

INVITED SPECIAL ARTICLE

For the Special Issue: Plant–Environment Interactions: Integrating Across Levels and Scales

Variation in the seasonal germination niche across an elevational gradient: the role of germination cueing in current and future climates

Jennifer R. Gremer^{1,2,6} , Alec Chiono^{1,3}, Elena Suglia^{1,4}, Megan Bontrager^{1,2}, Lauren Okafor⁵, and Johanna Schmitt^{1,2}

Manuscript received 16 May 2019; revision accepted 7 October 2019.

¹ Department of Evolution and Ecology, University of California–Davis, Davis, CA 95616 USA

² Center for Population Biology, University of California–Davis, Davis, CA, USA

³ Department of Biology, University of San Francisco, 2310 Fulton Street, San Francisco, CA 94117 USA

⁴ Population Biology Graduate Group, University of California–Davis, Davis, CA 95616 USA

⁵ Department of Biology, Howard University, 415 College St. NW, Washington D.C. 20059 USA

⁶ Author for correspondence (e-mail: jrgremer@ucdavis.edu)

Citation: Gremer, J. R., A. Chiono, E. Suglia, M. Bontrager, L. Okafor, and J. Schmitt. 2020. 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(2): 1–14.

doi:10.1002/ajb2.1425

PREMISE: The timing of germination has profound impacts on fitness, population dynamics, and species ranges. Many plants have evolved responses to seasonal environmental cues to time germination with favorable conditions; these responses interact with temporal variation in local climate to drive the seasonal climate niche and may reflect local adaptation. Here, we examined germination responses to temperature cues in *Streptanthus tortuosus* populations across an elevational gradient.

METHODS: Using common garden experiments, we evaluated differences among populations in response to cold stratification (chilling) and germination temperature and related them to observed germination phenology in the field. We then explored how these responses relate to past climate at each site and the implications of those patterns under future climate change.

RESULTS: Populations from high elevations had stronger stratification requirements for germination and narrower temperature ranges for germination without stratification. Differences in germination responses corresponded with elevation and variability in seasonal temperature and precipitation across populations. Further, they corresponded with germination phenology in the field; low-elevation populations germinated in the fall without chilling, whereas high-elevation populations germinated after winter chilling and snowmelt in spring and summer. Climate-change forecasts indicate increasing temperatures and decreasing snowpack, which will likely alter germination cues and timing, particularly for high-elevation populations.

CONCLUSIONS: The seasonal germination niche for *S. tortuosus* is highly influenced by temperature and varies across the elevational gradient. Climate change will likely affect germination timing, which may cascade to influence trait expression, fitness, and population persistence.

KEY WORDS *Arabidopsis*; Brassicaceae; climate change; dormancy; germination temperature; niche construction; phenology; plasticity; stratification; *Streptanthus tortuosus*.

Germination is a critical transition in the life cycle of plants, and the seasonal timing of this transition has profound impacts on survival at the vulnerable seedling stage. The timing of germination influences the ecological and selective environments that an individual will experience later in its life cycle, including the seasonal conditions experienced at seedling and adult stages (Donohue, 2002; Donohue et al., 2005a; Galloway and Etterson, 2007; Korves et al., 2007; Burghardt et al., 2015). As such, germination timing is critical for individual fitness and can scale to influence population dynamics, local persistence, and the distribution of species across the landscape (Kalisz, 1986; Kalisz and McPeck, 1992; Donohue et al., 2010; Kimball et al., 2010; Eckhart et al., 2011; Levine et al., 2011; Cochrane et al., 2015). Further, variation in germination timing has been shown to influence population and community dynamics in response to shifting climatic conditions (Kimball et al., 2010, 2011; Levine et al., 2011; Huang et al., 2016). Thus, the germination niche (the environmental conditions under which germination is possible) has important implications for population responses to current and future climate change.

Germination traits drive responses to proximal and seasonal environmental cues. Seeds may germinate in response to immediate cues such as light, soil water potential, and photoperiod, which signal the onset of favorable conditions (Finch-Savage and Leubner-Metzger, 2006; Baskin and Baskin, 2014; Springthorpe and Penfield, 2015; Finch-Savage and Footitt, 2017). Dormant seeds, however, cannot respond to those immediate cues until dormancy is released, which can occur after exposure to particular temperature, photoperiod, and other environmental factors (Baskin and Baskin, 2014; Finch-Savage and Footitt, 2017). For example, dormancy may be gradually released in response to experiencing a period of after-ripening at warm temperatures, which can act to prevent germination of summer-dispersed seeds until favorable fall conditions (Baskin and Baskin, 2014; Huang et al., 2016; Vidigal et al., 2016; Finch-Savage and Footitt, 2017). Conversely, seed dormancy may also be released by exposure to low temperatures, which may prevent germination from occurring until spring (Penfield and Springthorpe, 2012; Fernández-Pascual et al., 2017). As dormancy is lifted by these cues, germination can be induced by additional cues such as light under an increasing range of temperature and water availability. Seeds that do not experience such conditions do not germinate and instead remain in the seed bank (Finch-Savage and Footitt, 2017). Differences in dormancy requirements and responses to seasonal cues can drive differences in germination timing across individuals, populations, and species (Kalisz, 1986; Mayfield et al., 2014; Burghardt et al., 2015; Huang et al., 2016).

In variable and changing environments, timing germination to coincide with favorable conditions can be difficult or nearly impossible. In response, germination traits may evolve to either spread the risk of germinating into unfavorable conditions (Cohen, 1966; Seger and Brockmann, 1987; Philippi, 1993; Venable, 2007; Gremer and Venable, 2014) or to stimulate germination in response to environmental cues that signal favorable conditions (Finch-Savage and Leubner-Metzger, 2006; Donohue et al., 2010; Baskin and Baskin, 2014), or both (Cohen, 1967; Venable and Lawlor, 1980; Philippi and Seger, 1989; Simons, 2014; Gremer et al., 2016). Risk spreading can be achieved through producing offspring that have variation in germination traits, which can cause individual seeds to germinate at different times, a strategy known as bet hedging (Seger and Brockmann, 1987; Philippi, 1993; Simons, 2011). Variation among offspring in germination traits, such as primary dormancy and responsiveness to environmental cues, can thus act to spread germination either among years, across the growing season within years, or both (Simons, 2014;

Gremer et al., 2016). On the other hand, traits that enhance germination in response to reliable environmental cues, such as temperature and precipitation, can act to time germination with favorable conditions, and these traits define the conditions under which germination will proceed. The adaptive value of these traits (bet hedging and germination cueing) depends on the time scale of variation and the reliability of environmental cues (Cohen, 1967; Donaldson-Matasci et al., 2013; Botero et al., 2015), and observed germination strategies likely reflect past selection for bet hedging, germination cueing, or both (Donohue et al., 2010; Lampei and Tielborger, 2010; Gremer et al., 2016; Lampei et al., 2017).

Ecosystems across the globe are experiencing increased temperatures, shifts in the timing of precipitation, and increased variability in both temperature and precipitation (IPCC, 2014). Such shifts in environmental conditions can alter the availability and reliability of cues for life history timing and thus modify the seasonal niche. Cues may become decoupled, reducing the correlation between a cue and future conditions, or some cues may simply no longer occur (Miller-Rushing et al., 2010; Walck et al., 2011; Bonamour et al., 2019). Shifts in environmental conditions are expected to be particularly salient for early developmental stages, such as germination (Dagleish et al., 2010; Walck et al., 2011), but few studies have examined the impact of shifting cues on germination timing and the consequences under climate change (Kimball et al., 2010; Walck et al., 2011; Parmesan and Hanley, 2015). Those studies have found changes in precipitation and temperature regimes to have strong impacts on fitness, selection, and population dynamics. In an experimental field study of California annual plants, Levine et al. (2011) demonstrated substantial impacts of the timing of the first germination-triggering rain events of the season, with differences in population growth rates varying from 2- to 5-fold across treatments. In desert annual plants, Kimball et al. (2010) documented significant shifts in population dynamics and community composition in response to the timing of germination-triggering rain events and how those patterns interacted with temperature during the growing season. These studies highlight how understanding shifts in temperature, timing of precipitation, and how they interact with germination responses is critical for understanding the evolutionary ecology of germination timing and its consequences under current and future climatic conditions.

In this study, we examined variation in temperature cue responses mediating the timing of germination in a native California wildflower, *Streptanthus tortuosus* (Brassicaceae), across populations along an elevational cline. This species is ideal for investigating life history responses to shifting climate because it occupies a broad elevational and latitudinal range. It inhabits a variable Mediterranean climate that is characterized by strong intra- and inter-annual variability in temperature and precipitation (Baldwin, 2014; Rundel et al., 2016), which has already been strongly affected by climate change and is expected to continue to experience significant warming, drying, and increased variability in conditions (Cayan et al., 2008; Loarie et al., 2008). Further, *S. tortuosus* exhibits remarkable life-history variation both within and among populations, including differences in germination timing as well as the timing and frequency of reproduction. Moreover, the timing of germination has been demonstrated to affect life-history expression and fitness in two low-elevation populations of this species (Gremer et al., 2020), suggesting that seasonal germination timing cascades to affect trait expression and performance later in the life cycle. Here, we combined germination experiments in common gardens, field observations, and

data on past and future climate to (1) compare differences among populations in germination responses to chilling and germination temperature, (2) determine how differences in germination responses relate to local climate across populations, and (3) relate germination responses to observed germination phenology in the field. Further, we explored the implications of those patterns under future climate change to ask how climate change may shift seasonal germination niches and impact population persistence. We predicted that low-elevation populations, which experience a winter growing season and strong inter-annual variability in the timing of germination triggering rains in the fall and winter (Gremer et al., 2020), will require little to no chilling for germination and will germinate under a broader range of temperatures. Conversely, we expected that high-elevation populations, which experience colder temperatures and snowpack in the winter, will have cues that restrict germination to the spring and summer,

including strong chilling requirements and higher germination under warmer temperatures (Cavieres and Arroyo, 2000; Shimono and Kudo, 2005; Fernández-Pascual et al., 2017).

MATERIALS AND METHODS

Study system

Streptanthus tortuosus (Brassicaceae) is a native forb that occupies outcrops and dry, rocky slopes throughout northern California and southern Oregon (Preston, 1991; Calflora, 2014). This species is found across a broad elevational (200 to 4100 m a.s.l.) and latitudinal range (from southern California to southern Oregon), and populations tend to be discontinuously distributed (Preston, 1991; Calflora, 2014). We studied 21 populations across an elevational

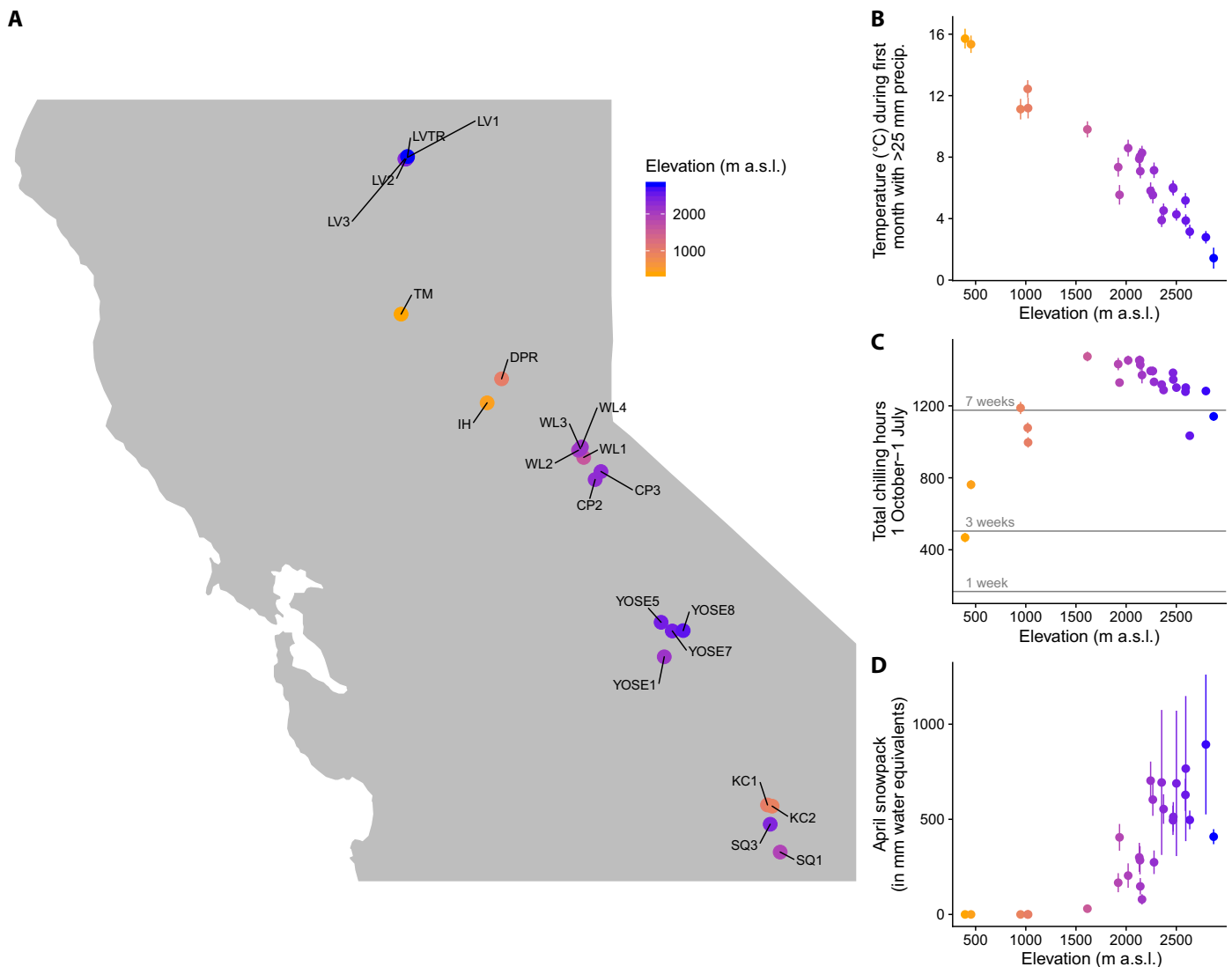


FIGURE 1. Map of *Streptanthus tortuosus* populations included in the study (A) and contemporary climate patterns for study populations (B–D). See Table 1 for site information. Colors indicate the elevation at each source population. For panels B–D, points are means across 30 years (1981–2010) \pm 1 SE for each population. (B) Temperature during the first month with sufficient germination triggering rain (first month with precipitation $>$ 25 mm). (C) Total chilling hours from 1 October to 1 July. Lines indicate the amount of chilling hours that correspond with stratification treatments (1, 3, 7 weeks). (D) April snowpack levels. Low-elevation populations do not accumulate snow.

TABLE 1. Sites and components included in study. C = cold stratification germination experiment, T = thermal germination experiment, F = field germination phenology.

Site name	Code	Experiment/study	Latitude	Longitude	Elevation (m a.s.l.)
Table Mountain	TM	C, T, F	39.5926	-121.551	379
Iowa Hill	IH	C, T	39.0933	-120.921	454
Kings Canyon 2	KC2	C	36.823	-118.835	948
Drum Powerhouse Road	DPR	C, T	39.2285	-120.815	1019
Kings Canyon 1	KC1	C	36.8297	-118.869	1023
Wrights Lake 1	WL1	C, F	38.7861	-120.214	1614
Sequoia 1	SQ1	C	36.5644	-118.776	1921
Wrights Lake 2	WL2	C, T, F	38.8263	-120.252	2020
Wrights Lake 4	WL4	C	38.8445	-120.231	2131
Wrights Lake 3	WL3	C, F	38.8353	-120.238	2138
Yosemite 1	YOSE1	C	37.6637	-119.625	2141
Carson Pass 2	CP2	C, F	38.6617	-120.131	2244
Carson Pass 3	CP3	C	38.7065	-120.088	2266
Lassen Volcanic 3	LV3	C	40.4664	-121.523	2354
Sequoia 3	SQ3	C	36.7211	-118.849	2373
Yosemite 5	YOSE5	C	37.8579	-119.648	2467
Yosemite 7	YOSE7	C, T	37.809	-119.566	2470
Lassen Volcanic 2	LV2	C	40.4656	-121.515	2501
Yosemite 8	YOSE8	C	37.8112	-119.486	2591
Lassen Volcanic 1	LV1	C, T	40.4747	-121.505	2594
Lassen Peak Trail	LVTR	C	40.4801	-121.504	2795

gradient (Fig. 1A, Table 1). Of these, all 21 were included in an experiment evaluating response to winter chilling (stratification), six were included in an experiment testing for differences in germination responses to temperature with and without stratification (thermal germination experiment), and five were surveyed for germination phenology in the field (Fig. 1, Table 1). All populations experience a Mediterranean climate in which precipitation comes mainly in the late fall and winter. Low-elevation populations experience warm temperatures when the first precipitation of the season arrives, and these temperatures remain high such that only 1–3 weeks of chilling (between 0–4°C) accumulate, and snow does not accrue (Fig. 1B–D; see below for details on climate data). Conversely, precipitation comes as either rain or snow at higher elevations, which experience cooler temperatures during these first fall and winter events, often accumulate 6–7 weeks of chilling over the winter, and have substantial snowpack in April (Fig. 1B–D).

Seeds for experiments were collected as maternal seed families at all populations between June and September, depending on the timing of fruit maturation for each population. We did not collect seed from plants that produced less than five siliques (fruits) or from plants within 1.5 m from a previously sampled plant. Seeds for the stratification experiment were collected in 2016; seeds for the thermal germination experiment were collected in 2016 or 2017. Before planting, seeds were stored dry at room temperature (~21°C).

Local climate patterns: current and future

We extracted contemporary and future climate data for these sites to examine differences among sites in seasonal conditions and generate predictor variables for later analyses. For each of our sites, we extracted contemporary and future climate using the Flint Basin Characterization Model, which downscales PRISM (PRISM Climate Group, Oregon State University, <http://www.prism.oregonstate.edu/>) data to a 270-m resolution for the California hydrologic region (Flint and Flint, 2014). From these data, we calculated eight variables of

interest using monthly precipitation, temperature, and snowpack records for 1981–2010. We calculated mean annual temperature (MAT), mean annual precipitation (MAP), interannual variance in temperature (variance in mean annual temperature across years), intra-annual variance in temperature (variance across months in the year, averaged across years), the mean and coefficient of interannual variation in fall precipitation (October to December), the mean and coefficient of interannual variation in total growing season precipitation (October to July), the average first month of the year without snow, the average temperature during the first month of the growing season with precipitation over 25 mm, and the average month in which that 25 mm of precipitation arrives. We additionally extracted daily maximum and minimum temperature records for each site from PRISM (PRISM Climate Group, 2004). From these, we interpolated hourly temperatures using the R package *chillR* (Luedeling, 2019) and calculated summed chilling hours (hours between 0° and 4°C) beginning 1 October at each site for each year between 1981–2010.

To evaluate how future climate change will influence seasonal cueing and conditions, we also extracted contemporary and future October mean temperature (calculated as the average of minimum and maximum temperature, °C), January minimum temperature (°C), and April snowpack (in mm water equivalent; Flint and Flint, 2014). For each of these variables, we extracted 30-year averages and detrended standard errors of contemporary climate (1981–2010) and four future climate projections for 2070–2099: the NOAA Geophysical Fluids Dynamics Laboratory Model (GFDL) and the NCAR Parallel Climate Model (PCM), which have been shown to perform well in this region (Maher et al., 2017). For these models, we extracted both the B1 (lower emissions scenario which includes reductions in future emissions) and the A2 (higher, “business-as-usual”, emissions scenario).

Stratification experiment

In fall of 2016, we exposed seeds from each of 21 populations to 0, 1, 3, or 7 weeks of cold stratification. These durations were chosen

based on expectations for how exposure to chilling would vary across the elevational gradient (Fig. 1B–D). The start date of each treatment was staggered so that all treatments would end on the same date and all seeds would be placed in inductive conditions at the same time. For each population, we used 5 or 10 maternal families depending on availability of seeds (10 maternal families were used for all populations except CP2, CP3, KC1, KC2, WL3, and WL4; each maternal family was replicated once, i.e., plated in one petri dish, in each treatment). To initiate each treatment group, we placed 10 seeds from each maternal family into a 60 × 15 mm plastic petri dish on top of germination paper and added 3.5 mL 0.2% plant preservation solution (Plant Preservation Mixture, Caisson Laboratories, UT, USA). Dishes receiving cold stratification were then placed in randomized locations in a dark 4°C chamber to begin treatments. Seeds assigned to the control (0 week) treatment were placed in dishes with solution when the other treatments had completed stratification, at which time all dishes from all treatments were placed in randomized locations in inductive conditions in 22°C chambers with 12-h daylight cycles (E7/2 growth chambers, Conviron, Winnipeg, Manitoba, Canada).

Germination was surveyed twice every week during stratification and daily once seeds were placed in inductive conditions. Seeds were removed from dishes upon germination, as evidenced by radicle emergence. Germination surveys under inductive conditions were conducted for 1 week, after which there was very little germination. We re-randomized the location of each petri dish during each survey and rotated dishes between shelves each day to minimize differences in light exposure across dishes. We added 1–2 mL plant preservation solution as needed to maintain moisture in the dishes.

To determine whether populations differed in their germination responses to stratification, we analyzed germination census data using mixed models (function `glmer` in R; Bates, 2015). First, we evaluated whether germination varied across populations in response to treatments using logistic regression (binomial family with logit link) with population and treatment and their interaction as fixed effects, and maternal family nested within population as a random effect. Because we observed germination during the stratification treatments, particularly the longest treatment (7 week), we also tested for differences among populations for dark germination in the 7-week treatment using the same mixed model structure, but without the treatment effect or interaction. For both total germination and dark germination, we also tested whether differences in germination responses varied along the elevational cline using models with elevation as a continuous variable, and included germination during stratification in analyses. For each of these tests, significance of fixed effects was evaluated using likelihood ratio tests on nested models (i.e., we compared models with and without interactions (if present) and then with and without each main effect).

Next we tested whether maximum germination rates varied across populations and in response to elevation, temperature, and precipitation. Here, maximum germination was calculated for each maternal family and represents the highest germination fraction observed across all treatments for each family. While not a direct estimate of primary seed dormancy, it can act as a proxy, since it indicates the maximum potential for germination across the range of thermal cues in our experiment. Similarly, we calculated variance in germination fractions across treatments for each maternal family. We consider this variance as a metric for specialization

in germination, since high variation can be achieved by having low to no germination in some treatments and higher germination in others. Conversely, low variation can be achieved by having low germination in all treatments or by having higher germination across all treatments. Both maximum and variance were estimated and analyzed on a logit scale for each maternal family. We used hierarchical partitioning analyses to determine which factors related to climate and elevation explained maximum or variance in germination fraction. Hierarchical partitioning analyses estimate the relative importance of each variable while accounting for multicollinearity (Murray and Connor, 2009). In our hierarchical partitioning (HP) analysis for maximum germination we included these nine variables describing mean and variance in conditions: mean annual temperature (MAT), mean annual precipitation (MAP), interannual variance in temperature, intra-annual variance in temperature, the mean and coefficient of variation in fall precipitation, the mean and coefficient of variation in total growing season precipitation, and elevation. For our HP analysis for variance in germination, we included these seven variables that related to mean conditions and seasonality: MAP, MAT, interannual and intra-annual variation in temperature, the average first month of the year without snow, the average temperature at the first month with precipitation over 25 mm, the mean month in which that 25 mm of precipitation arrives, and elevation.

Thermal experiment

To further quantify thermal conditions for germination and how these compared across populations, we conducted a thermal germination experiment using six populations across the elevation gradient (DPR, IH, TM, WL2, YOSE7, LV1). In this experiment, we exposed seeds to two treatments: 0 or 7 weeks of cold stratification. Seeds from the 7-week cold stratification were plated 7 weeks before being placed into inductive conditions, while seeds from the 0 week treatment were plated and placed into inductive conditions on the same day. Depending on seed availability, we pooled ~5–10 field-collected seeds from each of ~20–40 maternal families within each population. On 4 May 2018, we initiated the 7-week treatment; for each pooled sample from each population, we randomly drew 10 seeds, placed them into 60 × 15 mm petri dishes with 0.2% plant preservation solution and put them in a 4°C chamber in complete darkness. On 25 June 2018, we ended the cold stratification treatment, plated the remaining seeds for the control (0 week) treatment, and placed all dishes from all treatments in chambers to test for germination responses to temperature. Dishes were placed into six growth chambers set to inductive (light) conditions across a range of temperature treatments: 5, 10, 15, 20, 25, and 30°C, with 12-h daylight cycles. Four replicate dishes with seeds from each population and stratification treatment were randomly assigned locations in each temperature chamber.

Germination was surveyed while seeds were experiencing stratification, and once they were placed in inductive conditions. During stratification, we conducted three germination surveys under a green safe light to minimize light cues that could trigger germination. Seeds that germinated during the stratification were removed. Upon transfer to inductive conditions, dishes were surveyed daily. Germinants were removed from the dishes and discarded. Because the thermal germination experiment included lower temperatures expected to be suboptimal for germination, we continued germination censuses for 1 month when a decline in germination rates was

observed. An additional 10 surveys were then conducted through 21 November 2018 to capture the trailing edge of later germination, though there was little germination in any but the coldest treatments at these later dates.

For the thermal germination experiment, we fit logistic regressions (binomial GLMs with a logit link function) individually for each combination of population and stratification treatment. For each of these combinations, we compared fits of three models using AIC: one that included a linear term for temperature, one with a quadratic term for temperature, and a null model with random effects only (all models included random effects of dish nested within tray). We calculated parameters of interest based on the coefficients of the quadratic fits for each combination. We elected to calculate parameters based on quadratic fits because these fits are biologically appropriate for thermal performance curves which are expected to be nonmonotonic (Sheth and Angert, 2014) and were generally strongly favored over null models and ranked similarly to linear fits (Appendix S1a). These parameters included the temperature at which germination was maximized (the temperature where the quadratic fit peaked), the maximum proportion of germination achieved (the height of the peak of the quadratic), and the range of temperatures over which 50% germination was achieved. In the case of minimum or maximum temperature estimates that were outside our experimental range, we truncated them to 5° or 30°C. In two cases, the quadratic did not provide reasonable estimates for the maximum proportion of germination. For Table Mountain, the quadratic fit provided a convex curve precluding an estimate of the peak; in this case, we truncated the temperature at 30°C. For Wright's Lake 2 (WL2), the quadratic did not provide a strong fit and the parameters were instead estimated for a linear fit. We fit two sets of models: one in which we included seeds that had germinated during the stratification period and one in which we excluded them.

Germination phenology in the field

To determine germination phenology in the field, we established plots at 5 populations across an elevational gradient: TM, WL1, WL2, WL3, and CP2. Plots were arrayed along belt transects, in large square blocks, or dispersed plots depending on distribution of *S. tortuosus* and the number of plots needed to reach a minimum of 100 individuals at each site. Belt transects were established at TM (20 plots at each of 2 transects), WL1 (10–20 plots at each of 2 transects), WL3 (10–20 plots at each of 4 transects), while 26–35 plots in each of four large blocks were established at WL2, and six dispersed plots were established at CP2. All plots are 0.5 × 0.5 m except at TM (0.5 × 0.2 m). In these plots, surveys were conducted throughout the growing season from fall 2017 to summer 2018. At our low-elevation site (TM), plots were visited to record germination about 1 week after each rain event with at least 25.4 mm of precipitation. Surveys at this site (TM) were conducted throughout fall, winter, and spring until seasonal rains concluded and no new germination was observed. The higher-elevation sites (WL2, WL3, CP2) were surveyed in the fall before they were covered and inaccessible due to snowpack; we surveyed these sites until they were inaccessible, then returned after snowpack melted in spring. The mid-elevation site (WL1) was occasionally accessible during the winter when snow melted, and germination censuses were done when possible. At each survey, germinants were marked with colored toothpicks to indicate the timing of germination (i.e., germination cohort). We then estimated the cumulative proportion of germination at each

census relative to the total number of germinants in a plot, which were then averaged for each site and compared across sites.

RESULTS

Stratification experiment

Populations differed significantly in response to stratification (chilling) treatments (Fig. 2, population × stratification interaction: $\chi^2 = 534.4$, $df = 60$, $P < 0.0001$) as expected based on the large variation among sites in contemporary climate (Fig. 1B–D). Low-elevation populations had high-germination fractions in all treatments, and germination was strong without stratification (elevation × stratification: $\chi^2 = 237.1$, $df = 3$, $P < 0.0001$, Fig. 2A; Appendix S2). Conversely, high-elevation populations had low-germination fractions without stratification (Fig. 2A; Appendix S2), had high germination with the longest stratification treatment, and had intermediate germination for the 1- and 3-week treatments. Populations from intermediate elevations (~1000 m a.s.l., DPR, KC1, KC2) had variable responses to stratification, with one population having higher germination with little or no stratification (KC2), another with higher germination in the 7-week treatment (DPR), and another having low germination across all treatments (KC1).

In our experiment, seeds from some populations germinated while in the cold stratification treatment. Specifically, several low- and mid-elevation populations showed germination during the longest (7-week) stratification treatment, while high elevation populations did not germinate until they were moved to warm, inductive conditions after stratification (Fig. 2B, $\chi^2 = 50.25$, $df = 1$, $P < 0.001$). These patterns indicate that low- to mid-elevation populations have the ability to germinate in cold and dark conditions given sufficient time, while high-elevation populations do not.

To understand patterns of dormancy and the breadth of conditions in which germination occurred across populations, we compared the maximum germination seen across all treatments and variance in germination across treatments. Both variables showed significant variation across populations (maximum germination: $F_{21, 168} = 6.06$, $P < 0.0001$; variance in germination: $F_{21, 168} = 5.68$, $P < 0.0001$). Hierarchical partitioning analyses indicated that maximum germination was best explained by variation in fall precipitation (Table 2). Populations with high variance in fall precipitation had low germination fractions and vice versa (Fig. 3A). Conversely, variance in germination was best explained by the first month of the year without snow, with higher variance for populations that had later snowmelt (Table 2, Fig. 3B) and higher MAP (Table 2).

Thermal germination experiment

Results for our thermal germination experiment also demonstrated an elevational trend in stratification requirements (Fig. 4). Optimal temperatures for germination ranged from 19° to 30°C depending on elevation and stratification treatment, with stratification tending to increase optima for lower-elevation populations (IH and DPR) and lowering optima for higher-elevation populations (WL2, LV1; Fig. 4; Appendix S1b, c). Stratification increased the breadth of temperatures for germination for high-elevation populations by promoting germination at low temperatures, but had little to no effect on germination temperature ranges for

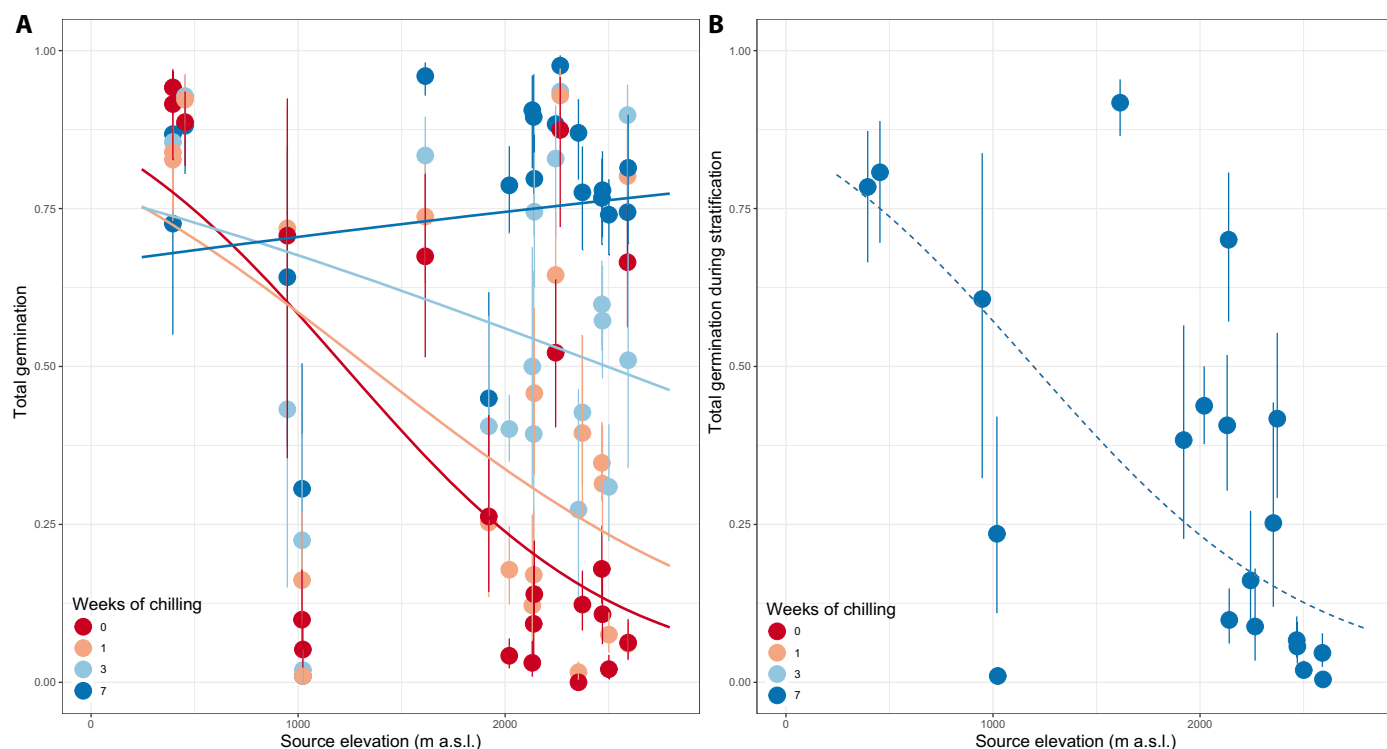


FIGURE 2. Total germination (A) and dark germination (B) in the stratification experiment across the elevational cline. (A) Germination fractions for populations across the cline in response to stratification (chilling) at 4°C for 0, 1, 3, or 7 weeks (colors indicate length of chilling treatment). Points represent means for each population \pm 1 SE (back-transformed from logit scale). Regression lines illustrate the patterns from the significant interaction between source-population elevation and stratification (back-transformed from logit scale, colors correspond with chilling treatment). (B) Points represent dark germination in the longest (7 week) stratification treatment for all populations (mean \pm 1 SE, back-transformed from logit scale). Regression line illustrates the significant effect of elevation (back-transformed from logit scale).

TABLE 2. Results of hierarchical partitioning analysis for maximum and variance in germination across stratification treatments. Direction of relationship is whether univariate relationship is either positive (+) or negative (–) based on simple linear regression. Independent percentage describes the amount of the explained variation that is explained by that variable relative to the others; all independent percentages sum to 100%.

Effect	Direction of relationship	Independent percentage
Maximum germination		
Coefficient of variation of fall precipitation	–	23.11
Elevation	–	14.54
CV of growing season precipitation	–	12.75
Mean annual temperature	+	11.67
Intra-annual variance in temperature	+	9.63
Mean growing season precipitation	–	7.84
Mean annual precipitation	–	7.73
Mean fall precipitation	–	6.89
Inter-annual variance in temperature	–	5.86
Variance in germination		
First month of year without snow	+	23.25
Mean annual precipitation	+	20.95
Mean annual temperature	–	15.91
Inter-annual variance in temperature	+	14.83
Elevation	+	10.52
Mean temperature of first month with precipitation >25 mm	–	9.72
Intra-annual variance in temperature	–	4.82

Note: CV = coefficient of variation.

low-elevation populations (Fig. 4; Appendix S1b). Germination remained above 50% for all populations at our highest temperature treatment (30°C), suggesting that germination does not drop off until even higher temperatures. Consistent with the results for the stratification experiment, there was substantial germination during stratification in the thermal experiment (Appendix S1d), and it varied across populations from different elevations in concordance with the stratification experiment. Patterns for thermal germination curves that exclude this germination during dark, cold treatments (Appendix S1a–c) show additional differences, particularly for low-elevation populations. Specifically, seeds that did not germinate while in stratification had lower-germination fractions overall and germinated at higher temperatures than nonstratified seeds (Appendix S1b, c). Maximum germination proportions across treatments in the thermal germination experiment were consistent with those from the stratification experiment (Figs. 3A, 4).

Germination phenology in the field

Patterns of germination in the field reveal strong differences in phenology across populations (Fig. 5). Germination at the low-elevation population at Table Mountain occurred from fall to spring, with the majority of germination occurring at the first germination-triggering rain event in the fall. Conversely, the high-elevation populations (WL2, WL3, CP2) germinated after snowmelt in the spring and summer, while the mid-elevation

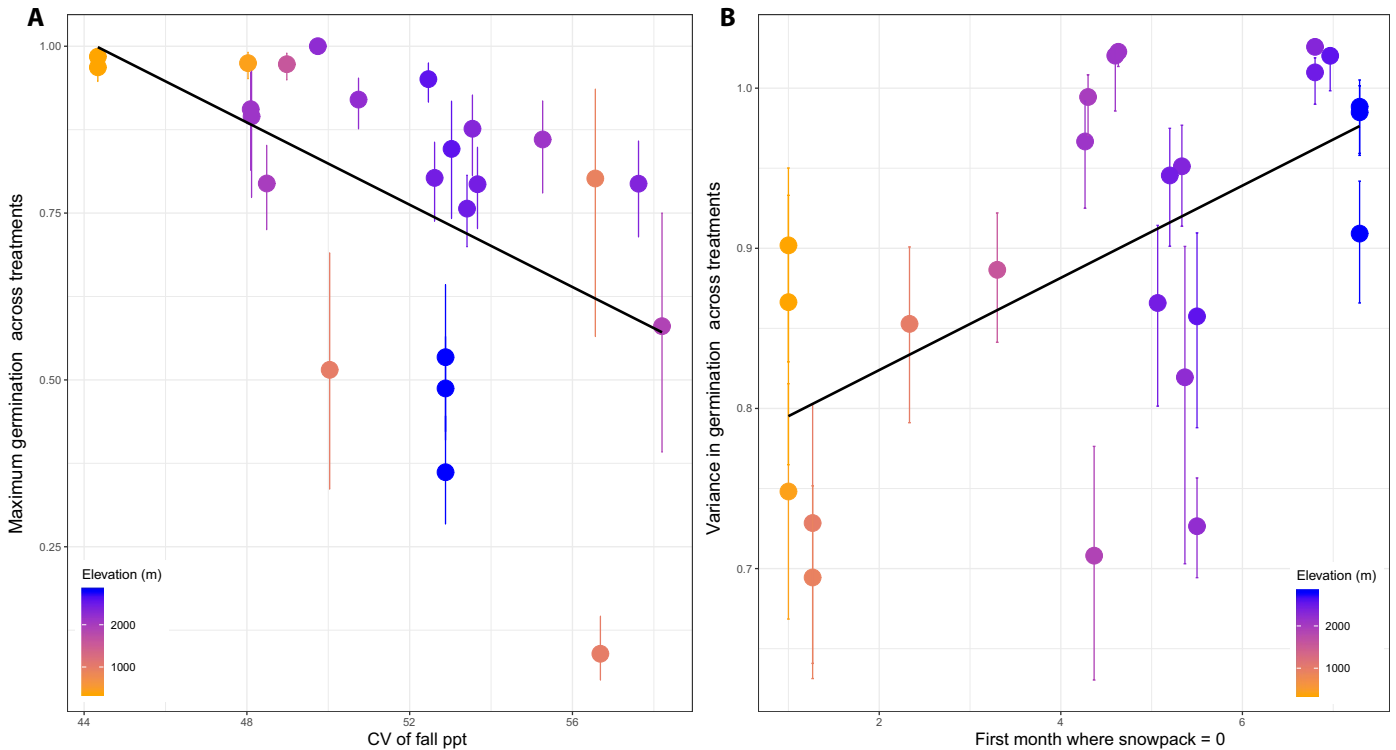


FIGURE 3. Maximum germination (A) and variance in germination (B) across treatments in the stratification experiment. Maxima and variances were estimated for each maternal family across treatments, then averaged across maternal families for each population (means \pm 1 SE, back-transformed from logit scale). (A) Maximum germination in relation to the coefficient of variation (CV) of fall precipitation. (B) Variance in germination in relation to the first month of the year in which there was no snow (snowpack = 0). Colors indicate the elevation at each source population.

population (WL1) had some germination in winter and some in spring.

Germination patterns in relation to current and future climate

Patterns for contemporary climate match expectations for differences among populations due to climate and correspond with germination responses in our experiment and field observations. Specifically, temperatures during the first rain event fall directly in the range of at least 50% germination for low-elevation populations (Fig. 4A–C), but are too cold for high-elevation populations to germinate without stratification (Figs. 1C, 4D–F). Similarly, low-elevation populations typically accumulate less than 3 weeks of chilling, mid-elevations accumulate 3–7 weeks of chilling, and the majority of high-elevation populations have the potential to accumulate at least 7 weeks of chilling in most years (Fig. 1B–D). These patterns nicely correspond with stratification requirements in both germination experiments. Lastly, patterns for April 1 snowpack indicate that higher elevation populations are still covered by snow in April in most years, which likely delays germination until snowmelt in May and June (Fig. 1D).

Forecasts from general circulation models indicate the potential for strong effects on fall and winter temperatures and declines in snowpack (Fig. 6). While there is variation across models in these impacts, all populations are expected to experience warming temperatures, with increases of 1–3.5°C in fall temperatures and 1.5–2.5°C in January minimum temperatures (Fig. 6), depending on model and population. High-elevation sites, in particular, will

likely experience the strongest changes in snowpack levels. Together these shifts are likely to affect temperature during germination and whether stratification requirements are met before spring snowmelt.

DISCUSSION

Seasonal germination timing is often under strong selection and may be critical for adaptation to local climate (Donohue et al., 2005b; Fenner, 2005; Baskin and Baskin, 2014). Optimal seasonal timing depends upon the ability of seeds to respond to appropriate environmental cues signaling favorable conditions. Temperature cues are particularly important for the release of dormancy to allow germination in response to light and moisture availability and may be particularly affected by rising temperatures due to climate change (Cayan et al., 2008; Loarie et al., 2008; Footitt et al., 2013, 2018; Baskin and Baskin, 2014; IPCC, 2014). However, the optimal response to temperature cues may vary with climate among populations. Although clinal within-species variation in dormancy and germination traits is often reported (Montesinos-Navarro et al., 2012; Vidigal et al., 2016; Barga et al., 2017; Fernández-Pascual et al., 2017; Hernández et al., 2019; López et al., 2019), fewer studies have examined intraspecific variation in seed chilling responses, particularly across climatic gradients (Cavieres and Arroyo, 2000; Debieu et al., 2013; Rubin and Friedman, 2018). Our results demonstrate extensive variation in stratification (chilling) requirements and ambient temperature responses in *S. tortuosus* populations across elevation.

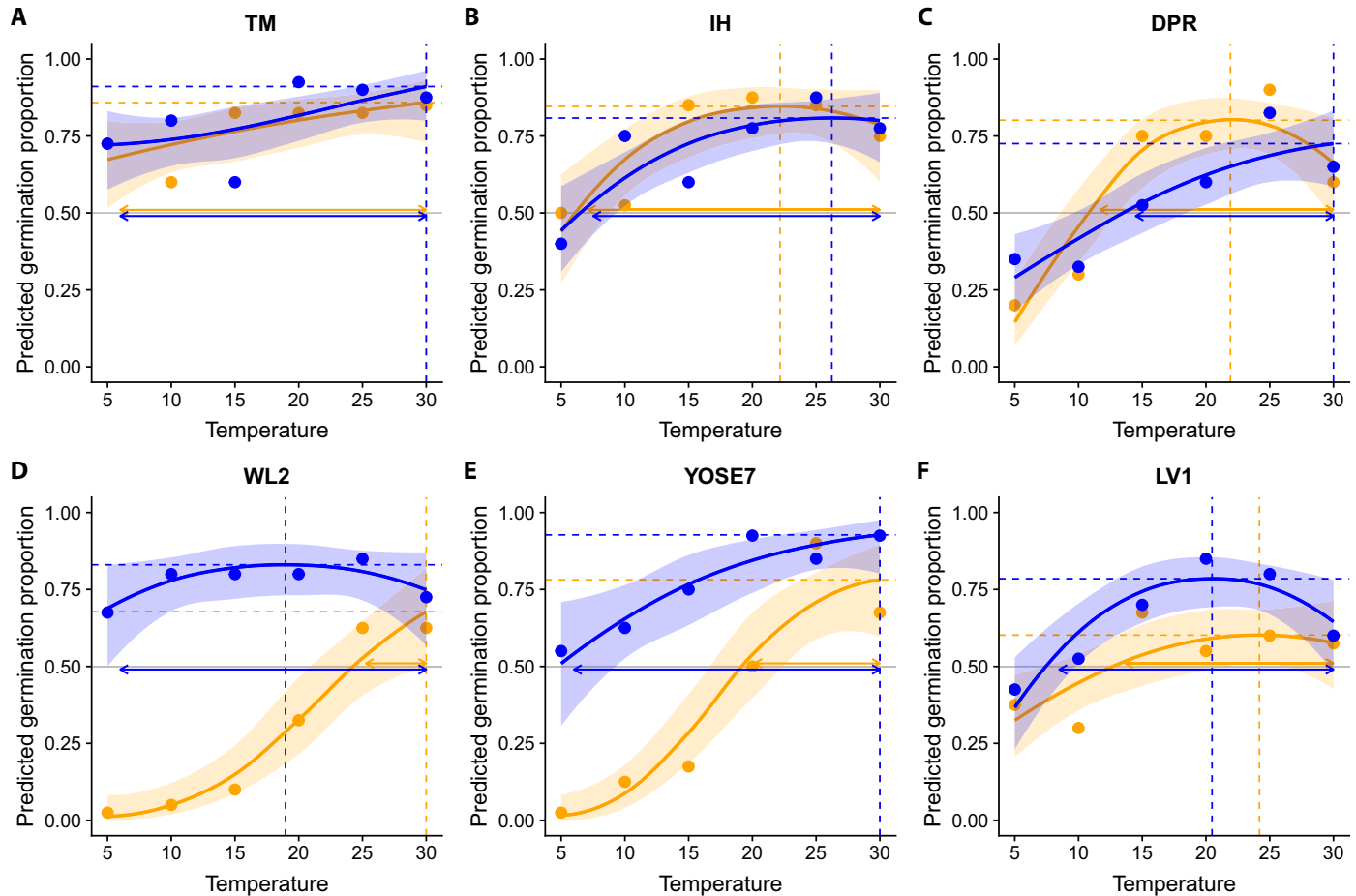


FIGURE 4. Germination in response to temperature and stratification treatments for six populations of *Streptanthus tortuosus*. Results illustrated here include seeds that germinated during stratification in analyses. Low-elevation populations illustrated on the top row (A–C) and high-elevation populations on the bottom row (D–F), in order of elevation. Stratified treatments in blue, nonstratified in orange. Points represent means; shaded areas represent 95% confidence intervals around fixed effects for quadratic model fits. Vertical dashed lines indicate the temperatures at which germination proportions were maximized; horizontal lines represent maximum germination proportions. Arrows indicate the breadth of temperatures at which germination was >50%; temperature breadths were truncated at the maximum temperature if germination remained above 50% at that temperature.

These differences in germination cueing correspond with dramatic elevational differences in seasonal climate and germination phenology in the wild. Further, observed differences among populations in maximum germination are consistent with predictions from bet-hedging theory. Although we cannot rule out a contribution from environmental parental effects, these results suggest a history of adaptive differentiation in the seed germination niche among populations across the species' elevational range. However, rapid climate change is bringing increasing temperatures and earlier snowmelt, which may lead to mismatches between changes in optimal germination timing and formerly adaptive environmental cues (Aitken et al., 2008; Donohue et al., 2010; Walck et al., 2011).

Stratification requirements for seed dormancy release are observed in many species (Baskin and Baskin, 2014) and can act to time germination with appropriate conditions for seedling establishment. Dormancy release after brief chilling exposure allows germination under cooling temperatures in fall. In many fall-germinating species, exposure to prolonged chilling then can re-induce secondary dormancy in the seed bank, preventing germination in

winter and spring (Penfield and Springthorpe, 2012; Baskin and Baskin, 2014). In contrast, some species and genotypes require prolonged cold exposure to break primary dormancy and therefore germinate in spring (Footitt et al., 2013; Baskin and Baskin, 2014). Cold stratification requirements are especially common in species from high elevations (Cavieres and Arroyo, 2000; Fernández-Pascual et al., 2017; Cavieres and Sierra-Almeida, 2018; Tudela-Isanta et al., 2018). Less is known about within-species variation, but there is some evidence for stronger stratification requirements in high-elevation populations of alpine species (Cavieres and Arroyo, 2000). Our results from *S. tortuosus* are consistent with this pattern. Low-elevation populations lack a cold stratification requirement and experience temperatures conducive for germination when precipitation begins in the fall, which would allow them to germinate with the first fall rains, as we observed for germination phenology in the field. High-elevation populations experience cold temperatures with the onset of seasonal precipitation and accumulate several weeks of chilling and substantial snowpack. For these populations, we would expect germination to be cued such that it is restricted to late spring and summer, after snowmelt, again consistent with our

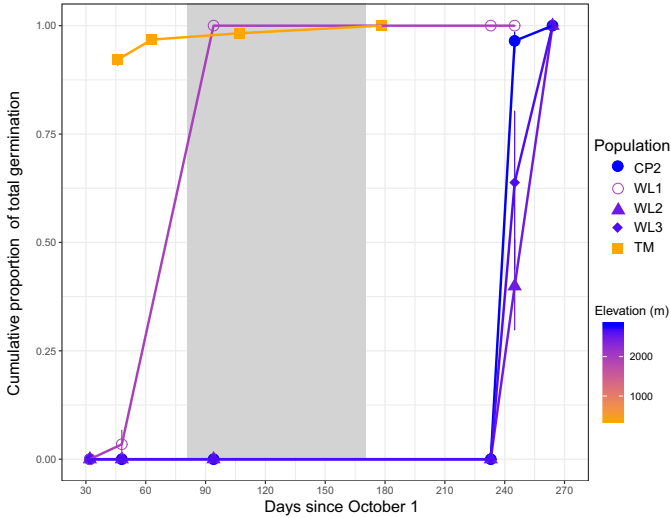
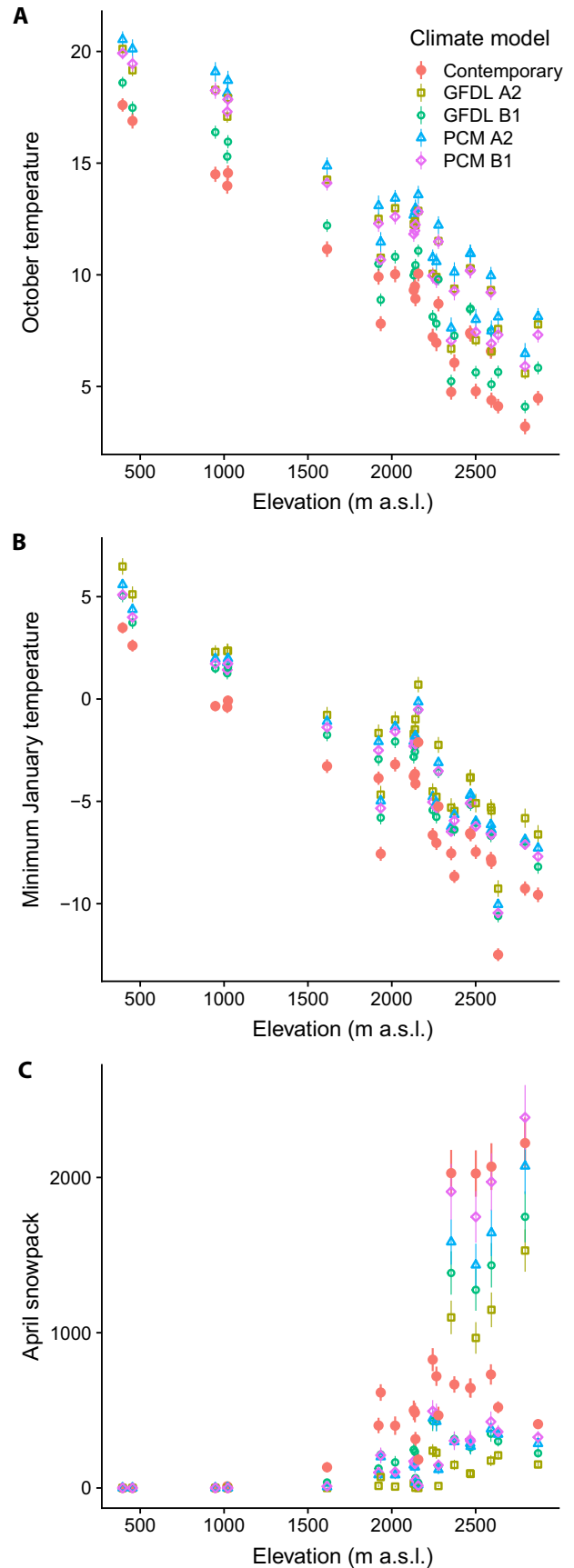


FIGURE 5. Germination phenology for five *Streptanthus tortuosus* populations. Points are average cumulative germination across plots at each site at each census date (± 1 SE, back-transformed from logit scale). Census dates are calculated as days since 1 October to illustrate the beginning of the water year (and growing season for low-elevation sites). Populations from low elevation to high: TM, WL1, WL2, WL3, CP2 (see Table 1 for site information). Shapes and colors indicate populations and elevations, respectively. The gray-shaded area indicates winter months, in which chilling may occur (depending on conditions and site).

field observations. This timing of germination seems to be achieved through the interaction of stratification requirements and temperature responses, since seeds from high elevations were confined to a narrow germination window at high temperatures until release of dormancy by cold stratification allowed them to germinate across a wider thermal range.

Delayed germination through seed dormancy is a classic example of biological bet hedging, which is an evolutionary strategy to maintain fitness in highly variable environments (Cohen, 1966; Seger and Brockmann, 1987; Philippi, 1993; Venable, 2007; Gremer and Venable, 2014). Indeed, delayed germination has been demonstrated to act as a bet-hedging strategy in deserts that experience high variability in the timing and extent of rainfall during the growing season (Philippi, 1993; Venable, 2007; Tielborger et al., 2012; Gremer and Venable, 2014; Gremer et al., 2016). In our study, we evaluated maximum levels of germination in response to treatments that simulated germination cues, namely, cues related to stratification (chilling) and germination temperature. While not a direct test of bet hedging, our results are consistent with expectations from bet-hedging theory, since populations that experience lower variability in fall precipitation had higher germination fractions and vice versa. Our results also correspond with a study in a California vernal pool endemic, *Lasthenia*

FIGURE 6. Future projections for temperature and snowpack across populations along the elevational cline. Points represent 30-year averages (2070–2099) ± 1 detrended SD for each population. Contemporary patterns indicated in orange, GFDL and PCM models were used to generate forecasts, each using either the B1 or A2 emissions scenarios. (A) October temperature, (B) minimum January temperature, and (C) April snowpack.



fremontii, which experiences high variability in water availability, due to interannual variation in the timing and extent of growing-season precipitation (Torres-Martínez et al., 2017). In that study, Torres-Martínez et al. (2017) found that among-population variability in germination fractions was significantly related to interannual variation in November precipitation, and this effect was stronger than that for total precipitation. In their study and in ours, relationships were stronger for fall precipitation than for total growing season precipitation, suggesting that fall precipitation may not be fully predictive of total growing-season precipitation and may be an unreliable cue of season quality, which would select for higher bet hedging. Similarly, the timing and extent of germination-triggering rain events in the fall and winter has been shown to be a key driver of bet-hedging germination strategies in desert annuals (Venable, 2007; Cuello et al., 2019) and scales to influence population and community dynamics in California annual communities (Levine et al., 2011) and in annual desert communities of the southwestern United States (Angert et al., 2009; Kimball et al., 2010, 2011). In our system, variation in the length of the seed stratification requirement within a population could potentially result in two seasonal germination cohorts, with some seeds germinating in fall and others in spring, as observed in other species (Galloway and Etterson, 2007; Montesinos-Navarro et al., 2012; Picó, 2012; Baskin and Baskin, 2014). Such variation could allow intra-annual bet hedging (Simons, 2014; Gremer et al., 2016), which might be adaptive in mid-elevation populations that experience variation in winter snowpack among years.

Plasticity to reliable environmental cues is an alternative strategy for dealing with variability in environmental conditions (Cohen, 1967; Simons, 2014; Botero et al., 2015; Gremer et al., 2016). Plasticity is not necessarily mutually exclusive with bet hedging, and the adaptive value of plasticity versus bet hedging depends on the timescale of that variation and reliability of available cues (Cohen, 1967; Donaldson-Matasci et al., 2013; Botero et al., 2015). In our study, we found strong responses of germination to temperature cues related to winter chilling (stratification) and seasonal temperatures, indicating plasticity to temperature. These responses varied, such that low-elevation populations did not respond to stratification and had high germination across treatments, and high-elevation populations had low germination unless they experienced substantial chilling (Figs. 2A, 4). For high-elevation populations, stratification is likely a reliable cue that favorable spring conditions are arriving, and a stratification requirement can prevent germination in the fall, which could lead to mortality over the winter. Moreover, stratification increased the range of temperatures for germination in high-elevation populations, consistent with results of Fernández et al. (2017). However, stratification is not an appropriate germination cue for low-elevation populations, since waiting until after winter chilling would vastly shorten the time for growth and reproduction before the onset of summer drought. Instead, lower-elevation populations germinated across a broad range of temperatures, with or without stratification. These results also correspond with the expectation that germination niches are narrower when cues are more reliable or more predictive of approaching favorable conditions (Barga et al., 2017; Fernández-Pascual et al., 2017). It is interesting that precipitation variability seems more important for predicting levels of maximum germination (i.e., dormancy), but that we saw strong plasticity in response to temperature cues, suggesting that temperature could be a more reliable cue of seasonal conditions than precipitation for these populations. We note that our clinal

gradient does include more variation in temperature than precipitation (Appendix S3a, b). We did not directly evaluate how both temperature and available moisture jointly affect germination in our experiments, but that is an interesting area for future study. Nonetheless, our results nicely correspond with observed germination phenology in the field, underscoring the strong role of temperature in our system.

The clinal population variation we found in germination traits suggests that the germination niche may be involved in local adaptation to elevation and climate. However, dormancy and germination traits can also be strongly influenced by the parental environment, and such transgenerational plasticity may itself have adaptive value (Galloway and Etterson, 2007; Springthorpe and Penfield, 2015; Auge et al., 2017; Lampei et al., 2017; Wadgymer et al., 2018). Thus, potentially adaptive phenotypic differences among populations may reflect transgenerational plasticity to local parental environments as well as local adaptation in response to natural selection. For example, in annual species of Israel, seed dormancy varies along a cline in aridity and precipitation variability consistent with adaptive bet hedging (Tielborger et al., 2012). Moreover, in those same species, the relative strength of parental effects on germination also corresponded with the cline in aridity and precipitation variability (Lampej et al., 2017). Our experiments used wild-collected seed from our study populations, so we cannot distinguish the contributions of genetic divergence and transgenerational plasticity across sites. However, this design allowed us to assess the realized germination niche of each population, that is, the thermal conditions under which seeds would actually germinate given each population's selection history and local parental environment.

The California Floristic Province has already experienced significant shifts in climate, and rates of climate change will continue to be rapid, with up to 66% of species expected to experience significant reductions in range size by the end of the century (Cayan et al., 2008; Loarie et al., 2008). For species that cannot disperse fast enough to track these changes through space, tracking the shifting conditions through time, through shifting seasonal niches, will be critical (Donohue et al., 2010; Walck et al., 2011; Hereford et al., 2017). Here we showed that the seasonal germination niche for *S. tortuosus* is highly influenced by temperature and that temperature cues are likely to shift among years and in response to climate change. Indeed, forecasts for seasonal temperature for our populations include increased temperatures in the fall and winter (Fig. 6) and decreasing snowpack for higher-elevation populations. Germination rates were higher than we expected in our warmest treatment (30°C) for all populations, though we expected germination to decline at this temperature, based on results from a study of several species of annual plants from the Sonoran Desert (Huang et al., 2016). However, follow-up studies suggest germination in *S. tortuosus* drastically declines past 30°C and does not occur at temperatures of 40°C for several populations (M. Bontrager, unpublished data). It may be that increases in germination temperature alone would have weak effects on germination timing, but the main effect of increased temperatures with climate change will be through reductions in chilling. Thus, these anticipated changes might have stronger impacts on germination at high-elevation populations, due to reductions in accumulation of chilling narrowing germination niches or preventing germination altogether. In addition to altering the timing and availability of cues for germination,

shifting temperature regimes under climate change may also affect other aspects of seed development and germination, including rates of seed maturation, seed aging, and maternal influences on seed traits (Donohue et al., 2010; Walck et al., 2011; Penfield and Springthorpe, 2012). Further, increased soil temperatures anticipated with climate change are likely to decrease seedbank persistence (Ooi et al., 2009; Ooi, 2012), which will alter the adaptive value of dormancy and germination timing. Of course, these effects early in the life cycle, at the seed and seedling stage, can cascade to influence trait expression and performance later in the life cycle (Kalisz, 1986; Galloway and Burgess, 2009; Wilczek et al., 2009; Donohue et al., 2010; Gremer et al., 2020).

Understanding how shifting environmental conditions under climate change affect the seasonal niche, through altering the timing and availability of cues, is critical for predicting future population persistence and distributions across the landscape. Here we showed that temperature cues that drive the seasonal germination niche for *S. tortuosus* are expected to shift substantially under future climate change (Fig. 6). The question is whether these populations can adapt in time, for instance, through evolutionary changes in stratification or germination temperature requirements. Evidence for rapid evolution of seed traits and germination during a range expansion was demonstrated in a study of an annual plant, *Helianthus annuus*, which occurred over a relatively short time frame (70 years; Hernández et al., 2019). Similar patterns were observed for trait variation, including germination phenology, in another invasive annual, *Brassica tournefortii*, across a range expansion in the southwestern United States occurring over about a century (Winkler et al., 2018). These studies suggest that rapid evolutionary response may be possible. Of course, evolutionary response depends on standing genetic variation, heritability, and constraints on response to selection (Antonovics and Vantienderen, 1991; Kopp and Matuszewski, 2014). In a study of germination responses to temperature and moisture across 240 species and 49 families across the globe, Arene et al. (2017) found negative correlations among seed and germination traits, as well as evidence for phylogenetic constraint in temperature responses. Such patterns could constrain the potential for evolutionary response to increased temperatures with climate change. Thus, it is unclear whether such rapid change can occur in our system, but understanding the potential for evolutionary response would provide key information on the fate of these populations and the future range distribution of this species.

CONCLUSIONS

Using a combination of common garden experiments and field observation, we demonstrated that the seasonal germination niche in *Streptanthus tortuosus* is strongly driven by temperature cues and varies across populations along an elevational cline. Further, differences in stratification requirements and how they interact with germination temperature cues explain differential patterns of germination phenology across populations in the field. These temperature cues exhibit strong inter- and intra-annual variation and are consistent with expectations under local adaptation. Perhaps more importantly, these cues will be strongly affected by climate change, which will shift germination timing and requirements, particularly for high-elevation populations. Our study demonstrates the key role of temperature in

germination timing across environmental gradients, reveals patterns consistent with local adaptation, and highlights the potential impact of climate change on life history timing, performance, and population persistence.

ACKNOWLEDGMENTS

The authors thank Chenoa Wilcox for identifying populations and collecting seed, Mireille Caton-Darby and Eva Beyen for help with experimental methods, design, and data collection, and numerous undergraduates including Joaquin Meckler-Pacheco, Helena Bayat, Sherry Zheng, Niel Gapal, Bryan Gonzalez, Josh Leung, Gautam Mathur, Grace Lewin, Chandler Stephenson, and Jillian Dyer. Sharon Strauss, Julin Maloof, and Alejandra Martínez-Berdeja provided invaluable discussion and advice. Two anonymous reviewers provided valuable comments. Funding was provided by UC Davis, USDA National Institute of Food and Agriculture Hatch project CA-D-EVE-3515-H-1002936 (J.Schmitt), and NSF DEB (1831913 to J. R. Gremer, J. Schmitt, Sharon Strauss, and Julin Maloof). L. Okafor received support from the UC Davis Colleges of Biological Sciences and Agriculture and Environmental Sciences through the Evolution and Ecology Graduate Admissions Pathways partnership with Howard University.

AUTHOR CONTRIBUTIONS

J.R.G., J.S., A.C., and E.S. conceived of and designed the study. A.C. and E.S. conducted the stratification experiment and preliminary data analyses. L.O. and E.S. conducted the thermal germination experiment and preliminary analyses. J.R.G., A.C., and M.B. analyzed data and prepared figures. J.R.G. wrote the manuscript with contributions from all authors.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

APPENDIX S1. Results from the thermal germination experiment including details on curve fitting and dark germination.

APPENDIX S2. Illustration of germination responses by population and stratification treatment.

APPENDIX S3. Mean annual temperature and mean annual precipitation across populations along an elevational cline.

LITERATURE CITED

- Aitken, S. N., S. Yeaman, J. A. Holliday, T. Wang, and S. Curtis-McLane. 2008. Adaptation, migration or extirpation: climate change outcomes for tree populations. *Evolutionary Applications* 1: 95–111.
- Angert, A. L., T. E. Huxman, P. Chesson, and D. L. Venable. 2009. Functional tradeoffs determine species coexistence via the storage effect. *Proceedings of the National Academy of Sciences, USA* 106: 11641–11645.
- Antonovics, J., and P. H. Vantienderen. 1991. Ontoecogenophyloconstraints? The chaos of constraint terminology. *Trends in Ecology & Evolution* 6: 166–168.

- Arene, F., L. Affre, A. Doxa, and A. Saatkamp. 2017. Temperature but not moisture response of germination shows phylogenetic constraints while both interact with seed mass and lifespan. *Seed Science Research* 27: 110–120.
- Auge, G. A., L. D. Leverett, B. R. Edwards, and K. Donohue. 2017. Adjusting phenotypes via within- and across-generational plasticity. *New Phytologist* 216: 343–349.
- Baldwin, B. G. 2014. Origins of plant diversity in the California Floristic Province. *Annual Review of Ecology, Evolution, and Systematics* 45: 347–369.
- Barga, S., T. E. Dilts, and E. A. Leger. 2017. Climate variability affects the germination strategies exhibited by arid land plants. *Oecologia* 185: 437–452.
- Baskin, C., and J. Baskin. 2014. *Seeds: Ecology, biogeography and evolution of dormancy and germination*. Academic Press, San Diego, CA, USA.
- Bates, D., M. Maechler, B. Boker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67: 1–48.
- 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, Biological Sciences* 374: 20180178.
- Botero, C. A., F. J. Weissing, J. Wright, and D. R. Rubenstein. 2015. Evolutionary tipping points in the capacity to adapt to environmental change. *Proceedings of the National Academy of Sciences, USA* 112: 184–189.
- 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.
- Calflora. 2014. Calflora: Information on California plants for education, research and conservation. The Calflora Database [a non-profit organization], Berkeley, CA, USA.
- Cavieres, L. A., and M. T. K. Arroyo. 2000. Seed germination response to cold stratification period and thermal regime in *Phacelia secunda* (Hydrophyllaceae) – altitudinal variation in the mediterranean Andes of central Chile. *Plant Ecology* 149: 1–8.
- Cavieres, L. A., and A. Sierra-Almeida. 2018. Assessing the importance of cold-stratification for seed germination in alpine plant species of the High-Andes of central Chile. *Perspectives in Plant Ecology, Evolution and Systematics* 30: 125–131.
- Cayan, D. R., E. P. Maurer, M. D. Dettinger, M. Tyree, and K. Hayhoe. 2008. Climate change scenarios for the California region. *Climatic Change* 87: 21–42.
- Cochrane, A., C. J. Yates, G. L. Hoyle, and A. B. Nicotra. 2015. Will among-population variation in seed traits improve the chance of species persistence under climate change? *Global Ecology and Biogeography* 24: 12–24.
- Cohen, D. 1966. Optimizing reproduction in a randomly varying environment. *Journal of Theoretical Biology* 12: 119–129.
- Cohen, D. 1967. Optimizing reproduction in a randomly varying environment when a correlation may exist between the conditions at the time a choice has to be made and the subsequent outcome. *Journal of Theoretical Biology* 16: 1–14.
- Cuello, W. S., J. R. Gremer, P. C. Trimmer, A. Sih, and S. J. Schreiber. 2019. Predicting evolutionarily stable strategies from functional responses of Sonoran Desert annuals to precipitation. *Proceedings of the Royal Society, B, Biological Sciences* 286: 20182613.
- Dalgleish, H. J., D. N. Koons, and P. B. Adler. 2010. Can life-history traits predict the response of forb populations to changes in climate variability? *Journal of Ecology* 98: 209–217.
- Debieu, M., C. Tang, B. Stich, T. Sikosek, S. Effgen, E. Josephs, J. Schmitt, et al. 2013. Co-variation between seed dormancy, growth rate and flowering time changes with latitude in *Arabidopsis thaliana*. *PLOS One* 8: e61075.
- Donaldson-Matasci, M. C., C. T. Bergstrom, and M. Lachmann. 2013. When unreliable cues are good enough. *American Naturalist* 182: 313–327.
- Donohue, K. 2002. Germination timing influences natural selection on life-history characters in *Arabidopsis thaliana*. *Ecology* 83: 1006–1016.
- Donohue, K., D. Dorn, C. Griffith, E. Kim, A. Aguilera, C. R. Polisetty, and J. Schmitt. 2005a. Niche construction through germination cueing: life-history responses to timing of germination in *Arabidopsis thaliana*. *Evolution* 59: 771–785.
- Donohue, K., L. Dorn, C. Griffith, E. Kim, A. Aguilera, C. R. Polisetty, and J. Schmitt. 2005b. The evolutionary ecology of seed germination of *Arabidopsis thaliana*: variable natural selection on germination timing. *Evolution* 59: 758–770.
- 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.
- Eckhart, V. M., M. A. Geber, W. F. Morris, E. S. Fabio, P. Tiffin, and D. A. Moeller. 2011. The geography of demography: Long-term demographic studies and species distribution models reveal a species border limited by adaptation. *American Naturalist* 178: S26–S43.
- Fenner, M., and K. Thompson. 2005. *The ecology of seeds*. Cambridge University Press, Cambridge, UK.
- Fernández-Pascual, E., A. Pérez-Arcoiza, J. A. Prieto, and T. E. Díaz. 2017. Environmental filtering drives the shape and breadth of the seed germination niche in coastal plant communities. *Annals of Botany* 119: 1169–1177.
- Finch-Savage, W. E., and S. Footitt. 2017. Seed dormancy cycling and the regulation of dormancy mechanisms to time germination in variable field environments. *Journal of Experimental Botany* 68: 843–856.
- Finch-Savage, W. E., and G. Leubner-Metzger. 2006. Seed dormancy and the control of germination. *New Phytologist* 171: 501–523.
- Flint, L. E., and A. L. Flint. 2014. California Basin characterization model: a dataset of historical and future hydrologic response to climate change., data release version 1.1. U.S. Geological Survey, Washington, D.C., USA. Available at https://ca.water.usgs.gov/projects/reg_hydro/basin-characterization-model.html.
- Footitt, S., Z. Huang, H. A. Clay, A. Mead, and W. E. Finch-Savage. 2013. Temperature, light and nitrate sensing coordinate *Arabidopsis* seed dormancy cycling, resulting in winter and summer annual phenotypes. *The Plant Journal* 74: 1003–1015.
- Footitt, S., Z. Huang, H. Ölcer-Footitt, H. Clay, and W. E. Finch-Savage. 2018. The impact of global warming on germination and seedling emergence in *Alliaria petiolata*, a woodland species with dormancy loss dependent on low temperature. *Plant Biology* 20: 682–690.
- Galloway, L. F., and K. S. Burgess. 2009. Manipulation of flowering time: phenological integration and maternal effects. *Ecology* 90: 2139–2148.
- Galloway, L. F., and J. R. Etterson. 2007. Transgenerational plasticity is adaptive in the wild. *Science* 318: 1134–1136.
- Gremer, J. R., and D. L. Venable. 2014. Bet hedging in desert winter annual plants: optimal germination strategies in a variable environment. *Ecology Letters* 17: 380–387.
- Gremer, J. R., S. Kimball, and D. L. Venable. 2016. Within- and among-year germination in Sonoran Desert winter annuals: bet hedging and predictive germination in a variable environment. *Ecology Letters* 19: 1209–1218.
- Gremer, J. R., C. J. Wilcox, A. Chiono, E. Suglia, and J. Schmitt. 2020. 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.
- Hereford, J., J. Schmitt, and D. D. Ackerly. 2017. The seasonal climate niche predicts phenology and distribution of an ephemeral annual plant, *Mollugo verticillata*. *Journal of Ecology* 105: 1323–1334.
- Hernández, F., M. Poverene, A. Garayalde, and A. Presotto. 2019. Re-establishment of latitudinal clines and local adaptation within the invaded area suggest rapid evolution of seed traits in Argentinean sunflower (*Helianthus annuus* L.). *Biological Invasions* 21: 2599–2612.
- Huang, Z., S. Liu, K. J. Bradford, T. E. Huxman, and D. L. Venable. 2016. The contribution of germination functional traits to population dynamics of a desert plant community. *Ecology* 97: 250–261.
- IPCC [Intergovernmental Panel on Climate Change]. 2014. Climate Change 2014: Impacts, adaptation, and vulnerability. Part B: Regional aspects. In V. R. Barros, C. B. Field, D. J. Dokken, M. D. Mastrandrea, K. J. Mach, T. E. Bilir, et al. [eds.], Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.

- Kalisz, S. 1986. Variable selection on the timing of germination in *Collinsia verna* (Scrophulariaceae). *Evolution* 40: 479–491.
- Kalisz, S., and M. A. McPeck. 1992. Demography of an age-structured annual—Resampled projection matrices, elasticity analyses, and seed bank effects. *Ecology* 73: 1082–1093.
- Kimball, S., A. L. Angert, 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.
- Kimball, S., A. L. Angert, T. E. Huxman, and D. L. Venable. 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.
- Kopp, M., and S. Matuszewski. 2014. Rapid evolution of quantitative traits: theoretical perspectives. *Evolutionary Applications* 7: 169–191.
- Korves, T. M., K. Schmidt, A. L. Caicedo, C. Mays, J. R. Stinchcombe, M. D. Purugganan, and J. Schmitt. 2007. Fitness effects associated with the major flowering time gene *FRIGIDA* in *Arabidopsis thaliana* in the field. *American Naturalist* 169: E141–E157.
- Lampe, C., and K. Tielborger. 2010. Evolvability of between-year seed dormancy in populations along an aridity gradient. *Biological Journal of the Linnean Society* 100: 924–934.
- Lampe, C., J. Metz, and K. Tielborger. 2017. Clinal population divergence in an adaptive parental environmental effect that adjusts seed banking. *New Phytologist* 214: 1230–1244.
- Levine, J. M., A. K. McEachern, and C. Cowan. 2011. Seasonal timing of first rain storms affects rare plant population dynamics. *Ecology* 92: 2236.
- Loarie, S. R., B. E. Carter, K. Hayhoe, S. McMahon, R. Moe, C. A. Knight, and D. D. Ackerly. 2008. Climate change and the future of California's endemic flora. *Plos One* 3: e2502.
- López, A. S., P. Marchelli, D. Batlla, D. R. López, and M. V. Arana. 2019. Seed responses to temperature indicate different germination strategies among *Festuca pallescens* populations from semi-arid environments in North Patagonia. *Agricultural and Forest Meteorology* 272–273: 81–90.
- Luedeling, E. 2019. chillR: Statistical methods for phenology analysis in temperate fruit trees, version 0.70.15.
- Maher, S. P., T. L. Morelli, M. Hershey, A. L. Flint, L. E. Flint, C. Moritz, and S. R. Beissinger. 2017. Erosion of refugia in the Sierra Nevada meadows network with climate change. *Ecosphere* 8: e01673.
- 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.
- Miller-Rushing, A. J., T. T. Hoye, D. W. Inouye, and E. Post. 2010. The effects of phenological mismatches on demography. *Philosophical Transactions of the Royal Society, B, Biological Sciences* 365: 3177–3186.
- Montesinos-Navarro, A., F. X. Pico, and S. J. Tonsor. 2012. Clinal variation in seed traits influencing life cycle timing in *Arabidopsis thaliana*. *Evolution* 66: 3417–3431.
- Murray, K., and M. M. Conner. 2009. Methods to quantify variable importance: implications for the analysis of noisy ecological data. *Ecology* 90: 348–355.
- Ooi, M. K. J. 2012. Seed bank persistence and climate change. *Seed Science Research* 22: S53–S60.
- Ooi, M. K. J., T. D. Auld, and A. J. Denham. 2009. Climate change and bet-hedging: interactions between increased soil temperatures and seed bank persistence. *Global Change Biology* 15: 2375–2386.
- Parmesan, C., and M. E. Hanley. 2015. Plants and climate change: complexities and surprises. *Annals of Botany* 116: 849–864.
- Penfield, S., and V. Springthorpe. 2012. Understanding chilling responses in *Arabidopsis* seeds and their contribution to life history. *Philosophical Transactions of the Royal Society, B, Biological Sciences* 367: 291–297.
- Philippi, T. 1993. Bet-hedging germination of desert annuals: variation among populations and maternal effects in *Lepidium lasiocarpum*. *American Naturalist* 142: 488–507.
- Philippi, T., and J. Seger. 1989. Hedging ones evolutionary bets, revisited. *Trends in Ecology & Evolution* 4: 41–44.
- 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.
- Preston, R. E. 1991. The intrafloral phenology of *Streptanthus tortuosus* (Brassicaceae). *American Journal of Botany* 78: 1044–1053.
- PRISM Climate Group. 2004. PRISM climate data. Northwest Alliance for Computational Science & Engineering, Oregon State University, Corvallis, OR, USA. Available at <http://prism.oregonstate.edu> [accessed 01 May 2019].
- Rubin, M. J., and J. Friedman. 2018. The role of cold cues at different life stages on germination and flowering phenology. *American Journal of Botany* 105: 749–759.
- Rundel, P. W., M. T. K. Arroyo, R. M. Cowling, J. E. Keeley, B. B. Lamont, and P. Vargas. 2016. Mediterranean biomes: evolution of their vegetation, floras, and climate. *Annual Review of Ecology, Evolution, and Systematics* 47: 383–407.
- Seger, J., and H. J. Brockmann. 1987. What is bet-hedging? *Oxford Surveys in Evolutionary Biology* 4: 182–211.
- Sheth, S. N., and A. L. Angert. 2014. The evolution of environmental tolerance and range size: a comparison of geographically restricted and widespread *Mimulus*. *Evolution* 68: 2917–2931.
- Shimono, Y., and G. Kudo. 2005. Comparisons of germination traits of alpine plants between fellfield and snowbed habitats. *Ecological Research* 20: 189–197.
- Simons, A. M. 2011. Modes of response to environmental change and the elusive empirical evidence for bet hedging. *Proceedings of the Royal Society, B, Biological Sciences* 278: 1601–1609.
- Simons, A. M. 2014. Playing smart vs. playing safe: the joint expression of phenotypic plasticity and potential bet hedging across and within thermal environments. *Journal of Evolutionary Biology* 27: 1047–1056.
- Springthorpe, V., and S. Penfield. 2015. Flowering time and seed dormancy control use external coincidence to generate life history strategy. *eLife* 4: e05557.
- Tielborger, K., M. Petru, and C. Lampe. 2012. Bet-hedging germination in annual plants: a sound empirical test of the theoretical foundations. *Oikos* 121: 1860–1868.
- Torres-Martínez, L., P. Weldy, M. Levy, and N. C. Emery. 2017. Spatiotemporal heterogeneity in precipitation patterns explain population-level germination strategies in an edaphic specialist. *Annals of Botany* 119: 253–265.
- Tudela-Isanta, M., E. Fernández-Pascual, M. Wijayasinghe, S. Orsenigo, G. Rossi, H. W. Pritchard, and A. Mondoni. 2018. Habitat-related seed germination traits in alpine habitats. *Ecology and Evolution* 8: 150–161.
- Venable, D. L. 2007. Bet hedging in a guild of desert annuals. *Ecology* 88: 1086–1090.
- Venable, D. L., and L. Lawlor. 1980. Delayed germination and dispersal in desert annuals: escape in space and time. *Oecologia* 46: 272–282.
- Vidigal, D. S., A. C. Marques, L. A. Willems, G. Buijs, B. Mendez-Vigo, H. W. Hilhorst, L. Bentsink, et al. 2016. Altitudinal and climatic associations of seed dormancy and flowering traits evidence adaptation of annual life cycle timing in *Arabidopsis thaliana*. *Plant, Cell & Environment* 39: 1737–1748.
- Wadgyar, S. M., R. M. Mactavish, and J. T. Anderson. 2018. Transgenerational and within-generation plasticity in response to climate change: insights from a manipulative field experiment across an elevational gradient. *American Naturalist* 192: 698–714.
- Walck, J. L., S. N. Hidayati, K. W. Dixon, K. E. N. Thompson, and P. Poschlod. 2011. Climate change and plant regeneration from seed. *Global Change Biology* 17: 2145–2161.
- 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.
- Winkler, D. E., J. R. Gremer, K. J. Chapin, M. Kao, and T. E. Huxman. 2018. Rapid alignment of functional trait variation with locality across the invaded range of Sahara mustard (*Brassica tournefortii*). *American Journal of Botany* 105: 1188–1197.