Title

Accelerated Phenology Fails to Buffer Fitness Loss from Delayed Rain Onset in a Clade of Wildflowers

Authors

Worthy, Samantha J
Ashlock, Sarah R
Miller, Arquel
et al.

Publication Date

2025

DOI

10.1086/735012

Peer reviewed

VOL. 205, NO. 5 THE AMERICAN NATURALIST MAY 2025

Accelerated Phenology Fails to Buffer Fitness Loss from Delayed Rain Onset in a Clade of Wildflowers

Samantha J. Worthy,[1,*] Sarah R. Ashlock,[1] Arquel Miller,[1] Julin N. Maloof,[2] Sharon Y. Strauss,[1,3] Jennifer R. Gremer,[1,3] and Johanna Schmitt[1,3]

1. Department of Evolution and Ecology, University of California, Davis, California 95616; 2. Department of Plant Biology, University of California, Davis, California 95616; 3. Center for Population Biology, University of California, Davis, California 95616

Submitted June 17, 2024; Accepted November 30, 2024; Electronically published March 17, 2025

Online enhancements: supplemental PDF.

ABSTRACT: The timing of early life cycle events has cascading effects on phenology and fitness. These effects may be critical for climate resilience of plant populations, especially in Mediterranean environments, where delayed rainfall onset causes delayed germination. To examine impacts of germination timing on 10 species of the *Streptanthus*/*Caulanthus* clade, we induced germination across a range of dates in ambient seasonal conditions and recorded phenological and fitness traits. Later-germinating cohorts accelerated flowering, partially stabilizing flowering date, but the degree of this compensatory plasticity differed across species. Fitness declined with later germination; the magnitude of this decline depended on the balance between direct negative effects of later germination and compensatory positive effects of accelerated flowering. The resulting species' differences in fitness responses suggest differential vulnerability to climate change. Species from wetter, cooler, less variable habitats exhibited greater phenological plasticity, accelerating flowering more and declining less in seed set with later germination than desert species. However, other fitness responses to germination timing, such as first-year fitness, were evolutionarily labile across the clade and unrelated to climate. Although compensatory phenological plasticity may buffer the impacts of delayed germination, it cannot prevent long-term declines in population fitness as fall rains come later with climate change.

Keywords: Brassicaceae, climate change, flowering time, germination time, phenotypic plasticity.

Introduction

The seasonal timing of early life cycle events, such as birth, hatching, or seed germination, has critical effects on fitness in many organisms (Kalisz 1986; Donohue 2002, 2005; Donohue et al. 2005; van Asch and Visser 2007). The timing of these events determines the effective length of the growing season and the environmental conditions organisms experience throughout the life cycle, including environmental cues mediating the timing of later life cycle events, such as reproduction (Galloway 2001; Donohue 2005; Donohue et al. 2005; Wilczek et al. 2009). However, climate change is altering the timing and length of the growing season as well as the environmental cues driving seasonal phenology for many organisms (Parmesan and Hanley 2015; Wadgymar et al. 2018; Bonamour et al. 2019; Bernhardt et al. 2020). An important question is whether phenological plasticity can buffer the population fitness impacts of such environmental change (Ghalambor et al. 2007; Chevin et al. 2010; Nicotra et al. 2010; Duputié et al. 2015; Kingsolver and Buckley 2017; Gauzere et al. 2020; Scheiner et al. 2020; Zettlemoyer et al. 2024). If so, the resilience of species' fitness to changing climate may depend on the phenological consequences of early life cycle events (Gremer et al. 2020*a*; Martínez-Berdeja et al. 2023).

In plants, seed germination timing is a critical early event that determines the seasonal conditions that plants experience throughout the life cycle (Donohue 2005). A species' germination niche—the range of environmental conditions under which seeds can germinate—determines its germination phenology (Donohue et al. 2010; Martínez-Berdeja et al. 2023; Worthy et al. 2024*b*). In seasonally dry climates, including Mediterranean climates, the timing of precipitation onset relative to other seasonal environmental cues regulating germination, such as temperature and day length, determines whether and when seedlings will emerge (Kimball et al. 2010; Martínez-Berdeja et al. 2020, 2023; Worthy et al. 2024*b*). Germination timing in turn determines the length of the growing season as well as exposure to environmental cues that mediate the timing of later

---

[*] Corresponding author; email: sjworthy@ucdavis.edu.

ORCIDs: Worthy, https://orcid.org/000-0003-0414-2607; Maloof, https://orcid.org/000-0002-9623-2599; Strauss, https://orcid.org/000-0002-6117-4085; Gremer, https://orcid.org/000-0001-8983-5482; Schmitt, https://orcid.org/0009-0009-5022-7485.

American Naturalist, volume 205, number 5, May 2025. © 2025 The University of Chicago. All rights reserved. Published by The University of Chicago Press for The American Society of Naturalists. https://doi.org/10.1086/735012

events, such as flowering and seed set. These cascading effects of germination timing may be important to species' persistence as climate change alters the timing and variability of seasonal precipitation in Mediterranean regions (Swain et al. 2018; Dong et al. 2019; Luković et al. 2021). In California, germination-triggering rains are coming later in fall, with a more compressed rainy season (Luković et al. 2021). This delay in rainfall onset constrains seeds to germinate later in the year, under different seasonal conditions and with a shorter potential growing season (Worthy et al. 2024*b*).

Seasonal delays in germination timing may affect species' fitness directly, through effects on growing season environment or length, or indirectly, through effects on reproductive phenology. Flowering time is often under strong selection, which usually favors earlier flowering (Munguía-Rosas et al. 2011; Anderson et al. 2012; Austen et al. 2017; Ensing et al. 2021; Zettlemoyer et al. 2024). In a shorter potential growing season, such selection may favor accelerated flowering at a smaller size to assure reproduction (Cohen 1976). If so, acceleration of flowering in later-germinating cohorts, mediated by seasonal environmental cues such as increasing day length or accumulation of photothermal units (Wilczek et al. 2009), could be a form of compensatory phenotypic plasticity mitigating fitness impacts of shorter growing seasons. On the other hand, if later germination prevents exposure to critical seasonal cues, such as accumulation of chilling hours (vernalization), the transition to flowering may be delayed or prevented with critical consequences for life history and fitness (Galloway and Etterson 2007; Gremer et al. 2020*a*). Species differences in phenological plasticity and fitness resilience to germination timing may contribute to differential vulnerability to climate change (Matesanz et al. 2010; Chevin et al. 2012).

Here, we examine the phenological and fitness consequences of germination timing in the *Streptanthus*/*Caulanthus* clade (Brassicaceae) by forcing plants to experience a range of natural seasonal environments both within and beyond their typical germination window. We asked the following. First, does flowering phenology respond to germination timing? Depending on species' responses to seasonal cues, flowering in later-germinating cohorts might be either accelerated (Wilczek et al. 2009; Wu and Owen 2014; Olliff-Yang and Ackerly 2021; Martínez-Berdeja et al. 2023) or delayed (Gremer et al. 2020*a*). Second, does germination timing affect fitness, either directly or indirectly, through effects on flowering phenology? Third, how have responses of flowering time and fitness to germination timing diversified across the clade, and do patterns reflect climate of origin? And fourth, can variation among species in responses to germination timing lead to differential vulnerability to climate change? Understanding variation in responses to germination timing can reveal species' differences in vulnerability to climate change at later life stages, compounding the potential effects of climate change on germination alone (Walck et al. 2011; Worthy et al. 2024*b*).

Methods

Study System

To investigate the potential impacts of germination delays on subsequent flowering phenology and fitness, we used 12 populations from 10 species that span the *Streptanthus* and *Caulanthus* genera of the *Streptanthus* clade of Brassicaceae: *Caulanthus anceps* (CAAN), *C. coulteri* (CACO), *C. inflatus* (CAIN), *Streptanthus breweri* (STBR), *S. diversifolius* (STDI), *S. drepanoides* (STDR), *S. glandulosus* (STGL), *S. insignis* (STIN), *S. polygaloides* (STPO), and *S. tortuosus* (STTO; table S1; tables S1–S21 are available online; Cacho et al. 2014). Henceforth, we refer to all species and populations by the abbreviations given above. This group has diversified from desert origins to across a broad latitudinal range that encompasses the California Floristic Province, spanning a wide range of mean and variability in temperature and precipitation (Axelrod 1958; Cacho et al. 2014, 2021; Worthy et al. 2024*b*). Species typically occur in sparsely populated, bare, harsh habitats growing on dry, rocky, or sandy substrates (Cacho and Strauss 2014; Pearse et al. 2022). They all experience growing seasons dictated by the Mediterranean climate of California, where germination-triggering rain events start the growing season in the fall and onset of drought ends the growing season. All species are winter annuals except for STTO, which has variation in life histories within and across populations, with facultative winter annual, biennial, and perennial life histories observed in some populations (Gremer et al. 2020*a*). The STTO population used in this study (TM2) is largely winter annual but also exhibits biennial and perennial life histories depending on germination timing and exposure to vernalization cues (Gremer et al. 2020*b*; J. R. Gremer, unpublished data). Hereafter, we will refer to the STTO life history as facultative biennial.

Eight of the species in this study were represented by one population approximately centrally located within the species' range-wide climatic space (fig. S1; figs. S1–S11 are available online). Two species, CAAN and CAIN, were opportunistically represented by two populations because of seed availability. We tested whether our conclusions varied on the basis of the inclusion of these different populations of CAAN and CAIN in models that revealed small differences in the level of statistical significance but no differences in trends.

Seeds for the experiment were collected as maternal families from the field in 2019 (June–August) or harvested from plants grown out simultaneously in a "screenhouse" common garden at the University of California, Davis (UC Davis; table S1). The screenhouse has a clear plastic roof and screened walls that allow exposure to ambient temperatures and day length but controlled watering and pollination. In the field, we collected seed only from plants with more than five fruits and more than 1.5 m from previously sampled plants. Unfortunately, sufficient fresh field-collected seed was not available for some species. For these species, we used maternal parents from seed collections in prior years, planted for a single generation of bulking in the screenhouse in September 2018 with experimental seeds harvested from these parents between June and August of 2019. Pools of seeds for the entire experiment ($n = 600$) were created from approximately 20 maternal families for each population. All seeds were stored dry at room temperature in the dark from collection until the start of the experiment.

Experimental Design

To examine phenological and fitness responses to seasonal germination timing, we induced germination on different dates to create eight staggered seasonal germination timing cohorts, one cohort planted every 3–4 weeks from September 20, 2021, to March 7, 2022. These cohorts spanned the natural germination timing in the field for these populations as well as extending timing earlier and later in the season. By forcing seeds to germinate outside their species' normal seasonal germination niche, we could observe phenology and fitness responses to germination timing across a wider range of seasonal environments, simulating historical extremes of rain onset and future climate change scenarios.

For each germination timing cohort, 75 randomly selected seeds from the original seed pool of each species were sown into individual cells of Landmark 98 germination plug trays with a goal of 24 seedlings for later transplant. Trays were filled with a mix of two-thirds UC Davis potting soil (equal parts sand, compost, and peat moss with dolomite) and one-third coarse 16 grit sand, watered until saturation. Seed coats of the *Caulanthus* species were scarified using a scalpel prior to sowing to remove physical dormancy barriers to germination observed in prior unpublished experiments (LoPresti et al. 2019; S. J. Worthy and J. R. Gremer, unpublished data). After planting, trays were placed into growth chambers (E7/2; Conviron, Winnipeg) for 17 days with 12-h daylight cycles at varying temperatures to promote germination (table S2). Germination of individual seeds was asynchronous within each cohort of each population across the 17 days, which also reflects germination behavior observed in a prior experiment (Worthy et al. 2024*b*) and in the field.

For each planting cohort, germination trays were placed in the screenhouse at UC Davis, after the 17-day germination period in growth chambers. After a 24-h adjustment period, seedlings were transplanted into individual conetainers (164 mL, SC10; Stuewe & Sons, Tangent, Oregon) filled with the same soil mixture as the germination trays. The height of each seedling was recorded to use as a size covariate in analyses, and cones were placed on a mist bench for 3 weeks to minimize transplant shock. Following this acclimation period, cones were placed randomly into population-specific racks distributed across four screenhouse benches. Sample size varied among populations and among cohorts due to variation in germination ranging from 0 to 24 individuals in each cohort (table S1). When plants flowered, we hand-pollinated them every 2 or 3 days to ensure pollination. We used cotton swabs to collect pollen from open flowers of at least two individuals per population and then distributed pollen to all flowering conspecifics. Two conspecifics were always available for pollination because of overlapping flowering among cohorts.

During the study, plants were watered using a drip irrigation system with each species assigned to one of three watering regimes: low (49.50 mL/week), medium (57.75 mL/week), or high (75.25 mL/week). In pilot experiments, we found that desert species got fungal disease with too much water, while species occupying wetter climates suffered under drier desert watering regimes. We therefore grouped species into watering regimes similar to annual rainfall at their field sites, determined by comparing 30-year average annual precipitation (1991–2020) for each population's collection site extracted from the PRISM database (PRISM Climate Group 2014; table S1). These precipitation amounts were converted to millimeters per week of the study and then to milliliters ($1 \text{ mm} = 1 \text{ L/m}^2$), after which they were used to calculate the length of time the irrigation system should run to deliver the desired quantity of water (based on the average flow rate of the drip irrigation system, 16.5 mL/min). When necessitated by prolonged temperatures greater than 38°C and plant wilting, additional water was supplied with proportional increases across the watering groups (table S3). Mean air temperature in Davis, California, during the experiment, ~15°C (9°C–21°C), was comparable to historical and contemporary field mean air temperatures populations experienced (table S4). To determine the end of the season, we visualized 30 years (1991–2020) of monthly precipitation values from the PRISM database, which showed that mid-June was a conservatively late choice considering differences in monthly precipitation among the populations' locations (fig. S2). To simulate a natural end to the season, watering was tapered off over a 3-week period prior to the end of the study on June 13, 2022. Later-germinating cohorts experienced shorter growing seasons, and thus less total irrigation, than earlier cohorts, which reflects expected costs to later germination.

Environmental Measurements

To quantify seasonal environments experienced by successive germination cohorts, we recorded hourly temperature in the screenhouse with temperature loggers (Thermochron DS1921G iButtons) buried in soil-filled cones from the date of transplant to the end of the study for each germination timing cohort. We used these data to calculate two metrics of cumulative growing season conditions for each germination timing cohort: accumulated chilling, expressed as chill portions, and photothermal units. Chill portions, a measure of cumulative exposure to cold temperatures (Fishman et al. 1987*a*, 1987*b*), were calculated using chillR (Luedeling et al. 2023). One chill portion is obtained after exposure to 6°C for approximately 28 h (Erez 2024). Accumulation of chill portions provides an index of progress toward fulfillment of potential vernalization requirements. Photothermal units were calculated according to Burghardt et al. (2015) such that each germination timing cohort accumulated thermal time during daylight hours with a base temperature rate of 4°C. This metric takes into account the combined impacts of photoperiod and ambient temperature on plant progress toward flowering (Wilczek et al. 2009; Burghardt et al. 2015). We also determined the day length for each day of the study for the location of the screenhouse using chillR (Luedeling et al. 2023).

Data Collection

We measured phenological and morphological traits for all transplanted individuals. To quantify phenology, we censused individuals three times a week and recorded dates of first bud, first flower, and first fruit. The dates of these phenological stages were highly correlated and results are concordant among the stages, so only first bud dates are considered in analyses here (table S5). We also recorded the height of each individual at these phenological stages. From these traits, we calculated time to first bud and first bud date for each individual. Time to first bud was calculated as the number of days between transplant date and date of first bud, an index of developmental speed. First bud date was calculated as the number of days from September 1 until first bud to standardize among germination timing cohorts. This metric represents the seasonal timing of first bud production.

To assess effects of germination timing on individual fitness, we recorded whether each plant flowered and scored seed number and total seed mass for all flowering individuals. We then calculated first-year fitness for each individual as the probability of flowering multiplied by the number of seeds produced. This metric is equivalent to lifetime fitness in annual species, but it does not account for reproduction in later years for biennials or perennials.

Data Analysis

Does Flowering Phenology Respond to Germination Timing? To examine phenological responses to germination timing, we fitted linear models to time to first bud, first bud date, and size at first bud. Each of these models included germination timing (transplant date coded as continuous), species, germination timing × species interaction, transplant height, and bench as predictors. Analysis of deviance tables were generated for fitted models to evaluate the significance of main effects. Marginal means of the relationships of time to first bud, first bud date, and size at first bud with germination timing were then estimated for each species using the emmeans package (Lenth 2023). We also tested for effects of seed source (screenhouse vs. field collected) by comparing mean (Student's *t*-test) and homogeneity of variance (Levene's test; car package; Fox and Weisberg 2019) in phenological responses to germination timing (slopes) between the groups.

Does Germination Timing Affect Fitness, Either Directly or Indirectly, through Flowering Phenology? To explore effects of germination timing on flowering probability, we fitted a group logistic regression with binomial error and a logit link function. Groups were benches ($n = 4$) within each cohort, and predictors were germination timing (transplant date coded as continuous), species, their interaction, and bench. Negative binomial generalized linear models (MASS package; Venables and Ripley 2002) were fitted to evaluate the relationships of number of seeds (for individuals that flowered) and first-year fitness with germination timing, whereas a linear model was fitted to model the same relationship for total seed mass. All of these fitness response models included germination timing (transplant date coded as continuous), species, their interaction, transplant height, and bench as predictors. Analysis of deviance tables were generated for fitted models to evaluate the significance of main effects, and then marginal means of the relationships between each fitness response and germination timing were estimated for each species using the emmeans package (Lenth 2023). We tested for effects of seed source on fitness responses to germination timing using the same models as for phenology responses above.

To decompose the effects of germination timing on fitness into direct effects and indirect effects through flowering phenology, we used structural equation models (SEMs) for time to first bud. Models were built separately for each species using piecewiseSEM (Lefcheck 2016). Prior analyses did not find significant differences among populations within species, so populations were pooled for SEM analysis. The models consisted of (1) a linear model fitted to the phenology response with germination timing (transplant date coded as continuous) and transplant height as predictors and (2) a negative binomial generalized linear model fitted to number of seeds with the phenology response, germination timing, and transplant height as predictors. Tests of directed separation and Fisher's *C* statistic were used to evaluate goodness of fit of the SEMs (Lefcheck 2016; Lefcheck 2021). The latent-theoretical approach was used to calculate standardized path coefficients for the linear phenology submodel, while the observation-empirical approach was used for the negative binomial fitness submodel (Grace et al. 2018; Lefcheck 2021). Diagrams of the SEMs were generated using DiagrammeR (Iannone 2023).

How Have Responses of Flowering Time and Fitness to Germination Timing Diversified across the Clade, and Do Patterns Reflect Climate of Origin? We evaluated how relationships between phenology, fitness, and germination timing were distributed across the phylogeny of these species to understand how these responses have diversified. The phylogenetic hypothesis for the Streptanthoid complex was previously generated by Cacho et al. (2014). We tested for phylogenetic signal in the marginal means estimated for each species from relationships between time to first bud, first bud date, probability of flowering, number of seeds, total seed mass, first-year fitness, and germination timing. Blomberg's K was estimated using phytools (Revell 2012) with standard errors of the marginal means included in the estimations. Values of Blomberg's K equal to 1 indicate that species variation in these relationships are indistinguishable from Brownian motion along the phylogeny (Blomberg et al. 2003). When values of K are greater than or less than 1, there is more or less variation, respectively, among species in the relationships than expected given Brownian motion (Blomberg et al. 2003).

We tested whether slopes of relationships between time to first bud, probability of flowering, number of seeds, first-year fitness, and germination timing were related to species' climate using phylogenetic generalized linear models (Orme et al. 2023). Six climate variables were extracted from the California Basin Characterization Model (Flint and Flint 2014) for species' locations across their ranges taken from herbarium records from the Consortium of California Herbaria (CCH2 Portal 2023; table S6). Average annual values of climate water deficit, precipitation, minimum and maximum temperatures, and interannual variability in precipitation (coefficient of variation) and temperature (standard deviation) over 25 years (1991–2015) were calculated, and a principal component analysis was used to reduce dimensionality of the data (table S6). The first principal component (PC1) was used in the models, as it explained 62% of the variation and was positively associated with precipitation and negatively associated with climate water deficit, minimum and maximum temperatures, and precipitation variability (table S6). This principal component contrasts cool, wet climates with less variation in precipitation (high values of PC1) from warm, dry climates with more variable precipitation (table S6).

We also used phylogenetic generalized linear models to test whether species with more specialized germination niches (i.e., those germinating in a narrower seasonal window with respect to rainfall onset) would also be more specialized in their postgermination niche requirements. If so, germination specialists should exhibit greater fitness reductions when forced to germinate outside their usual seasonal germination niche than species that germinate across a broader range of rainfall onset dates. In a previous study, we showed that germination fraction declined with later rainfall onset date in many of these species, but the magnitude of response varied significantly across the phylogeny (Worthy et al. 2024*b*). Here, we used the slope of this relationship as an index of germination specialization for each species; steeper slopes indicated narrower germination niches concentrated earlier in the season. To test our prediction, we asked whether such germination specialization was associated with species declines in number of seeds produced or first-year fitness with later germination timing in the present study. For this analysis, slopes of germination fraction for the species CAIN and CAAN, estimated in Worthy et al. (2024*b*), were averaged over two populations.

Last, we used phylogenetic generalized linear models to test the hypothesis that species with greater acceleration of flowering in later cohorts would better maintain fitness across a range of germination dates, as expected if this compensatory plasticity is adaptive. We tested this hypothesis by evaluating relationships between slopes of time to first bud against germination timing and slopes of three fitness metrics (flowering probability, number of seeds produced, and first-year fitness) against germination timing.

Results

Does Flowering Phenology Respond to Germination Timing?

Later-germinating cohorts encountered different seasonal environments, including decreases in the amount of chilling and photothermal units individuals accumulated during the growing season and variation in day length (fig. S3). Effects on reproductive phenology of these shifts in seasonal conditions with germination timing varied among species. In all species, the number of days to production of the first bud decreased significantly with later germination timing (fig. 1; tables S7, S8). Nevertheless, in all species except STTO, which did not flower in later cohorts, individuals that germinated in later rain events produced their first bud later in the season than individuals that germinated in earlier rain events (fig. S4; tables S7, S9). Thus, acceleration of bud production in later-germinating cohorts partially synchronized reproductive timing with earlier cohorts but did not completely prevent reproductive delays. Species differed in the degree of this compensatory plasticity of days to bud to germination timing (fig. 1) and consequently in the degree of synchronization of budding date across germination cohorts (fig. S4). Species with greater acceleration of budding in later-season germination cohorts exhibited more synchronization of budding date with respect to germination timing (figs. 1, S4). In four species, plants from later-season germination cohorts were significantly shorter when producing their first bud than individuals in earlier cohorts (fig. S5; tables S7, S10). Seed source (field vs. screenhouse) did not have a significant effect on species' phenological responses to germination timing (table S11).

Does Germination Timing Affect Fitness, Either Directly or Indirectly, through Flowering Phenology?

Germinating later in the season translated, for many species, into reduced fitness. For five species, the probability of flowering significantly decreased as the timing of germination came later in the season (fig. 2; tables S12, S13). The facultative biennial STTO failed to flower entirely in the last four germination cohorts (fig. 2, S5). One species, STDR, showed a significant increase in the probability of flowering with later germination, potentially due to high prereproductive mortality of individuals in the first cohort that resulted in low sample sizes for early cohort estimates (fig. S6).

Flowering individuals of six species produced significantly fewer seeds when germinating later in the season (fig. 3; tables S12, S14), and four of these species also had

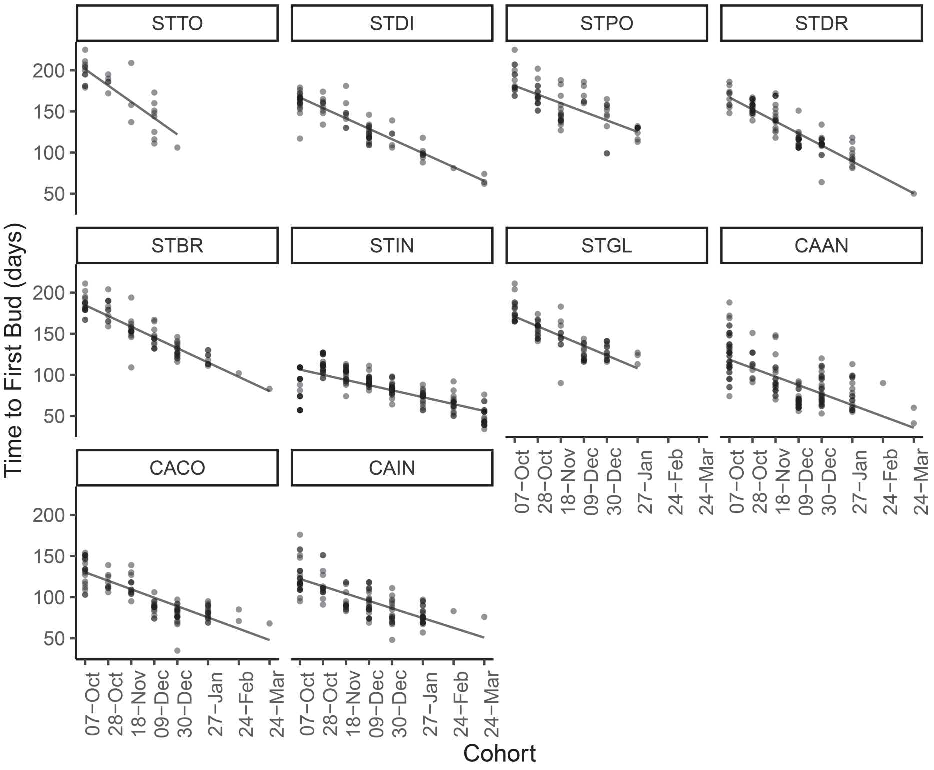


Figure 1: Relationships between amount of time to first bud (days) and germination timing. Time to first bud was calculated as the number of days between individual transplant date and date of first bud. Regression lines represent significant negative relationships where individuals that germinated in later cohorts took less time to produce their first bud. Points represent observed time to first bud for individuals of each species in each cohort. Points are opaque gray where darker points indicate overlap among points. Panels are ordered by species' phylogenetic relationships. See the main text for species abbreviations.

significantly lower total seed mass with later germination timing (fig. S7; tables S12, S15). Overall, seven of the 10 species showed significant decreases in their first-year fitness as the timing of rainfall events and subsequent germination occurred later in the season (fig. S8; tables S12, S16). There was no detectable effect of seed source on the fitness responses to germination timing (table S11).

SEMs revealed that germination timing influenced seed production both directly and indirectly through its effects on flowering phenology (fig. 4; table S17). Later germination timing had a significant and direct negative effect on seed number for all species except STTO and STPO, the latter of which had low overall seed set throughout the experiment (fig. 4). This negative effect was partially counteracted by a positive indirect effect through time to first bud, suggestive of adaptive phenotypic plasticity (table S17): later germination resulted in significantly fewer days to bud, which in turn had a significant positive effect on seed number in all species except STPO and STIN (fig. 4). Thus, acceleration of flowering in later cohorts partially ameliorated the fitness impacts of later germination. However, the relative magnitude of direct and indirect effects, and thus the total effect of germination timing on fitness, varied among species (fig. 4; table S17).

How Have Responses of Flowering Time and Fitness to Germination Timing Diversified across the Clade, and Do Patterns Reflect Climate of Origin?

Species' reproductive phenology and fitness responses to the timing of germination varied substantially across the clade. We did not find significant phylogenetic signal for responses of time to first bud or first bud date (K $=$ 1.19, $P = .15$; figs. 5, S9) to germination timing with K values consistent with Brownian motion; note that these phenological traits are linear transformations of one another, so the statistics are identical. Bloomberg's K for responses of flowering probability (K $=$ 0.95, $P = .90$; fig. S9), number of seeds produced (K $=$ 1.07, $P = .86$; fig. 5), seed mass (K $=$ 0.77, $P = .42$; fig. S9), and first-year fitness (K $=$ 0.68, $P = .99$; fig. S9) to germination timing were also consistent with Brownian motion.

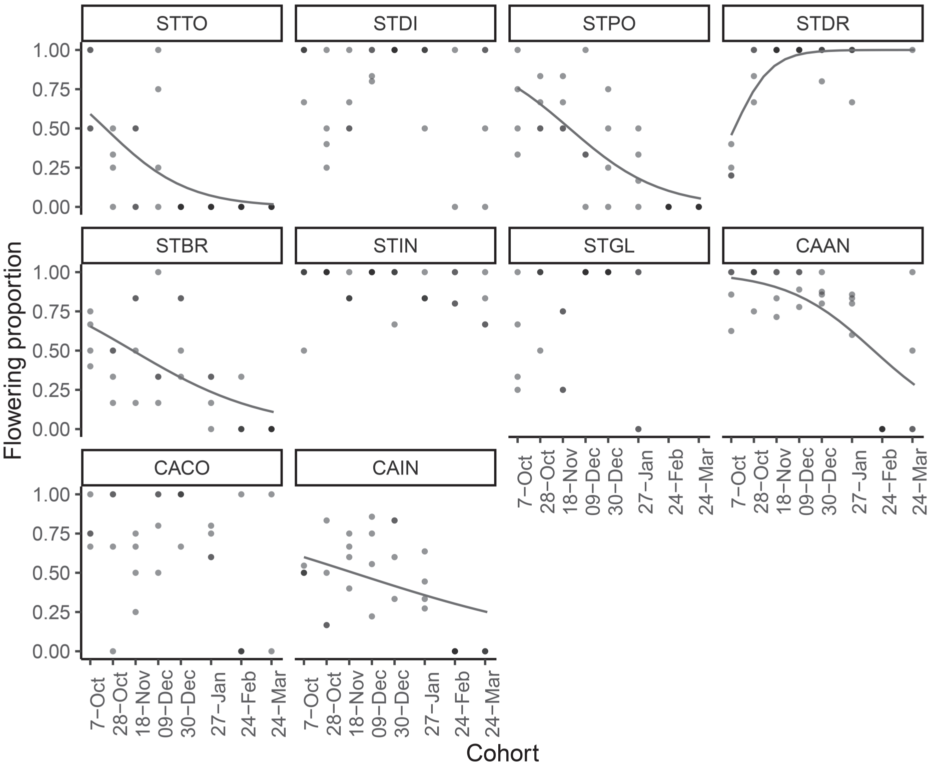


Figure 2: Relationships between probability of flowering and germination timing. Regression lines represent significant relationships (back transformed from logit scale) where later-germinating individuals had lower probability of flowering except for STDR, which had high prereproductive mortality of individuals in the first cohort (fig. S6). Points represent mean proportions of flowering individuals of each species in each cohort on each of four benches. Points are opaque gray where darker points indicate overlap among points. Panels are ordered by species' phylogenetic relationships. See the main text for species abbreviations.

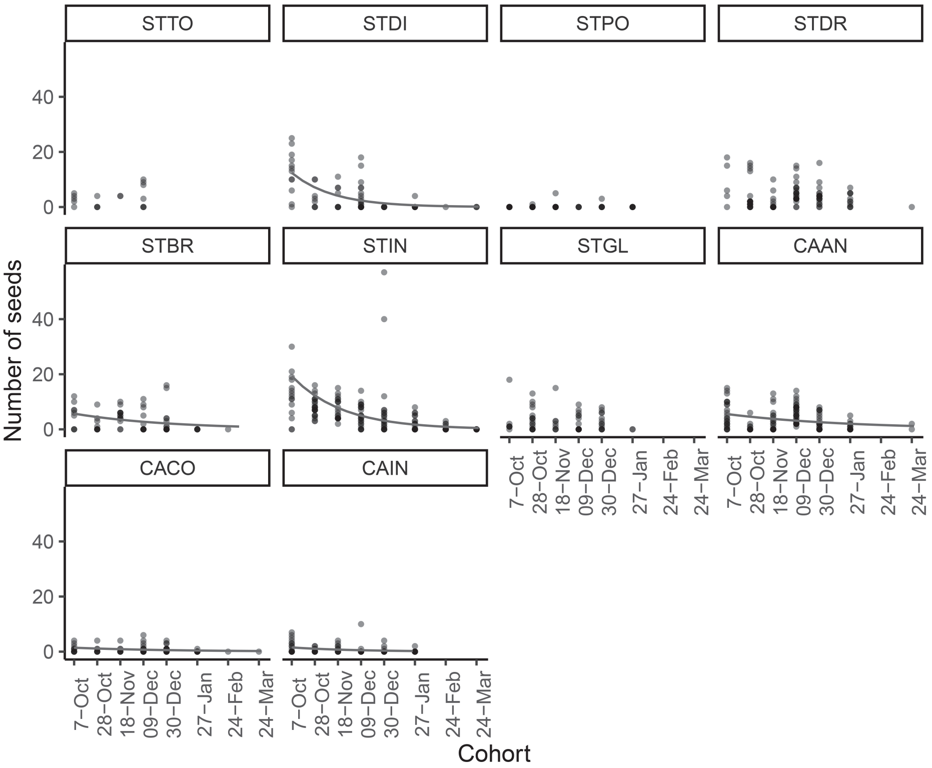


Figure 3: Relationships between number of seeds produced and germination timing. Regression lines represent significant negative relationships where later-germinating individuals produced fewer numbers of seeds. Points represent the number of seeds for individuals of each species in each germination timing cohort. Points are opaque gray where darker points indicate overlap among points. Many individuals included in this analysis flowered but did not produce any seeds ($n = 389$). Panels are ordered by species' phylogenetic relationships. See the main text for species abbreviations.

After accounting for phylogenetic relatedness, the responses of time to first bud and number of seeds to germination timing were significantly related to the PC1 of species' range-wide 25-year average annual climatic conditions (fig. 6*A*, 6*C*; table S18), suggesting a role of climate adaptation in species divergence. Species with steeper slopes of time to first bud (i.e., those whose reproductive phenology was more plastic to germination timing) were associated with lower climate water deficient, lower variability in precipitation, lower maximum temperature, and higher mean annual precipitation (fig. 6*A*; table S6). These species also had shallower decreases in number of seeds produced with later germination timing (less negative slopes; fig. 6*C*). Slopes of flowering probability and first-year fitness against germination time were unrelated to climate (fig. 6*B*, 6*D*; table S18).

We had hypothesized that species with narrower seasonal germination niches observed in our previous study (Worthy et al. 2024*b*) might have greater fitness sensitivity when forced to experience seasonal conditions under which they normally would avoid germinating. However, results of phylogenetic generalized linear models did not support that hypothesis: steeper declines in germination proportion in later seasonal cohorts (i.e., narrower seasonal germination niches) were not significantly associated with steeper declines in fitness with later germination (narrower postgermination seasonal niches; fig. S10; table S19) across species.

We also tested the hypothesis that compensatory plasticity of days to bud (or stasis of bud date) to germination timing would be associated with stabilization of fitness across germination cohorts. Accounting for phylogenetic relatedness, we observed a marginally significant negative relationship between species' phenological plasticity of days to bud (e.g., the slope of the relationship between time to first bud and germination timing) and response of seed number to germination timing (fig. S11*A*; table S20). Species with steeper decreases in time to first bud—and consequently smaller delays in bud date—had shallower declines in seed number with later germination timing, as predicted if acceleration of flowering in later cohorts is adaptive, compensatory plasticity. However, the relationships

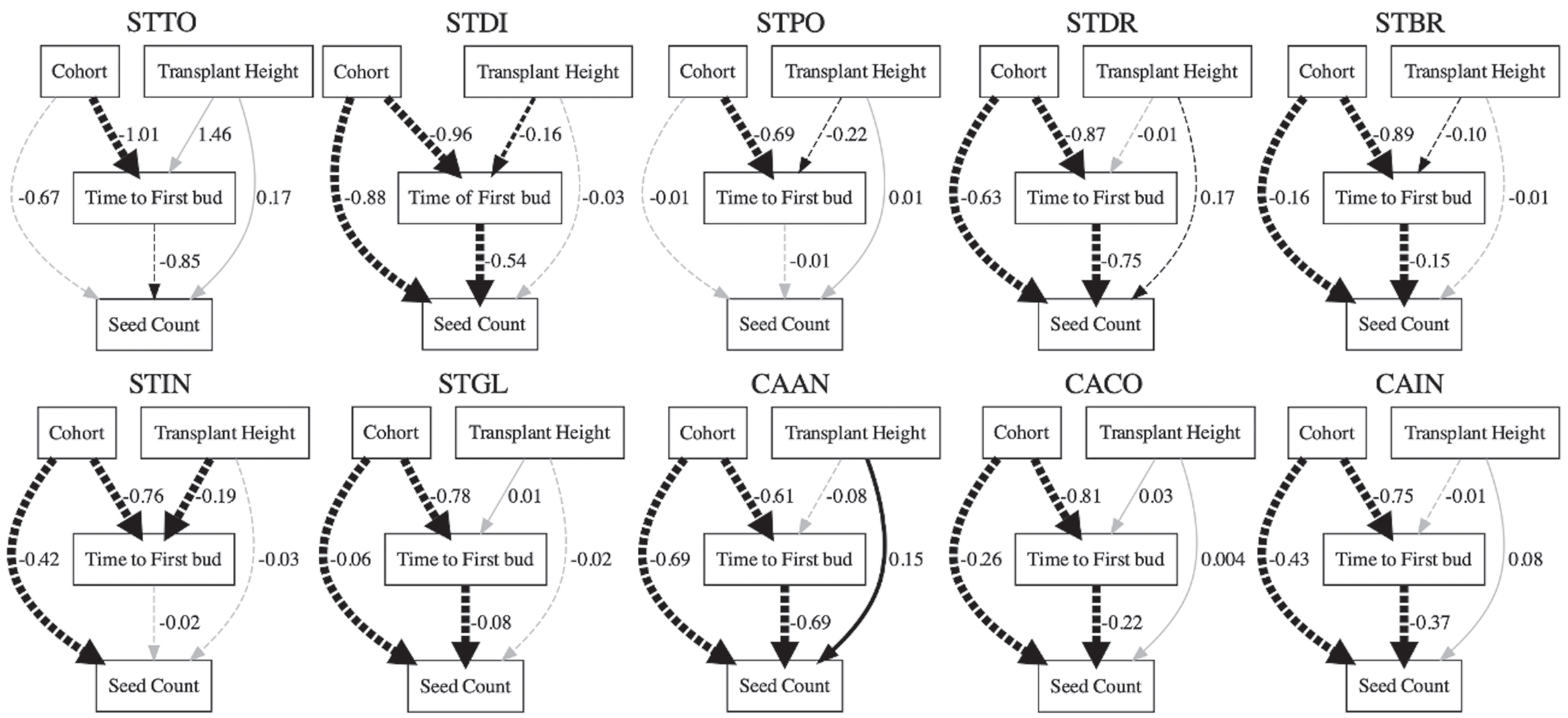


Figure 4: Results of structural equation models testing for direct effects of germination timing (cohort) on fitness (seed count) and indirect effects through phenology, time to first bud (days). Time to first bud was calculated as the number of days between individual transplant date and date of first bud. Numbers are standardized partial regression coefficients, and the width of the arrows is scaled based on their level of significance. Solid and broken lines represent positive and negative relationships, respectively. Line color represents significant (black) and nonsignificant (gray) relationships. Species are in order of phylogenetic relationships. See the main text for species abbreviations.

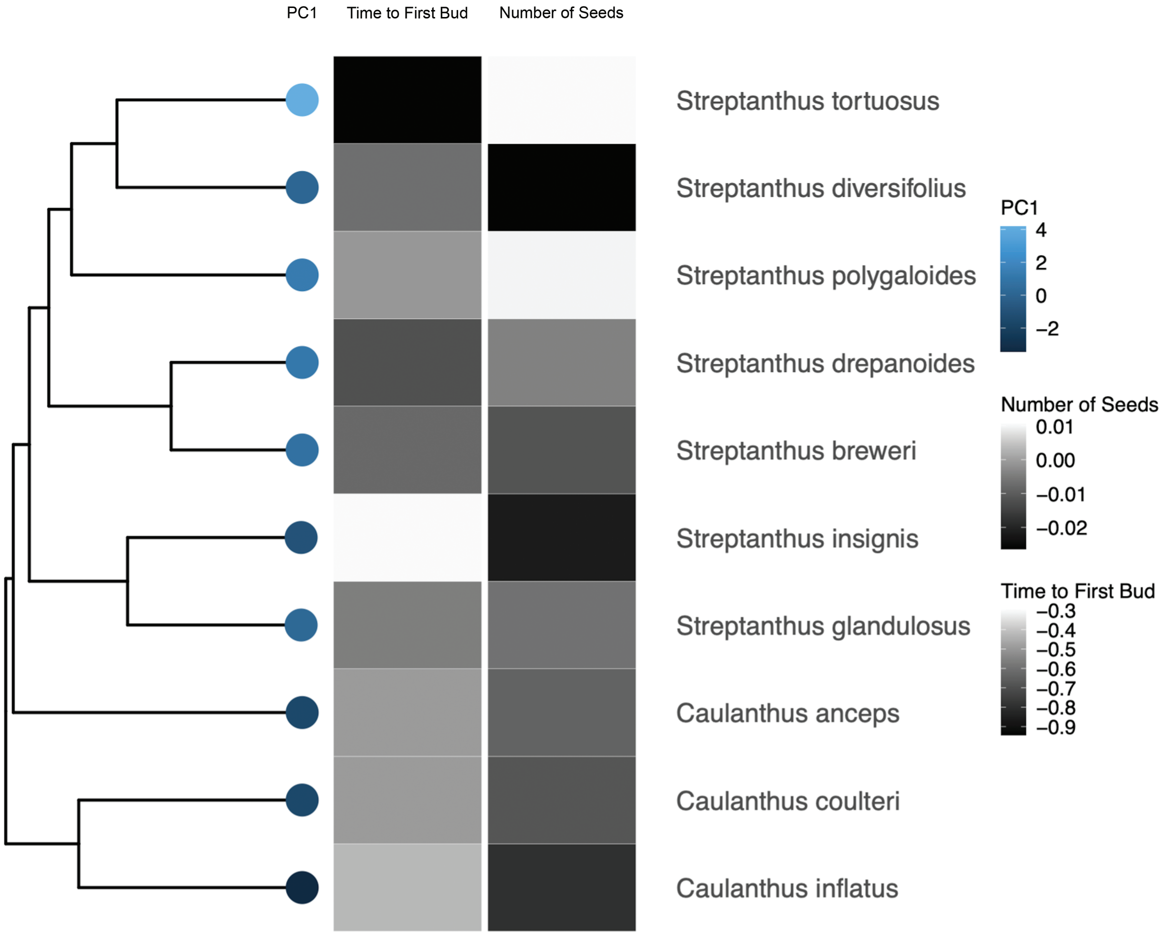


Figure 5: Slopes of relationships of time to first bud and number of seeds produced with timing of germination displayed across the phylogeny. Time to first bud was calculated as the number of days between individual transplant date and date of first bud. Phylogenetic signal of these relationships was evaluated with Blomberg's K: time to first bud ($K = 1.19$, $P = .15$), number of seeds ($K = 1.07$, $P = .86$). Scores associated with the first principal component (PC1) of an analysis of average yearly climate for 1991–2015 for species' locations are displayed (table S6). PC1 explained 62% of the variation and was positively associated with precipitation and negatively associated with climate water deficit, minimum and maximum temperatures, and precipitation variability.

between phenological plasticity, flowering probability (fig. S11*B*), and first-year fitness were not significant (fig. S11*C*).

Discussion

The seasonal timing of seed germination is a niche construction trait that determines the environmental conditions that plants experience during the growing season, thus shaping phenology and fitness (Donohue 2005; Donohue et al. 2005). As climate change alters seasonal environments, the resulting changes in seasonal germination timing may critically influence plant population performance (Kimball et al. 2011; Levine et al. 2011; Gremer et al. 2020*b*; Martínez-Berdeja et al. 2023). Our results reveal that later germination has significant impacts on flowering phenology and fitness. These findings suggest that later onset of the rainy season in Mediterranean climates due to climate change may affect persistence of plant populations, with impacts varying among species across the *Streptanthus*/*Caulanthus* clade. A critical component of these differences is species' variation in the degree of compensatory phenological plasticity: the ability of later-germinating plants to accelerate flowering, thus reducing delays in flowering date and stabilizing fitness responses to germination timing. This compensatory plasticity has diversified across the clade with a signal of climate adaptation. As climate change brings later average onset of the California rainy season (Luković et al. 2021),

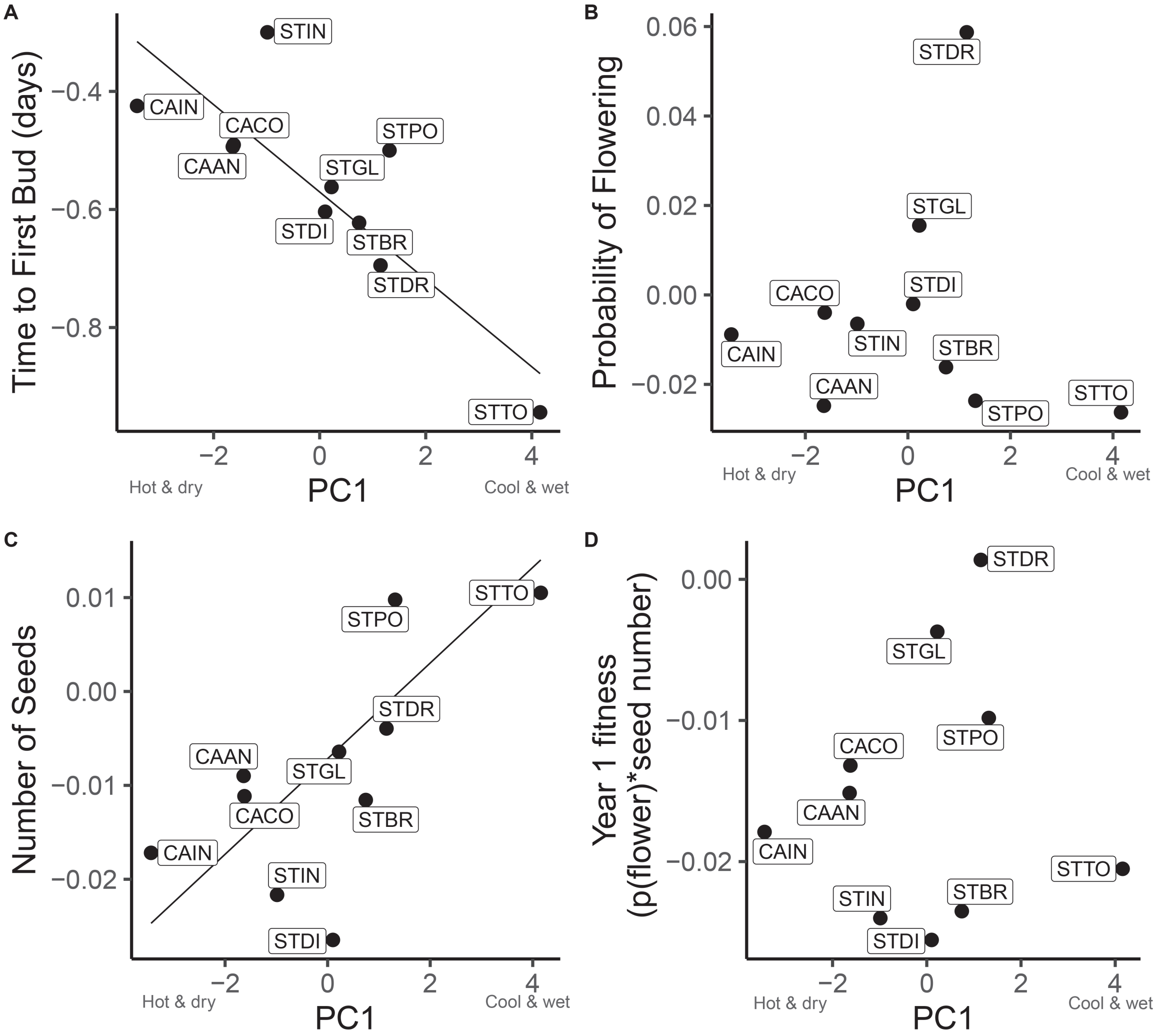


Figure 6: Relationships between phenology and fitness responses to germination timing and 25-year average annual climate variables tested using phylogenetic generalized linear models. Separate models were built for slopes of relationships of time to first bud (*A*), probability of flowering (*B*), number of seeds produced (*C*), and first-year fitness (*D*) with germination timing. Principal component analysis was used to reduce dimensionality of the climate variables (table S6). The first principal component (PC1) was positively associated with precipitation and negatively associated with climate water deficit, minimum and maximum temperatures, and precipitation variability. Points represent slope estimates for each species. See the main text for species abbreviations.

compensatory phenological plasticity may partially mitigate fitness impacts of delayed germination, but the majority of species are likely to suffer decreases in population fitness.

Does Flowering Phenology Respond to Germination Timing?

Germination timing often has cascading effects on flowering phenology, which may be mediated by availability of and species' responsiveness to seasonal cues (Donohue et al. 2002, 2010; Wilczek et al. 2009; Burghardt et al. 2015; Miryeganeh et al. 2018; Gremer et al. 2020*a*; Olliff-Yang and Ackerly 2021). In our study, later-germinating cohorts generally flowered in fewer days, but species differed in the degree of compensatory plasticity; species with greater plastic acceleration of days to bud in response to later germination had more synchronized flowering dates across germination cohorts. However, compensatory plasticity of days to bud was insufficient to synchronize flowering date completely, with only STTO (slope $= -0.94$) coming close to achieving complete compensation for late germination (slope of −1). Similarly, plastic acceleration of flowering with later germination does not entirely synchronize flowering date in *Arabidopsis thaliana* (Wilczek et al. 2009; Miryeganeh et al. 2018; Martínez-Berdeja et al. 2023; Huang et al. 2024).

Since all species experienced identical seasonal environments in our experiment, variation in phenological responses indicates that species differed in responses to seasonal cues. Day length changed dramatically throughout the study, while accumulation of chilling hours declined drastically in later-germinating cohorts, accompanied by significant declines in the probability of flowering in five species. One of these species was the facultative biennial STTO, in which we have experimentally demonstrated a vernalization requirement for flowering (Gremer et al. 2020*a*). That finding suggests that failure to flower in late-germinating cohorts of the other related species may also stem from unsatisfied vernalization requirements. However, the adaptive value of this requirement for fall-germinating winter annuals is unclear. Facultative vernalization requirements can prevent premature flowering in unfavorable winter conditions and synchronize flowering in spring, but flowering eventually occurs in the absence of chilling (Wilczek et al. 2009; Miryeganeh et al. 2018; Huang et al. 2024). However, failure to flower in spring due to insufficient vernalization means zero fitness for winter annuals, and spring germination may then be a lethal strategy. These temperature cues may interact with other factors, such as photoperiod and plant ontogeny or size, to influence flowering phenology (Donohue et al. 2010; Burghardt et al. 2015). In particular, variation among species in critical day length requirements and differences in photoperiod between the screenhouse and species' field environments could lead to differences in flowering responses to germination timing. Although our experimental design cannot distinguish the relative contributions of seasonal cues to species response differences, the results provide hypotheses to inform future experiments manipulating specific cues in controlled environments (e.g., Friedman and Willis 2013; Burghardt et al. 2016; Wolkovich et al. 2022).

Does Germination Timing Affect Fitness, Either Directly or Indirectly, through Flowering Phenology?

Germination timing is often under strong selection (Kalisz 1986; Donohue et al. 2005; Verdú and Traveset 2005; Picó 2012; Postma and Ågren 2016, 2022; Zacchello et al. 2020; Martínez-Berdeja et al. 2023). For annual plants in seasonal environments, both early and late germination may affect fitness (Zacchello et al. 2020). Early germination may expose seedlings to high temperatures and periods of drought (Mayfield et al. 2014; Harrison et al. 2015). Late germination may affect fitness in two ways: through exposure to cooler, less favorable conditions at the time of emergence and by decreasing the window of time available for growth and reproduction before the end of the growing season. Indeed, for all species in our experiment, these combined direct effects of later germination reduced seed production. The negative fitness impact of late germination was, however, partially mitigated by positive indirect effects of germination timing through its accelerating effect on phenology. Thus, acceleration of reproduction in later-germinating cohorts seems to be a form of adaptive plasticity that compensates for the negative direct effects of later germination. The degree of compensation and the balance of direct and indirect effects varied among species, resulting in the observed differences in fitness responses to germination timing. Direct and indirect effects of seasonal timing have also been observed in terrestrial and aquatic migratory species, where changes to environmental conditions, such as warming temperatures, have altered the timing of migration with direct effects on fitness and indirect effects through, for example, first egg date in birds (Both and Visser 2001; Winkler et al. 2014; Inouye 2022).

It is important to note that our fitness metrics did not account for effects of seasonal selective factors, such as pollinator or mate availability or herbivore abundance, that may be important in the field (Miryeganeh et al. 2018; Kehrberger and Holzschuh 2019; Kudo and Cooper 2019). For instance, by affecting synchronization of flowering, germination timing may affect pollination success of individuals in populations (Miryeganeh et al. 2018; Kehrberger and Holzschuh 2019). Through hand pollination in our experiment, this issue is avoided, but fitness may have still suffered from lower diversity of pollen when fewer individuals were flowering and less efficient pollination (Paschke et al. 2002). Our study system tends to have generalist pollinators, but species that rely on specialist pollinators may have more severe consequences of later germination timing if that leads to phenological mismatch and consequent reproductive failure (Kudo and Cooper 2019). Furthermore, greenhouse studies such as ours also preclude exploration of other selective factors, such as more natural variation in water availability throughout the season (Pearse et al. 2020), or effects of competition and herbivory.

Another limitation of our study is that species grown from wild-collected seed had different maternal environments than species grown from screenhouse-grown seed, which could have influenced the results. An ideal experiment would have used a single type of seed source to control for such effects, but this was not possible due to seed availability constraints. Our failure to detect significant effects of maternal environment on species responses to germination timing suggests that our conclusions are probably robust to this source of variation, but we cannot rule it out as a potential influence on our findings.

How Have Responses of Flowering Time and Fitness to Germination Timing Diversified across the Clade, and Do Patterns Reflect Climate of Origin?

Phylogenetic analyses suggest a signature of climate adaptation in the evolutionary diversification of phenological plasticity and seed production responses to rainfall onset across the Streptanthoid clade. Species from drier, warmer, more variable habitats in southern California accelerated flowering less in later cohorts and had less synchronized flowering dates than northern species. This finding suggests that compensatory phenological plasticity to germination timing may have evolved as the clade diversified out of the desert into cooler, wetter, more stable environments, with longer growing seasons. The desert species flowered rapidly even in the earliest-germinating cohorts, suggesting a constant developmental program across seasonal environments. This risk-averse, constitutively early flowering strategy may be adaptive in the short growing season and unpredictable rainfall of their home climates (Wesselingh et al. 1997; Metcalf et al. 2003; Rees et al. 2004; Austen et al. 2017). In contrast, Streptanthoid species from cool, wet environments were more plastic in flowering phenology (Pearse et al. 2020). Early-germinating cohorts flowered at a later age and larger size, which may help to maximize fitness in a longer growing season with early rainfall. Later cohorts accelerated development to flower at an earlier age and smaller size, synchronizing flowering date and allowing reproduction despite a shorter growing season. Responses of other fitness traits (first-year fitness and seed mass) to germination timing were more evolutionarily labile, with no climate association and no correlation with phenological plasticity across the clade. Fitness and life history metrics, in general, have previously been noted as less evolutionarily conserved when considering more than 400 plant species (Burns et al. 2010; Salguero-Gómez et al. 2016; Che-Castaldo et al. 2018), connected to colonization of new habitats (Herben et al. 2014) and higher intraspecific variation (Healy et al. 2019).

Consistent with our finding that compensatory phenological plasticity mitigated the direct negative fitness effects of later germination in most of our study species, we found that species with greater acceleration of days to bud in later cohorts had shallower declines in seed number after correcting for phylogeny. Such plasticity may buffer fitness declines in the face of delayed rainfall onset. Indeed, a phylogenetic analysis by Willis et al. (2008) showed that species with greater plasticity of flowering time to spring temperatures decreased less in abundance over approximately 150 years in the community of plants in Thoreau's woods in Massachusetts. Another strategy to mitigate the effects of shifting germination timing would be to avoid germinating outside favorable environmental windows. This strategy would require specialization on a narrower range of germination conditions, with higher fitness costs expected for species with this strategy forced to germinate in unfamiliar seasonal environments. We did not find support for this strategy here; responses of germination and postgermination fitness components were uncorrelated, suggesting that they have evolved independently across the phylogeny. Thus, compensatory phenological plasticity is likely the primary mechanism to buffer effects of variation in germination timing in this system.

Can Variation among Species in Responses to Germination Timing Lead to Differential Vulnerability to Climate Change?

Whether phenotypic plasticity can buffer fitness across changing environments is an important question for predicting population resilience to climate change (Ghalambor et al. 2007; Chevin and Lande 2010; Chevin et al. 2010; Nicotra et al. 2010; Vedder et al. 2013; Valladares et al. 2014; Anderson and Gezon 2015; Duputié et al. 2015; Kingsolver and Buckley 2017; DeMarche et al. 2018; Scheiner et al. 2020; Gauzere et al. 2020). Numerous studies have focused on plastic phenological responses to changing spring environments, such as early budburst or flowering in response to warmer springs and earlier snowmelt (Willis et al. 2008; Anderson et al. 2012; Anderson and Gezon 2015; Wadgymar et al. 2018; Zettlemoyer et al. 2024). Less attention has been paid to plant responses to changing fall environments (but see Kimball et al. 2010; Martínez-Berdeja et al. 2023; Worthy et al. 2024*b*). In desert and Mediterranean climates, later onset of fall rains (Luković et al. 2021) means that seeds are germinating in cooler conditions (Kimball et al. 2010; Worthy et al. 2024*b*) and may have less time to complete reproduction before the end of the growing season. This shorter growing season may therefore select for a faster transition to flowering, but at the expense of smaller size at reproduction and consequent lower fecundity (Cohen 1976).

In our study, species differences in degree of phenological compensation resulted in different sensitivities of seed production to seasonal germination delays; over half of the species significantly declined in fecundity with later germination. For these species, compensatory phenological plasticity partially mitigated fitness costs but was insufficient to stabilize fitness in the face of delayed germination. Thus, acceleration of flowering may be an adaptive response in short seasons but may still reduce population mean fitness

(Colautti et al. 2017). Plasticity of flowering time to germination timing may allow plants to maximize fecundity in years with early rainfall onset while mitigating fitness costs of shorter growing seasons in years with late rainfall, buffering mean population fitness across years. However, as the mean rainfall date moves later in the year, mean population fitness will decline. This finding adds to the growing body of evidence that adaptive phenological plasticity may be insufficient to fully maintain population fitness in the face of climate change (Franks et al. 2014; Duputié et al. 2015; Colautti et al 2017; Zettlemoyer et al. 2024).

Together, these findings suggest that populations of many Streptanthoid species are vulnerable to future delays in rainfall onset with climate change. This study does, however, trade off replicating populations within species for comparing species across the clade, making reported patterns somewhat preliminary. Populations were chosen for their approximate central location within climate space for their species, but future studies should more comprehensively examine how populations across the range respond to germination delays to fully capture variation within species in plasticity and fitness responsiveness. Species with vernalization requirements for flowering are especially likely to suffer greater impacts of later rainfall due to reproductive failure, especially if future warming temperatures reduce the seasonal accumulation of chilling hours (Cook et al. 2012; Ettinger et al. 2020; Anderson 2023). For such species, a formerly adaptive cue of seasonal conditions for flowering becomes maladaptive under novel climate conditions, and selection may act to weaken vernalization requirements in the future. We have previously demonstrated in this clade that germination declines with later rainfall onset, although species differ in the magnitude of this decline (Worthy et al. 2024*b*). This finding, combined with our current results, suggests that the impact of delayed rainfall onset on fitness will have cascading effects across life stages. Taken together, these findings suggest that species resilience to climate change across the Streptanthoid clade may depend on the cascading fitness consequences of phenological responses to seasonal cues across life stages.

Acknowledgments

We thank Chloe Abbasi, Eda Ceviker, Bryce Johnson, Hugo Mahatdejkul, Shannon Reilly, Emily Rushka, Samantha Swan, and Yasmiin Wadhwani for assistance with experimental setup, maintenance, and data collection. This research was supported by funding from National Science Foundation grant DEB-1831913 awarded to J. R. Gremer, J. Schmitt, S. Y. Strauss, and J. N. Maloof; USDA Hatch grant CA-D-PLB-2795-H awarded to J. N. Maloof; USDA Hatch grant CA-D-EVE-3515-H-1002936 awarded to J. Schmitt; and the University of California, Davis.

Statement of Authorship

J.R.G, J.S., S.Y.S., and J.N.M. conceptualized and designed the study. S.J.W., A.M, and S.R.A. performed the experiment and gathered the data. S.J.W., J.R.G., S.Y.S., and J.S. designed the data analyses. S.J.W. and J.R.G. analyzed the data with assistance from J.S., S.Y.S., and S.R.A. S.J.W., S.R.A., and J.S. wrote the manuscript with contributions from all other authors. All authors contributed to development of ideas, analyses, and interpretation of results.

Data and Code Availability

All data and code necessary to reproduce the results in this article are available on Zenodo (https://doi.org/10.5281/zenodo.14362672; (Worthy et al. 2024*a*).

Literature Cited

Anderson, J. T. 2023. The consequences of winter climate change for plant performance. American Journal of Botany 110:e16252.

Anderson, J. T., and Z. J. Gezon. 2015. Plasticity in functional traits in the context of climate change: a case study of the subalpine forb *Boechera stricta* (Brassicaceae). Global Change Biology 21:1689–1703.

Anderson, J. T., D. W. Inouye, A. M. McKinney, R. I. Colautti, and T. Michell-Olds. 2012. Phenotypic plasticity and adaptive evolution contribute to advancing flowering phenology in response to climate change. Proceedings of the Royal Society B 279:3843–3852.

Austen, E. J., L. Rowe, J. R. Stinchcombe, and J. R. K. Forrest. 2017. Explaining the apparent paradox of persistent selection for early flowering. New Phytologist 215:929–934.

Axelrod, D. I. 1958. Evolution of the madro-tertiary geoflora. Botanical Review 24:433–509.

Bernhardt, J. R., M. I. O'Connor, J. M. Sunday, and A. Gonzalez. 2020. Life in fluctuating environments. Philosophical Transactions of the Royal Society B 375:20190454.

Blomberg, S. P., T. Garland, and A. R. Ives. 2003. Testing for phylogenetic signal in comparative data: behavioral traits are more labile. Evolution 57:717–745.

Bonamour, S., L.-M. Chevin, A. Charmantier, and C. Teplitsky. 2019. Phenotypic plasticity in response to climate change: the importance of cue variation. Philosophical Transactions of the Royal Society B 374:20180178.

Both, C., and M. E. Visser. 2001. Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. Nature 411:296–298.

Burghardt, L. T., C. J. E. Metcalf, A. M. Wilczek, J. Schmitt, and K. Donohue. 2015. Modeling the influence of genetic and environmental variation on the expression of plant life cycles across landscapes. American Naturalist 185:212–227.

Burghardt, L. T., D. E. Runcie, A. M. Wilczek, M. D. Cooper, J. L. Roe, S. M. Welch, and J. Schmitt. 2016. Fluctuating, warm temperatures decrease the effect of a key floral repressor on flowering time in *Arabidopsis thaliana*. New Phytologist 210:564–576.

Burns, J. H., S. P. Blomberg, E. E. Crone, J. Ehrlén, T. M. Knight, J. Pichancourt, S. Ramula, et al. 2010. Empirical tests of life-history evolution theory using phylogenetic analysis of plant demography. Journal of Ecology 98:334–344.

Cacho, N. I., A. M. Burrell, A. E. Pepper, and S. Y. Strauss. 2014. Novel nuclear markers inform the systematics and the evolution of serpentine use in the Streptanthus and allies (Thelypodieae, Brassicaceae). Molecular Phylogenetics and Evolution 72:71–81.

Cacho, N. I., P. J. McIntyre, D. J. Kliebenstein, and S. Y. Strauss. 2021. Genome size evolution is associated with climate seasonality and glucosinolates, but not life history, soil nutrients or range size, across a clade of mustards. Annals of Botany 127:887–902.

CCH2 Portal. 2023. https://cch2.org/portal/index.php.

Che-Castaldo, J., C. Che-Castaldo, and M. C. Neel. 2018. Predictability of demographic rates based on phylogeny and biological similarity. Conservation Biology 32:1290–1300.

Chevin, L.-M., S. Collins, and F. Lefèvre. 2012. Phenotypic plasticity and evolutionary demographic responses to climate change: taking theory out to the field. Functional Ecology 27:967–979.

Chevin, L.-M., and R. Lande. 2010. When do adaptive plasticity and genetic evolution prevent extinction of a density-regulated population? Evolution 64:1143–1150.

Chevin, L.-M., R. Lande, and G. M. Mace. 2010. Adaptation, plasticity, and extinction in a changing environment: towards a predictive theory. PLoS Biology 8:e1000357.

Cohen, D. 1976. The optimal timing of reproduction. American Naturalist 110:801–807.

Colautti, R. I., J. Ågren, and J. T. Anderson. 2017. Phenological shifts of native and invasive species under climate change: insights from the Boechera–Lythrum model. Philosophical Transactions of the Royal Society B 372:20160032.

Cook, B. I., E. M. Wolkovich, and C. Parmesan. 2012. Divergent responses to spring and winter warming drive community level flowering trends. Proceedings of the National Academy of Sciences of the USA 109:9000–9005.

DeMarche, M. L., D. F. Doak, and W. F. Morris. 2018. Both life-history plasticity and local adaptation will shape range-wide responses to climate warming in the tundra plant *Silene acaulis*. Global Change Biology 24:1614–1625.

Dong, L., L. R. Leung, J. Lu, and Y. Gao. 2019. Contributions of extreme and non-extreme precipitation to California seasonality changes under warming. Geophysical Research Letters 46:13470–13478.

Donohue, K. 2002. Germination timing influences natural selection on life-history characters in *Arabidopsis thaliana*. Ecology 83:1006–1016.

———. 2005. Niche construction through phenological plasticity: life history dynamics and ecological consequences. New Phytologist 166:83–92.

Donohue, K., R. R. de Casas, L. Burghardt, K. Kovach, and C. G. Willis. 2010. Germination, postgermination adaptation, and species ecological ranges. Annual Review of Ecology, Evolution and Systematics 41:293–319.

Donohue, K., L. Dorn, C. Griffith, E. Kim, A. Aguilera, C. R. Polisetty, and J. Schmitt. 2005. Niche construction through germination cueing: life-history responses to timing of germination in *Arabidopsis thaliana*. Evolution 59:771–785.

Duputié, A., A. Rutschmann, O. Ronce, and I. Chuine. 2015. Phenological plasticity will not help all species adapt to climate change. Global Change Biology 21:3062–3073.

Ensing, D. J., D. M. D. H. Sora, and C. G. Eckert. 2021. Chronic selection for early reproductive phenology in an annual plant across a steep, elevational gradient of growing season length. Evolution 75:1681–1698.

Erez, A. 2024. Overcoming dormancy in *Prunus* species under conditions of insufficient winter chilling in Israel. Plants 13:764.

Ettinger, A. K., C. J. Chamberlain, I. Morales-Castilla, D. M. Buonaiuto, D. F. B. Flynn, T. Savas, J. A. Samaha, et al. 2020. Winter temperatures predominate in spring phenological responses to warming. Nature Climate Change 10:1137–1142.

Fishman, S., A. Erez, and G. A. Couvillon. 1987*a*. The temperature dependence of dormancy breaking in plants: computer simulation of processes studied under controlled temperatures. Journal of Theoretical Biology 126:309–321.

———. 1987*b*. The temperature dependence of dormancy breaking in plants: mathematical analysis of a two-step model involving a cooperative transition. Journal of Theoretical Biology 124:473–483.

Flint, L. E., and A. L. Flint. 2014. California Basin Characterization Model: a dataset of historical and future hydrologic response to climate change. US Geological Survey Data Release, https://doi.org/10.5066/F76T0JPB.

Fox, J., and S. Weisberg. 2019. An R companion to applied regression. 3rd ed. Sage, Thousand Oaks, CA.

Franks, S. J., J. J. Weber, and S. N. Aitken. 2014. Evolutionary and plastic responses to climate change in terrestrial plant populations. Evolutionary Applications 7:123–139.

Friedman, J., and J. H. Willis. 2013. Major QTLs for critical photoperiod and vernalization underlie extensive variation in flowering in the *Mimulus guttatus* species complex. New Phytologist 199:571–583.

Galloway, L. F. 2001. Parental environmental effects on life history in the herbaceous plant *Campanula americana*. Ecology 82:2781–2789.

Galloway, L. F., and J. R. Etterson. 2007. Transgenerational plasticity is adaptive in the wild. Science 318:1134–1136.

Gauzere, J., B. Teuf, H. Davi, L.-M. Chevin, T. Caignard, B. Leys, S. Delzon, et al. 2020. Where is the optimum? predicting the variation of selection along climatic gradients and the adaptive value of plasticity. A case study on tree phenology. Evolution Letters 4:109–123.

Ghalambor, C. K., J. K. McKay, S. P. Carroll, and D. N. Reznick. 2007. Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments. Functional Ecology 21:394–407.

Grace, J. B., D. J. Johnson, J. S. Lefcheck, and J. E. K. Byrnes. 2018. Quantifying relative importance: computing standardized effects in models with binary outcomes. Ecosphere 9:e02283.

Gremer, J. R., A. Chiono, E. Suglia, M. Bontrager, L. Okafor, and J. Schmitt. 2020*b*. Variation in the seasonal germination niche across an elevational gradient: the role of germination cueing in current and future climates. American Journal of Botany 107:350–363.

Gremer, J. R., C. J. Wilcox, A. Chiono, E. Suglia, and J. Schmitt. 2020*a*. Germination timing and chilling exposure create contingency in life history and influence fitness in the native wildflower *Streptanthus tortuosus*. Journal of Ecology 108:239–255.

Harrison, S. P., E. S. Gornish, and S. Copeland. 2015. Climate-driven diversity loss in a grassland community. Proceedings of the National Academy of Sciences of the USA 112:8672–8677.

Healy, K., T. H. G. Ezard, O. R. Jones, R. Salguero-Gómez, and Y. M. Buckley. 2019. Animal life history is shaped by the pace of life and the distribution of age-specific mortality and reproduction. Nature Ecology and Evolution 3:1217–1224.

Herben, T., V. Rydlová, T. Fér, J. Suda, Z. Münzbergová, R. Wildová, and J. Wild. 2014. Phylogenetic signal in growth and reproductive traits and in their plasticity: the *Descurainia* radiation in the Canary Islands: phylogenetic signal in growth and reproduction. Botanical Journal of the Linnean Society 174:384–398.

Huang, P., J. Schmitt, and D. E. Runcie. 2024. Exploring the molecular regulation of vernalization-induced flowering synchrony in Arabidopsis. New Phytologist 242:947–959.

Iannone, R. 2023. DiagrammeR: graph/network visualization. R package version 1.0.10.

Inouye, D. W. 2022. Climate change and phenology. WIREs Climate Change 13:e764.

Kalisz, S. 1986. Variable selection on the timing of germination in *Collinsia verna* (Scrophulariaceae). Evolution 40:479–491.

Kehrberger, S., and A. Holzschuh. 2019. How does timing of flowering affect competition for pollinators, flower visitation and seed set in an early spring grassland plant? Scientific Reports 9:15593.

Kimball, S., A. L. Anger, T. E. Huxman, and D. L. Venable. 2010. Contemporary climate change in the Sonoran Desert favors cold-adapted species. Global Change Biology 16:1555–1565.

———. 2011. Differences in the timing of germination and reproduction relate to growth physiology and population dynamics of Sonoran Desert winter annuals. American Journal of Botany 98:1773–1781.

Kingsolver, J. G., and L. B. Buckley. 2017. Evolution of plasticity and adaptive responses to climate change along climate gradients. Proceedings of the Royal Society B 284:20170386.

Kudo, G., and E. J. Cooper. 2019. When spring ephemerals fail to meet pollinators: mechanism of phenological mismatch and its impact on plant reproduction. Proceedings of the Royal Society B 286:20190573.

Lefcheck, J. S. 2016. piecewiseSEM: piecewise structural equation modelling in R for ecology, evolution, and systematics. Methods in Ecology and Evolution 7:573–579.

———. 2021. Composite variables. GitHub. https://jslefche.github.io/sem_book/index.html.

Lenth, R. 2023. emmeans: estimated marginal means, aka least-squares means. R package version 1.8.8.

Levine, J. M., K. McEachern, and C. Cowan. 2011. Seasonal timing of first rain storms affects rare plant population dynamics. Ecology 92:2236–2247.

LoPresti, E. F., V. Pan, J. Goidell, M. G. Weber, and R. Karban. 2019. Mucilage-bound sand reduces seed predation by ants but not by reducing apparency: a field test of 53 plant species. Ecology 100:e02809.

Luedeling, E., L. Caspersen, and E. Fernandez. 2023. chillR: statistical methods for phenology analysis in temperate fruit trees. R package version 0.73.1.

Luković, J., J. C. H. Chiang, D. Blagojević, and A. Sekulić. 2021. A later onset of the rainy season in California. Geophysical Research Letters 48:e2020GL090350.

Martínez-Berdeja, A., M. Okada, M. D. Cooper, D. E. Runcie, L. T. Burghardt, and J. Schmitt. 2023. Precipitation timing and soil substrate drive phenology and fitness of *Arabidopsis thaliana* in a Mediterranean environment. Functional Ecology 37:2471–2487.

Martínez-Berdeja, A., M. C. Stitzer, M. A. Taylor, M. Okada, E. Ezcurra, D. E. Runcie, and J. Schmitt. 2020. Functional variants of DOG1 control seed chilling responses and variation in seasonal life-history strategies in *Arabidopsis thaliana*. Proceedings of the National Academy of Sciences of the USA 117:2526–2534.

Matesanz, S., E. Gianoli, and F. Valladares. 2010. Global change and the evolution of phenotypic plasticity in plants. Annals of the New York Academy of Sciences 1206:35–55.

Mayfield, M. M., J. M. Dwyer, A. Main, and J. M. Levine. 2014. The germination strategies of widespread annual plants are unrelated to regional climate. Global Ecology and Biogeography 23:1430–1439.

Metcalf, J. C., K. E. Rose, and M. Rees. 2003. Evolutionary demography of monocarpic perennials. Trends in Ecology and Evolution 18:471–480.

Miryeganeh, M., M. Yamaguchi, and H. Kudoh. 2018. Synchronisation of *Arabidopsis* flowering time and whole-plant senescence in seasonal environments. Scientific Reports 8:10282.

Munguía-Rosas, M. A., J. Ollerton, V. Parra-Tabla, and J. A. De-Nova. 2011. Meta-analysis of phenotypic selection on flowering phenology suggests that early flowering plants are favoured. Ecology Letters 14:511–521.

Nicotra, A. B., O. K. Atkin, S. P. Bonser, A. M. Davidson, E. J. Finnegan, U. Mathesius, P. Poot, et al. 2010. Plant phenotypic plasticity in a changing climate. Trends in Plant Science 15:684–692.

Olliff-Yang, R. L., and D. D. Ackerly. 2021. Late planting shortens the flowering period and reduces fecundity in *Lasthenia californica*. Madroño 68:377–387.

Orme, D., R. Freckleton, G. Thomas, T. Petzoldt, S. Fritz, N. Isaac, and W. Pearse. 2023. caper: comparative analyses of phylogenetics and evolution in R. R package version 1.0.2.

Parmesan, C., and M. E. Hanley. 2015. Plants and climate change: complexities and surprises. Annals of Botany 116:849–864.

Paschke, M., C. Abs, and B. Schmid. 2002. Effects of population size and pollen diversity on reproductive success and offspring size in the narrow endemic *Cochlearia bavarica* (Brassicaceae). American Journal of Botany 89:1250–1259.

Pearse, I. S., J. M. Aguilar, and S. Y. Strauss. 2020. Life-history plasticity and water-use trade-offs associated with drought resistance in a clade of California jewelflowers. American Naturalist 195:691–704.

Picó, F. X. 2012. Demographic fate of *Arabidopsis thaliana* cohorts of autumn- and spring-germinated plants along an altitudinal gradient. Journal of Ecology 100:1009–1018.

Postma, F. M., and J. Ågren. 2016. Early life stages contribute strongly to local adaptation in *Arabidopsis thaliana*. Proceedings of the National Academy of Sciences of the USA 113:7590–7595.

———. 2022. Effects of primary seed dormancy on lifetime fitness of *Arabidopsis thaliana* in the field. Annals of Botany 129:795–808.

PRISM Climate Group. 2014. Oregon State University, https://prism.oregonstate.edu.

Rees, M., D. Z. Childs, K. E. Rose, and P. J. Grubb. 2004. Evolution of size-dependent flowering in a variable environment: partitioning the effects of fluctuating selection. Proceedings of the Royal Society B 271:471–475.

Revell, L. J. 2012. phytools: an R package for phylogenetic comparative biology (and other things). Methods in Ecology and Evolution 3:217–223.

Salguero-Gómez, J., O. R. Jones, E. Jongejans, S. P. Blomberg, D. J. Hodgson, C. Mbeau-Ache, P. A. Zuidema, et al. 2016. Fast-slow continuum and reproductive strategies structure plant life-history variation worldwide. Proceedings of the National Academy of Sciences of the USA 113:230–235.

Scheiner, S. M., M. Barfield, and R. D. Holt. 2020. The genetics of phenotypic plasticity. XVII. Response to climate change. Evolutionary Applications 13:388–399.

Swain, D. L., B. Langenbrunner, J. D. Neelin, and A. Hall. 2018. Increasing precipitation volatility in twenty-first-century California. Nature Climate Change 8:427–433.

Valladares, F., S. Matesanz, F. Guilhaumon, M. B. Araújo, L. Balaguer, M. Benito-Garzón, W. Cornwell, et al. 2014. The effects of phenotypic plasticity and local adaptation on forecasts of species range shifts under climate change. Ecology Letters 17:1351–1364.

van Asch, M., and M. E. Visser. 2007. Phenology of forest caterpillars and their host trees: the importance of synchrony. Annual Review of Entomology 52:37–55.

Vedder, O., S. Bouwhuis, and B. C. Sheldon. 2013. Quantitative assessment of the importance of phenotypic plasticity in adaptation to climate change in wild bird populations. PLoS Biology 11:e1001605.

Venables, W. N., and B. D. Ripley. 2002. Modern applied statistics with S: statistics and computing. Springer, New York.

Verdú, M., and A. Traveset. 2005. Early emergence enhances plant fitness: a phylogenetically controlled meta-analysis. Ecology 86:1385–1394.

Wadgymar, S. M., J. E. Ogilvie, D. W. Inouye, A. E. Weis, and J. T. Anderson. 2018. Phenological responses to multiple environmental drivers under climate change: insights from a long-term observational study and a manipulative field experiment. New Phytologist 218:517–529.

Walck, J. L., S. N. Hidayati, K. W. Dixon, K. Thompson, and P. Poschlod. 2011. Climate change and plant regeneration from seed. Global Change Biology 17:2145–2161.

Wesselingh, R. A., P. G. L. Klinkhamer, T. J. de Jong, and L. A. Boorman. 1997. Threshold size for flowering in different habitats: effects of size-dependent growth and survival. Ecology 78:2118–2132.

Wilczek, A. M., J. L. Roe, M. C. Knapp, M. D. Cooper, C. Lopez-Gallego, L. J. Martin, C. D. Muir, et al. 2009. Effects of genetic perturbation on seasonal life history plasticity. Science 323:930–934.

Willis, C. G., B. Ruhfel, R. B. Primack, A. J. Miller-Rushing, and C. C. Davis. 2008. Phylogenetic patterns of species loss in Thoreau's woods are driven by climate change. Proceedings of the National Academy of Sciences of the USA 105:17029–17033.

Winkler, D. W., C. Jørgensen, C. Both, A. I. Houston, J. M. McNamara, D. J. Levey, J. Partecke, et al. 2014. Cues, strategies, and outcomes: how migrating vertebrates track environmental change. Movement Ecology 2:10.

Wolkovich, E. M., C. J. Chamberlain, D. M. Buonaiuto, A. K. Ettinger, and I. Morales-Castilla. 2022. Integrating experiments to predict interactive cue effects on spring phenology with warming. New Phytologist 235:1719–1728.

Worthy, S. J., S. R. Ashlock, A. Miller, J. N. Maloof, S. Y. Strauss, J. R. Gremer, and J. Schmitt. 2024*a*. Data from: Accelerated phenology fails to buffer fitness loss from delayed rain onset in a clade of wildflowers. American Naturalist, Zenodo, https://doi.org/10.5281/zenodo.14362672.

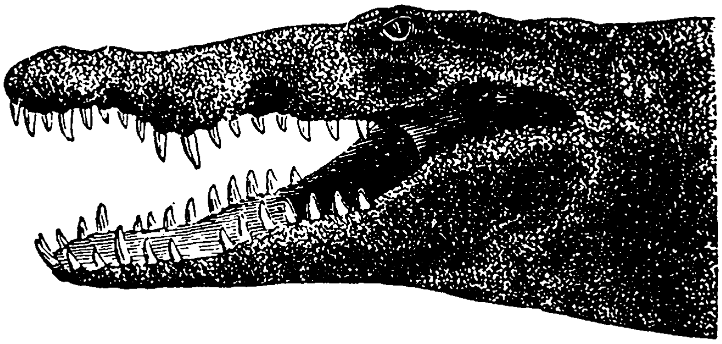
Worthy, S. J., A. Miller, S. R. Ashlock, E. Ceviker, J. N. Maloof, S. Y. Strauss, J. Schmitt, and J. R. Gremer. 2024*b*. Germination responses to changing rainfall timing reveal potential climate vulnerability in a clade of wildflowers. Ecology 105:e4423.

Wu, C., and M. D. K. Owen. 2014. When is the best time to emerge: reproductive phenology and success of natural common waterhemp (*Amaranthus rudis*) cohorts in the Midwest United States? Weed Science 62:107–117.

Zacchello, G., M. Vinyeta, and J. Ågren. 2020. Strong stabilizing selection on timing of germination in a Mediterranean population of *Arabidopsis thaliana*. American Journal of Botany 107:1518–1526.

Zettlemoyer, M. A., R. J. Conner, M. M. Seaver, E. Waddle, and M. L. DeMarche. 2024. A long-lived alpine perennial advances flowering under warmer conditions but not enough to maintain reproductive success. American Naturalist 203:E157–E174.

Associate Editor: Vincent M. Eckhart
Editor: Volker H. W. Rudolf



"About the middle of the day numbers may be seen lying lazily on the banks enjoying the heat, their polished scales shining in the sunlight, and all looking the very picture of tropical languor and repose. Its daily food is the fishes that inhabit its native element, but many a bright-plumed water-fowl and unsuspecting quadruped falls a prey to its rapacity." From "The Crocodile in Florida" by Wm. T. Hornaday (*The American Naturalist*, 1875, 9:498–504).