0.071	0.108	-0.091	0.058	0.119	0.543	0.041	< 0.001
Seed production	-0.055	0.047	0.249	-0.110	0.044	0.011	0.389	0.033	< 0.001

Table S4 Results of generalized linear mixed effects models of the effects of being a within-population cross vs. a between-population cross, while accounting for effects of absolute precipitation and temperature differences. Temperature and precipitation differences refer to absolute differences between the average historic conditions of an individual's parental populations and the conditions in the common gardens during the experiment. Positive estimates of the effects of between-population vs. within-populations indicate that having parents from two different populations ("gene flow") is beneficial. **(A)** Effects on lifetime fitness of *Clarkia pulchella*. **(B)** Effects on lifetime fitness when midparent precipitation differences are not included in the model. **(C)** Effects on component lifestages. Climate differences were calculated using climate data from only the months of that census period (i.e., September-November for germination and size after germination, December-March for overwinter survival and size after winter, and April-July for fruit counts and seed production). Analyses were conducted using only plants surviving the previous census window. Whenever applicable, size in the previous census was included as a covariate to account for differences accumulated during earlier lifestages. Significant parameters are indicated with bold text.

Response	Between-populations vs. within-populations			Absolute midparent temperature difference			Absolute midparent precipitation difference			Size during previous census		
	Estimate	SE	<i>P</i> -value	Estimate	SE	<i>P</i> -value	Estimate	SE	<i>P</i> -value	Estimate	SE	<i>P</i> -value
A. Lifetime fitness												
Lifetime fitness - zero inflation	0.008	0.047	0.860	-0.240	0.023	< 0.001	-	-	-	-	-	-
Lifetime fitness - conditional	0.047	0.049	0.345	-0.085	0.032	0.007	-0.072	0.036	0.045	-	-	-
B. Lifetime fitness without precipitation in model												
Lifetime fitness - zero inflation	0.008	0.047	0.860	-0.240	0.023	< 0.001	-	-	-	-	-	-
Lifetime fitness - conditional	-0.114	0.036	0.002	-0.059	0.029	0.041	-	-	-	-	-	-
C. Component lifestages												
Germination	-0.035	0.078	0.653	-0.088	0.029	0.003	-	-	-	-	-	-
Size after germination	-0.033	0.041	0.421	-0.028	0.015	0.058	-	-	-	-	-	-
Overwinter survival	-0.012	0.047	0.794	-0.058	0.022	0.009	-	-	-	0.336	0.023	< 0.001
Size after winter	-0.052	0.127	0.678	-0.274	0.068	< 0.001	-	-	-	0.721	0.031	< 0.001
Fruit count	-0.125	0.055	0.021	-0.081	0.032	0.011	-0.092	0.034	0.007	0.493	0.030	< 0.001
Seed production	0.092	0.047	0.052	-0.030	0.028	0.285	-0.092	0.030	0.002	0.357	0.024	< 0.001

Table S5 Results of generalized linear mixed effects models separately testing the effects of **(A)** genetic differentiation, **(B)** absolute midparent temperature differences, and **(C)** absolute midparent precipitation differences on performance of *Clarkia pulchella* in common gardens. Absolute midparent temperature and precipitation differences refer to absolute differences between the conditions in the common gardens during the experiment and the average historic conditions of an individual's parental populations. These analyses were performed using between-population crosses only, that is, every plant has one parent from a focal population and one parent from a donor population. For analyses of lifetime fitness, temperature differences were calculated using the duration of the experiment and precipitation differences were calculated using April-July values. Precipitation differences are only included as an effect in the conditional part of the model of lifetime fitness because precipitation effects are expected to manifest at later lifestages. For analyses of component lifestages, climate differences were calculated using climate data from only the months of that census period (i.e., September-November for germination and size after germination, December-March for overwinter survival and size after winter, and April-July for fruit counts and seed production). Component lifestage analyses were conducted using only plants surviving the previous census window. Whenever applicable, size in the previous census was included as a covariate to account for differences accumulated during earlier lifestages. Significant parameters are indicated with bold text.

A. F_{ST}						
Response	F _{ST}			Size during previous census		
	Estimate	SE	P-value	Estimate	SE	P-value
Lifetime fitness - zero inflation	0.086	0.028	0.002	-	-	-
Lifetime fitness - conditional	0.080	0.031	0.010	-	-	-
Germination	0.124	0.059	0.034	-	-	-
Size after germination	0.014	0.014	0.306	-	-	-
Overwinter survival	0.054	0.035	0.124	0.336	0.037	< 0.001
Size after winter	0.104	0.050	0.035	0.743	0.044	< 0.001
Fruit count	0.067	0.031	0.028	0.451	0.044	< 0.001
Seed production	0.081	0.029	0.005	0.334	0.035	< 0.001
B. Absolute midparent temperature differences						
Response	Temperature difference			Size during previous census		
	Estimate	SE	P-value	Estimate	SE	P-value
Lifetime fitness - zero inflation	-0.148	0.046	0.001	-	-	-
Lifetime fitness - conditional	-0.090	0.056	0.105	-	-	-
Germination	-0.088	0.070	0.212	-	-	-
Size after germination	-0.029	0.017	0.096	-	-	-
Overwinter survival	-0.054	0.049	0.275	0.335	0.037	< 0.001
Size after winter	-0.132	0.070	0.060	0.743	0.044	< 0.001
Fruit count	-0.121	0.063	0.057	0.457	0.044	< 0.001
Seed production	-0.071	0.066	0.285	0.336	0.035	< 0.001
C. Absolute midparent precipitation differences						
Response	Precipitation difference			Size during previous census		
	Estimate	SE	P-value	Estimate	SE	P-value
Lifetime fitness - conditional	0.123	0.078	0.113	-	-	-
Fruit count	0.047	0.083	0.574	0.452	0.044	< 0.001
Seed production	0.099	0.076	0.192	0.334	0.035	< 0.001

Table S6 Results of generalized linear mixed effects models of the effects of genetic differentiation between parental populations on performance of *Clarkia pulchella* in common gardens. Effects of absolute precipitation and temperature differences are also included in these models. Temperature and precipitation differences refer to the absolute midparent differences, i.e., the absolute differences between the conditions in the common gardens during the experiment and the average historic conditions of an individual's parental populations. These analyses were performed using between-population crosses only, that is, every plant has one parent from a focal population and one parent from a donor population. **(A)** Effects on lifetime fitness. **(B)** Effects on component lifestages. Climate differences were calculated using climate data from only the months of that census period (i.e., September-November for germination and size after germination, December-March for overwinter survival and size after winter, and April-July for fruit counts and seed production). Analyses were conducted using only plants surviving the previous census window. Whenever applicable, size in the previous census was included as a covariate to account for differences accumulated during earlier lifestages. Significant parameters are indicated with bold text.

Response	F _{ST}			Temperature difference			Precipitation difference			Size during previous census		
	Estimate	SE	P-value	Estimate	SE	P-value	Estimate	SE	P-value	Estimate	SE	P-value
A. Lifetime fitness												
Lifetime fitness - zero inflation	0.064	0.030	0.030	-0.117	0.048	0.014	-	-	-	-	-	-
Lifetime fitness - conditional	0.059	0.037	0.108	-0.031	0.055	0.574	0.053	0.082	0.520	-	-	-
B. Component lifestages												
Germination	0.111	0.062	0.073	-0.021	0.080	0.798	-	-	-	-	-	-
Size after germination	0.005	0.016	0.770	-0.026	0.020	0.179	-	-	-	-	-	-
Overwinter survival	0.047	0.044	0.286	-0.014	0.060	0.809	-	-	-	0.335	0.037	< 0.001
Size after winter	0.072	0.061	0.232	-0.073	0.082	0.376	-	-	-	0.742	0.044	< 0.001
Fruit count	0.058	0.034	0.089	-0.093	0.058	0.110	-0.010	0.084	0.905	0.455	0.044	< 0.001
Seed production	0.071	0.033	0.031	-0.035	0.055	0.522	0.028	0.077	0.719	0.334	0.035	< 0.001

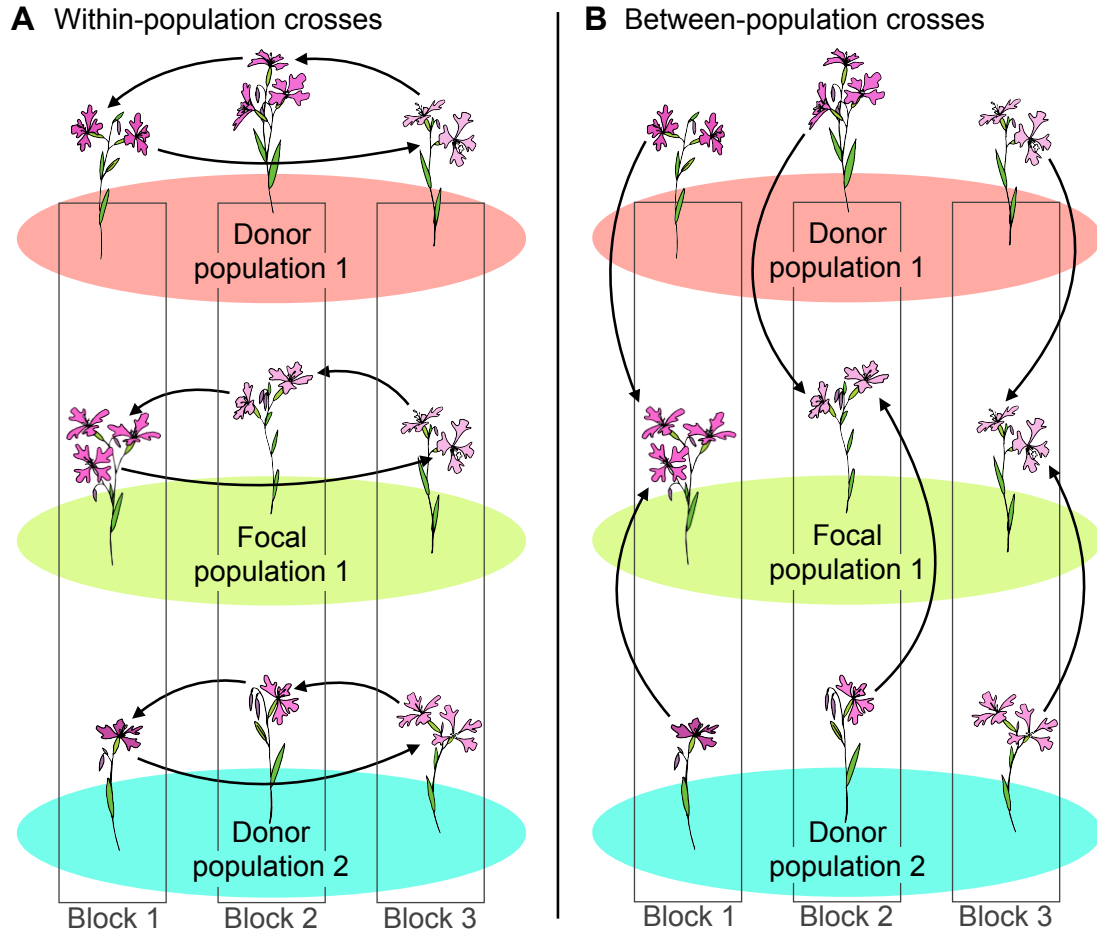


Figure S1 Schematic of the greenhouse crossing design to generate seeds for our common gardens. Three blocks are diagrammed here, but crosses were performed in 22 blocks and seeds from 15 blocks were transplanted into the field. **(A)** Within-population crosses: for each seed family from each of 15 populations (three are shown), plants were crossed in a “daisy chain” design, in which each plant was hand-pollinated using pollen from another individual of the same population from the subsequent block. **(B)** Between-population crosses: we used pollen from each of 13 donor populations (two are shown) to pollinate flowers on plants from each of the two focal populations (one is shown). Each focal plant served as a dam for multiple between-population crosses, that is, each focal seed family had one flower pollinated by a plant from each of 13 donor populations and from the other focal population.

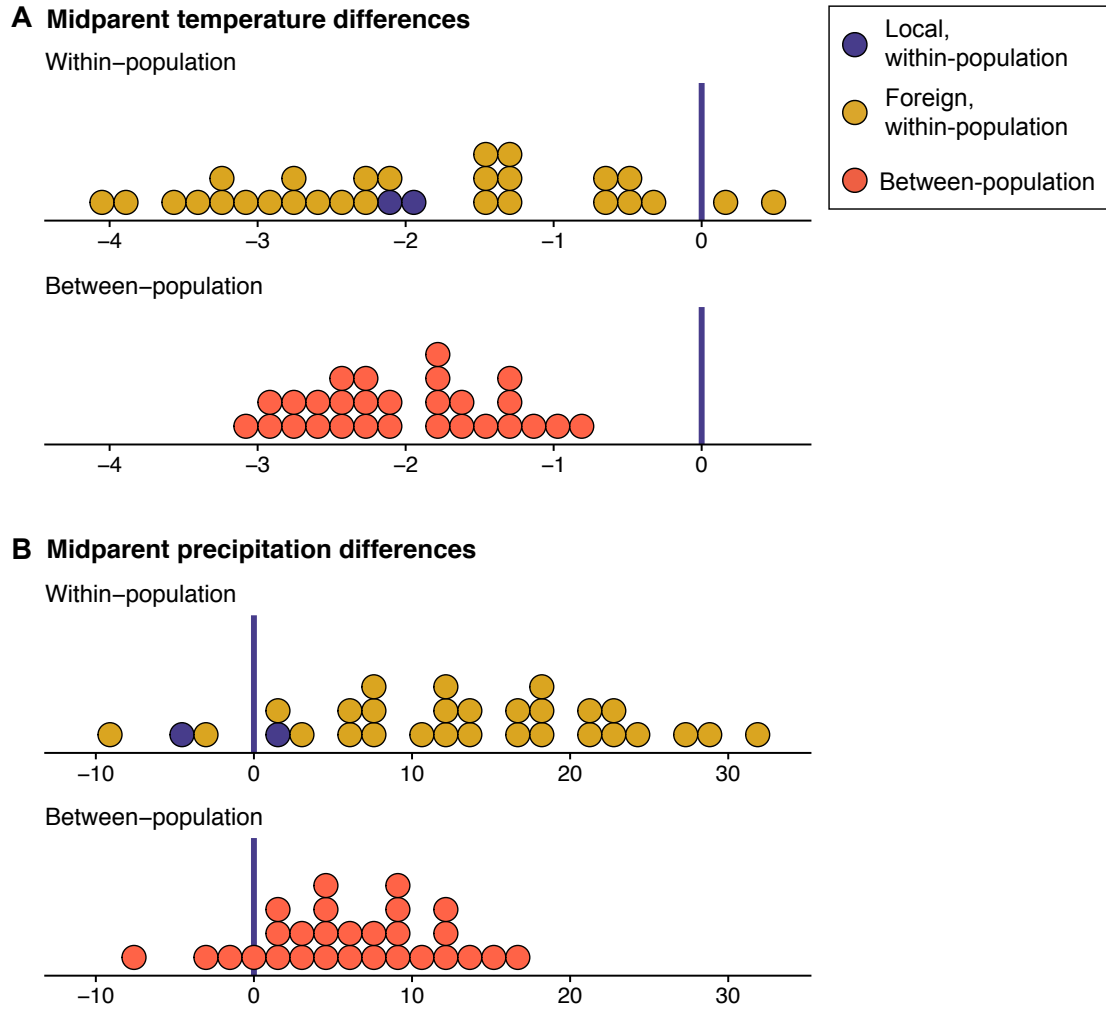


Figure S2 Distribution of climate differences of within- vs. between-population crosses of *Clarkia pulchella* relative to conditions during the experiment. Each dot represents a combination of maternal population, paternal population, and transplant site. Dark blue dots are within-population crosses of focal populations transplanted into their home sites. Gold dots are within-population crosses from donor populations planted into each of the two gardens, as well as the focal populations planted into each other's sites. Red dots are between-population crosses. Vertical blue bars are placed at zero, indicating where populations would be perfectly matched to the temperature or precipitation conditions during the experiment. **(A)** Distribution of the differences between the average temperature in the home sites of parental populations and conditions during the experiment. Focal populations are intermediate in temperature relative to other populations in the experiment; this results in similar average differences in temperature in between-population crosses and within-population crosses. **(B)** Distribution of differences between the average precipitation in the home sites of parental populations and conditions during the experiment. Focal populations are among the driest in the experiment; this results in smaller average differences in precipitation in between-population crosses compared to within-population crosses. Note that figures in the main text use absolute temperature differences: the absolute value of the midparent differences as they are plotted in this figure.

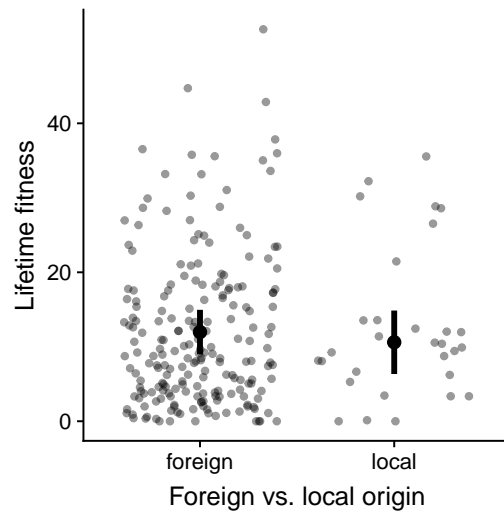


Figure S3 Lifetime fitness (seeds produced per seed planted) from populations of *Clarkia pulchella* with foreign vs. local parents. This analysis includes within-population plants only (no gene flow). Each point represents the average of a single family. Error bars are 95% confidence intervals of model estimated means, omitting variation from random effects.