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Germination timing and chilling exposure create contingency in life history and influence fitness in the native wildflower *Streptanthus tortuosus*

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Abstract

1. The timing of life history events, such as germination and reproduction, influences ecological and selective environments throughout the life cycle. Many organisms evolve responses to seasonal environmental cues to synchronize these key events with favourable conditions. Often the fitness consequences of each life history transition depend on previous and subsequent events in the life cycle. If so, shifts in environmental cues can create cascading effects throughout the life cycle, which can influence fitness, selection on life history traits, and population viability.
2. We examined variation in cue responses for contingent life history expression and fitness in a California native wildflower, *Streptanthus tortuosus*, by manipulating seasonal germination timing in a common garden experiment. We also manipulated chilling exposure to test the role of vernalization cues for seasonal life history contingency.
3. Plants germinating early in the growing season in autumn were more likely to flower in the first year and less likely to perennate than later germinants in spring. First-year reproduction and overall fitness was the highest for autumn cohorts. Sensitivity analyses showed that optimal germination date depended on survival beyond the first year and fruit production in later years.
4. Experimental chilling exposure induced first-year flowering in spring germinants, demonstrating that seasonal life history contingency is mediated by a vernalization requirement. This requirement reduced fitness of spring germinants without increasing survival or later fecundity and may be maladaptive. Such mismatches between cues and fitness may become more pervasive as predicted climate change reduces exposure to chilling, shortens growing seasons, and increases severity of summer drought.
5. *Synthesis*. Shifts in germination timing in seasonal environments can cause cascading effects on trait expression and fitness that extend beyond the first year of the life cycle. Climate change is likely to shift seasonal conditions, influencing such life history contingency, with significant impacts on trait expression, fitness, and

population persistence. These shifts may cause strong natural selection on cue sensitivity and life history expression, but it is an open question whether populations have the potential for rapid adaptation in response to this selection.

KEYWORDS

Arabidopsis, climate change, iteroparity, life history, perenniality, phenology, plant development and life-history traits, vernalization

1 | INTRODUCTION

In variable environments, organisms may evolve responses to seasonal environmental cues in order to time emergence, growth and reproduction to coincide with favourable conditions (Andres & Coupland, 2012; Blackman, 2017; Cohen, 1967; Gremer, Kimball, & Venable, 2016). The timing of events at each life history stage can affect phenological, physiological, morphological and demographic traits expressed at subsequent stages (Galloway & Burgess, 2009; Grime, 1977; Post, Pedersen, Wilmers, & Forchhammer, 2008; Wilczek et al., 2009) as well as the adaptive value of those traits (Donohue, 2002; Donohue, Casas, Burghardt, Kovach, & Willis, 2010; Galloway & Burgess, 2009; Kalisz, 1986). Thus, the contingency of developmental trajectories on seasonal timing and environmental cues can have important consequences for individual fitness, expression and selection on life history traits, and population viability (Galloway & Burgess, 2009; Post et al., 2008). In the face of a changing climate, it is critical to understand such contingent life histories and their implications under anticipated future conditions (Anderson, 2016; Donohue et al., 2010; Post et al., 2008).

A fundamental goal in evolutionary ecology is to understand life history timing in variable and changing environments. Largely, the field has focused on understanding variation in the timing of juvenile development, the timing of reproduction, and the scale and frequency of reproduction (Roff, 2001; Stearns, 1992). In plants, this translates into questions of when to germinate, when to transition from vegetative growth to reproduction, and whether to reproduce once or multiple times (semelparity vs. iteroparity). Generally, theory predicts that delaying germination and reproduction is costly to fitness, unless there is a benefit to delay, such as increased survival or fecundity (Cohen, 1966; Hart, 1977; Metcalf, Rose, & Rees, 2003; Tuljapurkar, 1990). Similarly, semelparous life histories are expected to be favoured under conditions with low adult survival and high variability in fecundity (Charnov & Schaffer, 1973; Ranta, Tesar, & Kaitala, 2002; Wilbur & Rudolf, 2006). Of course, these patterns depend on tradeoffs between survival and fecundity as well as the costs of current versus future reproduction (Charlesworth, 1994; Metcalf et al., 2003; Schaffer & Rosenzweig, 1977; Silvertown, Franco, & McConway, 1992). Although often studied separately, these life history traits are inherently linked and each can affect the adaptive value of the others.

For plants, the timing of germination is a key life history transition with profound effects on the rest of the life cycle (Burghardt, Metcalf, & Donohue, 2016; Burghardt, Metcalf, Wilczek, Schmitt, & Donohue, 2015; Donohue, 2005; Galloway & Burgess, 2009; Wilczek et al., 2009). Germination timing determines the conditions that a new, vulnerable seedling experiences and thus the probability of establishment (Akiyama & Agren, 2015; Postma & Agren, 2016) as well as the environmental niche experienced later in life, including growing conditions, resource availability, and interactions with other individuals and species (Donohue et al., 2010; Lortie & Turkington, 2002b, 2002a; Verdu & Traveset, 2005). For example, early germination can increase the amount of time to acquire resources for reproduction, but may increase the risk of encountering unfavourable conditions earlier in the season, such as mid-season drought, frost or predation, (Donohue et al., 2010; Lortie & Turkington, 2002a, 2002b; Mercer, Alexander, & Snow, 2011; Petru, Tielborger, Belkin, Sternberg, & Jeltsch, 2006; Tielborger & Valleriani, 2005; Verdu & Traveset, 2005). Germinating earlier within a season generally results in higher fecundity, but selection on survival may favour early, intermediate, or late germination (Akiyama & Agren, 2015; Donohue et al., 2010; Kalisz, 1986; Verdu & Traveset, 2005), potentially leading to conflicting selection on germination timing (Akiyama & Agren, 2015). Moreover, seasonal germination timing can influence the strength and direction of selection on traits expressed later in the life cycle, including growth, response to stress, and timing of reproduction (Donohue et al., 2005a; Korves et al., 2007; Mercer et al., 2011; Weinig, 2000). In addition to influencing performance, the seasonal timing of germination also determines exposure to environmental cues, such as day length, temperature, and water availability, which regulate expression of plastic life history traits such as reproductive timing within and across seasons (Burghardt et al., 2015; Galloway & Burgess, 2009; Wilczek et al., 2009). In particular, many plant species have winter chilling (vernalization) requirements, which prevent flowering until favourable spring conditions (Blackman, 2017; Bloomer & Dean, 2017). Variation within and among species in vernalization signaling pathways can determine whether a plant displays an annual, biennial, or iteroparous perennial life history (Albani et al., 2012; Baduel, Arnold, Weisman, Hunter, & Bomblies, 2016; Baduel, Hunter, Yeola, & Bomblies, 2018; Kiefer et al., 2017; Satake, 2010; Simpson & Dean, 2002; Wilczek et al., 2009). Therefore, germination timing can have cascading effects throughout the life cycle and influence individual fitness, trait expression and evolution, as well as population dynamics.

Within-season shifts in life history timing due to climate change are increasingly observed (Anderson, Inouye, McKinney, Colautti,

& Mitchell-Olds, 2012; Inouye, 2008; Kimball, Angert, Huxman, & Venable, 2010) and have been shown to affect fitness (Elzinga et al., 2007; Iler, Høye, Inouye, & Schmidt, 2013). For example, shifts in winter precipitation associated with climate change alter germination timing in annual plants (Kimball et al., 2010; Levine, McEachern, & Cowan, 2011), which in turn can affect flowering time (Kimball, Angert, Huxman, & Venable, 2011; Mercer et al., 2011; Wilczek et al., 2009) and fitness (Levine et al., 2011; Mercer et al., 2011). However, less is known about the effects of a shifting climate on the rest of the life cycle, particularly beyond the first year. Likewise, most studies of germination timing effects on phenotype and fitness have been conducted with annual plants (Kalisz, 1986; Weinig, 2000; Donohue et al., 2005a; Donohue et al., 2005b; Wilczek et al., 2009; Mercer et al., 2011; Gremer et al., 2016; but see Galloway & Etterson, 2007). In *Arabidopsis thaliana*, the seasonal timing of germination determines whether a plant displays a winter annual or summer annual life history (Burghardt et al., 2015; Taylor et al., 2017; Wilczek et al., 2009). For longer-lived plants, it is important to consider how germination timing affects life history expression across years and whether selection at different life history stages favours different life history schedules. If germination timing interacts with environmental conditions to affect trait expression and performance, it may shape selection on life span (annual vs. perennial), the timing of first reproduction (in the first year vs. later years), and the adaptive value of reproducing once (semelparity) or spreading reproduction over multiple seasons (iteroparity). Therefore, it is critical to understand how shifting environmental conditions that influence germination timing as well as conditions experienced later in the life cycle will influence life history schedules, selection and population viability.

In this study, we investigate the cascading effects of germination timing on contingent life history expression in two populations of the native wildflower *Streptanthus tortuosus* (Brassicaceae) and the implications of those patterns for response to future climate change. This species is ideal for investigating life history responses to shifting climate because it exhibits remarkable life history variation, including variation in germination timing as well as variation in both the timing and frequency of reproduction. Further, this variation is present both within and among populations. Within populations, multiple life histories have been observed, including individuals that live for one growing season and die after reproducing once (annual life history), live for more than one growing season and die after a single reproductive bout (biennial life history), or live for multiple growing seasons and reproduce multiple times (iteroparous perennial). Here, we focus on two highly variable populations near the warm low-elevation edge of the species range. These populations experience considerable interannual variability in the timing of germination-triggering precipitation events, which influences germination timing and subsequent exposure to seasonal temperature and precipitation. In this species, vernalization is required to induce flowering (Preston, 1991), and germination timing has the potential to influence growth, size, and exposure to sufficient chilling for first year flowering. Therefore, germination timing can create contingency in the life history for *S. tortuosus*, by determining the size and timing of reproduction. Here, we manipulated germination timing in a common garden study and evaluated the consequences for trait expression and fitness. Further, we conducted an experiment to determine how exposure to vernalization in the first year affects subsequent life history expression and fitness, and test whether the vernalization requirement for first year flowering enhances fitness. We then explored how shifts in future conditions expected with climate change may influence life history expression and fitness for these populations.

2 | MATERIALS AND METHODS

2.1 | Study system and seed collection

Streptanthus tortuosus (Brassicaceae) is a native forb that occupies outcrops and dry, rocky slopes throughout northern California and southern Oregon (Calflora, 2014; Preston, 1991). This species is found across a broad elevational (200 m to 4,100 m) and latitudinal range (from southern California to southern Oregon) and populations tend to be discontinuously distributed (Calflora, 2014; Preston, 1991). For this study we focus on two populations at the low-elevation margin of the species range (North Table Mountain Ecological Preserve, Butte County, CA 39°36′N, 121°33′W), where annual, biennial, and iteroparous perennial life histories coexist. The site has a Mediterranean climate; the growing season begins when rains come during the late autumn or winter and ends with the onset of summer drought. The two populations at the Table Mountain site (TM1 and TM2) occupy basalt outcrops separated by approximately 2 km (39°35′55.64″N, 121°32′44.77″W and 39°35′32.96″N, 121°33′3.20″W, elevation 411 m and 373 m respectively).

Seeds for the study were collected as maternal seed families at these two populations in August 2015. We did not collect seed from plants that produced less than 5 siliques or from plants within 1.5 m from a previously sampled plant. Prior to the start of each experiment, seeds were stored dry at room temperature (~21°C).

2.2 | Germination timing experiment

To understand how germination timing influences subsequent traits and fitness, we experimentally created distinct germination cohorts in a common garden at the University of California, Davis and measured life history traits and fates of individuals across three years of the study. This experiment was conducted in a "screenhouse," with a clear plastic roof but screened walls, exposing plants to ambient temperatures and day length while allowing control of the watering regime and excluding most external pests and potential pollinators. In the screenhouse, we created six germination cohorts by sowing seeds and watering them at distinct time intervals during the winter growing season, simulating variation in the onset of germination-triggering rain events in our system. The first cohort was initiated on November 2, 2015 with subsequent cohorts following at 4-week intervals (November 30, December 28, January 25, February 22, and March 21). Seeds

were stored dry in lightproof containers in the screenhouse under ambient temperature conditions from November 2 until their sowing dates. Seeds were sown on top of UC Davis potting soil (1:1:1 parts sand, compost, and peat moss with dolomite), and covered with approximately 1 cm of coarse 16 grit sand.

Nine maternal families from each of the two populations were included in the germination experiment. At each planting date (hereafter, "cohort"), 2–3 seeds were sown into each of six cells in a tray, with two trays per maternal family (N = 30 seeds from each of 18 maternal families for each planting). These two trays were then placed in random locations within each of two blocks in the screenhouse. Seeds were watered once or twice daily for 4–8 weeks as needed to maintain soil moisture, and total germination was scored at the end of this time. Once seedlings were ~2.5 cm tall, we transplanted three randomly selected seedlings per maternal family into separate cone-tainer pots (164 ml cone-tainer pots, Stuewe and Sons, Corvallis, Oregon), containing a 1:1 mixture of potting soil and sand, which were then randomized within two blocks in the screenhouse. The first cohort had lower sample sizes (1 seedling per maternal family); some maternal families had smaller sample sizes in some cohorts due to mortality. Subsequently, plants were watered as needed on a drip system, and fertilized twice a week with a dilute fertilizer mixture (equivalent to ~25% strength Hoagland's solution). Plants were bottom-watered during the first summer (2016) and then returned to drip irrigation and fertilizer for the remainder of the experiment.

The experiment was maintained for three years to evaluate patterns of trait expression and fitness across cohorts. Upon onset of flowering in spring 2016 and 2018, plants were moved to an outside bench with drip watering, which allowed for open pollination of flowers. Observed pollinators included honeybees (*Apis mellifera*), Syrphid flies, and other native bees and wasps (E. Suglia, *observation*), similar to the pollinators reported for natural populations in previous studies (Preston, 1991, 1994). Plants that survived and perennated were then returned to the screenhouse for the subsequent autumn and winter. In 2017 plants were not moved outside and stayed in the screenhouse in the spring.

2.3 | Phenotypic responses to germination timing

We measured life history, phenological and morphological traits for all transplanted individuals. Life history traits included whether plants flowered in their first year, whether they perennated to a second growing season, and how many times they flowered (number of reproductive events across the three years of the study, a measure of parity). To quantify phenology, we censused plants twice a week before peak flowering and every 2–3 days during peak flowering; we recorded the date that the first bud and first flower were observed in both 2016 and 2017 (1st and 2nd years of the study). Because patterns were concordant for bud and flower data, we present the latter here. We also measured stem diameter during the reproductive season, a non-destructive metric of size that could be measured consistently for both reproductive and vegetative plants. Measurements were taken on May 25, 2016 and June 29, 2016; since patterns are largely concordant, we present the earlier measurements here.

To determine whether germination probabilities varied across cohorts and, subsequently, whether germination timing influenced the probability of flowering and perennating, we used mixed models (function glmer in R, binomial distribution with a logit link, Bates 2015). In these models, we included cohort (coded as continuous) and local population (TM1 & TM2) as main effects, as well as their interaction. We included maternal family as a random effect, nested within population. For germination probabilities, we also included a block random effect. We used likelihood ratio tests on nested models to evaluate the significance of main effects, as well as the random effect of maternal family within population. To test whether the probability of perennating depended on whether plants flowered in their first year, we also evaluated models with and without a categorical variable for flowering. We analysed the number of reproductive events, flowering phenology and diameter during the reproductive season (census on May 25, 2016), using generalized linear mixed models with cohort, population, and their interaction as main effects with maternal family nested within population as a random effect (function lmer in R, Bates, 2015). We then tested for trait correlations within cohorts using mean trait values for each maternal family within each cohort.

2.4 | Fitness in response to germination timing

We determined how germination timing influenced fitness by measuring reproduction in each spring of the study (2016–2018), as well as calculating total fitness. In each year of the study, we counted mature fruits at the end of fruit production. In 2017, the second year of the study, we did not move plants to an outside bench to receive pollination from local pollinators. However, plants did successfully set fruit in 2017 at a rate only marginally lower than that for 2018 (χ^2 = 2.481, p = 0.12). Therefore, we used the observed fruit production counts for year 2, though we recognize this may slightly underestimate potential fruit production and we explore how this affects our conclusions in a sensitivity analysis described below. We calculated total fitness for each individual as:

$$\text{Total fitness} = \text{p(germ)} * f_1 + l_2 * \text{p(peren)}_2 * \text{fruits}_2 + l_3 * \text{p(peren)}_3 * f_3,$$

where p(germ) is the mean probability of germinating, and each individual was assigned the p(germ) for its maternal family and cohort. The rest of the metrics were calculated at the individual level, where f_t is fruit production in year t, l_t is the probability of surviving to year t and p(peren)_t is the probability of perennating to year t. Typically annual survival (l_t) and perennation (p(peren)_t) are combined into a single metric of survival, particularly for perennial plants, but here we distinguish them due to differences in

life history schedules (i.e. annual vs. perennial) seen in *S. tortuosus*. However, since survival of perennating plants in these well-watered conditions tends to be high (96%, J. Gremer unpublished data), we used a survival probability of 100% in our fitness calculations for simplicity. We also explore how this assumption affects conclusions as described below. Fitness was calculated for each individual using values for fruit production for that individual and whether or not that individual perennated to later years (0 or 1), as well as average p(germ) values estimated for the maternal family and cohort the individual belonged to.

We analysed fitness data using GLMMs as described above. We conducted these analyses separately for year 1 and year 2 fruit production, and total fitness. For fruit production, we evaluated models using negative binomial, Poisson, and normal distributions. We rescaled fruit count values by dividing by the global mean and used negative binomial GLMMs (function glmer.nb in R; Bates, 2015) for first year fruit production and a Poisson distribution (function glmer in R; Bates, 2015) for second-year fruit production. We log transformed the values for total fitness data (ln(x + 1)) for analysis (function lmer in R; Bates, 2015). Note that results from this mixed model approach were largely concordant with those from aster models (Shaw, Geyer, Wagenius, Hangelbroek, & Etterson, 2008; Table S2-3 in Appendix S2). We then explored tradeoffs among fitness metrics by testing for correlations among maternal family mean fitness values within cohorts.

Our fitness comparisons rely on estimates of survival to subsequent seasons, as well as estimates of successfully producing fruit in later years. As mentioned, our estimates of second year fruit production in the screenhouse may be low and it is possible that fruit set in our common garden could have been limited by pollen, pollinators or other factors, and that observed values in our experiment may not directly relate to patterns in the field. Further, survival probabilities are likely to vary more in the field than in our well-watered common garden conditions. Therefore, we performed sensitivity analyses to test how values for fruit set and survival in years 2 and 3 affected conclusions about patterns of fitness in relation to germination timing. To do so, we independently varied fruit set (*p(fruitset)*) by exploring a range of values from 0 (no fruit set in years 2 and 3) to 2 (double the fruit set we observed in our experiment). Similarly, we varied survival (*l*) to years 2 and 3 (0 to 1 in 0.05 increments) and calculated total fitness using maternal family mean values for each cohort and population. These calculations follow the equation presented above, with the exception that fruit production for years 2 or 3 = $p(fruitset)^*fruits_i$. We assumed that survival and fruit set were the same for year 2 and 3 in these calculations ($l_2 = l_3$; $p(fruitset)_2 = p(fruitset)_3$).

2.5 | Vernalization experiment

Germination cohorts experienced changing ambient temperatures throughout the season in our common garden, leading to differences in plant exposure to cold temperatures across cohorts (Figure S3-1 in Appendix S3). Early cohorts (November–December) experienced cooler temperatures that likely satisfied vernalization requirements for first-year flowering, while later cohorts (Jan – March) were exposed to less chilling (Figure S3-1 in Appendix S3). To isolate the effect of this exposure to cold temperature in the first year and evaluate the effects on subsequent life history traits and fitness, we experimentally manipulated exposure to vernalization for a late season cohort and followed the fates of control and treatment plants. For this experiment, seeds from both populations were germinated and transplanted as described above. Treatment plants were sown on February 2, 2016 in a growth chamber with 14/10 hr light/dark cycles and temperatures cycling between 32°C daytime maximum and 23°C nighttime minimum. Once they were 2 weeks old and were approximately 2.5 cm tall, they were transferred to growth chambers set at 4°C with 8/16 hr cycles of light and dark conditions, respectively, for 4 weeks. After this cold treatment, plants were returned to the screenhouse on March 16, 2016. To create control groups with which to compare these vernalized plants, we initiated germination for control plants on March 1, 2016 in the same growth chamber conditions as treatment plants. These plants were approximately 2 weeks old and 2.5 cm tall on March 16. Thus, plants in control and treatment groups were slightly different ages (control = 2 weeks, vernalized = 6 weeks), but were approximately the same size when all plants were returned to screenhouse conditions. From there, plants in this experiment were maintained as described above for the germination timing experiment and the same data on probability of flowering, perennating and fitness were also collected. Total fitness was calculated as described above, using estimates for *p(germ)* for the 22-February germination timing experiment cohort. Due to loss of labels in a watering mishap, families and populations could not be distinguished so all plants were pooled for analysis. We analysed the effect of the vernalization treatment on the probability of flowering and perennating and the consequences for fitness using general linear models (glm function in R, R Core Team, 2018). We used logistic regression for the probability of flowering and perennating (binomial family with logit link) and regression (lm function in R, R Core Team, 2018) for year 1 and year 2 fruit production as well as total fitness.

2.6 | Contemporary and future climate data

To understand the implications of contemporary and future climate change, we evaluated contemporary patterns of germination triggering rains, winter temperatures and summer drought and explored potential future patterns. We extracted climate data for growing seasons from 1954 to 2016 from NOAA's Climate Data Online Daily Summaries search tool, using daily temperature and precipitation data from the Oroville weather station (Station ID GHCND:USC00046521), though data are not available for 1976–1982. We estimated the timing of the first germination triggering rain by aggregating precipitation into unique events, which we considered to be events that occurred on multiple days with no intervening days without precipitation. Germination-triggering rain events were those first rain events in the growing season year (from October to June) that totaled at least 12.7 mm of precipitation, based on observation. We explored different precipitation

thresholds with similar results. Based on results for potential chilling hours in the screenhouse (see Figure S3-1 in Appendix S3), we calculated the number of days that could meet a vernalization requirement (chilling days) as the total number of days after the first germination-triggering rain event in which the minimum temperature was below 6°C and above 0°C. To explore contemporary trends in summer drought, we retrieved monthly data to estimate summer drought from the California Basin Characterization Model (CA BCM) from 1980 to 2014, which incorporates fine-scale climate projections with digital maps of soils and geology to estimate water availability (Flint, Flint, Thorne, & Boynton, 2013). These monthly data correspond well with monthly averages of temperature and precipitation data recorded by the NOAA weather station (Pearson correlation coefficient, $r > .93$, $p < .0001$). The monthly CA BCM data include climatic water deficit, which describes the evaporative demand that exceeds available soil moisture (in units of mm H_2O), which we averaged for the summer months (June–September) for each year. The CA BCM data were retrieved for each of our populations, but results were nearly identical across the two sites (with only 3 years being slightly drier at Table Mountain 2), and we present data for the Table Mountain 1 population here. We explored whether there were temporal trends in the timing of germination rains, chilling days and summer drought using linear regression (lm function in R, R Core Team, 2018).

To compare current conditions with anticipated future conditions, we retrieved climate projections for years 2070–2099 from the 2014 California Basin Characterization Model through the California Landscape Conservation Cooperative's Climate Commons 30-year summary tool, which downscales data to a 270m resolution for the California hydrologic region (Flint & Flint, 2014; Maher et al., 2017). We used the models GFDL and PCM each with Special Report on Emissions Scenarios (SRES) A2 and B1 for four sets of data (i.e. GFDL+A2, GFDL+B1, PCM+A2 and PCM+B1). The data were reported as averages across the 30 years; we then averaged across the four GCMs. We compared monthly minimum temperature, precipitation and climatic water deficit (potential evapotranspiration minus actual evapotranspiration; a measure of drought stress) across three time frames: historic (1951–1980), contemporary (1981–2010) and projections for the late 21st century (2070–2099).

3 | RESULTS

3.1 | Life history responses to germination timing

Germination probabilities significantly varied among cohorts (Figure 1). Germination was lowest for the 21-March cohort and peaked for both populations in the 25-January cohort (quadratic effect of cohort: $\chi^2 = 99.597$, $p < .0001$). Differences in germination probabilities among populations were not significant ($\chi^2 = 1.461$, $p = .227$), and neither was the interaction between cohort and population (both linear and quadratic; $p > .49$). Maternal families showed significant variation in germination probabilities ($\chi^2 = 239.88$, $p < .0001$; Figure S1-1 in Appendix S1).

The timing of germination influenced life history transitions later in the life cycle, including both flowering in the first year and probability of perennating to the second year. The probability of flowering in the first year significantly decreased with later germination (Figure 2a, Table 1, Table S2-1 in Appendix S2, Gremer, Wilcox, Chiono, Suglia, & Schmitt, 2019). Local populations varied significantly in flowering probabilities, but they responded similarly in terms of flowering responses to cohort. The probability of perennating varied significantly among cohorts, and responses varied by population (Figure 2b, Table 1, Table S2-1 in Appendix S2). The probability of perennating was significantly lower if plants flowered in their first year (main effect of flowering: $\chi^2 = 4.319$, $p = .038$; Table S2-1 in Appendix S2). There was significant variation among maternal families within populations for both flowering in the first year and perennating to the second year (Figure S1-2b,c in Appendix S1, Table 1). Plants that perennated to later seasons had high probabilities of flowering in those later seasons (Tables S2–1 and S2–2 in Appendix S2).

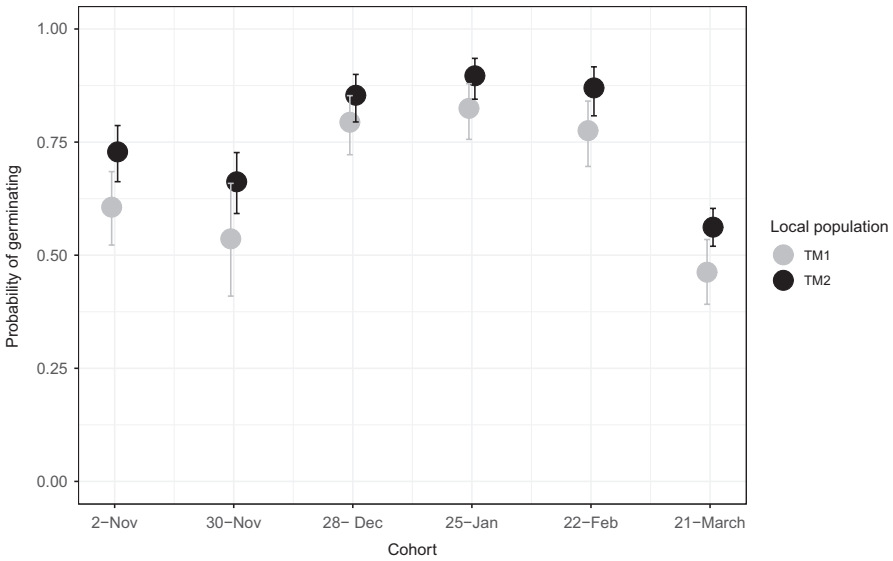

FIGURE 1 Germination probability of *Streptanthus tortuous* seeds (mean ± *SE*) varies with date of planting (cohort). Table Mountain 1 (TM1) population shown in gray, Table Mountain 2 (TM2) in black

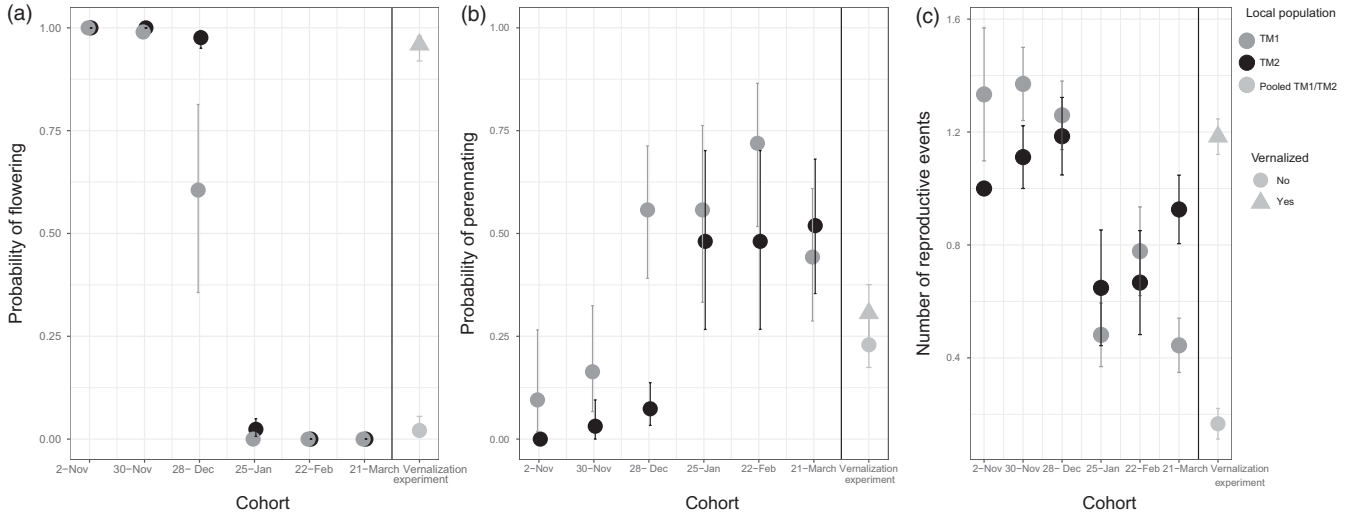

FIGURE 2 Probability of flowering in the first year (a), perennating to the second year (b), and total number of reproductive events (c) of *Streptanthus tortuosus* plants with date of planting (cohort). *N* = 9 maternal families per population (means ± *SE*). Table Mountain 1 (TM1) population shown in gray, Table Mountain 2 (TM2) in black. Right panels on each graph show results of the vernalization experiment, which used bulked seed from both populations (*N* = 48–49 per treatment, means ± *SE*; light gray); triangles represent vernalized plants, circles represent controls

TABLE 1 Results from generalized linear mixed models (GLMMs) for life history and phenology traits for *Streptanthus tortuosus*; statistics are results from likelihood ratio tests

	Flowering in first year		Perennating to 2nd year		# Reproductive events		Flowering date (year 1)		Size at reproduction (year 1)	
	χ^2	*p*	χ^2	*p*	χ^2	*p*	χ^2	*p*	χ^2	*p*
Cohort	**293.23**	**<.001**	**23.109**	**<.001**	**26.548**	**<.001**	**57.162**	**<.001**	.039	.843
Cohort^2	1.944	.163	–	–	.864	.353	**6.299**	**.012**	**85.646**	**<.001**
Population	**6.486**	**.011**	2.417	.120	.004	.951	**26.937**	**<.001**	**11.635**	**.001**
Cohort × Population	.756	.385	**5.027**	**.025**	**7.476**	**.006**	.096	.757	1.556	.212
Cohort^2 × Population	.020	.889	–	–	.410	.522	.115	.735	**5.047**	**.025**
Maternal family (random effect)	**4.767**	**.029**	**15.105**	**<.001**	1.461	.227	0	1	.004	.952

Note that the full model did not converge with the quadratic effect included for the probability of perennating (indicated by a dash in the table). $p < 0.05$ (in bold).

While the probability of perennating was lower for November and December cohorts, the plants that did perennate had more lifetime reproductive events, (Figure 2c, Figure S1-2c in Appendix S1, Table 1, Tables S2–1 and S2–2 in Appendix S2). Interestingly, Table Mountain 1 had a higher average number of reproductive events in earlier cohorts than Table Mountain 2, while Table Mountain 2 had more events in the 21-March cohort (Figure 2c, Table 1). While few individual plants in the two November cohorts and the 28-December cohort flowered every year of the study (3 years; *N* = 5 for TM1, *N* = 3 for TM2), most plants reproduced once and many in the later cohorts never reproduced (Figure S1-2c in Appendix S1, Table S2-2 in Appendix S2).

Differences in trait expression were likely due to differences across cohorts in exposure to chilling in the screenhouse (Figure S3-1 in Appendix S3). Our vernalization experiment tested this hypothesis by exposing a late season cohort to a chilling treatment and comparing responses with a control treatment with no chilling. Few plants in the control treatment flowered in the first year, while most plants in the vernalization treatment did flower (control: 2% flowered, 95% CI (0.29, 13.36); vernalized: 96%, 95% CI (85.10, 98.98); Z = 5.642, $p < .0001$; Gremer et al., 2019). Vernalization did not affect the probability of perennating to the second year (Z = 0.853, $p = .394$, control mean = 22.9%, 95% CI (13.17, 36.82); vernalized mean 28.6%, 95% CI (17.71, 42.64). However, vernalized plants had more reproductive events than non-vernalized plants ($F_{1,95} = 111.9$, $p < .0001$), because several vernalized plants perennated and reproduced twice (*N* = 9), while no control plants did.

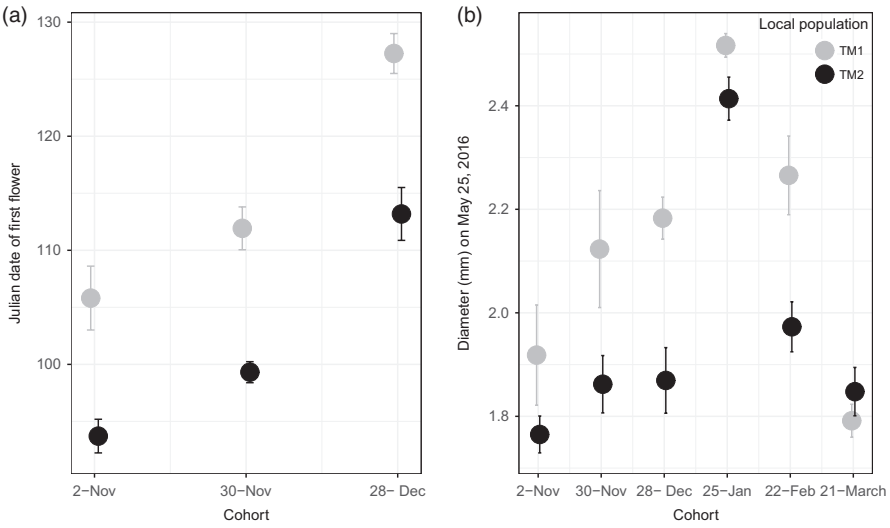

FIGURE 3 Flowering phenology (a) and size (b) of *Streptanthus tortuosus* (mean ± SE) in response to planting date (cohort). (a) Julian date on which first flower was observed in 2016, for the three cohorts in which plants flowered in the first year. (b) Stem diameter (mm) during the reproductive census on May 25, 2016 for cohorts

3.2 | Phenology and size

Flowering phenology was strongly influenced by germination cohort and source population (Figure 3a; Table 1). Plants in the 28-December cohort first flowered approximately 19–22 days later than the 02- November cohort, despite being planted 56 days later. Table Mountain 1 had later phenology than Table Mountain 2, but the interaction between source population and cohort was not significant. Flowering phenology in the second year, when all plants experienced the same chilling exposure over the winter, was not significantly affected by planting date (cohort main effect: $\chi^2 = 0.038$, $p = .85$).

Plant size, measured as basal stem diameter, varied nonlinearly with cohort (Figure 3b, Table 1). Plants were largest in the 25-January cohort for both populations, and smallest in the earliest and latest cohorts. The Table Mountain 1 population plants were larger overall and responded differently to cohort than Table Mountain 2. Plant size also marginally influenced the probability of flowering in the first year; flowering probabilities were lower for plants with larger stem diameter (coefficient = −2.862 (logit scale), $p = .058$).

3.3 | Fitness in relation to germination timing

Consistent with our results for the patterns of flowering and perennating, fitness also varied across germination cohorts (Figure 4). First-year fruit production was lower in later cohorts (Figure 4a; Table 2). Despite having smaller plant sizes, Table Mountain 2 had higher fruit production in year 1. For second year fruit production there was a nonsignificant trend towards higher fruit production in later cohorts (Figure 4b, Table 2). Similarly, total fitness was strongly affected by germination cohort, with a marginally significant interaction with population (quadratic x population interaction in Table 2; linear interaction is significant using aster models, Table S2-3 in Appendix S2). Cohorts before the 28-December cohort had higher total fitness than later ones for both populations, though fitness seemed to peak at different cohorts for different populations (Figure 4c). We did not see evidence for significant variation in fruit production or fitness across maternal families.

These differences in fruit production and fitness were likely mediated by exposure to cold temperatures, as demonstrated by the vernalization experiment. As expected from patterns for first-year flowering, first-year fruit production was higher for vernalized plants than controls (Figure 4a, $F_{1,95} = 86.036$, $p < .0001$), and similar to first year fruit production for the December cohort of the germination experiment. Second year fruit production was not different between vernalized and control plants (Figure 4b, $F_{1,95} = 0.600$, $p = .0.446$); only two plants survived to the third year, so no differences in fruit set in year 3 were apparent. However, vernalized plants had higher total fitness than controls (Figure 4c; $F_{1,95} = 35.3$, $p < .0001$). Thus, we did not observe any cost to flowering in the first year for vernalized plants.

The survival of perennating plants in our well-watered experimental conditions may have been higher than would be seen in field populations. Further, our estimates of second-year fruit production in 2017 might also have been biased if fruit production was low in the absence of pollinators. Indeed, estimation of fruit set using counts of flowers and fruits in our experiment in 2017 and 2018 were low (average = 23%) compared to those we expected from previous studies (75%, Preston, 1994). To further explore the robustness of our conclusions to different values for survival and fruit set in later years, we performed a sensitivity analysis (Figure 5). This analysis revealed patterns consistent with our empirical results for first year fruit production, with fitness highest for early cohorts if survival or fruit set is low beyond the first year. However, if either survival or fruit set is moderate to high in later years, fitness is higher for later cohorts. Interesting patterns arise among the two populations under these high survival

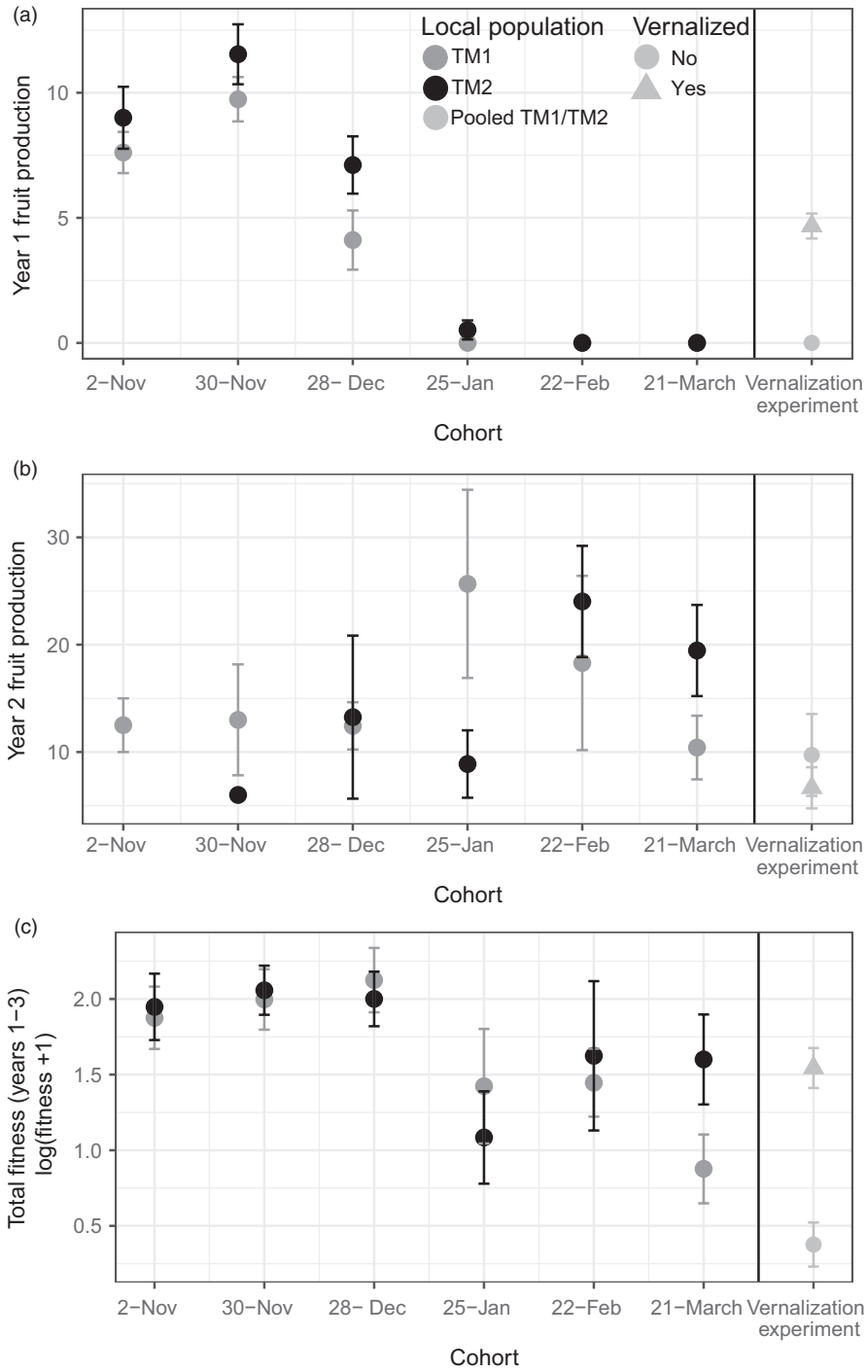

FIGURE 4 Fitness in relation to planting date (cohort) for *Streptanthus tortuosus* (mean ± *SE*). (a) First year fruit production, (b) Second year fruit production for plants that perennated, and (c) total fitness across all cohorts. Table Mountain 1 (TM1) population shown in dark gray, Table Mountain 2 (TM2) in black. Right panels on each graph show results of the vernalization experiment, which used bulked seed from both populations (N = 48–49 per treatment, means ± *SE*; light gray); triangles represent treatment plants, circles represent controls

and fruit set scenarios, since fitness is highest for 28-December cohorts for Table Mountain 1, but there are two peaks of fitness for Table Mountain 2 (28-December and 22-February). Together, these patterns suggest that earlier germination is optimal for annual life histories, while later germination is better for perennial and iteroparous life histories.

3.4 | Correlations among traits and fitness

Correlations among traits revealed positive relationships as well as tradeoffs. In the November cohorts, larger plants (larger diameter at reproductive census) flowered later (02- November: r = .55, p = .041; 30- November: r = .50, p = .037; 28-December: r = .39, p = .2048) and reproduced more often (02- November: r = .76, p = .0006; 30- November: r = .47, p = .048; 28-December: r = 0.33, p = .18). A negative correlation between the probability of flowering and the probability of perennating in the 30- November and 28-December cohorts revealed a tradeoff between these life history transitions (30- November: r = −.62, p = .006; 28-December: r = −.75, p = .0003). In that same 28-December cohort, larger plants were more likely to perennate (r = .70, p = .0011), and less likely to flower (r = −.53, p = .0223). Analyses that account for differences among populations

TABLE 2 Results from generalized linear mixed models (GLMMs) for fruit production and total fitness for *Streptanthus tortuosus*; statistics are results from likelihood ratio tests

	Fruit production year 1		Fruit production year 2		Total fitness	
	χ^2	*p*	χ^2	*p*	χ^2	*p*
Cohort	**206.13**	**<0.001**	0.074	0.786	**12.410**	**0.0004**
Cohort^2	–	–	0.729	0.393	0.018	0.894
Population	**6.272**	**0.012**	0.037	0.848	0.180	0.672
Cohort × Population	0.062	0.803	4.288	0.117	1.701	0.192
Cohort^2 × Population	–	–	–	–	2.667	0.102

Note that models for fruit production that included quadratic terms did not converge and did not provide a good fit to the data (indicated by a dash in the table). $p < 0.05$ (in bold).

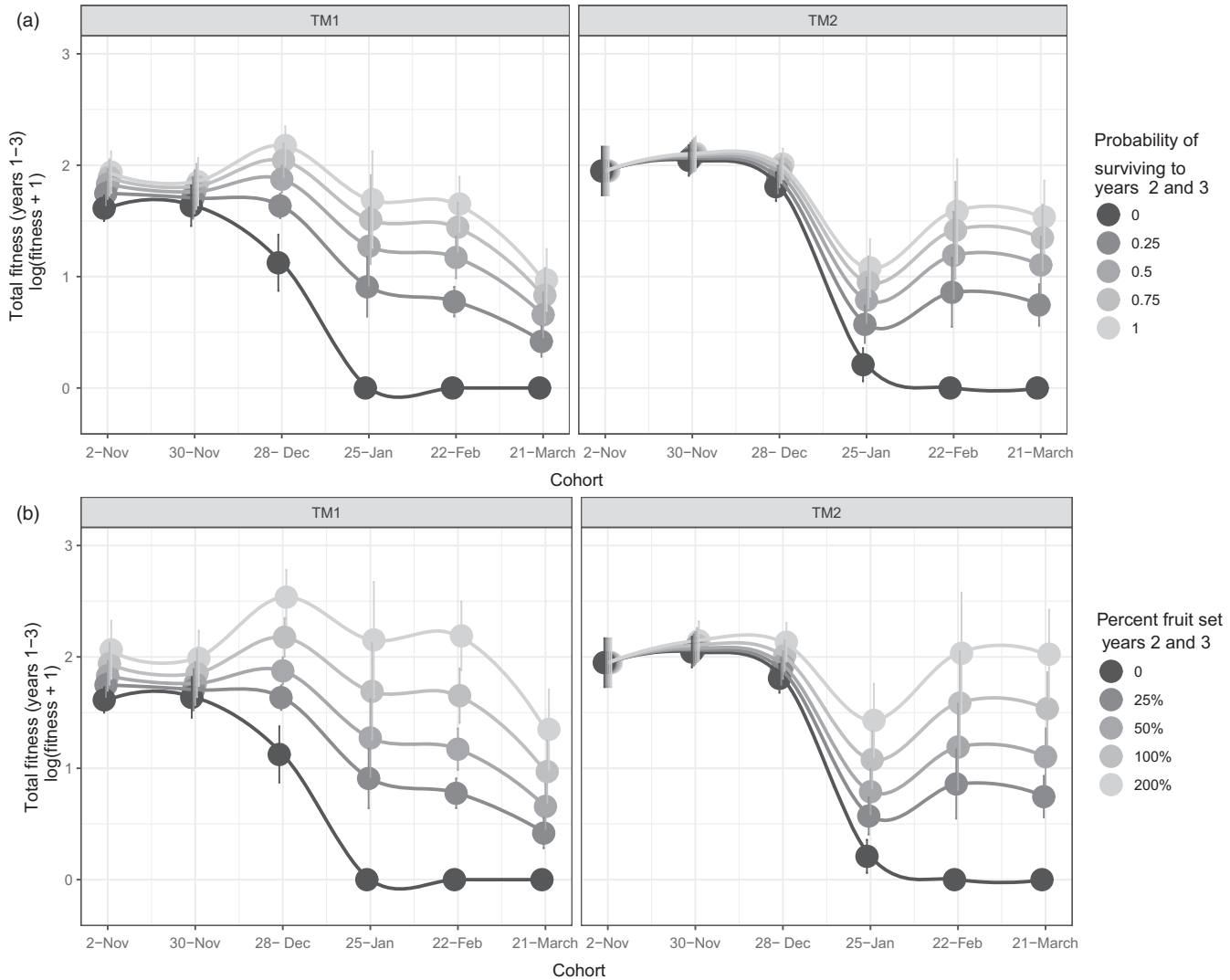

FIGURE 5 Simulations of total fitness as a function of planting date and scenarios for (a) probability of survival to later years and (b) successful fruit production (fruit set). Colours represent different estimates for survival and fruit set, panels are separated for Table Mountain 1 (TM1) and Table Mountain 2 (TM2). Illustrations reflect patterns for when fruit set is set to 100% of values observed per cohort & population in the germination timing experiment in (a), and for when survival is 100% for patterns in (b). Error bars represent one standard error of the mean across maternal families, lines are Loess fitted curves

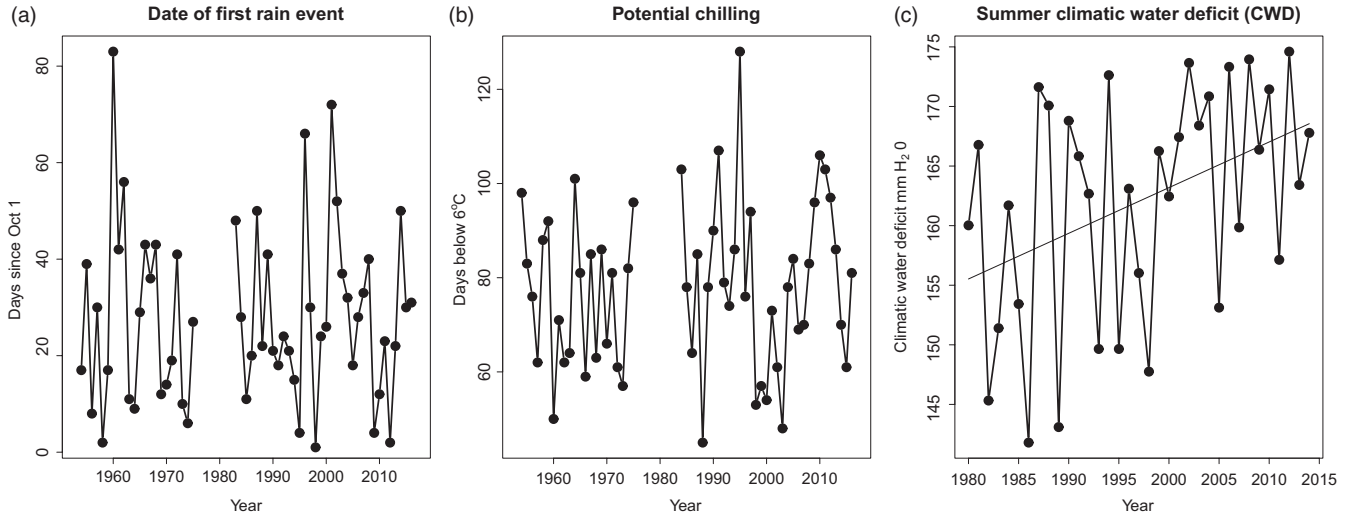

FIGURE 6 Contemporary patterns for germination triggering rain events, days with potential chilling hours, and drought. (a) Date of first rain event, measured as the first rain event of the growing season with at least 12.7 mm total precipitation. (b) Number of days with a minimum temperature below 6°C during the growing season (from the date of the first germination triggering rain event through June). (c) Mean summer climatic water deficit (CWD), averaged across the summer months of June through September, in mm H_2O. Regression line represents a significant positive trend through time. Data for a & b are from the National Climatic Data Center (NCDC) for 1953–2016 (missing data from 1976–1982), from the CA BCM dataset (1980–2014; Flint et al., 2013)

(ANCOVAs with local population as a covariate) were consistent with these results (not shown).

We also explored correlations with fitness, particularly between first- and second-year fruit production. Here we focus on results for the 28-December cohort, since cohorts before that had few perennating plants (no second-year fruit production), and cohorts after that had few plants that flowered in the first year (no first-year fruit production), but that cohort had both. For all plants in that 28-December cohort, first-year fruit production traded off with second-year fruit production ($r = -0.55$, $p = .0176$).

3.5 | Current and future climate

Contemporary patterns for the timing of germination rains, exposure to cold temperatures, and exposure to drought highlight the variability of climate for these *S. tortuosus* populations (Figure 6). There were no significant directional trends for the date of the first rain event for historic (before 1980, here 1954–1975; $F_{1,20} = .295$, $p = .59$) or contemporary (here 1983–2016; $F_{1,32} = 0.04$, $p = .83$) time frames or the number of days with potential chilling (days with a minimum temperature below 6°C; historic: $F_{1,20} = .23$, $p = .64$; contemporary: $F_{1,32} = .15$, $p = .71$), but there is substantial variability in both. There were strong trends for increasing summer drought during the contemporary time frame (here 1980–2014), measured as average climatic water deficit (CWD) for the summer (June–September; $F_{1,33} = 6.675$, $p = .014$), suggesting that plants attempting to perennate to future years have been experiencing increasingly more intense drought conditions through time.

Comparison of patterns from the historic (1951–1980) and contemporary (1981–2010) time frames with future projections (2070–2099) reveal clear patterns of increasing monthly minimum temperatures and increasing late spring and summer drought (CWD; Figure 7). Patterns of the average total monthly precipitation were more variable within timeframes and differences across time frames were not evident. These patterns indicate less exposure to cold temperatures for vernalization, a reduction in the length of the growing season due to earlier drought conditions, and increased intensity of summer drought conditions for these populations in the future.

4 | DISCUSSION

Germination timing determines not only the environment that a newly emerged seedling will experience, but also conditions experienced at later life stages. As such, germination timing can have profound impacts on trait expression, selection on morphological traits and life history schedules, individual fitness and population persistence. Here, we investigated this life history contingency in a species whose remarkable variation in life history schedules provides the rare opportunity to study these processes within populations. Our results illustrate that the timing of germination-triggering rain events has the potential to drive not only the timing and extent of germination, but also if and when an individual flowers in its first year, if it perennates, and, ultimately, its fitness (Figure S4-1 in Appendix S4). These life history differences among germination cohorts are mediated by vernalization responses to winter chilling, which early cohorts likely experience in the first year, and later cohorts may experience only if they survive to later years. However, our failure to detect fitness costs of first-year flowering induced in late germination cohorts suggests that the vernalization requirement for first-year flowering is maladaptive for these populations. This requirement may become

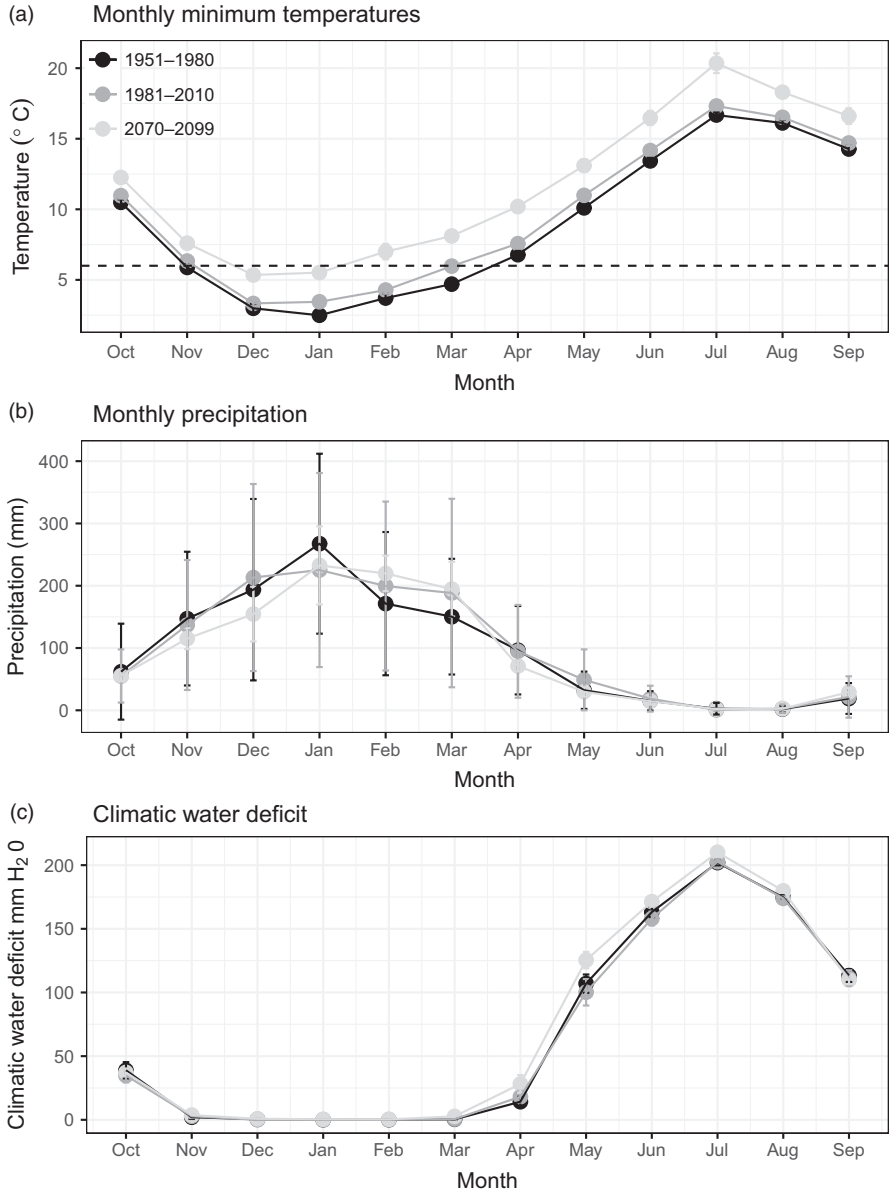

FIGURE 7 Mean minimum monthly temperatures (a), precipitation (b), and climatic water deficit (c) for historic, contemporary, and future timeframes. Means for minimum temperature and precipitation are across 30 year periods; for future projections means were taken across four global circulation models. The dashed line in (a) indicates the likely threshold for vernalization for these populations (6°C)

even more maladaptive in the future, as winter warming will reduce exposure to vernalization and prevent first-year flowering, while intensifying summer drought is likely to reduce survival to subsequent seasons and select for annual life histories.

Our results reveal profound impacts of the timing of seasonal rains on phenology, life history, and fitness in *S. tortuosus*. Cohorts that germinated before December had lower germination fractions, high probabilities of flowering in the first year, and lower likelihood of perennating than later cohorts. Thus, most early germinants expressed annual life histories, with a few plants surviving to the next year and flowering, thus expressing iteroparous perennial life histories. Among these autumn cohorts, later germination resulted in later flowering in spring, but flowering was much less delayed than germination, suggesting synchronization of flowering by seasonal environmental cues (Miryeganeh, Yamaguchi, & Kudoh, 2018). In contrast, later cohorts did not flower in the first year and were mostly biennials with a few iteroparous perennials. Thus, interannual variation in the onset of seasonal rains likely has major consequences for life history expression and demography across years. Moreover, in years with early rainfall, there may be conflicting selection on germination timing since different life history schedules (e.g. first-year fruit production vs. perennation and later fruit production) favoured different optimal germination dates. Similarly conflicting viability and fecundity selection on germination timing (Akiyama et al., 2013) and flowering time (Wadgymar, Daws, & Anderson, 2017) have been observed in other species. Such discordance in optimal phenotypes among life history schedules may be an important constraint on evolutionary response to environmental change (Cotto, Sandell, Chevin, & Ronce, 2019).

For these *Streptanthus tortuosus* populations, optimal germination timing and life history schedules hinge on the likelihood of surviving to subsequent seasons. Low survival to later years would favour autumn germination, whereas a high probability of survival

would favour later germination (Figure 5), even in years with early rainfall. Likewise, low probability of fruit set in later years also favours earlier germination and annual life histories, but high probabilities of fruit set favour later germination and biennial or perennial life histories. However, increasing drought severity and shorter growing seasons forecasted in the future may result in reduced survival between growing seasons, favouring autumn germination and annual life histories. Of course, when germination can actually occur depends on the timing of precipitation and how it interacts with other germination requirements, such as temperature and light. Similarly, annual plants in the Sonoran Desert often exhibit sub-optimal variation seasonal germination timing (Gremer et al., 2016), which is likely due to strong intra-annual variation in the timing of germination-triggering rain and among-species variation in germination requirements (Huang, Liu, Bradford, Huxman, & Venable, 2016). Thus, the evolution of optimal germination timing may be constrained by strong inter- and intra-annual variation in water availability and temperature.

Life history theory predicts that optimal life history schedules will depend on stage-specific survival and tradeoffs between current and future reproduction. Annual life histories are expected to be favoured when adult survival is low or variable (Charnov & Schaffer, 1973), but selection should favour reproductive delay when there is a benefit to delay, namely higher reproductive output (Cohen, 1966; Hart, 1977; Metcalf et al., 2003; Tuljapurkar, 1990). In our study, autumn germinants had higher first year fruit production, lower probabilities of perennating, and mostly annual life histories. However, winter germinants had higher second year fruit production and were mostly biennial. Generally, these patterns correspond with predictions from life history theory. Our results also revealed tradeoffs between current and future reproduction (i.e. fruit production in year 1 vs. year 2) as well as tradeoffs between current reproduction and survival (i.e. probability of flowering vs. probability of perennating), particularly in the late December cohort, as expected by theory (Charlesworth, 1994; Roff, 1992; Schaffer, 1974).

Our results illustrate the importance of vernalization signaling for the expression of contingent life histories across different germination cohorts. In many species of Brassicaceae, exposure to prolonged cold acts through the vernalization pathway to lift repression of genes promoting the transition from vegetative to reproductive growth (Bloomer & Dean, 2017). The strength of initial repression and vernalization response to cold interact with germination timing to determine flowering time and seasonal life history in annual plants such as *Arabidopsis thaliana* (Bloomer & Dean, 2017; Shindo et al., 2005; Wilczek et al., 2009). Moreover, variation within and among species in vernalization pathways may determine whether a plant exhibits an annual, semelparous perennial or iteroparous perennial life history in a given environment (Albani et al., 2012; Baduel et al., 2016, 2018; Friedman & Willis, 2013; Kiefer et al., 2017; Satake, 2010). In our study populations of *S. tortuosus*, vernalization is required to induce flowering in the first year and exposure to sufficient chilling affected whether annual, biennial, or iteroparous perennial life histories were expressed. Early germinating cohorts received sufficient chilling to induce flowering in the first spring, whereas later-germinating plants remained vegetative unless they were experimentally exposed to the vernalization cue. A similar pattern has been observed in *Campanula americana*, in which autumn germinants are winter annuals and spring germinants are biennials (Galloway & Etterson, 2007).

Vernalization requirements are often considered to be adaptive because they prevent plants from flowering during unfavourable conditions before winter has passed (Blackman, 2017; Simpson & Dean, 2002). Vernalization requirements may also function to promote reproductive synchrony, and thus enhance mating opportunities, for plants germinating on different dates (Miryeganeh et al., 2018). Moreover, delayed reproduction allows plants to accumulate more biomass, which could increase fecundity or survival of perennial plants to subsequent years, and thus lifetime fitness. This could be particularly beneficial for late-germinating plants that have less time before the flowering season and may experience vernalization in their second winter or growing season. In this way, vernalization requirements can force late germinants to delay reproduction until their second season (or later). We therefore predicted that the vernalization requirement would be adaptive in our study populations; if so, artificial induction of first-year flowering in late germinating cohorts should have reduced lifetime fitness compared with late germinants that remained vegetative until the following year. Surprisingly, although we observed an apparent tradeoff between first- and second-year fitness in the December cohort, experimental induction of first-year flowering by vernalization in a late season cohort had no apparent cost to survival or later fecundity and resulted in higher lifetime fitness than controls. Therefore, the chilling requirement appears to be maladaptive for these populations, particularly if survival to the next year is low. However, resource availability, competition, and herbivory are all likely to show much stronger variation in field conditions and will influence the adaptive value of first-year flowering for late germinants. If survival to the second year is very low, selection should favour plants with weak vernalization requirements capable of first-year reproduction. Phenotypic manipulation to assess the costs and benefits of observed life history cueing is a powerful way to evaluate the adaptive value of such traits (Dudley, 1996; Galloway & Burgess, 2009; Schmitt, Dudley, & Pigliucci, 1999). Manipulating first-year flowering and comparing performance of plants under field conditions would provide a more comprehensive understanding of whether the vernalization requirement for first year flowering is indeed maladaptive for these low-elevation populations.

Considering the rapid pace of climate change, evolutionary responses to shifts in climate are likely to depend on standing genetic variation and phenotypic plasticity (Barrett & Schluter, 2009; Jump & Peñuelas, 2005; Merilä & Hendry, 2014). This may be particularly true for *S. tortuosus* populations, which inhabit rocky outcrops that are patchily distributed throughout the species range, making it difficult for populations to track suitable climatic conditions through dispersal. Low-elevation populations are expected to experience increases in winter temperatures, which will likely reduce the exposure to sufficient chilling to satisfy vernalization requirements for first year flowering, particularly in years with late onset

of autumn rains. In addition, drought conditions are expected to come earlier in the season and be more severe (Figure 7), which is likely to reduce the survival of perennating plants. Together, these patterns are problematic, since individuals would be less likely to flower in their first year, and less likely to survive to reproduce in later years. Thus, contrary to the theoretical predictions that plasticity will facilitate climate change response in the short term (Chevin, Collins, & Lefèvre, 2013; Chevin, Lande, & Mace, 2010; Ghalambor, McKay, Carroll, & Reznick, 2007; Hendry, 2016), we found that plasticity of life history to germination timing in these populations may be maladaptive in the face of rapid climate change. We predict that selection should favour a reduction in the vernalization requirement and earlier germination to maximize fitness of plants with an annual life history. The key question is whether these populations can respond to that selection. Although we observed significant variation in flowering responses to germination timing across field-collected maternal families, it remains to be determined whether that variation is heritable and whether it is sufficient for rapid evolutionary response. Loss of vernalization requirements has been observed in other species where early mortality may select for early reproduction (Baduel et al., 2016; Lowry & Willis, 2010; Toomajian et al., 2006). There is also evidence for adaptive evolution of germination timing in different climates (Postma & Agren, 2016; Vidigal et al., 2016). The persistence of these *S. tortuosus* populations will critically depend on the potential for similar adaptive evolution.

5 | CONCLUSIONS

In a variable world, organisms must have strategies to time critical life history functions, such as emergence, growth, and reproduction, with favourable conditions. Often, these strategies involve responding to environmental cues, though shifting conditions with climate change will likely change the adaptive value of those cue responses. Our study demonstrates that shifts in the timing of germination-triggering precipitation can influence exposure to seasonal temperature cues, which not only affected life history trait expression in the first year, but also in later years, with strong effects on fitness. We also found that a chilling requirement for first-year flowering decreased fitness and may be maladaptive, and both flowering and over-summer survival may be negatively affected by increasing temperatures and drought expected with climate change. Therefore, cues for germination and flowering may be even less reliable in the future. Together, our study provides insight into the forces shaping life history variation in a changing environment, the impacts of shifting conditions on contingent life history expression, and the implications for future population persistence.

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AUTHORS' CONTRIBUTIONS

J.S., C.J.W. and J.R.G. conceived and designed the study. C.J.W., A.C. and E.S. performed experiments and collected data. J.R.G. analysed data and wrote the manuscript, with contributions from all authors. All authors contributed to development of ideas, analyses and interpretation of results and writing of the manuscript.

DATA AVAILABILITY STATEMENT

Data for the germination timing and vernalization experiments are available from the Dryad Digital repository: https://doi.org/10.5061/dryad.8g71v4s (Gremer et al., 2019). Weather and climate data are available from the National Centers for Environmental Information NOAA Climate Data Online summaries search tool and from the California Basin Characterization Model (Flint et al., 2013).

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