

1 **A resurrection study reveals limited evolution of thermal performance in response to**
2 **recent climate change across the geographic range of the scarlet monkeyflower**

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30 Introduction

31 Evolution can facilitate species persistence in the face of changing climate (Hoffmann and Sgrò
32 2011; Carlson et al. 2014), especially when extensive habitat fragmentation prevents migration
33 (Collingham and Huntley 2000) or plasticity is not sufficient to suit organisms to novel
34 environments (Visser 2008). Because climate change is causing mismatches between species'
35 geographic ranges and thermal niches, thermal adaptation is an important driver of population
36 responses to climate change (Geerts et al. 2015). Evolutionary rescue in the face of
37 environmental change occurs when adaptive evolution restores positive growth rates to
38 populations in decline, and it is most likely when the rate of environmental change is gradual and
39 the amount of standing genetic variation for ecologically important traits is high (Carlson et al.
40 2014). Yet, there is severe uncertainty regarding how extreme selection events associated with
41 changing climate (as opposed to gradual environmental change) will impact the extent to which
42 adaptive evolution can rescue populations in decline, and whether adaptive evolution varies
43 across species' geographic ranges.

44 Capacities for thermal adaptation may vary among populations across a species' range for
45 at least three reasons. First, populations may experience different magnitudes of climate
46 anomalies (departures of contemporary climate from historical averages), and thus different
47 selective pressures on thermal tolerance. For example, temperature increases associated with
48 climate change are often greater at higher latitudes relative to lower latitudes (IPCC 2013).
49 Second, populations may differ in the ability to evolve earlier phenology that would enable
50 avoidance of drought or extreme heat encountered during the growing season, consequently
51 relaxing selection for heat tolerance (Franks et al. 2007; Sheth and Angert 2016; Socolar et al.
52 2017; Dickman et al. 2019). In fact, empirical studies indicate that selection for early flowering

53 can result in correlated reductions in stress tolerance (Franks 2011; Hamann et al. 2018). Third,
54 populations may differ in adaptive genetic variation due to connectivity with other populations.
55 High-latitude, leading-edge populations may have ample genetic variation to evolve as they
56 receive warm-adapted alleles from lower-latitude populations, but low-latitude, trailing-edge
57 populations may lack genetic variation due to a scarcity of populations adapted to warmer
58 temperatures (Davis and Shaw 2001; Hampe and Petit 2005; Hu and He 2006). Nonetheless,
59 recent work suggests that evolutionary rescue may not occur fast enough for populations to keep
60 up with the pace of climate change. The probability of evolutionary rescue may be especially low
61 if amelioration of climate extremes induces reversals in trait evolution (Hamann et al. 2018) or if
62 long generation times slow the rate of evolution (Hoffmann and Sgrò 2011). Ultimately,
63 understanding variation in thermal niche evolution among populations could improve models
64 that predict how species' distributions will shift with climate change, most of which currently
65 assume evolutionary stasis of species' climatic niches across space and time (Angert et al. 2011;
66 Hällfors et al. 2016; Peterson et al. 2019).

67 Temperature can shape species' distributions via its effects on fitness and other
68 performance metrics, yet we have only recently begun to understand the evolution of thermal
69 performance across space and time (Araújo et al. 2013; Diamond 2017). A thermal performance
70 curve (TPC) describes the performance of a genotype, population, or species across a
71 temperature gradient (Huey and Stevenson 1979; Angilletta 2009; Fig. 1A). A TPC peaks at an
72 intermediate temperature (thermal optimum) and is bounded by a temperature on either side
73 where performance falls to zero (upper and lower thermal limits). The span of temperatures
74 across which organisms achieve a designated percentage of the maximum performance is called

75 the thermal performance breadth (hereafter referred to as breadth), and narrower breadth
76 suggests greater thermal specialization.

77 These TPC parameters, like many other traits such as phenology or resource acquisition,
78 can exhibit adaptive clines across spatial climatic gradients such as latitude (Lynch and Gabriel
79 1987; Angilletta 2009). Performance trade-offs between low and high temperatures, manifested
80 by shifts in the TPC along the temperature axis, yield the expectation that thermal optima
81 increase with environmental temperature (Angert et al. 2011). For example, thermal optima of
82 populations of *Mimulus cardinalis* in western North America increased with average July
83 temperatures and decreased with latitude, suggesting adaptive differentiation across the species'
84 range (Angert et al. 2011; Paul et al. 2011). If these patterns across space also apply across time,
85 climate change-induced increases in mean temperatures should result in the evolution of
86 increased thermal optima. The climate variability hypothesis posits that populations inhabiting
87 regions that are climatically stable should evolve narrower climatic tolerances relative to those
88 from climatically heterogeneous areas (Dobzhansky 1950; Janzen 1967; Stevens 1989). For
89 ectothermic animals, thermal breadth decreases towards the equator because organisms at lower
90 latitudes experience lower temperature variation (Sunday et al. 2010). This hypothesis has
91 primarily been tested in temperate-tropical comparisons, but also applies to situations where
92 climate variability changes across time, including recent climate change. That is, shifts in
93 seasonality related to climate change could result in the evolution of altered breadth. Although
94 there is some evidence of rapid evolution of thermal performance in response to climate change
95 in vertebrates and invertebrates (Kingsolver et al. 2013; Higgins et al. 2014; Geerts et al. 2015),
96 little is known about the evolution of TPCs in response to climate change in plants.

97 To explore how thermal performance has evolved in response to recent climate change
98 and how the direction and magnitude of shifts vary across populations, we implemented a
99 resurrection experiment (Franks et al. 2008) with populations across the broad geographic range
100 of the scarlet monkeyflower, *Mimulus cardinalis* (Lowry et al. 2019). For each of two northern-
101 edge, two central, and two southern-edge populations that collectively span broad climatic
102 gradients in western North America (Fig. 2), we grew ancestors from 2010 alongside
103 descendants from 2017 in growth chambers. Ancestors and descendants were respectively
104 derived from seed collected before and after a seven-year period of record-setting drought and
105 heat in western North America. Specifically, northern and central populations experienced the
106 most extreme increases in temperature relative to historical conditions (Fig. 2B; Table 1).
107 Further, temperature seasonality and annual precipitation decreased substantially in southern
108 populations in recent years (Fig. 2C; Tables 1, S1). Recent population declines, coupled with low
109 probabilities of survival and high probabilities of reproduction at the southern range edge,
110 suggest that drought and warming could select for an “annualized” life history in this perennial
111 species (Sheth and Angert 2018). Thus, decreased generation times could enhance the potential
112 for evolutionary responses in some populations. We performed growth chamber experiments in
113 eight temperature regimes to build TPCs for ancestors and descendants within each population.
114 Because we held all aspects of the environment other than temperature constant, and produced
115 seed families for both ancestors and descendants in a common environment, we can confidently
116 attribute differences in TPCs between ancestors and descendants to genetic changes, rather than
117 plastic developmental responses, seed storage/age effects, or maternal effects (Franks et al. 2018,
118 2019). We tested two hypotheses about evolutionary responses of TPCs to climate change. First,
119 under directional warming, particularly in northern and central populations, increased thermal

120 optima should evolve (Table 1; Fig. 1B). Second, under lower temperature seasonality,
121 particularly in southern populations, decreased breadth should evolve (Table 1; Fig. 1C).
122 Differences in evolutionary change in these TPC parameters among populations would suggest
123 that thermal adaptation is dependent upon variation in climate anomalies, evolution of avoidance
124 traits, and/or genetic variation in thermal performance. We also explored whether thermal optima
125 and breadths are associated with geographic temperature gradients, allowing us to test for
126 evolutionary divergence in thermal performance parameters across space.

127

128 Methods

129 *Study system, seed sampling, and refresher generation*

130 *Mimulus cardinalis* is a perennial herb that occurs along seeps and streams from central Oregon,
131 USA to northern Baja, Mexico (Fig. 2A). It has been the subject of numerous investigations of
132 local adaptation, geographic range limits (Angert and Schemske 2005; Angert 2006; Paul et al.
133 2011; Muir and Angert 2017; Angert et al. 2018; Bayly and Angert 2019), and physiological,
134 evolutionary, and demographic responses to climate change (Angert et al. 2011; Sheth and
135 Angert 2016, 2018). Previous work indicates that populations in our study have been in decline,
136 but differences in generation time and gene flow across the range may affect the potential for
137 evolutionary rescue. Specifically, a demography study showed that during a five-year period of
138 severe drought and warming (2010-2014), growth rates of 32 *M. cardinalis* populations
139 decreased from the leading to trailing edges of the geographic range (Sheth and Angert 2018).
140 Three of these populations are included in our study (N1, C2, and S1; Table 1), and each of these
141 showed a significant population decline during the study period (Sheth and Angert 2018).
142 Further, the demography study showed that the probability of survival from one year to the next

143 was highest in central populations and declined towards northern and southern range edges. A
144 majority of adults marked in 2010 in N1 and S1 populations did not survive to 2011 (Sheth and
145 Angert 2018), and data collected beyond 2014 suggest that a few C2 plants could survive at least
146 6-7 years (Angert and Sheth unpubl. data). Thus, populations in the range center likely have
147 longer generation times and lower potential for rapid evolution than those at range edges. A
148 genetic study of the northern half of the range of *M. cardinalis* showed that northern populations
149 have recently received a net influx of migrants from hotter environments (Paul et al. 2011),
150 which could enhance genetic variation in thermal performance and facilitate adaptation to a
151 warming climate.

152 We collected seeds from 80-100 individuals in each of the six study populations in 2010
153 (ancestors) and 2017 (descendants). Ancestors were collected as described in Sheth and Angert
154 (2016), and descendants were re-collected using the same protocol. Although there is a
155 possibility that a seedbank could have introduced individuals into the descendent populations
156 whose parents were not exposed to the period of anomalous climate during the study period (i.e.,
157 pre-2010), previous observations have pointed towards limited seed dormancy in *M. cardinalis*.
158 In particular, a study of mid-latitude populations (2002-2003) found that only a small fraction of
159 seeds can remain viable in the seed bank for at least one year (Angert 2006), but a recent study of
160 7 populations spanning the latitudinal range (2011-2014) demonstrated that no germination
161 occurred after the first year in the seed bank (Sheth and Angert 2018). To minimize maternal and
162 storage/age effects, we grew seeds in the greenhouse for a ‘refresher’ generation and performed
163 controlled crosses to produce 18 seed families within each population/cohort combination
164 ([Franks et al. 2018, 2019; Appendix S1](#)). Most seed families had unique sires and dams (full-
165 sibs), with the exception of some crosses that shared the same sire (half-sibs) in four

166 population/cohort combinations with low parental sample sizes (N1 2010, N2 2010, C2 2010,
167 and C2 2017; Table S2).

168 *Resurrection experiment*

169 To determine whether *M. cardinalis* TPCs have evolved in response to recent climate change
170 across the geographic range, we implemented a resurrection experiment in growth chambers
171 using ancestral and descendent seed families of the six populations from the refresher generation
172 (Appendix S1). In summary, we grew seedlings in one of eight 16h day/8h night temperature
173 regimes (10/-5, 15/0, 20/5, 25/10, 30/15, 35/20, 40/25, or 45/30 °C) for one week. These
174 temperature regimes encompass temperatures experienced by each of the six populations (Fig.
175 S1) and capture full TPCs for *M. cardinalis* and close relatives (Paul et al. 2011; Sheth and
176 Angert 2014). Previous work in *Mimulus* has documented substantial variation in growth across
177 temperatures during the short time frame of one week (Paul et al. 2011; Sheth and Angert 2014).
178 In each growth chamber run, we included seedlings from each of the 18 seed families within
179 each of the 12 population/cohort combinations. Temperature regimes were replicated twice to
180 reduce chamber effects. Each seed family was replicated four times in each temperature regime,
181 with two replicates in each chamber run (6,912 plants total).

182 Prior to chamber runs, we planted seeds into 72-cell plug trays. We planted into sets of
183 six trays, which together eventually went into each growth chamber run and contained the two
184 replicate plants for all 216 seed families planted in a randomized design. Two to ten seeds were
185 planted for each replicate. Seeds were germinated under a benign day/night temperature regime
186 (20/15 °C) and a 16-hour photoperiod (6:00-22:00). Three to four weeks after planting, when
187 most seedlings had germinated but were small enough that roots were not yet entangled, we
188 thinned seedlings to one central-most seedling in each cell. Two weeks after thinning, when most

189 seedlings had at least two true leaves, we put each tray set (i.e., six trays containing two
190 replicates of all seed families) into one of four reach-in growth chambers (Percival LT-105X,
191 Percival Scientific, Inc., Perry, Iowa, USA) that was set to one of the eight day/night temperature
192 regimes (Appendix S1).

193 We measured the performance of all seedlings based on the relative change in leaf
194 number over the course of growth chamber runs. We recorded the number of true leaves >1 mm
195 in length on each individual immediately prior to, and one week after, being placed in the growth
196 chamber ($leaf_{in}$ and $leaf_{out}$, respectively). We then calculated relative growth rate (RGR) as:

$$\frac{(leaf_{out} - leaf_{in})}{(leaf_{in} \times number\ of\ days)} \quad (Eq. 1)$$

197 This metric does not incorporate total fitness in terms of reproductive output, and alternative
198 performance metrics could yield different results. However, size is positively related to fruit
199 number in natural populations of *M. cardinalis* (Sheth and Angert 2018). Because rapid growth
200 at early life stages during which plants are smaller and more vulnerable should increase the
201 chances of juvenile survival and thus the probability that a plant will reproduce, relative growth
202 rate is likely correlated with total fitness. Nonetheless, we emphasize that relative growth rate is
203 a metric of plant performance that is a component of fitness, rather than a metric of total fitness.
204 We excluded 866 plants that died, did not germinate, or did not have true leaves by the start of
205 chamber runs, and 13 that were accidentally damaged before final leaf number was
206 measured. Thus, at the end of the experiment, we measured RGR for 6,033 plants (of the 6,912
207 initially planted). For 718 individuals that died during chamber runs (59% of plants at 10/-5 °C,
208 25% of plants at 45/30 °C, and <1% of plants at each of the other temperature regimes), we set
209 RGR equal to zero. No individual had fewer leaves coming out of the chamber than going in, so
210 all RGR values were greater than or equal to zero.

211 *Statistical analysis*

212 We used RGR data to build TPCs for ancestors and descendants within each of the six *M.*
213 *cardinalis* populations. To determine how thermal performance has evolved in response to recent
214 climate change across the species' range, we compared thermal optima and breadths of ancestors
215 vs. descendants within each population using probabilistic comparisons (i.e., the proportion of
216 times that the parameter for a descendent group was greater than its respective ancestral group).
217 We used a hierarchical Bayesian model (R package *performr* v0.2;
218 <https://github.com/silastittes/performr>; Tittes et al. 2019) to fit TPCs to our data. This method
219 allowed us to simultaneously estimate responses (RGR) of our 12 biological groups (6
220 populations x 2 cohorts) across an environmental gradient (daytime temperature) using a
221 derivation of Kumaraswamy's probability density function. There are two limitations to the
222 model in its current form. First, although there are more complex ways to model RGR as change
223 in leaf number (Rees et al. 2010), the model is unable to handle complex response variables.
224 Second, the model does not allow for random effects. Thus, prior to model implementation, we
225 averaged RGR among replicates of each family in each temperature regime to avoid
226 pseudoreplication within families and to minimize growth chamber effects (N=1,717; Table S2).
227 We scaled RGR by the overall mean and centered daytime temperature around zero to improve
228 model performance. We used the default model settings, except we increased iterations per chain
229 to 10,000 and max_treedepth to 12. These settings increased convergence and reliability of
230 posterior sampling according to \hat{R} statistics of 1 and large numbers of effective samples (at least
231 10,000; Table S3; [Gelman et al. 2014](#)). While we did not compare our model to alternatives, we
232 quantified the adequacy of the model's fit to the data using a Bayesian p-value (Gelman et al.
233 2014). An adequate model should have a Bayesian p-value near 0.5, indicating a lack of

234 discrepancy between the data generated by the model and the empirical data. To compute the
235 Bayesian p-value, we compared 1) the sum of squares between the model's expected value and
236 the RGR values generated from each model's posterior draws, and 2) the sum of squares when
237 comparing posterior expectations to the empirical data. The Bayesian p-value was calculated as
238 the proportion of posterior draws where the former sum of squares was greater than the latter.
239 When simulating RGR values, all negative predictions were set to zero. The Bayesian p-value of
240 our model was 0.19 (Fig. S2), indicating that the model adequately described the data generating
241 process. Bayesian p-values for each population and cohort combination were also generally close
242 to 0.5, though there were a few exceptions (Fig. S2). Lack of strong correlations in posterior
243 draws between the core parameters of this model indicate that variance inflation does not
244 influence posterior uncertainty (Fig. S3).

245 We derived thermal performance parameters of interest (thermal optimum and breadth)
246 from each posterior draw of the TPC model and placed the parameters back in their original scale
247 to aid interpretation. We calculated thermal optimum as the temperature at which RGR is
248 maximized (Tittes et al. 2019), and breadth as the range of temperatures across which plants
249 achieved at least 50% (B_{50}) and 80% (B_{80}) of maximum performance (Huey and Stevenson
250 1979). We calculated breadth by finding the approximate lower and upper temperature values
251 that corresponded to 50% or 80% of the maximum height of the curve. Lacking an exact solution
252 for the critical values, we selected them from a grid of 100 equally spaced points along the
253 temperature axis, choosing the two points that had the minimum distance to the desired
254 percentage of curve height. Results were qualitatively similar for B_{50} and B_{80} (Fig. S4B-C), so
255 we report results for only B_{50} along with differences in results in cases where they influence
256 interpretation. We performed pairwise comparisons of thermal optimum and breadth among all

257 12 population-by-cohort groups, focusing on comparisons between cohorts within populations.
258 Specifically, we calculated the average and 95% credible interval of the difference in the
259 predicted parameter estimate of ancestors vs. descendants of each population. A 95% credible
260 interval that did not overlap zero would indicate a highly plausible difference between
261 descendants and ancestors (i.e., we had the statistical power to detect evolutionary change). A
262 95% credible interval that did overlap zero would indicate that evolutionary change was not
263 highly plausible.

264 To test for evolutionary divergence in thermal optima and breadth across the geographic
265 temperature gradient, we implemented two linear models using the functions *lm* and *anova* from
266 the *stats* package in R. We estimated means of thermal optima and breadths for each population
267 and cohort combination from posterior draws of the TPC model. Historical maximum July
268 temperature and historical temperature seasonality (maximum temperature of the warmest month
269 minus minimum temperature of the coolest month) were estimated for each population and
270 cohort combination as means from the years 1951-2000 (Table S1). The first model predicted
271 thermal optimum as a function of maximum July temperature, cohort, and their interaction. A
272 positive relationship between thermal optimum and maximum July temperature would confirm
273 that there are performance trade-offs between low and high temperatures. The second model
274 predicted breadth as a function of seasonality, cohort, and their interaction. A positive
275 relationship between breadth and seasonality would support the climate variability hypothesis.
276 For both models, we removed interactive and/or main effects of cohort when they were not
277 significant at $\alpha < 0.05$. We used R v3.6.1 for all analyses (R Core Team 2019).

278

279

Results

280

Evolution of thermal optimum

281 Overall, there was no support for the hypothesis that populations have evolved higher thermal
282 optima. The thermal optimum increased by averages of about 0.5 °C from ancestors to
283 descendants in three populations—one population from each of the northern edge (N1), central
284 (C1), and southern edge (S1) regions of the geographic range (Figs. 3, 4A, S4A; Table 1).
285 Thermal optimum decreased in each of the three other populations (N2, C2, and S2) by averages
286 of less than 0.5 °C (Figs. 3, 4A, S4A; Table 1). However, because the credible intervals for all
287 shifts in thermal optimum (both positive and negative) included 0, we inferred that evolutionary
288 change was not highly plausible. Means and 95% credible intervals for thermal optima and other
289 TPC parameters for all population/cohort combinations are reported in Table S4.

290

Evolution of thermal performance breadth

291 We found mixed support for the second hypothesis that populations have evolved narrower
292 breadths. On average, breadth increased in two populations (N1 and C2) and decreased in the
293 other four populations (Figs. 3, 4B, S4B; Table 1). Among these, the only highly plausible
294 evolutionary change detected was for S1, whose descendants had an average breadth that was
295 1.25 °C narrower than ancestors (Figs. 3, 4B, S4B; Table 1). When comparing breadth at the
296 80% threshold (B_{80}), the direction of evolutionary change from ancestors to descendants was the
297 same as B_{50} for each population, but that of S1 was no longer highly plausible (descendants had
298 an average B_{80} that was 0.87 °C narrower than ancestors; Fig. S4C).

299

Evolutionary divergence in thermal optimum and breadth across temperature gradients

300 Overall, thermal optimum did not significantly vary with maximum July temperature
301 ($F_{1,8}=0.744$, $p=0.414$) or between cohorts ($F_{1,8}=0.236$, $p=0.640$). The relationship between

302 thermal optimum and maximum July temperature did not differ between cohorts ($F_{1,8}=0.0001$,
303 $p=0.991$). After removing cohort as a main effect in the model, maximum July temperature
304 explained no variation in thermal optimum ($b=0.063$, $R^2_{adj}=-0.009$, $p=0.364$; Fig. 4A).

305 Breadth showed no significant differences between ancestors and descendants
306 ($F_{1,8}=0.384$, $p=0.552$), nor did breadth vary differently with seasonality between cohorts
307 ($F_{1,8}=1.877$, $p=0.208$). However, breadth increased with seasonality overall ($F_{1,8}=6.648$,
308 $p=0.033$). After removing cohort as a main effect in the model, seasonality explained 39% of the
309 variation in breadth ($b=0.253$, $R^2_{adj}=0.386$, $p=0.018$; Fig. 4B).

310

311 Discussion

312 We combined a resurrection study with a hierarchical Bayesian model to test key hypotheses
313 about how thermal performance has evolved in response to recent climate change across a plant
314 species' range. Since the introduction of resurrection studies over a decade ago (Franks et al.
315 2008), this is the first to test whether plant TPCs can rapidly evolve in response to contemporary
316 climate change. In only seven years encompassing anomalous temperatures and record drought,
317 we detected rapid evolution of the TPC in a southern, trailing-edge population of a perennial
318 herb. However, we show that rapid evolution is the exception rather than the norm across
319 multiple populations. Overall, there was no support for the hypothesis that the populations have
320 evolved higher thermal optima, and little support for the hypothesis that the populations have
321 evolved narrower breadths. One southern-edge population evolved a narrower breadth, indicating
322 increased thermal specialization. There was no apparent evolutionary change in the breadth of
323 northern-edge and central populations and the other southern-edge population. Below, we
324 interpret these findings in light of genetic variation, natural selection, and the evolution of

325 avoidance traits across the species' geographic range, and we discuss their implications for
326 evolutionary rescue.

327 *Genetic variation and selection*

328 Genetic variation in thermal performance within populations and selective pressures from recent
329 trends in climate may explain the observed evolutionary shifts in TPCs. Directional warming,
330 estimated as the average anomaly in maximum July temperature during the study period, was
331 greatest in the central and northern populations (Table 1; Fig. 2B). Further, anomalies in
332 maximum July temperature steadily increased from 2010 to 2017 across populations (Fig. S5A,
333 Appendix S2), reducing the likelihood that amelioration in climate would have induced reversals
334 in trait shifts. Thus, upward evolutionary shifts in thermal optima (Fig. 1B) should have been
335 greatest in the central and northern populations if they are successfully adapting to climate
336 change. However, we did not detect significant increases in thermal optima in these populations
337 (Table 1; Figs. 3, S4A). One interpretation of this result is that evolutionary rescue is not
338 occurring rapidly enough for these populations to keep up with the pace of rapid climate change
339 (Hamann et al. 2018).

340 There are multiple potential explanations for the lack of evolutionary responses of
341 thermal optimum. First, climate-driven selection on thermal performance may not have been
342 strong enough to cause significant directional change in thermal optima. Average anomalies in
343 maximum July temperature were negative in southern populations (Table 1), so selection for
344 higher thermal optima could have been weak. In central and northern populations, average
345 anomalies in maximum July temperature were positive but less than 1 °C across populations.
346 Ancestors within all four of these populations had a thermal optimum that is at least 1 °C greater
347 than their respective historical maximum July temperatures (Fig. 4A; Tables S1, S4). Thus,

348 ancestors were already equipped to tolerate the increased temperatures experienced throughout
349 the study period. Three populations showed shifts in thermal optima that were opposite to their
350 respective anomalies in maximum July temperature (N2, C2, and S1; Table 1). However, it is
351 worth noting that C1—whose ancestors had the lowest thermal optimum of all populations
352 (31.71 °C) and experienced the greatest average increase in maximum July temperature (+0.66
353 °C)—showed a similar average increase in thermal optimum (+0.63 °C; Table 1), though the
354 credible intervals for this shift in thermal optimum overlap zero. Two other populations showed
355 an increase in thermal optimum that matched the magnitude of increase in maximum July
356 temperature (N1 and S2). Interestingly, although S2 did not experience maximum July
357 temperatures during the study period that were greater than historical averages, both cohorts
358 within S2 have a thermal optimum that is almost 1 °C less than its historical maximum July
359 temperature average (Fig. 4A; Tables S1, S4), and thus there may still be future selection for
360 higher thermal optimum. Given more time under elevated temperatures, N1, C1, and S2 may
361 have the greatest potential to track further increases in mean temperature through a shift in
362 thermal optimum.

363 Second, lack of gene flow from populations adapted to warmer temperatures could
364 constrain the evolution of thermal optima across the species' range. Northern populations have
365 recently received an influx of migrants from central populations that occur in hotter temperatures
366 (Paul et al. 2011). However, contemporary populations owe less than 1% of their genotypes to
367 recent migrants (i.e., within the last two generations; Paul et al. 2011). Further, the limited gene
368 flow from central to northern populations that may have occurred over our study period may not
369 have introduced genotypes with higher thermal optima. This is because central populations,
370 though they occur in hotter environments (Fig. 2A), did not have higher thermal optima than

371 northern populations (Figs. 4A, S4A). However, on average, the southern populations in our
372 study had higher thermal optima than central populations (Figs. 4A, S4A). One potential
373 explanation for this pattern is limited gene flow between southern and central populations, which
374 has preliminarily been shown by a range-wide population genetics dataset of *M. cardinalis* (J. R.
375 Paul, T. Parchman, A. Buerkle, and A. L. Angert, unpublished manuscript). Limited gene flow
376 between southern and central populations, paired with our finding that central populations have
377 not evolved higher thermal optima (Table 1), suggests that gene flow from southern populations
378 has not enhanced adaptation to warmer temperatures in central populations. Further, the southern
379 populations in our study may not have evolved higher thermal optima because their location
380 within the geographic range limits the opportunity to receive alleles from warmer-adapted
381 populations. A third reason for lack of evolution of thermal optimum is that ancestors lack
382 genetic variation in thermal optimum, a possibility that we are currently assessing. Overall, these
383 results indicate that evolutionary rescue has not yet occurred in *M. cardinalis* populations that
384 have declined during years of severe warming and drought. Evolution of thermal optima may not
385 have played an important role in buffering against *M. cardinalis* population declines in response
386 to recent climate change, but further work is needed to assess whether populations are able to
387 evolve in the long term.

388 According to the climate variability hypothesis, populations that experienced the lowest
389 temperature variation relative to historical averages should exhibit the greatest decreases in
390 breadth (Dobzhansky 1950; Janzen 1967; Stevens 1989). When climate is stable within the
391 lifetime of organisms, genotypes with high performance within the narrow climatic gradient are
392 favored (Etterson 2004). In support of the climate variability hypothesis, seasonality, which
393 represents the span of temperatures experienced during the year, was on average dramatically

394 lower than historical conditions in the S1 population (Table 1; Fig. 2C), and this population
395 showed plausible evolution towards thermal specialization (i.e., breadth became narrower in
396 descendants relative to ancestors; Figs. 3, S4B). Two factors aside from decreased seasonality
397 could have contributed to the evolution of thermal specialization in S1. First, southern
398 populations of *M. cardinalis* have become increasingly annualized (i.e., high probabilities of
399 flowering and low probabilities of survival from one year to the next; Sheth and Angert 2018).
400 Annualization could enhance the rate of evolution due to shorter generation times. Second, S1
401 has experienced recent drought, receiving on average 111 mm less precipitation per year
402 compared to the historical average (the strongest drought across all six populations; Table S1).
403 Heat compounded by drought may have truncated the growing season and reduced the range of
404 temperatures the population encounters, thus increasing selection for thermal specialization.
405 Lower annual precipitation could also explain trends towards decreasing breadth in two other
406 populations, S2 and C1. Average anomalies in seasonality have been small but positive in the
407 northern populations (Table 1; Fig. 2C). Inconsistent with the climate variability hypothesis,
408 these northern populations did not evolve broader TPCs (Table 1; Figs. 3, S4B). However,
409 seasonality of each study year was not always greater compared to historical conditions and did
410 not follow a unidirectional trend across the study period (Figs. 2C, S5B), so it is possible that
411 selection for greater breadth was neither strong nor consistent across years. Further, populations
412 whose breadth did not evolve may have lacked standing genetic variation in breadth. Overall,
413 these results suggest that in *M. cardinalis*, breadth may be a more evolutionarily labile trait than
414 thermal optimum, but lack of breadth evolution in response to recent climate change in a
415 majority of populations indicates that evolutionary rescue has not occurred in populations that
416 are declining as temperatures have become more variable.

440 2019). At the same time, these avoidance traits, including earlier flowering, may come with the
441 cost of lower tolerance to environmental stress. For example, when populations of *Brassica rapa*
442 evolved earlier flowering after a multi-year drought, they concurrently evolved decreased water-
443 use efficiency, and thus lower ability to tolerate drought conditions (Franks 2011; Hamann et al.
444 2018). Using the ancestral populations from our study, Sheth and Angert (2016) quantified the
445 response to artificial selection for early and late flowering as a proxy for each population's
446 adaptive potential. They found that the two southern populations rapidly responded to selection
447 on flowering time, with early- and late-flowering selection lines diverging by ~15 days. Thus,
448 the ancestors of the southern populations had ample genetic variation to evolve earlier flowering
449 times, potentially allowing them to avoid the extreme drought and increased temperatures that
450 they have recently experienced (Table S1). Additionally, early-flowering selection lines, though
451 they did not have decreased water-use efficiency, had higher specific leaf area and leaf nitrogen
452 content, representing a partial shift toward a fast, resource-acquisitive life history (Sheth and
453 Angert 2016). Thus, if southern populations have evolved earlier flowering in situ since 2010
454 (which we are currently assessing), they may have also evolved acquisitive life histories at the
455 expense of more resource-conservative functional traits that would promote thermal tolerance. In
456 line with this prediction, we found that the both southern populations tended to evolve narrower
457 TPCs (though not significant in S2; Table 1; Figs. 3, S4B), meaning that the descendants did not
458 tolerate extreme temperatures as well as their ancestors. Populations could have exhibited
459 evolutionary shifts in other TPC parameters, including lower and upper thermal limits, critical
460 breadth (the difference between upper and lower limit), performance maximum, and area under
461 the performance curve. For example, if S1 evolved a more competitive growth strategy, we
462 might predict that it has evolved a higher performance maximum. Though descendants of the

486 organisms have relied on performance metrics that are partial components of total fitness (e.g.,
487 heart rate in crabs: [Gaitán-Espitia et al. 2014](#), feeding rate in butterfly larvae: [Higgins et al. 2014](#),
488 growth rate in nymphalid caterpillars, sockeye salmon, and tropical tree seedlings: [Brett et al.](#)
489 [1969](#); [Berger et al. 2011](#); [Cheesman and Winter 2013](#), locomotor activity in *Drosophila*: [Latimer](#)
490 [et al. 2011](#), swimming speed in tadpoles: [Bartheld et al. 2017](#), sprinting speed in skinks and
491 lizards: [Crowley 1985](#); [Phillips et al. 2014](#)). Importantly, our study represents an important first
492 step in quantifying physiological tolerances for ancestors and descendants of plants in a
493 resurrection study, which is complementary to many other studies of *M. cardinalis* that have
494 explored geographic range limits and responses to climate change (e.g., [Angert et al. 2011](#); [Paul](#)
495 [et al. 2011](#); [Sheth and Angert 2016, 2018](#)).

496 Our study has several additional caveats which might limit our inferences about the
497 evolution of TPCs in response to recent climate change. First, we maintained a constant
498 day/night temperature regime in growth chambers, yet it is increasingly recognized that
499 temperature variability and frequency of temperature extremes have important consequences for
500 physiological, ecological, and evolutionary processes. Second, the cohorts in our resurrection
501 study are derived from two sampling periods that are only seven years apart, which may not be
502 enough time to detect evolutionary responses in a perennial plant. Based on previously collected
503 demography data ([Sheth and Angert 2018](#)) and personal observation, we speculate that plants
504 could have plausibly completed one to seven generations between our sampling periods.
505 Strikingly, despite this potential drawback, we still detected rapid evolution of breadth in the S1
506 population, which is particularly interesting given that individuals in southern populations tend
507 to be shorter-lived than those in northern and central populations ([Sheth and Angert 2018](#)).
508 Third, if seeds that remained dormant in the seed bank for multiple years contributed to the

509 descendant cohort in our study, they could slow the rate of evolutionary change (Hairston and De
510 Stasio 1988), but the likelihood of this is low (Sheth and Angert 2018). Fourth, the hierarchical
511 model assumes that seed families are statistically independent, however many seed families
512 shared a parent and were thus not genetically independent (Table S2). As a result, our estimates
513 of TPCs could be artificially more precise for those population/cohort combinations that had
514 fewer genetically unique families (N1 2010, N2 2010, C2 2010, and C2 2017). However, we did
515 not identify highly plausible evolutionary patterns in these populations, suggesting that greater
516 numbers of genetically non-independent families do not inflate estimates of evolutionary
517 response. Thus, future studies that consider additional life stages, performance metrics,
518 temperature regimes, and sampling years are still needed to gain a comprehensive view of long-
519 term evolutionary responses of TPCs in *M. cardinalis*.

520 *Conclusions and future directions*

521 A key question in ecology and evolutionary biology is whether populations can evolve rapidly
522 enough to keep up with the pace of climate change. Although rates of projected climate change
523 exceeded past rates of climatic niche evolution in a macroevolutionary study of vertebrates
524 (Quintero and Wiens 2013), we showed that in only seven years, breadth has decreased by over 1
525 °C in a southern population of a perennial plant. This pattern of evolution may be due to a period
526 of drought experienced in situ from 2010 to 2017, which would have truncated the growing
527 season and reduced the range of temperatures encountered, or a trade-off in which evolution of
528 earlier flowering comes with the cost of thermal specialization. Breadth did not significantly shift
529 in any of the other five populations, and thermal optima did not significantly shift in any of the
530 six populations across the species' range, likely due to a combination insufficient time for
531 evolutionary change, weak selection, or lack of genetic variation in thermal performance. We

532 conclude that populations, even those that are in the same region of a geographic range (e.g., the
533 two southern-edge populations in our study), can vary in their evolutionary responses to climate
534 change, having important, but often overlooked, impacts on forecasts of range shifts. More
535 importantly, our findings demonstrate that thermal performance evolution may not occur rapidly
536 in a majority of populations, even those where it is most expected. Overall, determining the
537 potential for population-level TPCs to evolve in response to recent climate change represents an
538 important step forward in understanding and predicting whether evolution can rescue populations
539 in the face of climate change.

540

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552

553 Author contributions

554 SNS conceived of the study; RCW and SNS designed the experiment. RCW conducted the
555 experiments and collected the data. RCW analyzed the data with the assistance of SBT. RCW
556 and SNS wrote the first draft of the manuscript and all authors contributed to editing the final
557 manuscript.

558

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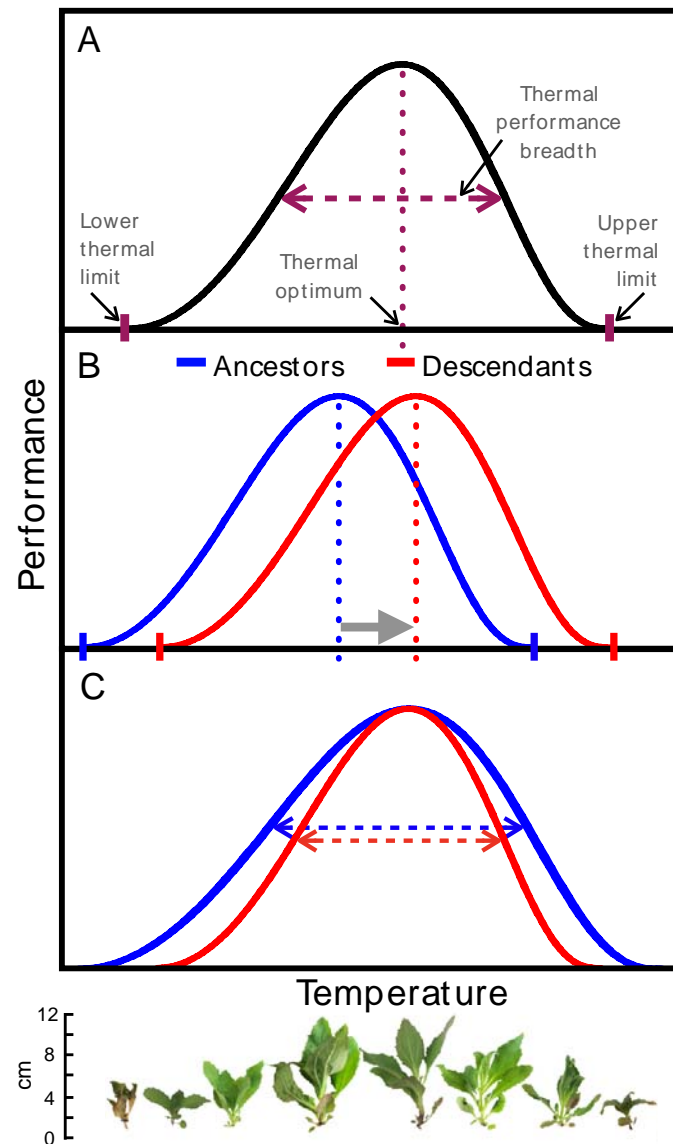
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704 **Table 1.** Observed evolutionary change (with 95% credible interval) in thermal optimum and
 705 breadth of six populations of *Mimulus cardinalis* (N, C, and S designate northern, central, and
 706 southern populations shown in Fig. 1A), alongside the average recent temperature anomalies
 707 (difference between historical mean and each study year from 2010 to 2017; Fig. 1B-C) for each
 708 population. Observed changes represent the mean differences in thermal optima and breadth
 709 between descendants (derived from seed collected in 2017) and ancestors (derived from seed
 710 collected in 2010) within each population. Positive values indicate that the thermal optimum or
 711 breadth was higher for descendants compared to ancestors, and negative values indicate that the
 712 thermal optimum or breadth was lower for descendants compared to ancestors. Highly plausible
 713 differences (where credible intervals do not overlap zero) are bolded. All units are in °C. Climate
 714 data were generated for population localities (Table S1) using the ClimateWNA v5.51 software
 715 package (available at <http://tinyurl.com/ClimateWNA>; [Wang et al. 2016](#)).

Population	Anomaly in maximum July temperature	Observed change in thermal optimum	Anomaly in seasonality	Observed change in breadth
N1 [†]	+0.61	+0.49 [-0.73, 1.68]	+ 0.15	+0.88 [-0.94, 2.64]
N2	+0.50	-0.46 [-1.48, 0.61]	+ 0.02	-0.50 [-1.89, 0.93]
C1	+0.66	+0.63 [-0.27, 1.52]	- 0.90	-0.47 [-1.63, 0.71]
C2 [†]	+0.61	-0.16 [-1.02, 0.71]	- 0.87	+0.31 [-0.81, 1.47]
S1 ^{†,‡}	-0.11	+0.57 [-0.26, 1.39]	- 1.86	-1.25 [-2.35, -0.14]
S2 [‡]	-0.13	-0.20 [-1.00, 0.59]	- 1.75	-0.34 [-1.38, 0.68]

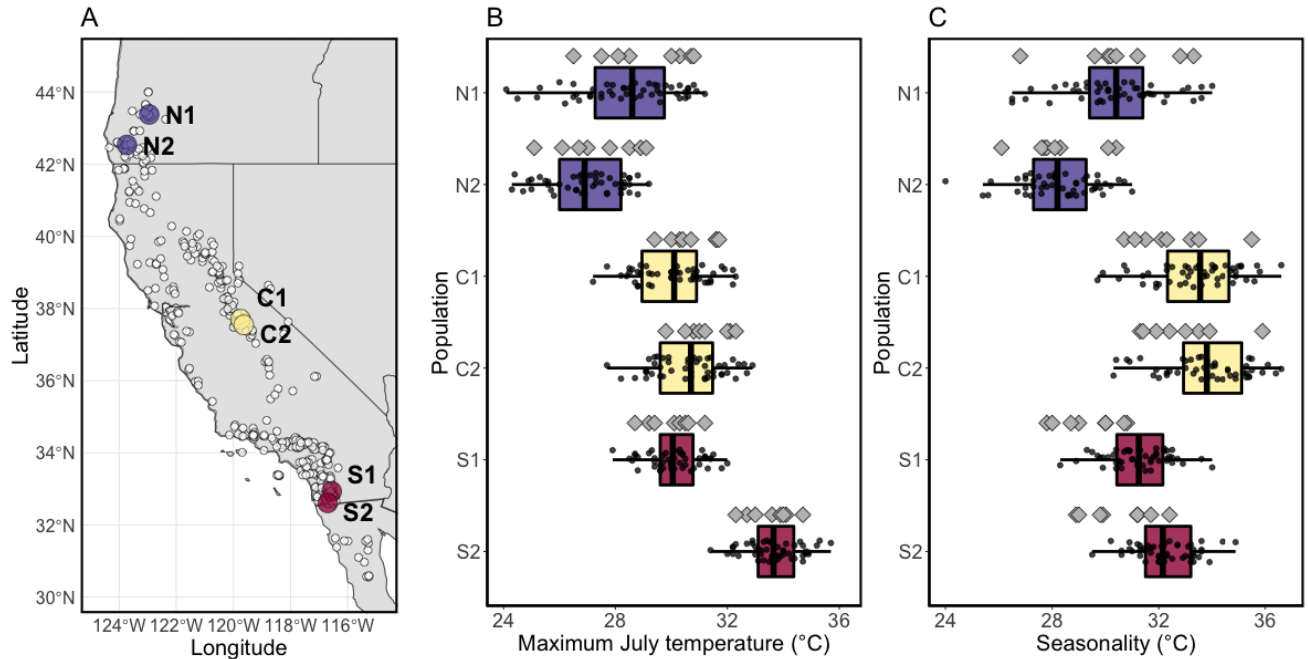
716 [†], populations which showed significant decline from 2010 to 2014 according the a demography study by [Sheth and](#)
 717 [Angert \(2018\)](#). Populations not marked with an asterisk were not included in this demography study, thus we do not
 718 know their status. [‡], populations whose ancestors showed ample genetic variation to evolve earlier flowering times
 719 in an artificial selection experiment by [Sheth and Angert \(2016\)](#).



720

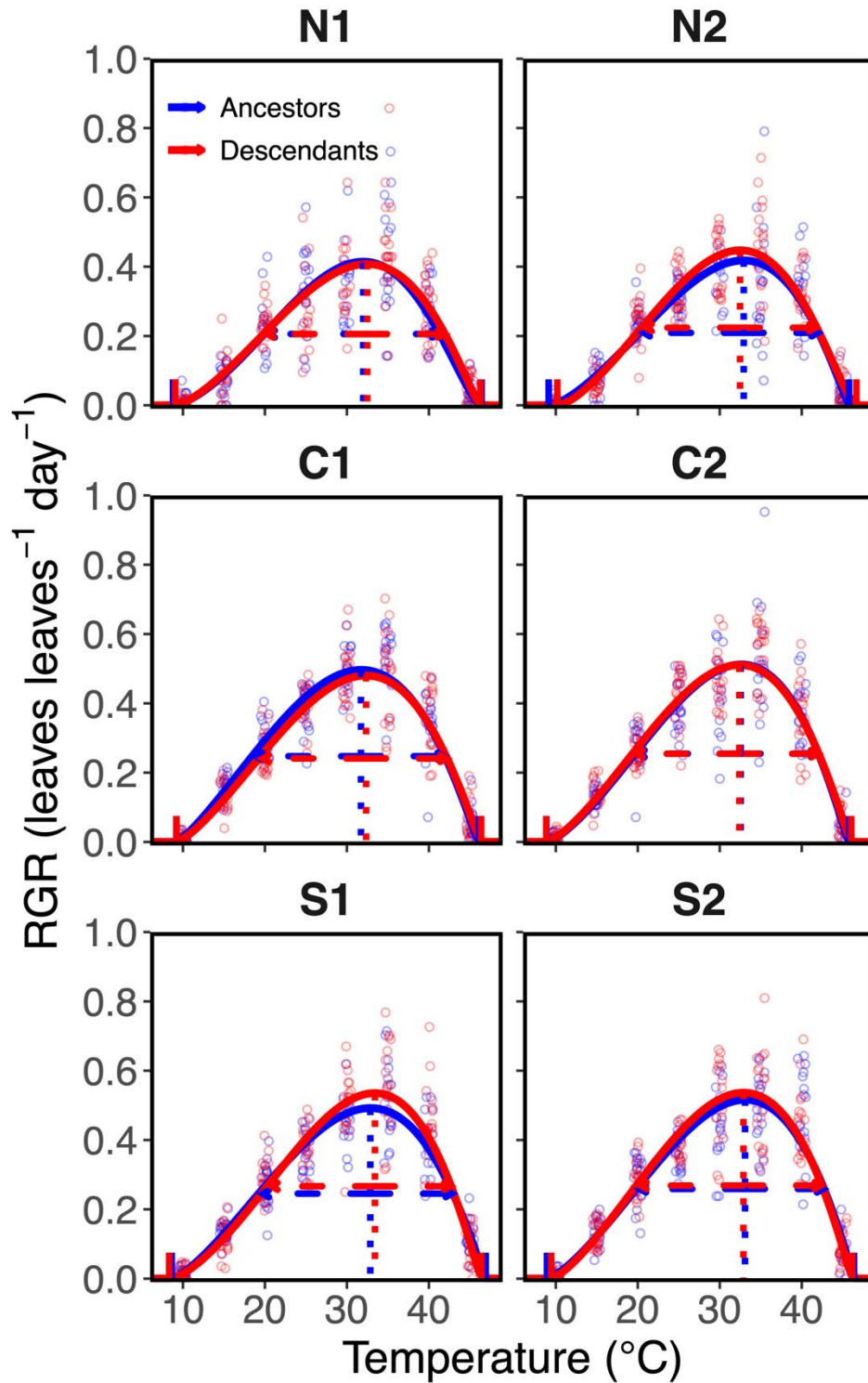
721 **Figure 1.** Predictions for evolution of thermal performance curves of *Mimulus cardinalis* in
722 response to recent climate change. A) Thermal performance curves are described by parameters
723 including the thermal optimum, thermal performance breadth, and lower and upper thermal
724 limits. B) Thermal optima of descendants should evolve to be higher than ancestors, especially in
725 northern and central populations where recent increases in maximum July temperatures have
726 been most extreme, and C) breadths of descendants should evolve to be narrower than ancestors,
727 especially in southern populations where recent decreases in temperature seasonality have been

728 most extreme (Table 1). Images of a single S2 2010 seed family grown across the experimental
729 temperature gradient are shown below panel C, with a scale for size.



730

731 **Figure 2.** A) Map of seed collection sites of two northern-edge (purple), two central (yellow),
732 and two southern-edge (red) populations of *Mimulus cardinalis*, superimposed on herbarium
733 specimen locations (white circles; [Angert et al. 2018](#)). Recent (2010-2017) B) maximum July
734 temperatures and C) temperature seasonality for each population (gray diamonds), superimposed
735 on boxplots of historical values (1951-2000). Climate data are described in Table S1.

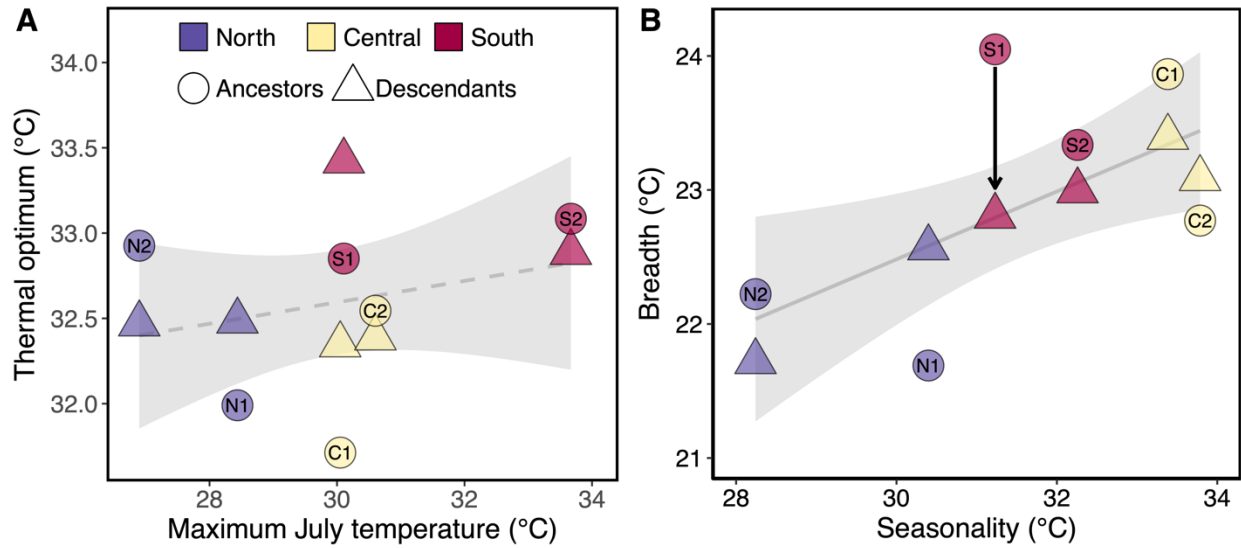


736

737 **Figure 3.** Thermal performance curves of the ancestors and descendants in each of six *Mimulus*

738 *cardinalis* populations. Vertical dotted lines represent thermal optima, horizontal dashed lines

739 represent thermal performance breadths (range of temperatures across which plants achieve 50%
740 of maximum growth), and notches on the x-axis indicate lower and upper thermal limits. The x-
741 axis represents daytime temperatures in growth chambers. Open points represent family means at
742 each temperature, which are horizontally scattered around each temperature at random to aid
743 visualization.



744

745 **Figure 4.** Variation in A) thermal optima across historical mean temperatures and B) breadth

746 across historical seasonality. Thermal optima and breadth values represent mean estimates

747 derived from a hierarchical Bayesian model, and are colored by the region where populations

748 occur within the species' geographic range (Fig. 2A). The arrow indicates highly plausible

749 evolutionary change from 2010 (ancestors) to 2017 (descendants) (Table 1). Population codes

750 are overlaid onto ancestral values. The regression in panel A was not significant at $\alpha=0.05$

751 (dashed line), but breadth significantly increased with seasonality (solid line; see results in the

752 main text). Shaded intervals represent 95% confidence intervals. Climate data are described in

753 Table S1.