Predicting the contribution of single trait evolution to rescuing a plant population from demographic impacts of climate change

Campbell, Diane R.[1,2], Powers, John M.[1,2] and Justin Kipness[2]

1. Department of Ecology & Evolutionary Biology, University of California, Irvine, CA 92697
2. Rocky Mountain Biological Laboratory, Crested Butte, CO 81224

Abstract

Evolutionary adaptation can allow a population to persist in the face of a new environmental challenge. With many populations now threatened by environmental change, it is important to understand whether this process of evolutionary rescue is feasible under natural conditions, yet work on this topic has been largely theoretical. We used unique long-term data to parameterize deterministic and stochastic models of evolutionary rescue with field estimates for the subalpine plant *Ipomopsis aggregata* and hybrids with its close relative *I. tenuituba*. In the absence of evolution or plasticity, the two studied populations are projected to go locally extinct due to earlier snowmelt under climate change, which imposes drought conditions. Phenotypic selection on specific leaf area (SLA) was estimated in 12 years and multiple populations. Those data on selection and its environmental sensitivity to annual snowmelt timing in the spring were combined with previous data on heritability of the trait, phenotypic plasticity of the trait, and the impact of snowmelt timing on mean absolute fitness. Selection favored low values of SLA (thicker leaves). The evolutionary response to selection on that single trait was insufficient to allow evolutionary rescue by itself, but in combination with phenotypic plasticity it promoted evolutionary rescue in one of the two populations. The number of years until population size would stop declining and begin to rise again was heavily dependent upon stochastic environmental changes in snowmelt timing around the trend line. Our study illustrates how field estimates of quantitative genetic parameters can be used to predict the likelihood of evolutionary rescue. Although a complete set of parameter estimates are generally unavailable, it may also be possible to predict the general likelihood of evolutionary rescue based on published ranges for phenotypic selection and heritability and the extent to which early snowmelt impacts fitness.

Key words: adaptation, climate change, environmental stochasticity, evolutionary rescue, genetic variation, *Ipomopsis*, phenotypic plasticity, phenotypic selection, snowmelt, specific leaf area.

Lay summary

Climate change is threatening many populations around the world. A population can avoid extinction by dispersal to more favorable locations, but that is not possible for many plants with limited seed dispersal. An alternative is evolutionary change in which changes in traits increase fitness and result in rescue of an otherwise endangered population. Some populations of a subalpine herb, Scarlet gilia, are threatened by increasingly early spring snowmelt due to climate change. Long-term field data on this species generated a unique opportunity to examine if evolutionary rescue is likely in a plant population. We estimated the strength of natural selection on specific leaf area (leaf thinness) in 12 years and its dependence on the date of snowmelt that year. Combined with previous estimates of the heritability of the trait (which affects speed of evolution), the direct response of the trait to date of snowmelt (plasticity) and the demographic impact of early snowmelt, models predicted that evolutionary rescue is possible in one of two threatened populations. Evolutionary rescue occurred in part because the plastic change to thicker leaves under early snowmelt and drought was adaptive. Our work provides one of the first examples to apply evolutionary rescue models to natural populations.

Introduction

Climate change is putting many populations at risk of extinction (Bellard et al., 2012; MacLean & Wilson, 2011). At-risk species could persist in the face of climate change by (1) dispersal to new localities with more favorable environmental conditions, (2) altering phenology to match abiotic conditions that change temporally, or (3) expressing new trait values that are adaptive under the new conditions, through a response to selection, phenotypic plasticity, or both. Whereas examples of the first mechanisms are relatively well-known, the third mechanism of persisting in the face of climate change has been less well documented under natural conditions (Parmesan, 2006). With rapid environmental changes around the world, understanding adaptive responses to the changing climate is urgently important, particularly for species with limited dispersal ability, such as many plants.

Adaptive responses to climate change could result from genetic changes due to evolution in response to the new conditions or to phenotypic plasticity (Chevin et al., 2013). The process by which adaptive evolutionary change occurs sufficiently rapidly to counteract a decline in population size under initially unfavorable conditions has been called evolutionary rescue (Bell & Gonzalez, 2011). Evolutionary rescue has been modeled primarily using classical quantitative genetic approaches (Chevin et al., 2013; Chevin et al., 2010; Gomulkiewicz & Holt, 1995; Kopp & Matuszewski, 2014), although there is increasing interest in incorporating genomics (Bay et al., 2017; Urban et al., 2023). The likelihood of evolutionary rescue depends upon the balance between the speed of evolutionary adaptation and the initial maladaptation of the population (Gomulkiewicz & Holt, 1995). A population declines initially in size due to the environmental challenge, then alleles or traits adaptive in the new environment increase in frequency, leading to higher mean absolute fitness and eventually a rebound in population size, if fitness is increased enough before the population goes extinct (Carlson et al., 2014). Evolutionary rescue can occur under greater environmental change when (1) genetic variance in a trait is high, (2) selection on the trait has a high sensitivity to the environment, and (3) generation time is short (Chevin et al., 2010). Phenotypic plasticity can enhance adaptation and further promote population persistence if plasticity is not costly to the organism (Scheiner et al., 2019). Despite that theoretical understanding, and laboratory demonstrations with microbes (Bell, 2017), we currently lack much understanding of how often conditions are sufficient for multicellular organisms in nature (Gomulkiewicz & Shaw, 2013; Urban et al., 2023), but see Peschel & Shaw (2024).

Here we use a well-studied plant system to determine how evolution in a single trait influences the likelihood of population persistence under climate change. Whereas the analysis of a single trait under selection does not capture some important features of evolutionary rescue, such as shifts in multiple genetically correlated traits, the approach illustrates how theoretical models of evolutionary rescue can be applied to real systems with all the challenges in estimating parameters under field conditions. At least three kinds of information are necessary: genetic variance, strength and environmental sensitivity of natural selection, and effect of an environmental challenge on mean fitness. All of these are difficult to measure under natural conditions, although information on one or two of them is sometimes available for a given plant species, including estimates of selection on functional traits (Dudley, 1996), genetic variation (Ahrens et al., 2019), or change in mean fitness in a novel environment (Walter et al., 2023). Here we leverage 12 years of data on natural selection and plasticity, in combination with previously published data, to provide for the first time all three kinds of information for natural plant populations.

We focus on specific leaf area (SLA) in subalpine plants, especially Scarlet gilia, *Ipomopsis aggregata,* and its close congener *Ipomopsis tenuituba* (Polemoniaceae), in the Rocky Mountains, Colorado, USA. In the western USA including Colorado, there is already a 10-20% loss in water contained in the snowpack since the 1980s, with a further loss of 60% projected over the next 30 years (Fyfe et al., 2017), and this reduced snowpack has caused shifts towards earlier melting in the spring (Clow, 2010). In the Colorado Rocky Mountains, *Ipomopsis* populations are threatened by earlier snowmelt, which currently causes lower seedling emergence, lower chance of survival to the next year, and lower seed production, projecting declines in local abundance (Campbell, 2019). Whereas pollen dispersal could introduce new genes that aid persistence, seed dispersal and migration to more suitable habitat are unlikely to contribute to persistence as seeds rarely disperse > 1 m (Campbell et al., 2017). On the other hand, several traits of *I. aggregata* experience ongoing natural selection and show genetic variance (Campbell et al., 2022), thus providing the raw material for evolutionary rescue from these deleterious impacts of climate change. One such trait is specific leaf area (SLA): the ratio of leaf area to dry mass. On a global scale, low SLA (i.e. thick leaves) is often associated with dry conditions as it reduces surface area, thereby reducing water loss from the leaf, at the cost of reduced photosynthesis (Poorter et al., 2009). In some natural populations of *Ipomopsis*, plants with low SLA had higher survival (Campbell et al., 2024), demonstrating selection on the trait. In a short-term experimental study of *I. aggregata*, selection on this trait depended upon snowmelt timing in the spring; plants with low SLA were more likely to survive to flower when snowmelt was artificially accelerated, but not so under later snowmelt (Navarro et al., 2022). In a quantitative genetic study in the field, SLA showed significant narrow sense heritability of 10%, indicating its potential to evolve in response to phenotypic selection (Campbell et al., 2022).

Finally, the trait shows phenotypic plasticity; in repeated measures of the same plants over several years, SLA is lower in years of earlier snowmelt (Campbell et al., 2022), which is adaptive (Navarro et al., 2022).

We first use 12 years of field data on SLA and its impact on fitness from years that varied greatly in snowmelt timing to determine overall selection on SLA and its environmental sensitivity under natural conditions. Only one rare study of flowering time measured selection in natural plant populations over a longer period (Ehrlén & Valdés, 2020). We then develop models of evolutionary rescue, incorporating the known genetic variance in that trait, and use them to determine whether evolutionary response to the selection is sufficient to counteract the impact of snowmelt timing on population growth. We address four specific questions:

1. How does selection on specific leaf area (SLA) depend on snowmelt timing?
2. How do magnitudes of heritability and selection intensity affect the likelihood of evolutionary rescue, and do actual field estimates for SLA fall in the range needed for evolutionary rescue?
3. Is population persistence likely given the overall temporal trend towards earlier snowmelt, and how does environmental stochasticity, in the form of variability around that trend, affect persistence? With climate change likely to increase extremes (IPCC, 2022) as well as average temperature, it is important to consider the impact of that variability.
4. How does phenotypic plasticity affect the likelihood of evolutionary rescue in this natural system?

Materials and Methods

Study System

The study sites consisted of three "Poverty Gulch" sites in Gunnsion National Forest and one site "Vera Falls" at the Rocky Mountain Biological Laboratory, all in Gunnison County, CO, USA. At Poverty Gulch there is a natural hybrid zone between *Ipomopsis aggregata* ssp. *aggregata* and *I. tenuituba* ssp. *tenuituba* (Campbell et al., 1997). Focal plants included two sets of plants. One set (data from 2009-2019) consisted of plants in common gardens at three sites: an *I. aggregata* site (hereafter "agg"; site L in Campbell et al., 1997), an *I. tenuituba* site (hereafter "ten"; site C) and a site at the center of the natural hybrid zone (hereafter "hyb"; site I). The second set consisted of plants growing in situ at the Poverty Gulch *I. aggregata* site (also included in "agg"), the Poverty Gulch hybrid site (also included in "hyb"), and an *I. aggregata* site at Vera Falls (hereafter "VF"; data from 2017-2023). Natural populations of *Ipomopsis* at these sites are relatively small, with typically 30 to 70 flowering individuals, along with plants in the vegetative state, in a given year.

At these sites, plants of *Ipomopsis* emerge as seedlings in the spring, and spend 2 to 12+ years as a rosette of leaves before sending up a flowering stalk during the year of flowering (Campbell et al., 2008). The mean generation time is 5 years in this locality (Campbell & Waser, 2007). The plants bloom during a single season, set seed, and then die. The plants have hermaphroditic flowers and are self-incompatible. The primary pollinators are hummingbirds and hawkmoths, with occasional flower visits from butterflies and solitary bees (Campbell et al., 1997; Price et al., 2005). The common gardens were started from seed in 2007 and 2008 (details in (Campbell, 2019; Campbell & Powers, 2015). Measurements of SLA in these gardens began when plants were 2 years old, either 2009 or 2010 depending upon the garden, as they are only small seedlings during their first summer after seed maturation. By 2018, all but 15 of the 4512 plants originally planted had died, with or without blooming, and we stopped following these gardens. Starting in 2017, in situ vegetative plants at the *I. aggregata* site and the hybrid site whose longest leaf exceeded 25 mm were marked with metal tags to facilitate identification.

Measurements of trait and fitness

In each year of the study, one leaf from each vegetative plant was collected in the field and transported on ice to the nearby Rocky Mountain Biological Laboratory (RMBL), 8 km distant. There each leaf was scanned with a flatbed scanner and analyzed using ImageJ (National Institutes of Health, Bethesda, MD, USA) to measure leaf area. The leaf was dried at 70 deg C for 2 hours and then weighed to obtain dry mass and calculate SLA as area/dry mass. For plants in the common gardens, SLA was measured on 982 leaves from 383 plants in 2009 – 2014. For in situ plants, SLA was measured on one leaf from each of 877 plants in 2017 – 2022.

Fitness was estimated as the binary variable of survival to flowering. Plants that were still alive in 2019 in the common gardens or in 2023 at the end of the study were assumed to survive to flowering. Whereas it is theoretically possible SLA could also influence flower number or seeds per survivor through effects on resource acquisition during earlier parts of the lifecycle, a previous study of *I. aggregata* found no evidence that selection on SLA differed whether flower number was included or not in the fitness estimate (Navarro et al., 2022).

Question 1: Selection on SLA and its environmental sensitivity

All data analysis and modeling was done in R ver. 4.4.2. To determine the overall average standardized selection differential on SLA, we first averaged SLA across repeated measurements in multiple years for a given plant. This simplification ignored the extent to which an individual plant matched SLA in a given year to local conditions, but that aspect is partly captured by the addition of plasticity (see below). We then performed analysis of covariance to model relative fitness (fitness divided by global mean fitness) as a function of mean SLA and the factor of site, after expressing SLA in units of standard deviation by subtracting the mean and dividing by the standard deviation across plants. The within-site regression coefficient for the effect of the standardized trait value on relative fitness (fitness divided by mean fitness) gives the SD-standardized selection differential (Kingsolver et al., 2001). Site was included as a fixed factor because survival differed on average across the three sites ($P < 0.0001$ in this analysis of covariance).

To evaluate the environmental sensitivity of SLA, we used individual measurements in each year and found the separate standardized selection differential in each year, including site along with the effect of standardized SLA in the model. The selection differential was standardized within year but not within site for this analysis. We then regressed the selection differential (both standardized and unstandardized for use in models) on date of snowmelt in that year. Because we had much longer time series for the agg and hybrid sites, we evaluated environmental sensitivity of selection only for those two sites. A steeper slope would indicate greater environmental sensitivity of selection. We examined trends in snowmelt date from 1985-2023 at sites agg, hyb, VF and the RMBL, at a similar elevation to our agg and VF sites (Supplementary Methods S1). The RMBL data were included because previous studies of how demography depends on snowmelt timing relied on those values (Campbell, 2019), and we therefore calibrated the evolutionary rescue models in the next sections the same way. Snowmelt date was 6 days later at the agg site than at RMBL, 17 days later at the hyb site than at RMBL, and 3 days earlier at site VF, with a common slope of 0.20 days earlier per year.

Most models of evolutionary rescue assume that selection on the trait is stabilizing, with an optimum that moves with the environment (Gomulkiewicz & Houle, 2009). In separate analyses, we also tested for stabilizing selection in each year using a model with site, the standardized trait value and the squared value of the standardized trait value. A negative slope of survival on the squared value would indicate curvature to the fitness relationship that corresponds with stabilizing selection. The quadratic regression coefficients were multiplied by 2 to obtain the quadratic selection gradients (Stinchcombe et al., 2008). Since the fitness component was binary, for all tests we employed function *glm* to perform generalized linear models with a binomial distribution to test for statistical significance while reporting quantitative estimates of the selection differentials based on ordinary least squares regression (Kingsolver et al., 2012).

Question 2: Modeling dependence of evolutionary rescue on selection intensity and heritability

As the observed selection on SLA was always directional, with no significant stabilizing or disruptive selection in any year (see Results), we used iterative models of evolutionary rescue based on directional selection rather than previous models that assumed stabilizing selection. We developed several models, building from simple to complex. Our first model (*Scenario 1*) was designed to examine how much evolutionary response (and hence selection intensity and heritatbility) was required to counter a particular drop in mean absolute fitness due to early snowmelt, and for this purpose we used a model for directional selection proposed by Campbell (2008):

$$N_t = \overline{W}_{t-1} N_{t-1} \quad (1)$$

$$\overline{W}_t = \overline{W}_0 \left[1 + \frac{b}{v} \Delta z_t\right] \quad (2)$$

where N_t = population size in generation t, $\overline{W}_t$ = mean absolute fitness in generation t, and $\overline{W}_0$= mean absolute fitness after the environmental challenge but prior to allowing for evolution. The portion in brackets expresses how absolute fitness is altered by the evolutionary response given an abrupt environmental shift to earlier snowmelt. The value Δz_t is the cumulative evolutionary response after t generations in the mean value for trait z. Following standard quantitative genetic theory:

$$\Delta z_t = h^2 S + \Delta z_{t-1} \quad (3)$$

where $h^2$is heritability and S is the selection differential, which in turn is the covariance between relative fitness and the trait value (Falconer & MacKay, 1996). Heritability of SLA was set to 0.10, as estimated in the field at these sites (Campbell et al., 2022). The expression *b/v* converts Δz_t into an effect on fitness; it equals b, the slope of fitness on z, divided by mean fitness, v. We assumed a starting stable population of 200 individuals based on historical demographic studies of *I. aggregata* (Price et al., 2008; Waser et al., 2010) and then a step change to constant prolonged drought, as in 2012, corresponding to the lowest annual value for absolute fitness observed across 15 years of study by Campbell (2019). That year had the earliest snowmelt date (RMBL day in year = 114) in the study, and we used the average of fitness across the *I. aggregata* site ($\overline{W}_0$ = 0.82) and the hybrid site ($\overline{W}_0$ = 0.93; average = 0.88). These values for fitness were estimated by the intrinsic rate of increase (λ) in integral population models that took into account all stages of the lifecycle from seed to seedling to vegetative plant to flowering plant to seed in the next generation (Campbell, 2019). For the strength of selection on SLA, we first used values from 2010, the year in which we observed the strongest selection favoring low SLA (Table 1). Since selection was estimated from survival, we are assuming that overall fitness would be reduced by the same amount as survival. This scenario corresponds to a situation involving prolonged extreme drought and prolonged strong selection.

To fully answer question 2, we examined the sensitivity of the results to changes in heritability and the selection intensity, in both cases by stepping the parameter from 0.05 to 1.00 by a step of 0.05. Since the plants are hermaphroditic and self-incompatible, in the deterministic case we assumed that the population would be functionally extinct if population size fell below 2. To investigate the impact of demographic stochasticity, instead of obtaining the population size in the next generation by multiplying by average fitness, for each individual we drew the number of individuals in the next generation by sampling from a Poisson distribution with a mean equal to average fitness (λ), as justified in Ellner et al. (2016). *Scenario 1* provides a baseline for understanding how population persistence is affected by a particular drop in mean absolute fitness, but has the disadvantage that the environmental change is unrealistic.

Question 3: Population persistence given mean and variance of temporal trend in snowmelt

To determine whether evolutionary rescue can occur given the projected temporal trends in snowmelt date, we modeled *scenario 2* in which snowmelt date was assumed to continue advancing linearly following the trend estimated since 1984 of 0.20 days per year. Because the environmental change is expressed in terms of years rather than generations, we modeled population size over years for this scenario. For simplicity, we retained discrete generations and assumed that the evolutionary response in SLA per year was 0.2 as high as the evolutionary response per generation (= 5 years). We then modeled the effect separately for the hyb and agg populations, for which we have the longest time series of data. These two populations differ in demography, in that the hybrid population is already below replacement ($\lambda<1$), whereas the *I. aggregata* population currently has $\lambda> 1$ but is predicted to fall below replacement in the near future with earlier snowmelt (Campbell, 2019). For these two population, we allowed absolute fitness in the absence of evolution ($\overline{W}_0$) to decline with snowmelt day at RMBL as determined from fitting quadratic models (Table 2) to the results of integrated projection models in a long-term demographic study (Campbell, 2019).

To incorporate the effect of evolution of SLA, we first modeled how the strength of selection on SLA changes with snowmelt day by regressing the selection differential (S) on annual snowmelt date for our 12 years of study (Table 2) and substituting that for S in equation 3. As Δz is the change in mean phenotype between two generations and generation time is 5 years, we divided h^2S by 5 in incrementing it each generation (see expression for Δz_tin Table 2). Similarly, to obtain how b/v (the change in fitness with the trait) changes with snowmelt day, we used the regression coefficient b in each year, and regressed that divided by mean survival against snowmelt day (Table 2).

We then used our *scenario 2* with its gradual change in snowmelt date to evaluate the influences of environmental stochasticity and phenotypic plasticity. We added environmental stochasticity in the form of observed variation around the trend line for snowmelt day as a function of year. Using again the linear relationship from Wadgymar et al. (2018), we used the *predict* function in base R to find the residual standard deviation of the predicted values during the timespan of 1984 to 2023, which equaled 11.4 days. In each year, we drew a value for snowmelt day from a normal distribution with mean as predicted but now with a standard deviation around it of 11.4 days. Due to the addition of this random element, we ran this model 10 times. To incoporate demographic stochasticity, as in *scenario 1*, for each individual we drew the number of individuals in the next generation by sampling from a Poisson distribution with a mean equal to average fitness (λ).

Question 4: Impact of phenotypic plasticity on population persistence

To investigate the impact of phenotypic plasticity on population persistence, we added plasticity in SLA to *scenario 2* both with and without stochastic environmental variability around the temporal trend line in snowmelt. To do so we used an equation for SLA as a function of snowmelt day for a set of plants that were measured repeatedly in different years by Campbell et al. (2022). Thus plasticity was modeled as a linear function of the present environment as detected by the individual plant (Greenspoon & Spencer, 2021). Using repeated measures ANOVA, SLA increased by 1.323 for every day later the snow melted. Assuming no cost of reduced SLA, to our prediction for the trait value in a given year, we added 1.323 times the difference in snowmelt day from the previous year.

Results

Question 1: Selection on SLA

Using mean values for SLA for individual plants, the overall standardized selection differential was S' = -0.12 (SE = 0.04, P = 0.0012; Fig. 1) for effect of the trait in a model that also included site, as compared to the values of S' = -0.33 and -0.19 (P = 0.007) in *I. aggregata* and *I. tenuituba* sites measured previously in 2009-2014 only (Campbell et al., 2024). These values all indicate that lower values (thicker leaves) led to higher survival to flowering. Selection was detectably different from zero in four years (Table 1), with the strongest value of S' = -0.23 (SE = 0.08, P < 0.01) in 2010. The selection differential (S) did not correlate significantly with snowmelt date in the spring (r = -0.21; P > 0.05), but was negative, favoring thicker leaves, in 19 of 24 site-year combinations (Fig 2). When broken up by site, it showed a positive trend (but not significant) at the hybrid site only; in other words in the direction expected with stronger selection for lower SLA when snowmelt was earlier (Fig 2).

Question 2: Modeling dependence of evolutionary rescue on selection intensity and heritability

With the assumption that early snowmelt made $\overline{W}_0$ = 0.88, in the absence of evolution, a population starting at size 200 would fall below 2 and thus be functionally extinct by the 38th

generation (Fig. 3). With the predicted evolution of SLA towards lower values in response to the strongest selection observed (S' = -0.23 and *scenario 1*; Fig. 3A), the expected population size fell only as low as 20 individuals (in generations 34-44) before rising again as mean fitness crossed zero and eventually followed exponential growth to above its starting level, showing evolutionary rescue (Fig. 3B). With demographic stochasticity added, 2 of 10 populations starting at size 200 went extinct by the year 2400 (75 generations; Supplementary Figure 1).

Increasing the heritability would increase the likelihood of evolutionary rescue (Fig. 4A), whereas halving it would prevent it, given that a population starting at 200 individuals would drop below 2 (the minimum that can perpetuate a self-incompatible species) by generation 66 and thus be functionally extinct at that time (Supplementary Figure 2). Doubling the selection intensity in the same way has an even larger effect (Fig. 4; Supplementary Figure 2) because it not only doubles the rate at which the trait value changes but also increases the influence of that change on absolute fitness.

Using the overall average value for selection (S' = 0.13), as the best estimate, rather than its value of -0.23 in the most extreme year of 2010, the estimated heritability would put *Ipomopsis* right on the dividing line between local extinction and population persistence in a deterministic model (Fig. 4A). With demographic stochasticity added, only 10% of simulated *Ipomopsis* populations persisted to generation 80 (white circle in Fig. 4C). All of these models so far examined evolutionary rescue only in the face of an abrupt shift to earlier snowmelt.

Question 3: Population persistence given mean and variance of temporal trend in snowmelt

Scenario 2 allowed a more realistic continuous change in the day of snowmelt in the spring (Fig. 5A,B) rather than a shift to extreme drought. In this case, in the absence of evolution, a hybrid population starting at size 200 would fall below 2 in the year 2128 and thus be functionally extinct by the 21th generation (Fig. 5A). Allowing for the observed trend in selection on SLA would not allow evolutionary rescue at the hybrid site, as the population size would still fall below 2, in this case in 2138 and stay below 2 for a very lengthy time (blue line in Fig. 5C shows population size still decreasing in the year 2400). Thus adding the extra realism of the actual trendline for snowmelt timing and selection eliminated the opportunity for evolutionary rescue. Even though the initial environmental hit to survival was less strong than in *scenario 1* (mean fitness in generation 1 = 0.92 as compared with 0.88 in model 1), selection was weaker and would not reach the value used in *scenario 1* until the year 2175 (supplementary Table S1). Increasing heritability to 0.30 would make evolutionary rescue possible even in this more realistic scenario, as a hybrid population starting at size 200 would not drop below 3 individuals (green line in Fig. 5C).

In contrast, *scenario 2* with a realistic trendline for snowmelt in an *I. aggregata* population showed very little effect of heritability on population persistence (Fig. 5B). This population is not yet below replacement (Campbell 2019), so allowing for selection and using the best fitting quadratic relationship for how mean fitness has previously changed with snowmelt, the population would initially increase in size, but start to decline by 2045 as fitness drops below 1 due to earlier snowmelt. Selection on SLA is not only weaker at the start in this population than in the *I. aggregata* population, but it also trends towards favoring larger SLA with earlier snowmelt in this population (Fig. 2). Even raising heritability of SLA to 0.30 would have little effect on the population dynamics, and the population is predicted to drop below its starting value by 2073 and be functionally extinct ($N < 2$) by around 2128, a value similar to that for the hybrid population (Fig. 5D) despite the difference in population dynamics to arrive at that point.

Adding variability in prediction of snowmelt date did not change the basic pattern that both populations would go extinct in the absence of plasticity (Fig. 6). Variability in snowmelt date had, however, more effect on the dynamics in the *I. aggregata* population, causing extreme swings in population size in the first several decades that would greatly change the predicted date for population extinction (Fig. 6B). The two populations showed different magnitudes of response to variability in snowmelt date because fitness in the absence of evolution is more sensitive to snowmelt date in the *I. aggregata* population. Allowing for demographic stochasticity had little effect except that all very small populations were predicted to go locally extinct by 2181 (Fig. 6C and 6D).

Question 4: Impact of phenotypic plasticity on population persistence

Adding phenotypic plasticity of SLA had a large effect for the hybrid population, allowing the simulated population to persist, never dropping below N = 10, when it had not in its absence, and allowing the population to grow starting in 2202 (compare blue line in Fig. 7C with blue line in Fig. 5C). This was not so for the *I. aggregata* population; even though phenotypic plasticity now made SLA decrease over time, it did not do so rapidly enough to generate evolutionary rescue (Fig. 7). For the hybrid population, adding environmental stochasticity in snowmelt timing on top of plasticity, the number of years until population growth became positive was extremely variable across runs of the model, spanning a range from the start until approximately 2300 (Fig. 8A). The variation arose because strong phenotypic plasticity made SLA highly responsive to the yearly fluctuations in snowmelt. Number of years until population growth became positive was highly responsive to initial changes in SLA, with a few early low values leading to early evolutionary rescue due to strong increases in absolute fitness (see brown line in Fig. 8A). Even with demographic stochasticity, however, the population had an 80%

chance of being rescued by evolution in this case (Fig. 8C), in comparison with the case without plasticity in which the hybrid population always went extinct (Fig. 6C). Adding environmental and/or demographic stochasticity on top of selection and plasticity still did not allow evolutionary rescue in the *I. aggregata* population (Fig. 8B, D).

Discussion

Climate change is projected to cause earlier snowmelt in mountains around the world due to higher temperatures and reduced snowpacks (Clow, 2010; IPCC, 2022; Kraaijenbrink et al. 2021). Here we modeled how earlier snowmelt affects absolute fitness, trait evolution, and the impact of that evolution on population persistence in a subalpine herb. A simple model based on directional selection (*scenario* 1) confirmed results of other models in which evolutionary rescue is more likely with higher heritability and lower initial maladaptation (Gomulkiewicz & Holt, 1995). Using field estimates of parameters, and a gradual trend in snowmelt date (*scenario* 2) we projected local population extinction even if adaptive evolution of the trait of specific leaf area is allowed, but that phenotypic plasticity in combination with evolution would likely rescue one of the two populations modeled. The simulated hybrid population is currently below replacement but is projected to be rescued by evolution of that single trait due to the combination of strong selection and plasticity. Although the simulated *I. aggregata* population is currently growing, it is projected to fall below replacement due to earlier snowmelt, and the weaker selection on SLA in that population is likely insufficient to rescue the population, even allowing for adaptive plasticity. Thus in this case the population most threatened in the near term is the one with better prospects for long-term persistence. Note that these models predict local population extinctions, not species extinction. *Ipomopsis aggregata* is widespread and common across the mountains of the western USA, encompassing a very wide range of environmental conditions (Grant &

Wilken, 1986). Furthermore, there is evidence that recruitment of vegetative rosettes is enhanced by soil disturbance, suggesting that populations may have historically arisen and went locally extinct (Juenger & Bergelson, 2000).

. Our models are relatively simplistic in comparison with some models of evolutionary rescue (Xu et al., 2023), but we viewed that as necessary to fit to the kind of information typically available. In developing the models, we made many key assumptions. First, we assumed that climate change can cause snowmelt to get progressively earlier following its current linear fit trend over the past four decades, and that no other environmental changes will affect these populations. While recognizing that simplicity, and the increase in extinction that can be caused by a non-linear environmental change (Greenspoon & Spencer, 2021), we view incorporation of alternative climate scenarios (Thomas et al., 2004) as beyond the scope of this paper. Second, we assumed natural selection was linear, which may be true in the short-term but is unlikely in the longer term as specific leaf area approaches its optimal value for survival. As SLA gets lower, surface areas for photosynthesis decreases, and at some point carbon assimilation may then limit fitness more than reduction of water loss. This could occur if a plant escapes drought by rapid growth early in the season. Tests of this drought escape strategy in other species have produced mixed results (Sherrard & Maherali, 2006; Wolfe & Tonsor, 2014). Third, we assumed that phenotypic plasticity would continue indefinitely along a linear trend. Although unlikely in the very long term, SLA in our models with plasticity did not fall below the minimum observed value (81 cm^2/g) in a recent study of *I. aggregata* (Navarro et al., 2022) until well after absolute fitness rose above 1 causing population size to increase (Fig. 8A). Fourth, we assumed that allowing for variation in time to flowering and thus overlapping generations would not alter population dynamics significantly. Fifth we assumed no cost to phenotypic plasticity, as defined by a fitness decrement of a highly plastic genotype relative to a less plastic genotype, an assumption that may often be met (Murren et al., 2015). Six, we had to make some assumptions about initial population size and when a small population would go extinct, either if population size dropped below 2, or with number of surviving offspring following a Poisson distribution. The populations we studied are small, with 30 to 70 flowering individuals, along with vegetative individuals, in a given year, and local extinction was not very sensitive to population size between 100 and 200. But demographic stochasticity would cause local extinction even in some cases when population size could otherwise eventually recover, and neither extinction criterion captures fully the reality of variation in lifetime fitness (Shaw et al., 2008). We saw a large interactive effect of environmental stochasticity and phenotypic plasticity, which allowed for evolutionary rescue to take a very wide range of possible times to occur in the hybrid population. Other forms of stochasticity would likely add to that variation in outcome. Thus, even though we predicted that the hybrid population could eventually be rescued by selection and adaptive plasticity in SLA, it is not currently possible to predict for a given local population precisely when population growth would become positive again.

In addition to these assumptions for a closed population, we also assumed no gene flow or dispersal between populations. Gene flow via pollen could introduce genes that increase adaptation (Wolf & Campbell, 1995). Seed dispersal on the other hand is very limited with seeds rarely moving > 1 m (Campbell et al., 2017). The two populations modeled here are 700 m apart and differ in snowmelt date by 11 days on average, meaning that 64 years of seed dispersal upslope would be required to gain just one day later of snowmelt, which is insufficient to keep up with the trend in snowmelt timing.

The information needed to project population persistence with evolution is rarely available. But for *Ipomopsis*, we have long-term estimates of how snowmelt timing affects mean absolute fitness (Campbell, 2019), heritabilities of some functional traits (Campbell et al., 2022), and now 12 years of selection estimates, allowing us to estimate environmental sensitivity. We are unaware of other plant systems for which all of these data are available, but a few cases come close. For example, data on genetic variation and selection were combined to compare the number of generations for northern populations of a primose to evolve some traits of southern populations separated by a temperature difference that climate change could produce in 70-140 years (Mattila et al., 2024). Besides *Ipomopsis*, we are aware of one other plant system for which similar information on the three parameters in our *scenario* 1 model (drop in mean absolute fitness, selection, and heritability) are available: *Boechera stricta*, another herbaceous species in the Rocky Mountains. We repeated the deterministic and stochastic versions of that model with two sets of parameter estimates for *B. stricta* (Supplementary Methods S2). Conditions appear to allow for evolutionary rescue in some parts of the range based on the earlier study (black circles in Fig. 4C, D; (Wadgymar et al., 2017)) but not under snow removal conditions that mimic climate change (white circles in Fig. 4C,D; Bemmels & Anderson, 2019). Extending the model to other plants, we plotted 95% confidence intervals for 653 selection differentials and 1214 estimates of heritabilities for functional traits reviewed by (Geber & Griffen, 2003). The majority of the space, but by no means all, overlapped with conditions where evolutionary rescue could take place (Fig. 4B) , with the important caveat that an abrupt shift to an environment resulting in mean absolute fitness of 0.79 is assumed and the additional caveat that many of the studies estimated heritability in a greenhouse or growth chamber where values were higher than in the field (mean = 0.42 vs 0.12).

Our models incorporated adaptive evolution and plasticity of only one quantitative trait. All else equal, adding more traits could likely increase the potential for evolutionary rescue by increasing absolute fitness more quickly. But phenotypic plasticity may modify that result. Note that we chose the trait of SLA because of prior evidence that it was under strong natural selection in the field environments (Campbell et al., 2024) and was plastic with respect to snowmelt timing in a concordant direction (Campbell et al., 2022). A recent meta-analysis found that plastic traits tend to have more additive genetic variation and thus higher evolvability (Noble, et al., 2019). Some other traits of *Ipomopsis* that are also under selection may not show plasticity, or may not show it in an adaptive direction. For example, earlier snowmelt leads to smaller flowers and reduced nectar production and yet those traits values are expected to reduce pollination and seed production (Powers et al., 2022). Furthermore, selection on flower length has gotten weaker over time with earlier snowmelt (Campbell & Powers, 2015). We are currently testing how allowing for multivariate trait evolution would affect evolutionary rescue in *Ipomopsis*.

With a single trait, the increase in mean fitness due to evolution of SLA was small compared to an upper bound on the rate of adaptation, following Fisher's fundamental theorem of natural selection (Fisher, 1930):

$$\bar{W}_{t+1} = \bar{W}_t + \frac{V_A(W)}{\bar{W}_t} \quad (4)$$

where $V_A(W)$ = additive genetic variance in fitness (Peschel & Shaw, 2024). That was previously estimated in a quantitative genetic study of *Ipomopsis aggregata* under field conditions as 54% of mean fitness (with a large confidence interval), based on survival from seed to flowering (Campbell, 1997). With heritability at 0.10, adaptation per generation in our models was much lower than that theoretical maximum based on all traits. For example, in generation 1 it equaled 0.4 % in *scenario 1* (supplementary Table S1).

We modelled expected evolutionary rescue with a quantitative genetic approach. Another promising approach is to use genomics and perform genomic sequencing over time (Urban et al., 2023). A few studies have detected genome evolution by comparisons over time, as in the European great tit (Stonehouse et al., 2023) or over different habitats that differ in ways expected under climate change, as in corals (Bay et al., 2017). These results have occasionally been used to make projections for persistence under climate change, but notably they have had to assume how many loci are involved in thermal tolerance and affect fitness in the field (Bay et al., 2017), whereas we had field data on how the trait affected fitness in particular years. This is one advantage of the quantitative genetic approach; whereas it does not identify particular loci, it is easier to measure field impacts on fitness, as shown by hundreds of studies (Kingsolver et al., 2012) and also how mean fitness changes over time (Shaw, 2019). That may make it a more feasible way to add evolutionary potential to extinction-risk assessments (Forester et al., 2022).

Conclusions

Using a long-term study of natural selection in the field, in combination with prior field information on heritability and mean absolute fitness, we were able to show that evolutionary rescue of a plant population due to evolution of specific leaf area is possible, if we also allow for the high phenotypic plasticity in the trait. Selection and plasticity in combination were projected to rescue one of two populations, and it was the population currently more threatened in which selection was strongest and evolutionary rescue appeared most likely. Our work provides one of the first examples to estimate the major parameters in evolutionary rescue models under natural conditions.

Data and code availability

Data and scripts will be made available in Dryad Digital Repository and Zenodo upon acceptance of the manuscript.

Author contributions

D.C. conceived the study, supervised the data collection, performed the data analysis and modeling, and drafted the initial version of the manuscript. All authors collected field data and contributed to later versions of the manuscript.

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Conflicts of interest

The authors declare no conflicts of interest.

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Table 1. Standardized selection differentials on SLA in each year. Directional selection differentials were estimated from models with a linear term of standardized SLA along with the factor of site. Quadratic selection gradients were estimated by doubling the quadratic regression coefficient in models with linear and quadratic terms of standardized SLA along with site. Statistical departure from zero was assessed using models with a binomial distribution of residuals and was not based on standard errors from the estimates in ordinary least squares regression.

Year	Directional selection differential	Quadratic selection gradient
2009	**-0.171 ± 0.081***	0.092 ± 0.108
2010	**-0.230 ± 0.087***	-0.004 ± 0.090
2011	-0.039 ± 0.065	0.094 ± 0.050
2012	-0.033 ± 0.067	0.084 ± 0.048
2013	**-0.174 ± 0.063****	-0.002 ± 0.074
2014	-0.063 ± 0.060	0.098 ± 0.070
2017	**-0.213 ±0.081***	-0.160 ± 0.122
2018	0.022 ± 0.112	-0.102 ± 0.105
2019	-0.058 ± 0.133	0.268 ± 0.282
2020	0.060 ± 0.135	0.057 ± 0.160
2021	0.125 ± 0.117	0.002 ± 0.135
2022	-0.114 ± 0.075	-0.037 ± 0.109

* $P < 0.05$. * $P < 0.01$.

Table 2. Parameter expressions used in modeling the impact of a linear trend in snowmelt timing and selection on specific leaf area (*scenario 2*).

Site	Process	Parameter expression
Both sites	Trend in snowmelt timing	d = 539.2 – 0.20*year
	SD in predicted snowmelt	11.4d
hybrid	Absolute fitness in absence of evolution	$\overline{W}_0$ = 1.352 – 0.0202*d + 0.000126*d^2
	Selection differential	S = -10.041 + $0.040d_t$
	Change in trait value by time t	$\Delta z_t = \frac{h^2(-10.041 + 0.040d_t)}{5} + \Delta z_{t-1}$
	Effect of trait value on absolute fitness relative to the mean	$\frac{b_t}{v_t} = (-0.0224 + 0.00012d_t)/\overline{W}_{0_t}$
I. aggregata	Absolute fitness in absence of evolution	$\overline{W}_0$ = 7.504– 0.1378*d + 0.00067*d^2
	Selection differential	S = 31.493-0.252d_t
	Change in trait value	$\Delta z_t = \frac{h^2(31.493 - 0.252d_t)}{5} + \Delta z_{t-1}$
	Increase in absolute fitness relative to the mean	$\frac{b_t}{v_t} = (0.0144 - 0.00012d_t)/\overline{W}_{0_t}$

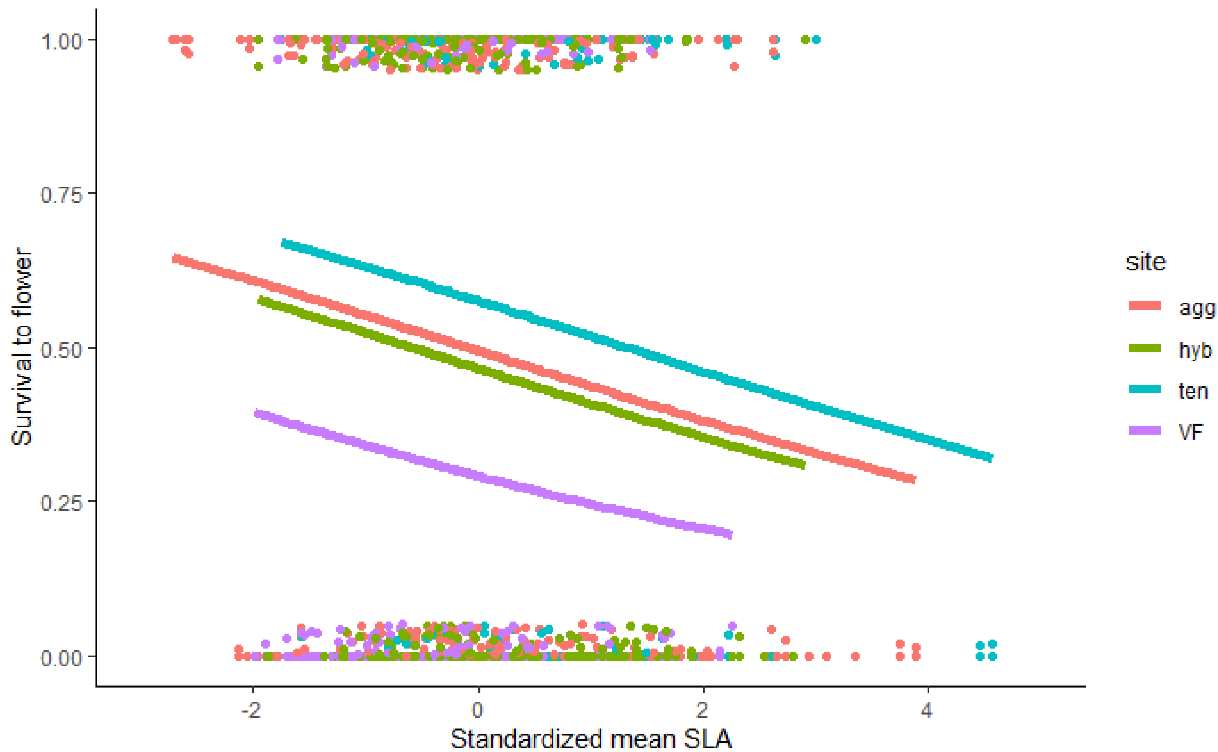


Figure 1. Survival to flowering as a function of mean SLA for a plant. Points are jiggered for visibility. Lines are predicted values obtained by inverse prediction from analysis of covariance with a binomial distribution: glm(survtoflr ~ site + rsla, family = binomial). These are bounded by 1 and 0 but appear approximately linear over the range of observed SLA. Sites “agg” and “VF” both contain *Ipomopsis aggregata*. Site “ten” contains *I. tenuituba*, and site “hyb” contains natural hybrids between the two parental species.

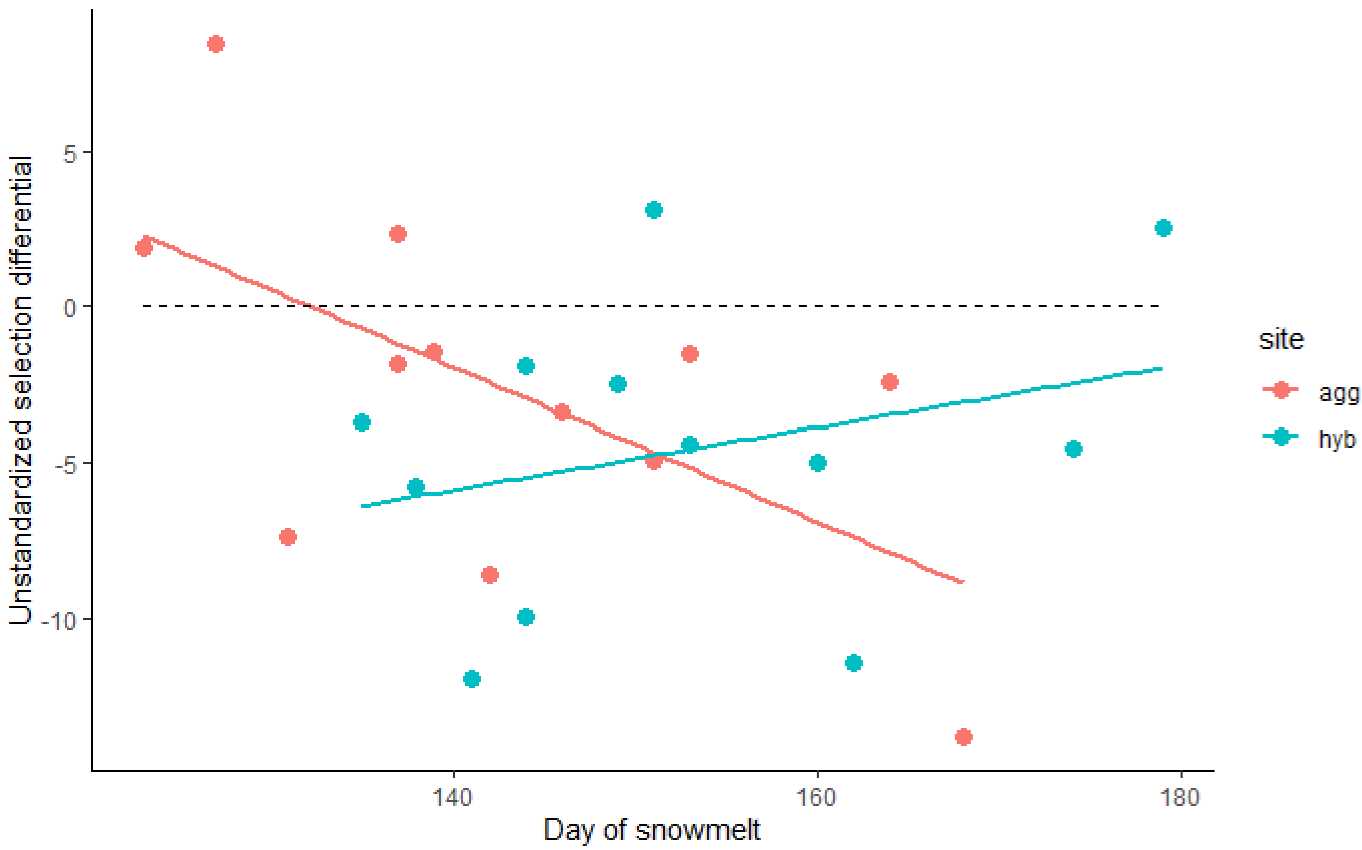


Figure 2. Unstandardized selection differential as a function of day of snowmelt in two sites. The models were originally fit to RMBL day of snowmelt and then adjusted by a constant to reflect accurate estimates of snowmelt in the individual sites. The selection estimate was negative (below the dashed line) in 19 of 24 site-year combinations, but did not show significant environmental sensitivity to day of snowmelt.

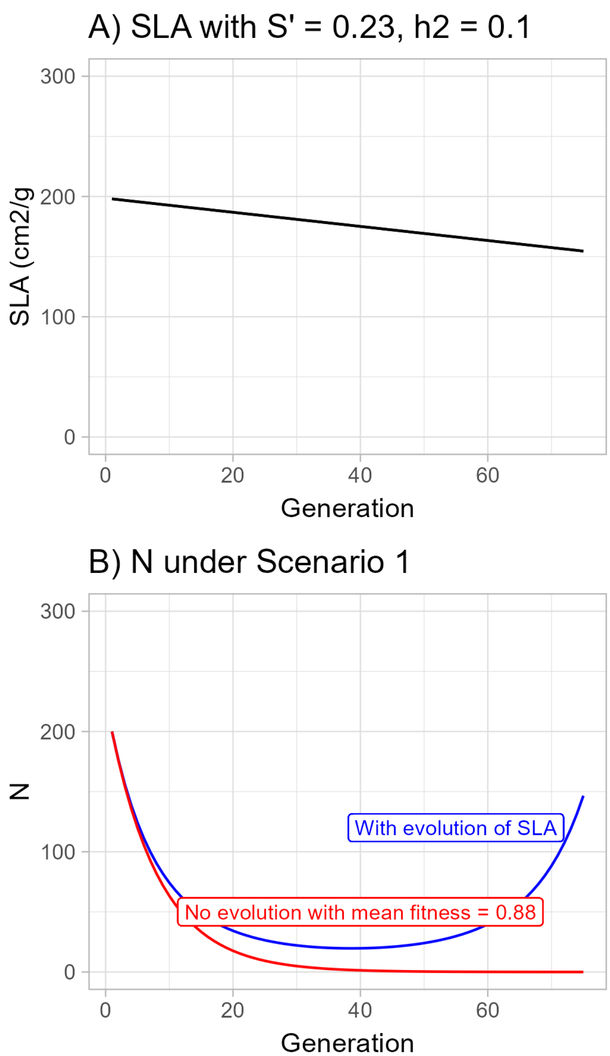


Figure 3. *Scenario 1* with constant extreme environment. A) Evolution of SLA with constant selection (S' = 0.23) and heritability = 0.10. B) Change in population size (N) for the case of no evolution (red line) and case of constant selection (blue line). In 2010, the year with strongest selection for smaller SLA, mean survival (v) = 0.554, and the regression coefficient (b) of absolute survival on raw SLA was -0.0034, making b/v (the relative amount by which absolute fitness is changed per cm^2/g increase in SLA) = -0.0061. The selection differential (S) obtained from the covariance of relative survival with raw SLA was -5.866, and heritability was assumed to be 0.10, making Δz = -0.59, a drop in SLA of 0.59 cm2/g per generation.

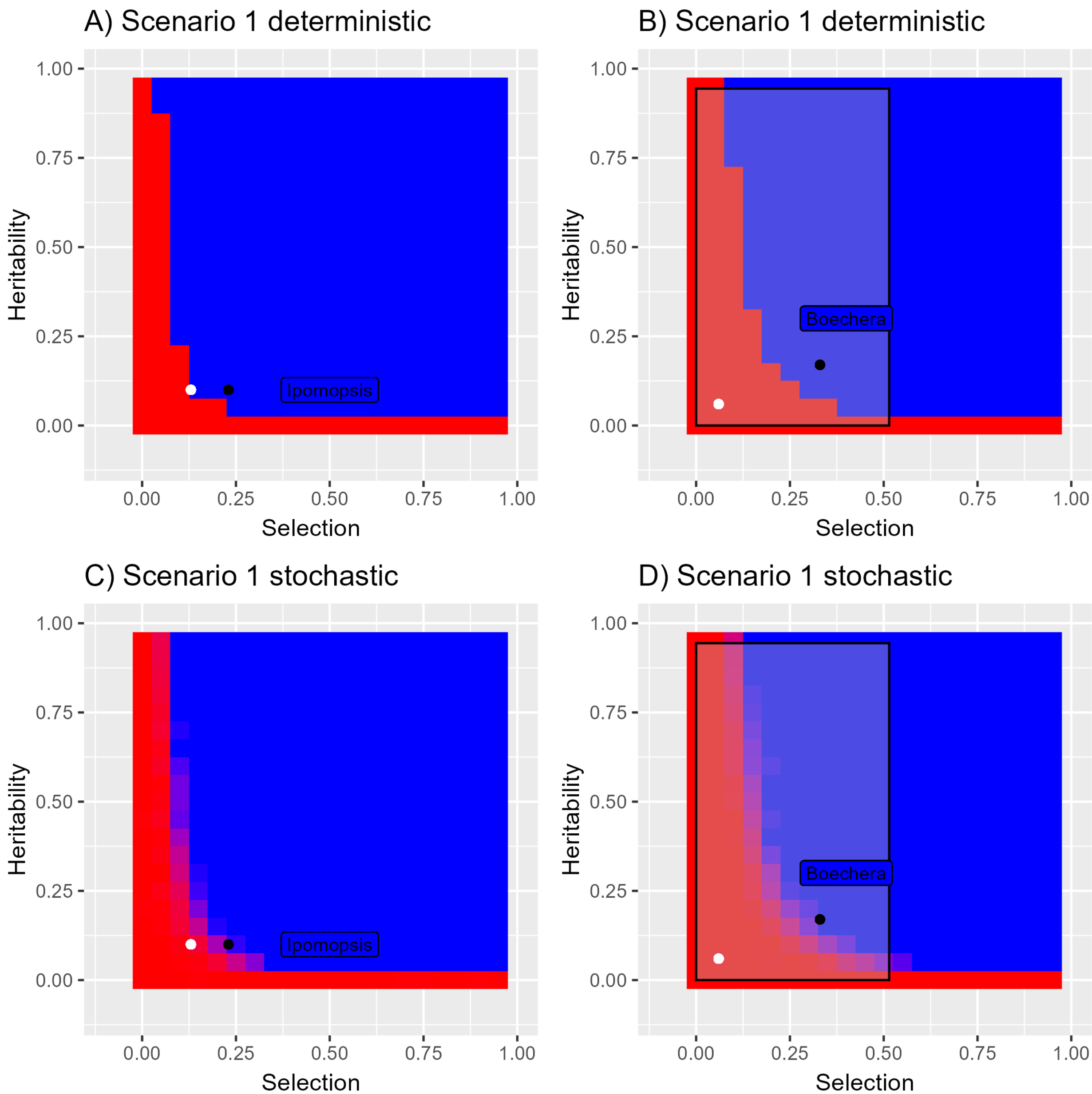


Figure 4. Parameter space for heritability and standardized selection differential showing conditions allowing evolutionary rescue in response to a constant extreme environment (*scenario 1*). Starting population size = 200. Red indicates extinction. Blue indicates evolutionary rescue by generation 75. Deterministic models shown for (A) Mean absolute fitness under early snowmelt in the absence of evolution = 0.88 in *Ipomopsis aggregata* and (B) 0.79 in *Boechera*

stricta. Points for species are plotted at their field-estimated parameter values. For *Ipomopsis* (A,C) the black circle indicates the strongest selection observed (S' = 0.23) and the white circle indicates mean selection (S' = 0.13). For *Boechera* (B,D), the two points correspond to two sets of parameters from different common garden experiments (see supplementary methods S2). Panels (C) and (D) include demographic stochasticity. In that case, approximately 90% of runs for *Ipomopsis* values went extinct when S' = 0.13. The gray rectangle in (B) and (D) encompasses a 95% confidence interval around the mean values for the selection differential and heritability in a review of plant functional traits (Geber & Griffen, 2003).

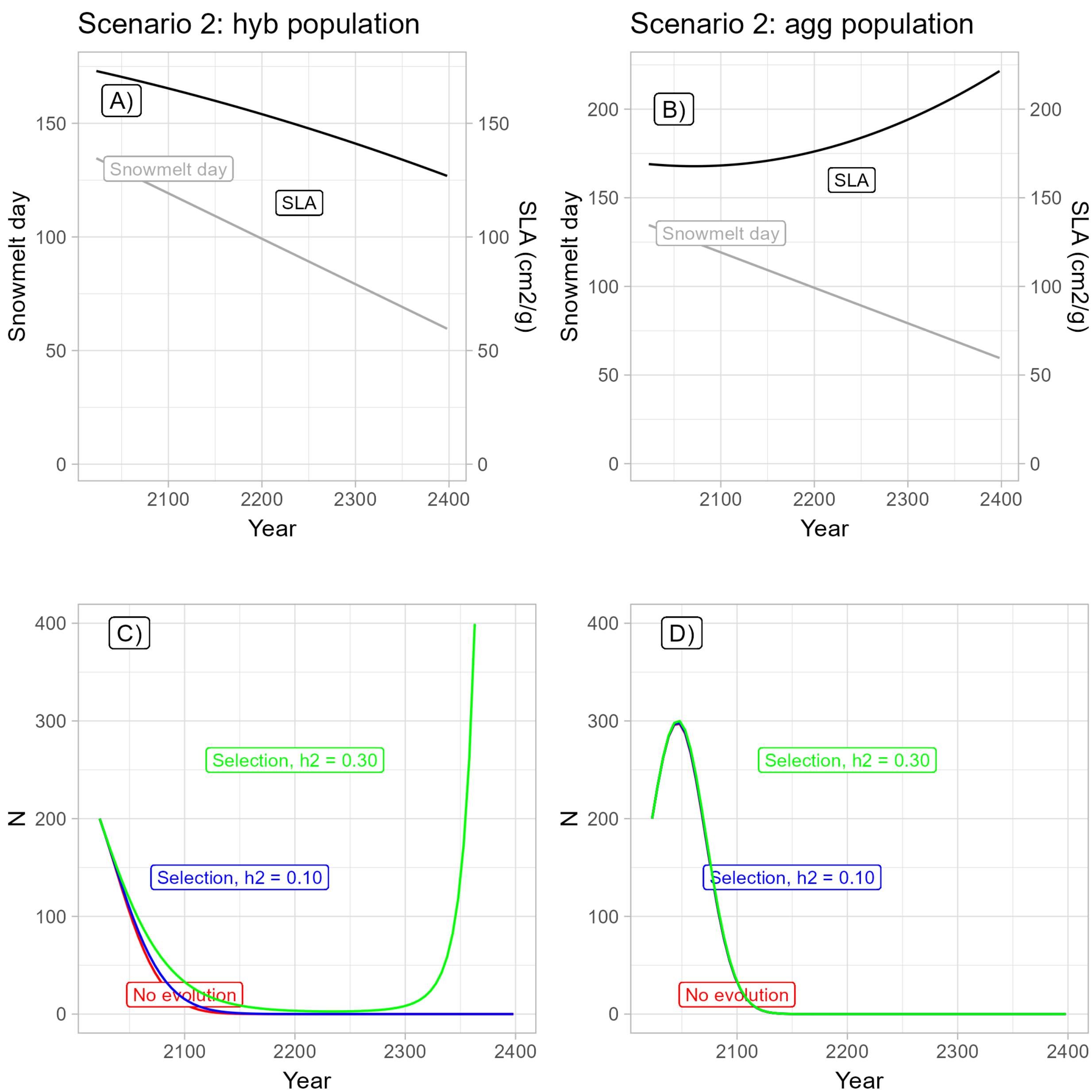


Figure 5. Predictions for selection but no plasticity or stochasticity in *scenario 2* with gradually earlier snowmelt. Snowmelt date (days since 1 January) and the evolutionary response of SLA shown for the (A) hybrid population and (B) *I. aggregata* population. Population size (N) for the

case of no selection (red line), selection with observed heritability of 0.10 (blue line), and selection with heritability of 0.30 (green line) for approximately 75 generations shown for the hybrid population (C) and *I. aggregata* population (D).

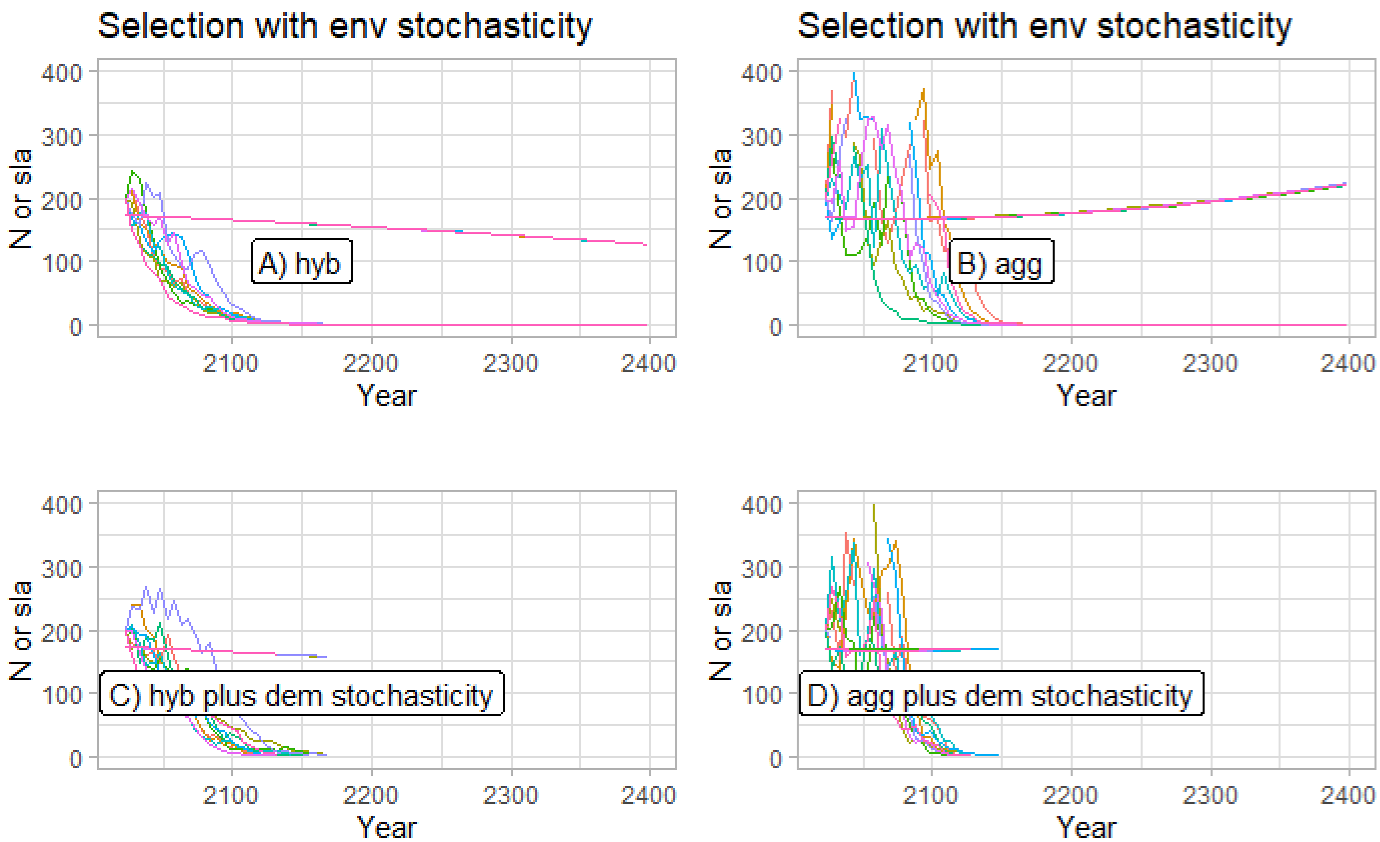


Figure 6. Predicted population size and the evolutionary response of SLA as a function of year with environmental stochasticity in the form of variance in snowmelt around the trendline. The model includes selection on SLA but not phenotypic plasticity. Heritability was set at 0.10. A separate line is plotted for each of 10 replicates for (A) hybrid population without demographic stochasticity, (B) *I. aggregata* population without demographic stochasticity, (C) hybrid population with demographic stochasticity, and (D) *I. aggregata* population with demographic stochasticity.

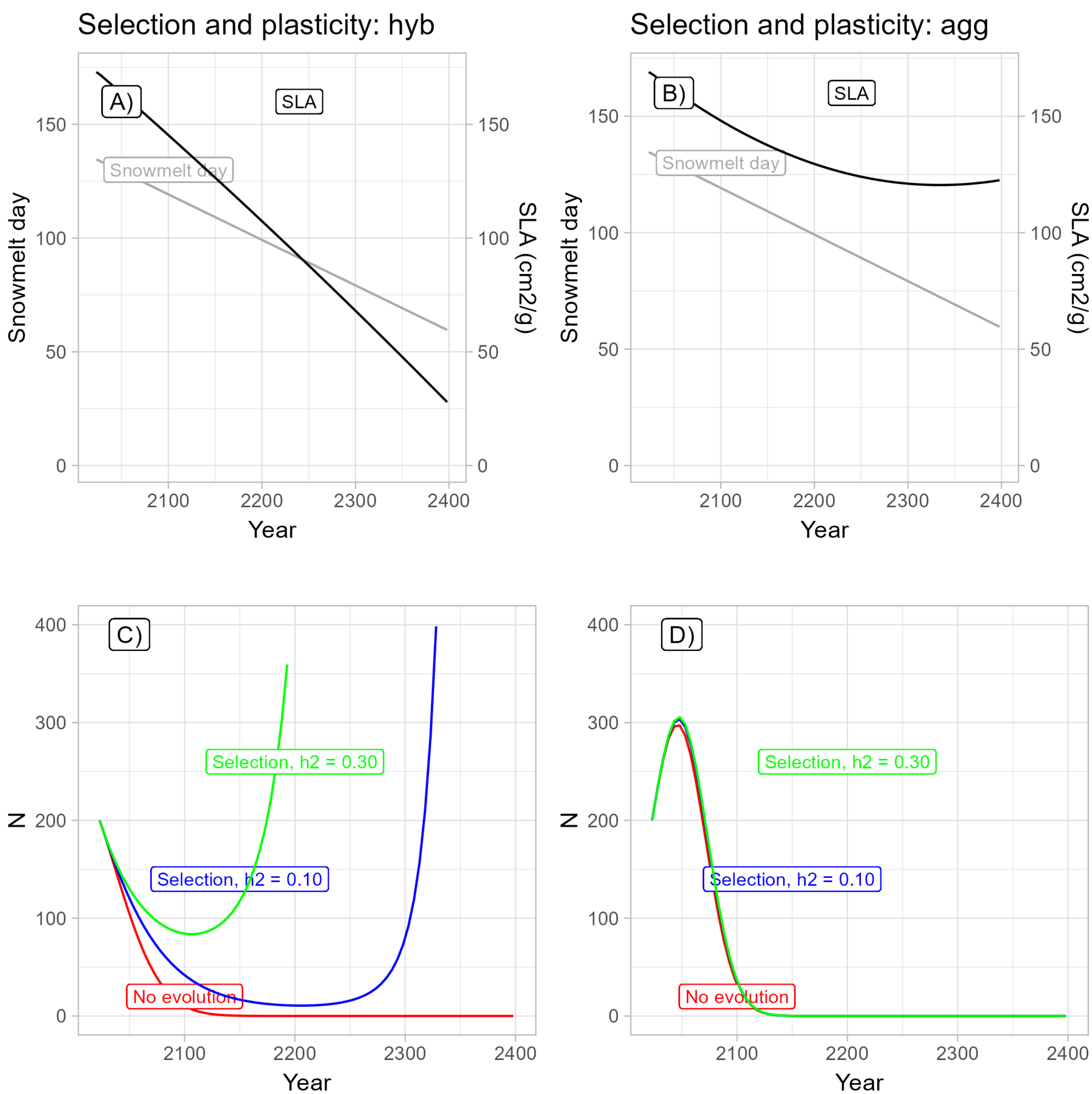


Fig. 7. Predictions for selection with added plasticity but no stochasticity in *scenario 2* with gradually earlier snowmelt.. Starting population size = 200. Snowmelt date (days since 1 January) and the evolutionary response of SLA shown for the (A) hybrid population and (B) *I.*

aggregata population. Population size (N) for the case of no selection (red line), selection with observed heritability of 0.10 (blue line), and selection with heritability of 0.30 (green line) for approximately 75 generations shown for the hybrid population (C) and *I. aggregata* population (D).

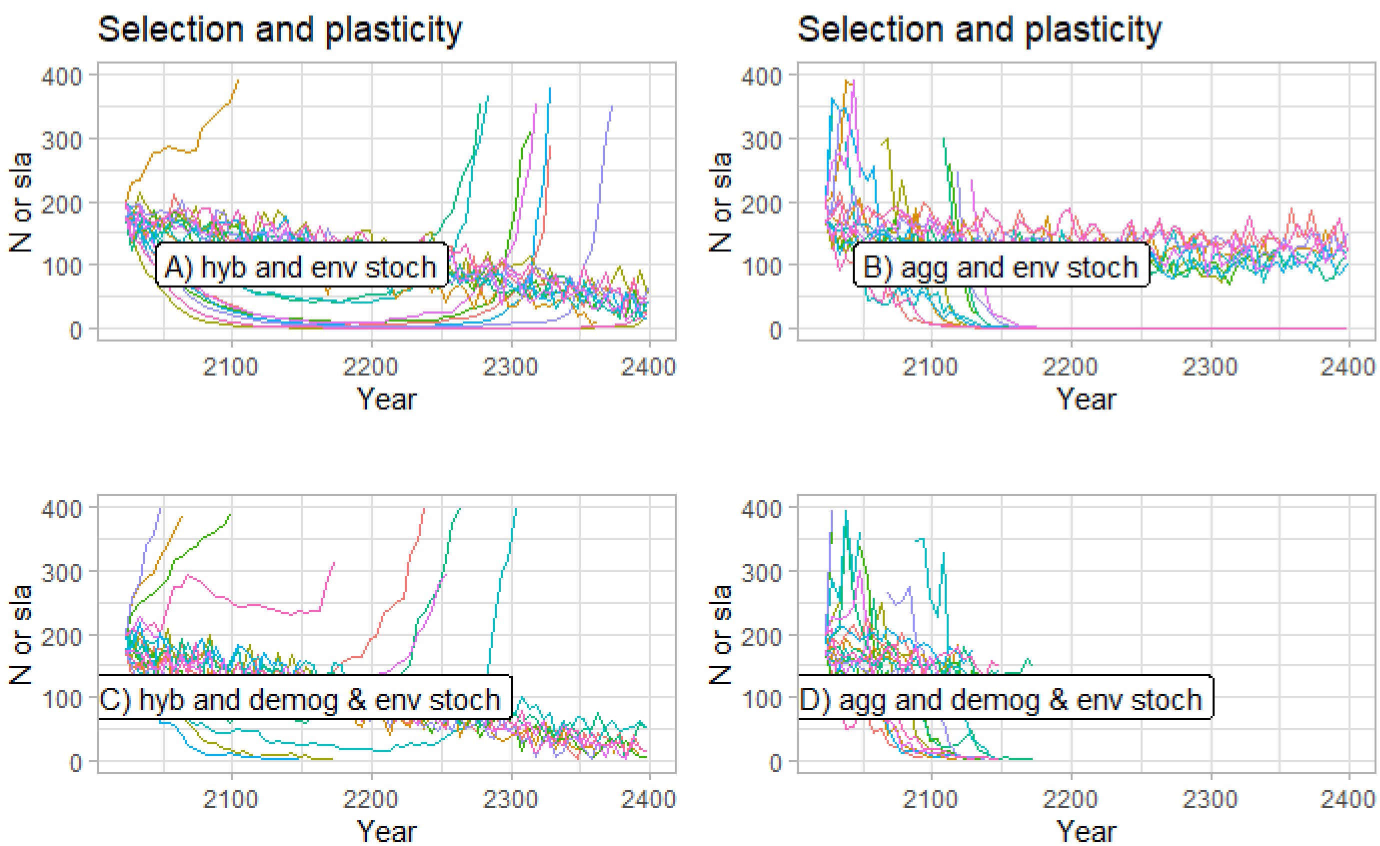


Figure 8. Predicted size of population (N) and mean SLA (cm^2/g) as a function of generation with selection, phenotypic plasticity and environmental stochasticity in the form of variance in snowmelt around the trendline. The observed heritability of 0.10 was used. All populations started with size N = 200. The response of SLA is shown in the same color as the population size for the corresponding run. Ten sample runs are shown for (A) the hybrid population and (B) the *I. aggregata* population without demographic stochasticity and (C) the hybrid population and (D) the *I. aggregata* population with demographic stochasticity.

Supplementary Materials

Methods S1. Snowmelt timing

We examined trends in snowmelt date (date of bare ground) from 1985-2023 at sites agg, hyb, and VF and 1984-2022 at the Rocky Mountain Biological Laboratory, 8 km distant and at a similar elevation to our *I. aggregata* site (http://www.gothicwx.org/ground-cover.html). The RMBL data were included because previous studies of how demography depends on snowmelt timing that are incorporated into modeling here relied on those values (Campbell, 2019), and we therefore calibrated the evolutionary rescue models in the next sections the same way. Snowmelt timing at the two actual sites (agg and hyb) differs only by a constant, as shown by the following analysis. We obtained estimates of snowmelt date at each site in each year from maps of snow persistence prepared by I. Breckheimer from an analysis of Landsat data and the size of the snowpack measured in snow water equivalent near snow telemetry sites (https://arcg.is/1yzKDG). In a model of snowmelt day as a function of year, site (RMBL, agg, hyb, VF) and the site x year interaction, the interaction was not significant ($F_{3, 144} = 0.06$, $P = 0.9800$). Removing the interaction from the model, snowmelt date was 6 days later at the agg site than at RMBL, 17 days later at the hyb site than at RMBL, and 3 days earlier at site VF, with a common slope of 0.20 days earlier per year (SE = 0.09, P = 0.0294).

Methods S2. Evolutionary rescue in *Boechera stricta*

Information on the three parameters needed for the model of extreme drought and prolonged selection (drop in mean absolute fitness, selection, and heritability) is available for another species in the Colorado Rocky Mountains, *Boechera stricta* (Brassicaceae). This small mustard is primarily self-pollinating, but for comparison with *Ipomopsis*, we still considered population extinction to occur if N < 2. At an elevation of 3133 m, the species has historically stable population size, but in more recent common garden studies, $\lambda = 0.79$ (Anderson & Wadgymar, 2020). One set of parameter values came from (Wadgymar et al., 2017) who estimated significant heritability of SLA as 0.17 (mean of three provided estimates) and significant standardized selection intensity at -0.33. The second set came from snow removal plots mimicking climate change conditions that found little evidence for an evolutionary response in SLA and non-significant heritability of 0.06 (mean of three estimates; (Bemmels & Anderson, 2019)). We repeated the deterministic and stochastic versions of the model for a constant extreme drought and selection (*scenario* 1) with these parameter estimates and compared the results with those for *Ipomopsis* using its overall average standardized selection differential on SLA.

References for Supplementary Material

Anderson, J. T., & Wadgymar, S. M. (2020). Climate change disrupts local adaptation and favours upslope migration. *Ecology Letters, 23*, 181-192.

Bemmels, J. B., & Anderson, J. T. (2019). Climate change shifts natural selection and the adaptive potential of the perennial forb *Boechera stricta* in the Rocky Mountains. *Evolution, 73*, 2247-2262.

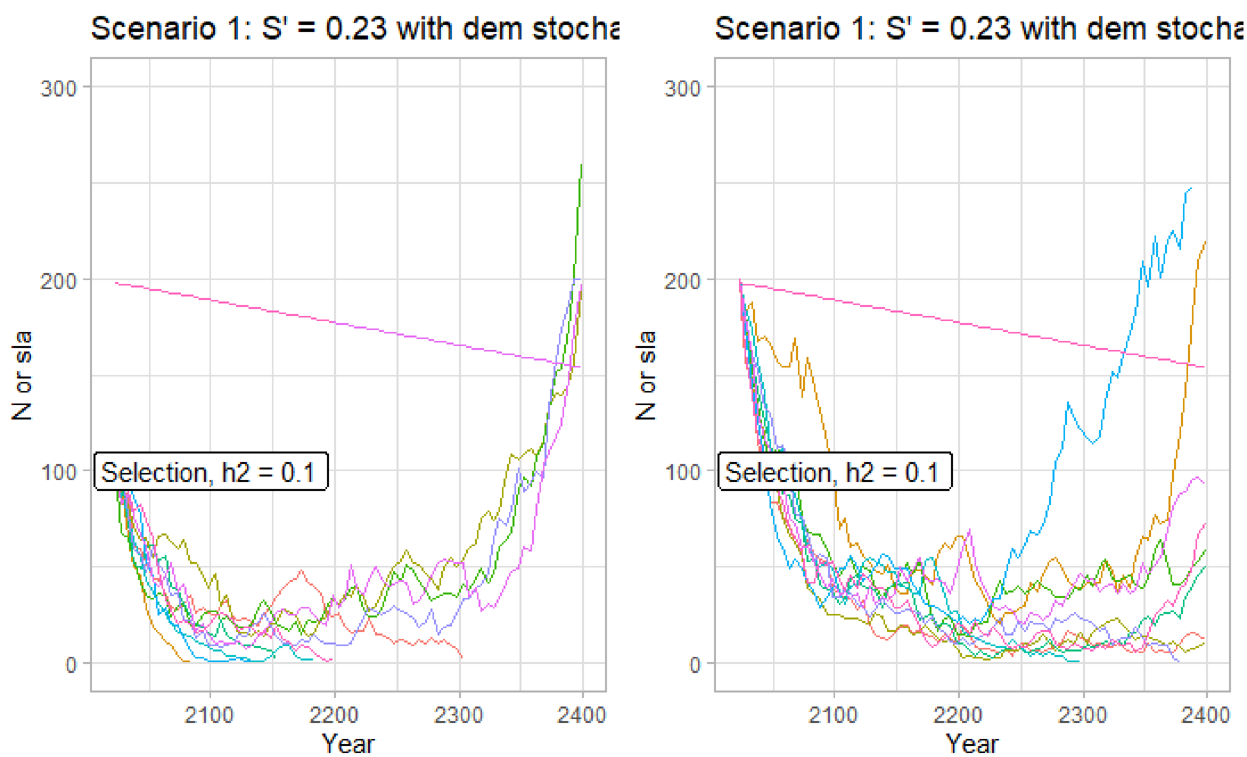
Campbell, D. R. (2019). Early snowmelt projected to cause population decline in a subalpine plant. *Proceedings of the National Academy of Sciences USA, 116*(26), 12901-12906.

Wadgymar, S. M., Daws, C., & Anderson, J. T. (2017). Integrating viability and fecundity selection to illuminate the adaptive nature of genetic clines. *Evolution Letters, 1*, 26-39.

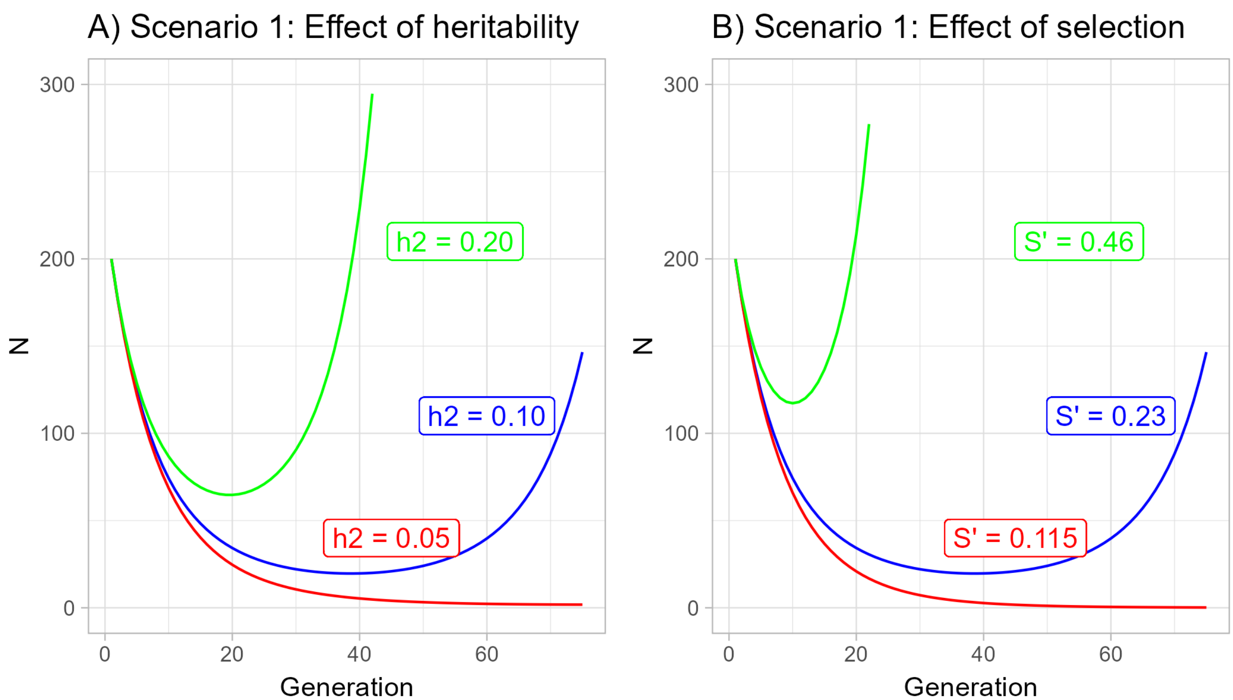
Table S1. Intermediate dynamics in iterative models for population size. Heritability of the trait was set at 0.10, and starting population size at 200. Adaptation (increase in mean fitness) is given by $\frac{b}{v}\Delta z_t$. $\overline{W}_0$ = mean absolute fitness in absence of evolution.

Scenario 1: Constant environment and constant selection							
Generation	Year	$\overline{W}_0$	S	$\frac{b}{v}$	Δz_t	$\frac{b}{v}\Delta z_t$	N with evolution
1	2028	0.88	-5.866	-0.0061	-0.587	.0035807	176.6
2	2033	0.88	-5.866	-0.0061	-1.174	.0071614	156.5
3	2038	0.88	-5.866	-0.0061	-1.761	0.0107421	139.2
4	2043	0.88	-5.866	-0.0061	-2.348	0.0143228	124.3
5	2048	0.88	-5.866	-0.0061	-2.935	0.0179305	111.3
6	2053	0.88	-5.866	-0.0061	-3.522	0.0214842	100.1
7	2058	0.88	-5.866	-0.0061	-4.109	0.0250649	90.3
8	2063	0.88	-5.866	-0.0061	-4.696	0.0286456	81.7
9	2068	0.88	-5.866	-0.0061	-5.283	0.0322263	74.2
10	2073	0.88	-5.866	-0.0061	-5.870	0.035807	67.7
Scenario 2: Mean fitness and selection change with snowmelt date as in hybrid population.							
Generation	Year	$\overline{W}_0$	S	$\frac{b}{v}$	Δz_t	$\frac{b}{v}\Delta z_t$	N with evolution

1	2028	0.905	-4.697	-0.0064	-0.56	0.003584	183.3
2	2033	0.889	-4.737	-0.0065	-1.03	0.006695	166
3	2038	0.876	-4.777	-0.0066	-1.51	0.009966	148.5
4	2043	0.863	-4.817	-0.0067	-1.99	0.013333	131.4
5	2048	0.850	-4.857	-0.0068	-2.47	0.016796	114.9
6	2053	0.838	-4.897	-0.0070	-2.96	0.02072	99.3
7	2058	0.826	-4.937	-0.0071	-3.45	0.024495	85
8	2063	0.814	-4.977	-0.0072	-3.95	0.02844	71.9
9	2068	0.802	-5.017	-0.0073	-4.45	0.032485	60.2
10	2073	0.791	-5.057	-0.0074	-4.95	0.03663	49.9



Supplementary Figure 1. *Scenario 1* of constant selection in an extreme environment with demographic stochasticity added. Ten sample runs are shown starting with N = 100 (left panel) or N = 200 (right panel). Parameter values are the same as in Fig. 3 with the exception of the addition of demographic stochasticity.



Supplementary Figure 2. Effects of heritability and selection on population dynamics in *scenario 1* with constant extreme environment. A) Selection is kept at S’ = 0.23, and heritability varies. B) Heritability is kept at 0.10 and selection varies. Predicted population size is shown as a function of generation.