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Snow melt timing acts independently and in conjunction with temperature accumulation to drive subalpine plant phenology

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Abstract

Organisms use environmental cues to align their phenology—the timing of life events—with sets of abiotic and biotic conditions that favor the successful completion of their life cycle. Climate change has altered the environmental cues organisms use to track climate, leading to shifts in phenology with the potential to affect a variety of ecological processes. Understanding the drivers of phenological shifts is critical to predicting future responses, but disentangling the effects of temperature from precipitation on phenology is often challenging because they tend to covary. We addressed this knowledge gap in a high-elevation environment where phenological shifts are associated with both the timing of spring snow melt and temperature. We factorially crossed early snow melt and passive warming treatments to (1) disentangle the effects of snow melt timing and warming on the phenology of flowering and fruiting and reproductive success in three subalpine plant species (*Delphinium nuttallianum*, *Valeriana edulis*, and *Potentilla pulcherrima*); and (2) assess whether snow melt acts via temperature accumulation or some other aspect of the environment (e.g., soil moisture) to affect phenological events. Both the timing and duration of flowering and fruiting responded to the climate treatments, but the effect of snow melt timing and warming varied among species and phenological stages. The combined effects of the treatments on phenology were always additive, and the snow melt treatment often affected phenology even when the warming treatment did not. Despite marked responses of phenology to climate manipulations, the species showed little change in reproductive success, with only one species producing fewer seeds in response to warming (*Delphinium*, −56%). We also found that snow melt timing can act both through temperature accumulation and as a distinct cue for phenology, and these effects are not mutually exclusive. Our results show that one environmental cue, here snow melt timing, may act through multiple mechanisms to shift phenology.

KEYWORDS
climate change, flower duration, flower timing, fruit duration, fruit timing, growing degree days, passive warming, subalpine plant community

1 | INTRODUCTION

Virtually all organisms require specific optimal environmental conditions to complete their life-history events. As such, the timing of life cycle events with respect to the environment is critical to organism success (Forrest & Miller-Rushing, 2010). Failure to respond to changing seasonal conditions can have considerable consequences for an individual's survival and reproduction. In theory, the timing of life cycle events—phenology—should closely track climatic fluctuations through time by following changes to environmental cues, defined here as an aspect of the environment that initiates a phenological response (Chmura et al., 2018). However, climate change is rapidly altering the environmental cues that organisms use to track optimal climates, namely temperature and precipitation (Forrest et al., 2010; IPCC, 2014). Some organisms have shifted their phenology, appearing to maintain performance by tracking changing climatic conditions. Indeed, there is evidence that failure to shift the timing of life cycle events might cause decreased performance and population size (Cleland et al., 2007, 2012; Miller-Rushing et al., 2010; Møller et al., 2008).

The reliability of a phenological cue depends on its ability to detect the suitability of forthcoming environmental conditions (Bernhardt et al., 2020). Unless all axes of environmental suitability change synchronously, phenological cues can become unreliable and expose organisms to suboptimal abiotic conditions and fitness declines (Høye et al., 2007; Inouye, 2008; Ludwig et al., 2006). For example, an organism that relies on thawing as a cue for favorable temperatures, day length, or mutualist activity could be adversely affected if changes in the timing of thawing becomes decoupled from one or more of the organism's environmental requirements. Organisms that integrate multiple cues to predict the suitability of future conditions may not fare well if their phenological cues change at different rates (Bernhardt et al., 2020). This highlights the importance of understanding whether different climate drivers act independently (additively) or whether their effects when combined interact to affect phenology. If climate drivers interact, they may amplify the effects of one another when combined, more so than expected from their individual additive effects. In contrast, interacting climate drivers may have subadditive effects when combined, so that the effect of one driver is masked or muted compared to when it is considered in isolation. Additionally, phenological events happen as part of a larger cycle, and sequential phenological stages may be sensitive to different environmental cues. Disparate changes to the start and end of phenological stages may cause changes to the duration of phenological events, or changes to early season events may have consequences for events later in the season (Inouye et al., 2003; Li et al., 2016). If we do not know what aspect (or aspects) of climate is driving phenological shifts, then we cannot make accurate predictions of future phenology and how that phenology will affect fitness (Richardson et al., 2013).

Temperature and snow melt timing are important phenological cues in high-elevation and high-latitude plant communities, where climate change is occurring rapidly (Dunne et al., 2003; Høye et al., 2007; Inouye & Wielgolaski, 2013; Jabis et al., 2020; Price & Waser, 1998; Quaglia et al., 2020; Saavedra et al., 2003; Wielgolaski & Inouye, 2013; Wipf & Rixen, 2010; Ziello et al., 2009). Rising temperatures due to climate change are strongly associated with earlier phenology (Forrest & Miller-Rushing, 2010; Parmesan, 2006; Parmesan & Yohe, 2003; Thackeray et al., 2010). Temperature catalyzes the onset of phenological events through the accumulation of heat (measured as growing degree days [GDD]) or by reaching a temperature threshold for activity (e.g., above freezing; Forrest & Thomson, 2011; Oberbauer et al., 2013; Schwartz, 2003). In areas with seasonal snow cover, the timing of snow melt is also an important driver of phenology (Høye, Mølgaard Ellebjerg, et al., 2007; Iler et al., 2013; Lambert et al., 2010). However, the mechanism underlying snow melt timing as a driver of phenology is not as well understood as temperature. Snow melt timing may cue phenology by exposing plants to light once the snow has melted, through temperature accumulation, or through soil moisture. For example, the snowpack holds plants at or below their lower thermal activity limit, and snow melt removes this insulation, allowing physiological processes to resume (depending on air temperatures). Snow melt could also affect phenology through changes in soil moisture, because as the snow melts, the soil receives an influx of moisture, alerting plants to seasonal change and potentially inducing physiological processes. Evidence for this comes from studies where the advancement or delay of snow melt timing is no longer tied to a change in temperature, and the timing of flowering still changes (Bjorkman et al., 2015; Steltzer et al., 2009). Warmer temperatures and early snow melt are often strongly correlated, yet have largely been studied in isolation. This has prevented us from: (i) identifying the mechanism behind phenological responses to snow melt; (ii) assessing the relative importance of these two cues individually; and (iii) determining whether phenological responses are caused by interactions between these cues.

Here we study the timing, duration, and success of flowering and fruiting in three subalpine wildflower species. The timing and length of events such as flowering and fruiting are important because they can affect interactions with pollinators, herbivores, other plants (via co-flowering overlap), and season length (Augspurger & Zaya, 2020; Forrest et al., 2010; Inouye et al., 2003; Li et al., 2016). We factorially crossed warming with early snow melt within a subalpine plant community in the Colorado Rocky Mountains to answer the following questions. (1) *How does snow melt timing and warming individually and in combination affect the timing, duration, and success of flowering and fruiting in subalpine wildflowers?* We expected that early snow melt and warming would both advance reproductive timing, with the earliest phenology in the combined treatments. Because reproductive duration depends to some extent on the timing of events, we also expect changes to the duration of flowering and fruiting. If plants are tracking their preferred environments by shifting their phenological events, flower and seed production should not be affected by early snow melt and warming. Alternatively, if phenological shifts expose plants to unfavorable environmental conditions, then flower and seed production may decrease. (2) *Do the climate treatments* *affect reproductive phenology through temperature accumulation?* If the effects of snow melt timing and warming are independent, then snow melt timing will affect phenology beyond the accumulation of temperature.

2 | METHODS

2.1 | Study site

This study was conducted in a subalpine meadow in Gunnison National Forest at 3000 m a.s.l., approximately 4 km north of the Rocky Mountain Biological Laboratory (RMBL) in Gothic, Colorado (38°57′ N, 106°59′W). The timing of spring snow melt in this area is variable year to year, but there is a trend toward earlier snow melt with an average 12.8-day shift earlier over 42 years (1975–2016; Ogilvie et al., 2017). Spring temperatures have warmed, with a 1.14°C increase in average April–May temperature and a 1.63°C increase in minimum April–May temperature over 38 years (1973–2011; Anderson et al., 2012).

2.2 | Study species

Phenological events were tracked in three focal species: *Delphinium nuttallianum* (Ranunculaceae), *Valeriana edulis* (Caprifoliaceae), and *Potentilla pulcherrima* (Rosaceae), hereafter referred to as *Delphinium*, *Valeriana*, and *Potentilla*, respectively. All three species are common long-lived perennial forbs commonly found near the RMBL. *Delphinium* flowers shortly after the snow melts in early spring (early June on average), *Valeriana* flowers in mid-June, and *Potentilla* flowers in late June (CaraDonna et al., 2014). *Delphinium* is facultatively outcrossing (Waser & Price, 1981). *Valeriana* is dioecious and thus obligately outcrossing (Meyer, 1951). *Potentilla* is capable of autonomous self-pollination but sets more seed with outcross pollen (Burkle & Irwin, 2010; Vail, 1983).

2.3 | Experimental design

2.3.1 | Climate treatments

This study implemented a factorial design of warming and early snow melt treatments to disentangle the potentially independent effects that snow melt timing and temperature have on flowering and fruiting phenology. We used four climate treatments, namely control, early snow melt, warming, and combined warming × early snow melt. There were fourteen 7 × 7 m plots in total spread across a 2-ha meadow. Seven plots received an early snow melt manipulation, and seven were snow melt control-plots. Treatments were arranged in a split plot design, so that warming and control subplots were placed within each of the 14 plots (three of each per plot). Ambient air temperatures were increased via passive warming open-top chambers (OTC), made out of clear polycarbonate paneling (*following* Marion et al., 1997). The chambers were hexagonal in shape with a base diameter of ~1 m, an opening diameter of ~0.5 m, and a height of ~0.5 m. Chambers each had a ~15-cm wide by 5-cm high open hole in the south facing side midway up the panel for increased ventilation and were attached to the ground with 6″ metal landscape staples. Each control subplot was ca. 1 m^2. Controls for *Valeriana*, a substantially larger sized plant than the other two focal species, were not in subplots and instead were scattered individuals within the plot (these plants were already tagged as part of a preexisting demographic study). Warming chambers were deployed after the snow had melted in all plots to avoid affecting the date of snow melt. The OTC were setup on June 17–19, 2019 and remained in place through August 22, 2019. Early snow melt treatments used a 9 × 9 m black shade cloth to advance spring snow melt timing within the plot, plus a 1 m buffer on all sides to reduce edge effects. Snow melt timing was manipulated by placing black shade cloths directly on the snow surface, thereby decreasing albedo and increasing heat absorption. The shade cloth blocked 50% of light transmission and was secured to metal poles at the four plot corners by metal rings that allowed the cloth to settle and remain in contact with the snow surface as the snow melted. The shade cloth was deployed in the early spring (April 27), and was removed over the course of 1 week as the snow melted in each plot (June 4–June 10).

2.3.2 | Assessing climate

Both the snow melt and the warming treatments were analyzed as categorical variables; however, to assess the effectiveness of the treatments, we measured snow melt date and temperature quantitatively. Mounted time-lapse cameras recorded snow melt timing for four quadrants within each plot. Snow melt timing was defined as at least 50% visible bare ground within the quadrant. The largest variation in snow melt timing among quadrants within the same plot was 2 days (and the mean difference among quadrants within the same plot was less than 1 day). Therefore, since there was very little variation in melt dates within plots, the mean melt date across all four quadrants was used to represent the melt date for all subplots within each plot. A data logger was mounted in the center of each plot from July 3 to August 22, recording the air temperature every 15 min (HOBO data loggers; Onset Computer Corporation). Additional data loggers rotated among *Valeriana* individuals for 1 week at a time throughout the season.

To assess whether the warming chambers and the snow melt treatment acted through accumulated temperature, we calculated the GDD accumulated under each treatment. To calculate GDD, we used an interpolation model with early season temperature data from a weather station ca. 4 km away in Gothic (billy barr, unpublished data) to fill in temperatures between snow melt timing (early to mid-June, depending on the plot) and the date on which we began collecting temperature data (July 3), as well as temperatures for weeks when there was no data logger stationed at an individual

Valeriana (detailed in Appendix 1). GDD was calculated as the mean of the daily temperature low and daily temperature high minus a baseline temperature of 1°C. Forrest and Thomson (2011) show that temperature accumulation for species in this ecosystem is best understood using baseline temperatures between 0 and 1°C. GDD calculated with the baselines of 0 and 1°C, respectively, were highly correlated (Table S1); we therefore used a baseline of 1°C because that was the best baseline temperature for *D. nuttallianum* according to Forrest and Thomson (2011). GDD was calculated from the date of snow melt in each plot to the date of flowering onset (for the responses of peak flowering date and flowering duration) or the date of fruiting onset (for peak fruiting date and fruiting duration). GDD was calculated for each *Valeriana* individual, based on the interpolated data. Since data loggers were not stationed at *Potentilla* and *Delphinium* individuals, their GDD was calculated at the subplot level as the GDD of the closest *Valeriana* individual, or the mean of the closest *Valeriana* individuals if the nearest individuals were equidistant.

2.3.3 | Tracking phenology

Before reproductive structures were visible, five individuals from *Delphinium* and five from *Potentilla* were tagged in each subplot (5 individuals × 3 subplots × 2 warming treatments × 14 plots = 420 individuals per species). *Valeriana* were warmed as part of a larger study, and we were able to increase our sample size of this species by using additional warmed and unwarmed plants in each plot. Because we focused on the timing of reproductive events, we excluded tagged individuals that did not flower (Table S2).

Individual plants within each plot were followed throughout the growing season to determine the timing and duration of flowering and fruiting. Flowering was recorded when flowers were fully open, and the reproductive structures were mature. The number of open flowers was counted on each individual 3 days per week. For *Valeriana*, the number of flowering stalks was counted because *Valeriana* produces hundreds to thousands of small flowers within each inflorescence. Fruiting was recorded when fruits became fully ripe, indicated by fruit drying or color change. Flowering (fruiting) duration was defined as the number of days between the first and last flower (fruit). Peak flowering (fruiting) was defined as the day on which 50% of the cumulative total number of flowers (fruits) were counted on an individual (following Høye, Post, et al., 2007; Iler et al., 2013).

2.3.4 | Measuring reproduction

Plant size is a strong predictor of reproductive output in many species, and size can also affect phenology (Forrest, 2014; Ollerton & Lack, 1998). We therefore included plant size as a covariate when testing for climate effects on plant phenology and reproductive output. Multiple measurements were taken for each species: leaf length, leaf width, and leaf number for *Delphinium*; tallest stem, perimeter, the widest diameter of the plant, and the diameter perpendicular to the widest diameter for *Valeriana*; and leaf length and leaf number for *Potentilla*. Size was measured after flowering started, under the assumption that plants were done growing for the season once they started allocating resources to reproduction. For the two species that produce multiple seeds per fruit, *Delphinium* and *Potentilla*, we collected all mature fruits and counted the total number of seeds produced by each individual in the laboratory. *Valeriana* produces a single seed per flower, thus we were able to quantify seed production for this species in the field using a robust estimation method (following Petry et al. 2016)—seeds were counted in a subset of the inflorescence, then the number of these subsets needed to fill the entire inflorescence was estimated visually. At the end of the field season, some individual *Potentilla* plants still had immature fruit, which were collected in order to count their seeds, so we excluded fruit duration for *Potentilla* from our analysis because the end fruiting date was unknown.

2.4 | Analysis

Sequential phenological events may not be independent of one another, potentially leading to misattribution of cause when dependent events are shifted in time (Li et al., 2016). Therefore, we tested for (i) the dependence of peak fruiting date on peak flowering date; and (ii) the dependence of fruiting duration on flowering duration across the climate treatments using a multivariate ANOVA separately for each species. For each analysis, the response variables (peak dates or durations) were averaged across subplot (plot for the larger *Valeriana*) because the individual-level data violated the assumptions of normality; treatment was analyzed as a categorical variable with four levels because we were only interested in the overall effect of treatment for this analysis. In all three species, fruiting responses to the treatments in terms of peak date and duration were independent of flowering responses (Table S3). Without any evidence that earlier phenological responses constrained later responses, we proceeded to analyze flowering and fruiting responses separately.

Our first set of inferential analyses was designed to test for individual and interactive effects of our climate treatments on plant reproductive phenology and output. We fit generalized linear mixed effects models (GLMMs) to our experimental data using the glmmTMB and lme4 packages (Bates et al., 2015; Brooks et al., 2017) in the r Statistical Environment version 3.5 (R Core Team, 2019). For each response variable, we included fixed effects of snow melt treatment category, warming treatment category, and their interaction. Plant size and sex (for *Valeriana*) were included as fixed effect covariates to control for the dependence of reproductive timing and output on size (or sex). We fit random intercepts for plot (all species) and subplot nested within plot (*Delphinium* and *Potentilla* only) to account for nonindependence among replicate plants caused by the scales at which the snow melt (plot-sized tarp) and warming (subplot-sized chamber) treatments were applied. Model errors were found to be normally distributed (peak date response variables), Poisson-distributed with a log-link (fruit duration in *Valeriana* and flower count in *Delphinium*), or negative binomial distributed with a log-link (all other duration, flower, and seed count variables).

Our second set of inferential analyses was designed to partition out the effect of temperature accumulation from both the warming chamber and advanced snow melt treatments. Doing so allowed us to test whether early snow melt had a distinct cueing effect on plant reproductive responses, or if plants simply were responding to an early start of GDD accumulation. To do these analyses, we simply added the cumulative GDD experienced by individual plants as a fixed effect covariate to the GLMMs described in the previous paragraph. If the effect of snow melt timing on plant reproductive responses functions merely by starting the accumulation of GDD earlier, we would expect that any statistically significant coefficients for snow melt treatment in the first GLMM would no longer be significant when controlling for GDD. Moreover, the addition of the GDD term allows us to test whether warming chambers had effects on plants that were not mediated by temperature accumulation. We expect that the effect of chamber treatment should disappear entirely when GDD is added to the model under the idealized circumstances that warming chambers have no side effects on other drivers of plant performance (e.g., soil moisture, attractiveness to pollinators, etc.). By examining the remaining effect of chamber treatment, we can quantify the extent to which plant responses were affected by these unintended side effects.

We determined which size measurements explained the most variation in phenology for each species by conducting simple linear regression models with each size measurement as a continuous predictor and peak flowering or peak fruiting dates as a continuous response. The measurement with the highest R^2 value was used to represent plant size (Table S4). The best size measurements for each species were tallest stem for *Valeriana*, length of longest leaf for *Potentilla*, and leaf number for *Delphinium*.

3 | RESULTS

3.1 | Treatment effects

Our tarp treatment caused snow to melt on average 9 days earlier compared to un-tarped control plots. Mean (±1 SE henceforth) melt date for control plots was June 12 (±0.06 days) and for early snow melt plots was June 3 (±0.04 days). Open top chambers warmed overall air temperatures an average of 2.1°C; mean temperature for the warming treatment was 16 ± 0.02°C and mean temperature for the control treatment was 13.9 ± 0.03°C. Daytime (06:00–18:00 h) temperatures differed by 2.5°C between treatments, and nighttime (18:00–06:00 h) temperatures differed by 1.7°C between treatments.

Both early snow melt and warming treatments increased the accumulation of temperature (i.e., GDD; Table S5; Figure S1). In the early snow melt treatment, plants gained a 9-day head start on GDD accumulation, whereas the warming treatment accumulated more GDD each calendar day. At the time of flowering and fruiting, the two treatments had a similar magnitude of effect on cumulative GDD, with the highest cumulative GDD in the combined treatment that matched the additive expectation from both treatments individually.

3.2 | Treatment effects on phenology and reproductive success

3.2.1 | Timing

In all three species, the early snow melt treatment shifted flowering earlier (Table 1; Figure 1a–c). In *Delphinium* and *Potentilla*, the warming treatment also shifted flowering earlier (Table 1; Figure 1a,b). For fruiting, in all three species, the early snow melt treatment was at least marginally significant and shifted fruiting earlier (marginally significant for *Potentilla*; Table 1; Figure 1d–f). In *Delphinium* only, the warming treatment also shifted fruiting earlier (Table 1; Figure 1d). There was no significant interaction between snow melt and warming for the timing of flowering or fruiting for any species.

3.2.2 | Duration

Flowering duration for *Delphinium* was only affected by size, with larger plants flowering for a longer period of time, likely because they have more flowers, which flower sequentially (Table 2). For *Valeriana*, the early snow melt treatment led to a 13.6% longer flowering duration and the warming treatment led to a 9% longer flowering duration (Table 2; Figure 2c). In contrast, for *Potentilla*, the warming treatment shortened flowering duration by 36% (Table 2; Figure 2c). Fruit duration for *Delphinium* and *Valeriana* was lengthened only by the early melt treatment (158% and 6%, respectively), and this effect was marginally significant for *Valeriana* (Table 3; Figure 2d,e). There was no significant interaction between snow melt and warming for the duration of flowering or fruiting for any species.

3.2.3 | Reproductive success

We found no evidence that the climate treatments affected the reproductive output of *Valeriana* and *Potentilla*. Only plant size had a significant effect on the number of flowers and seeds, with larger plants having more flowers and seeds in these species (Table 3). However, for *Delphinium*, the warming treatment increased the number of flowers per individual and decreased the total number of seeds per individual, 31% increase and 56% decrease, respectively (Table 3; Figure 3a,d). There also was an interaction between the treatments such that the combined treatment did not see as large of a decline in total individual seed production as expected if the effects of snow melt and warming were additive. Additionally, there

TABLE 1 Summary tables from linear mixed effects models (LMMs) for *Delphinium*, *Valeriana*, and *Potentilla* for the effect of climate manipulations (warming and early snow melt) and plant size on the timing of flowering and fruiting (peak flowering date and peak fruiting date). Subplot or plot was a random effect in LMMs. Bold indicates $p < 0.05$

Response	Species	Predictor	Estimate	SE	*df*	*t* value	*p*
Peak flowering	*Delphinium*	Intercept	193.62	0.92	108.80	209.93	**<0.0001**
		Warming	−2.00	0.82	68.03	−2.44	**0.02**
		Early melt	−6.44	0.82	56.53	−7.81	**<0.0001**
		Warming × Early melt	−0.55	1.18	62.98	−0.47	0.64
		Size	−0.08	0.20	122.91	−0.39	0.70
	Valeriana	Intercept	205.56	1.16	162.67	177.11	**<0.0001**
		Warming	−1.21	0.73	344.61	−1.66	0.10
		Early melt	−4.58	0.78	16.67	−5.89	**<0.0001**
		Warming × Early melt	1.01	1.01	363.99	1.00	0.32
		Size	0.07	0.01	363.00	6.10	**<0.0001**
		Sex	1.97	0.53	357.80	3.69	**<0.001**
	Potentilla	Intercept	211.93	1.84	207.20	115.47	**<0.0001**
		Warming	−4.83	1.31	67.18	−3.70	**<0.001**
		Early melt	−6.33	1.24	59.66	−5.08	**<0.0001**
		Warming × Early melt	−0.65	1.86	66.75	−0.35	0.73
		Size	1.04	0.31	200.77	3.32	**<0.01**
Peak fruiting	*Delphinium*	Intercept	212.85	1.55	49.22	137.65	**<0.0001**
		Warming	−4.61	1.55	36.16	−2.98	**0.01**
		Early melt	−4.81	1.43	30.72	−3.35	**<0.01**
		Warming × Early melt	1.90	2.16	34.73	0.88	0.38
		Size	−0.20	0.34	45.90	−0.60	0.55
	Valeriana	Intercept	218.14	0.94	247.00	232.81	**<0.0001**
		Warming	−0.35	0.61	247.00	−0.57	0.57
		Early melt	−1.89	0.51	247.00	−3.73	**<0.001**
		Warming × Early melt	−0.22	0.83	247.00	−0.27	0.79
		Size	0.01	0.01	247.00	1.40	0.16
	Potentilla	Intercept	231.78	1.40	93.84	165.73	**<0.0001**
		Warming	−0.52	0.94	41.64	−0.55	0.58
		Early melt	−1.52	0.88	28.84	−1.73	0.09
		Warming × Early melt	−0.10	1.30	39.33	−0.08	0.94
		Size	0.22	0.24	104.82	0.90	0.37

was a marginally significant interaction in *Potentilla* such that the combined treatment had more flowers than expected if the nonsignificant positive effects of snow melt and the nonsignificant negative effects of warming were additive.

3.3 | Temperature accumulation effects on phenology

In our first analysis, we found no subadditive interactions between the two treatments in the phenological responses (the only significant interaction was for seed production in *Delphinium*), which we would have expected if the snow melt treatment was masking the effect of temperature and acting through temperature accumulation. To investigate further and more explicitly test if the treatments were acting through temperature accumulation, we ran additional analyses looking at the effect of GDD.

The effect of the snow melt treatment on the timing of flowering persisted after accounting for GDD in all three species (Table 4; Figure 4). In both *Delphinium* and *Valeriana*, there was evidence for GDD shifting the timing of flowering in conjunction with snow melt (as both snow melt and GDD were significant in the second analysis). However, the effect of GDD in *Delphinium* and *Valeriana* seems to be driven by different mechanisms. A previously significant warming effect for *Delphinium* became nonsignificant in the second analysis when the effect of GDD was included, showing that effects of warming were due to temperature accumulation. For *Valeriana*, there was no evidence of the warming treatment shifting flowering

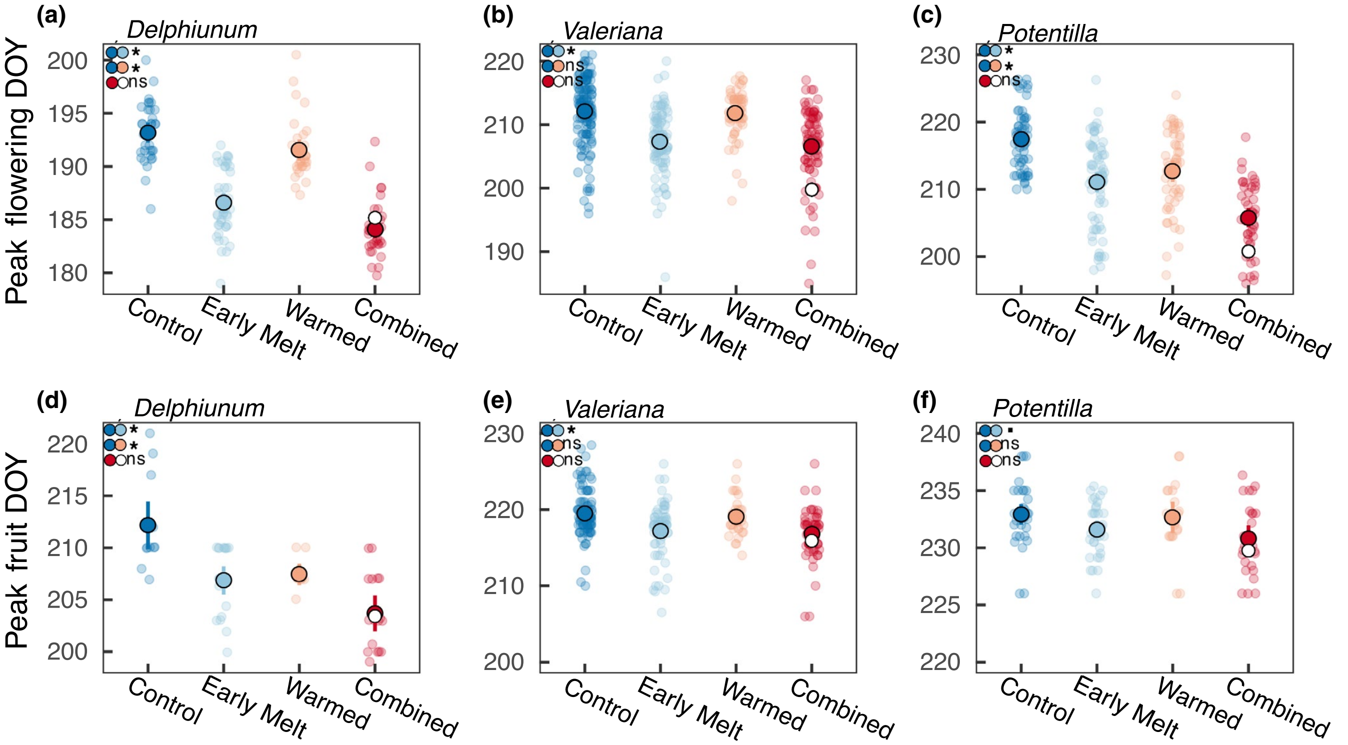


FIGURE 1 Timing of flowering and fruiting, shown in day of year (DOY) across four treatments: control, early melt, warming, and a combination of early melt and warming. Solid dots are means, and error bars represent 95% confidence intervals. Open circles represent the additive expectation when the warming and melt treatment effects are combined. In the legends, asterisks indicate significant differences at $p < 0.05$, dots indicate marginally significant comparisons at $0.05 < p < 0.10$, and "ns" indicates nonsignificant comparisons. Note that y-axes are on different scales because species flower and fruit on different dates [Colour figure can be viewed at wileyonlinelibrary.com]

timing in the first analysis, therefore the effect of GDD in the second analysis is a result of the early snow melt treatment. There was no evidence for GDD shifting the timing of flowering in *Potentilla*.

The timing of fruiting for *Delphinium* was driven by GDD, because in the second analysis the snow melt treatment was no longer significant and GDD was significant (Table 4; Figure 4). For *Potentilla*, there was no evidence for any of climate variables (including GDD) shifting the timing of fruiting in the second analysis. For *Valeriana*, the effect of the snow melt treatment persisted after accounting for GDD.

The effects of the snow melt treatment on flower duration persisted after accounting for GDD for *Valeriana* (Table 5; Figure 4). In the other two species, the snow melt treatment was not significant in the first analysis. For *Potentilla*, the effect of the warming treatment persisted after accounting for GDD, indicating that something other than warming may have affected flowering duration in the OTC. The effects of both the snow melt and warming treatments on fruit duration persisted after accounting for GDD for *Valeriana* (Table 5; Figure 4). However, for *Delphinium* the effect of the snow melt treatment was no longer significant after GDD was included in the model.

4 | DISCUSSION

Multiple aspects of climate may cue a single phenological event, and these cues often change at different rates as the climate changes (Bernhardt et al., 2020). Climatic cues may also covary, making it difficult to tease apart their independent effects. Disentangling the effects of correlated climatic cues that are being altered by climate change at different rates is a substantial challenge, but doing so will improve our mechanistic understanding of phenology. This study disentangled the effects of two correlated climatic cues, snow melt timing and temperature, on the reproductive phenology of subalpine plants. Our results indicate that multiple climatic cues can drive reproductive phenology simultaneously and that a single climatic cue can have multiple mechanisms for affecting phenology. We find that snow melt timing is a consistently important cue of plant phenology, but that the mechanisms behind snow melt as a cue of phenology vary among species and phenological stages. In some species, snow melt is driving phenology through the earlier accumulation of temperature, while in others snow melt is driving phenology through mechanisms other than temperature accumulation (e.g., perhaps soil moisture). Additionally, these mechanisms are not mutually exclusive, with examples of plant reproductive phenology responding to both temperature accumulation and snow melt cues.

We provide novel experimental evidence that snow melt can act independently of temperature accumulation, by examining whether the effects of experimentally advanced snow melt persist after statistically accounting for the effects of GDD. We observed that snow melt timing can act independently from the warming treatment, when early snow melt and the combined treatments advance

TABLE 2 Summary tables from generalized linear mixed effects models (GLMMs) for *Delphinium*, *Valeriana*, and *Potentilla* for the effect of climate manipulations (warming and early snow melt) and plant size on the duration of flowering and fruiting. Plot or subplot was a random effect in GLMMs. Bold indicates $p < 0.05$

Response	Species	Predictor	Estimate	SE	*z* value	*p*
Flower duration	*Delphinium*	Intercept	1.66	0.18	9.08	**<0.0001**
		Warming	0.18	0.14	1.32	0.19
		Early melt	0.01	0.14	0.08	0.94
		Warming × Early melt	−0.15	0.21	−0.74	0.46
		Size	0.17	0.04	3.91	**<0.0001**
	Valeriana	Intercept	3.34	0.05	60.85	**<0.0001**
		Warming	0.09	0.03	2.57	**0.01**
		Early melt	0.13	0.03	4.06	**<0.0001**
		Warming × Early melt	−0.04	0.05	−0.83	0.41
		Size	0.00	0.00	5.41	**<0.0001**
		Sex	0.10	0.02	3.83	**<0.001**
	Potentilla	Intercept	2.31	0.22	10.72	**<0.0001**
		Warming	−0.31	0.13	−2.39	**0.02**
		Early melt	−0.11	0.12	−0.86	0.39
		Warming × Early melt	0.08	0.19	0.42	0.67
		Size	0.16	0.04	4.18	**<0.0001**
Fruit duration	*Delphinium*	Intercept	−0.60	0.43	−1.40	0.16
		Warming	0.31	0.41	0.75	0.45
		Early melt	0.95	0.36	2.66	**0.01**
		Warming × Early melt	−0.14	0.49	−0.28	0.78
		Size	0.24	0.08	3.25	**<0.01**
	Valeriana	Intercept	3.23	0.05	59.35	**<0.0001**
		Warming	0.01	0.03	0.25	0.80
		Early melt	0.06	0.03	1.92	0.06
		Warming × Early melt	−0.05	0.05	−1.01	0.31
		Size	0.00	0.00	5.80	**<0.0001**

phenology but warming does not (e.g., peak fruiting in *Valeriana*). However, this does not preclude the possibility that snow melt timing is simply acting through temperature accumulation, as early snow melt would expose plants to spring temperatures and light earlier. In six out of nine cases where the snow melt treatment shifted phenology, either alone or in conjunction with the warming treatment, the effect of the snow melt treatment persisted after GDD was included in the model (Figure 4), supporting the hypothesis that snow melt affects phenology independent of temperature accumulation. It has been previously suggested that the influx of soil moisture after snow melt helps drive the onset of flowering (Dorji et al., 2013; Song et al., 2020; Walker et al., 1995), and this may be the mechanism behind our observed effect of snow melt on phenology. There is also observational evidence that rainfall and soil moisture affect flowering phenology in other, arid ecosystems (Crimmins et al., 2010; Gordo & Sanz, 2010; Peñuelas et al., 2004; Pérez-Ramos et al., 2020; Song et al., 2020). We also find that in two of these cases, both the snow melt treatment and temperature accumulation changed the timing of flowering, indicating that the timing of snow melt has multiple, nonmutually exclusive mechanisms for affecting plant phenology (Figure 4).

The relative ability of temperature accumulation and snow melt timing to predict spring phenology in high-elevation and high-latitude environments appears to vary among species as well as between phenological stages (Kelsey et al., 2020; Quaglia et al., 2020; Theobald et al., 2017; Wipf, 2010). Following this, we found that temperature accumulation did cue phenology (in tandem with other drivers) for some, but not all species and not all responses. Temperature accumulation was the sole cue of phenological changes in only two out of nine cases (Figure 4: timing and duration of fruiting in *Delphinium*), and temperature accumulation worked in tandem with other drivers in an additional two cases (Figure 4: timing of flowering in *Delphinium* and *Valeriana*). Temperature accumulation as a phenological cue may be less important in ecosystems with seasonal snow cover compared to those where temperature is the main climate driver (Augspurger & Zaya, 2020).

Many studies use passive warming chambers to simulate climate change, and while we show that they do raise temperatures and shift

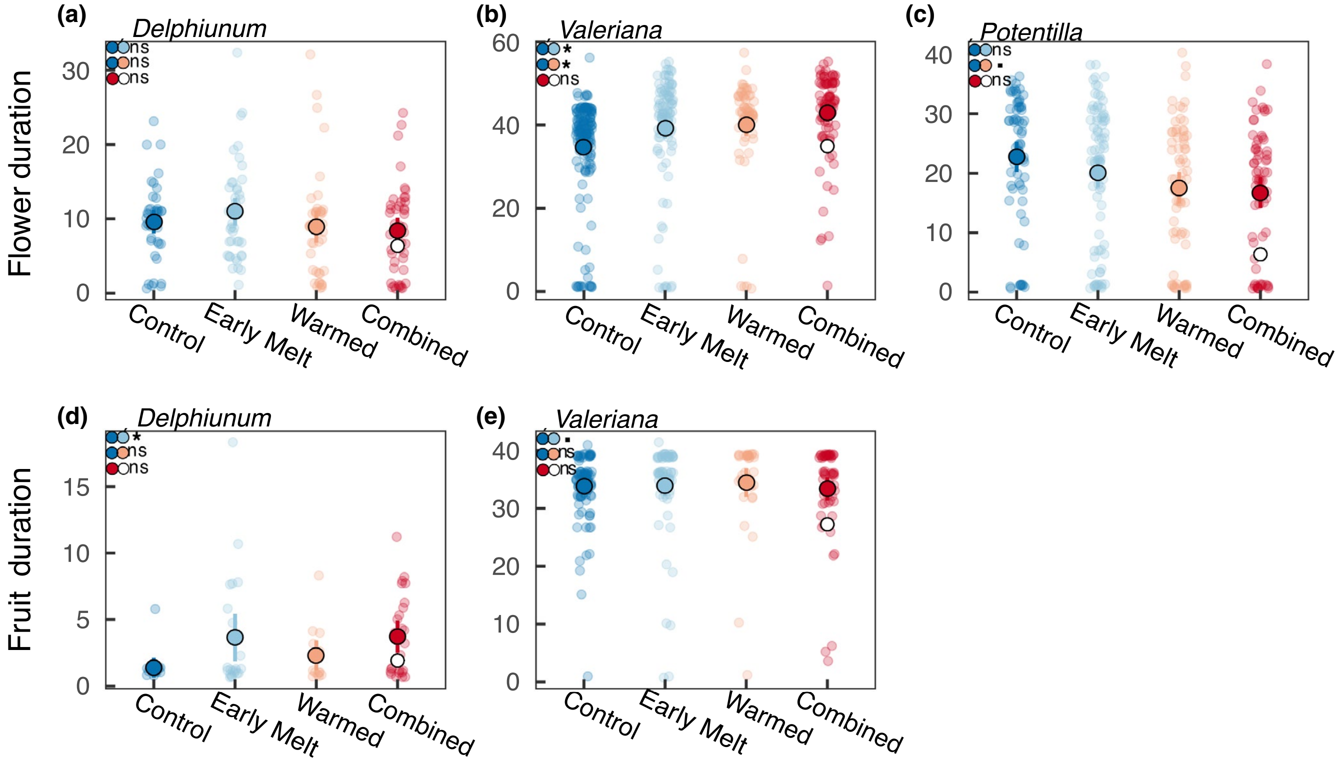


FIGURE 2 Duration flowering and fruiting, shown in number of days across four treatments: control, early melt, warming, and a combination of early melt and warming. Solid dots are means, and error bars represent 95% confidence intervals. Open circles represent the additive expectation when the warming and melt treatment effects are combined. In the legends, asterisks indicate significant differences at $p < 0.05$, dots indicate marginally significant comparisons at $0.05 < p < 0.10$, and "ns" indicates nonsignificant comparisons. Note that y-axes are on different scales because species flower and fruit on different dates [Colour figure can be viewed at wileyonlinelibrary.com]

phenology as expected, they also have been shown to have other effects, such as reduced winds and lower humidity (e.g., Marion et al., 1997). We found three cases where the warming chambers had effects other than a change to temperature accumulation, though our experiment was not designed to identify the exact cause of these side effects. These effects were exhibited when the warming treatment continued to be significant in the second analysis after accounting for temperature accumulation (flowering date and duration in two species; Figure 4). These results indicate that there may be other climatic factors that influence phenology and the duration of life cycle events in this ecosystem for which we have yet to account.

The duration of life-history events is responding to climate change in part because of disparate shifts in the onset and ending of events (CaraDonna et al., 2014), but climate-induced changes to the duration of events are not as well studied as their timing and the findings are not as consistent. Some studies have found that flower duration or season length changed in response to climate change, although the direction and magnitude were not always the same (Dunne et al., 2003; Li et al., 2016; Sethi et al., 2020). However, several studies have found the duration of phenological stages to be unresponsive to climate change (Jabis et al., 2020; Price & Waser, 1998; Semenchuk et al., 2016). Similarly, we found that the duration of flowering and fruiting of some species did not change significantly under warming and earlier snow melt, whereas other species showed shorter or longer duration of reproductive phases. If climate change causes the duration of flowering to lengthen in some species, but shorten, or remain unchanged in others as we find here, this may change co-flowering overlap, potentially shifting competition for resources, such as pollinators (Forrest et al., 2010; Mitchell et al., 2009; Faust & Iler, unpublished). Much less is known about whether species co-fruiting periods will also be shifted under climate change, but our results suggest this to be the case. Altered patterns of fruiting overlap may have implications for interactions among seed predators and seed dispersers in species with animal-dispersed seeds.

We found no evidence for changes to reproductive success because of climate manipulation in two of the species, potentially because phenological shifts in these species allowed them to track optimal conditions for flowering and fruiting. Both the warming and the snow melt treatments gave rise to climatic changes on par with previous climate changes in subalpine ecosystems (Anderson et al., 2012; IPCC, 2014; Ogilvie et al., 2017). However, 2019 was a relatively late snow melt year, occurring 18 days later than the long-term average at the RMBL (1975–2018; barr, 2020). Therefore, the early snow melt treatment was more reflective of current conditions, and the control treatment was more reflective of historic climatic conditions. Previous studies found decreased flowering under early snow melt due to increased frost damage (Gezon et al., 2016; Høye, Mølgaard Ellebjerg, et al., 2007; Inouye, 2008; Thomson, 2010), but *Delphinium* and *Potentilla* are not particularly sensitive to frost

TABLE 3 Summary tables from generalized linear mixed effects models (GLMMs) for *Delphinium*, *Valeriana*, and *Potentilla* for the effect of climate manipulations (warming and early snow melt) and plant size on the number of flowers and seeds per individual. Plot or subplot was a random effect in GLMMs. Bold indicates $p < 0.05$

Response	Species	Predictor	Estimate	SE	*z* value	*p*
Flower count	*Delphinium*	Intercept	0.55	0.15	3.58	**<0.001**
		Warming	0.27	0.14	1.96	**0.05**
		Early melt	0.04	0.14	0.29	0.77
		Warming × Early melt	0.00	0.20	0.00	1.00
		Size	0.14	0.03	4.24	**<0.0001**
	Valeriana	Intercept	0.49	0.17	2.89	**<0.01**
		Warming	0.09	0.10	0.86	0.39
		Early melt	0.06	0.10	0.65	0.52
		Warming × Early melt	−0.08	0.14	−0.57	0.57
		Size	0.01	0.00	3.88	**<0.001**
		Sex	0.10	0.07	1.38	0.17
	Potentilla	Intercept	0.79	0.18	4.33	**<0.0001**
		Warming	−0.07	0.13	−0.54	0.59
		Early melt	0.19	0.12	1.58	0.11
		Warming × Early melt	−0.30	0.18	−1.68	0.09
		Size	0.13	0.03	4.22	**<0.0001**
Seed count	*Delphinium*	Intercept	3.60	0.27	13.19	**<0.0001**
		Warming	−0.82	0.23	−3.53	**<0.001**
		Early melt	−0.21	0.21	−0.99	0.32
		Warming × Early melt	0.67	0.33	2.05	**0.04**
		Size	0.22	0.07	3.23	**<0.01**
	Valeriana	Intercept	3.71	0.35	10.56	**<0.0001**
		Warming	−0.17	0.19	−0.85	0.39
		Early melt	0.30	0.22	1.35	0.18
		Warming × Early melt	−0.33	0.26	−1.26	0.21
		Size	0.03	0.00	10.01	**<0.0001**
	Potentilla	Intercept	4.64	0.35	13.34	**<0.0001**
		Warming	−0.26	0.19	−1.37	0.17
		Early melt	0.10	0.19	0.55	0.59
		Warming × Early melt	−0.32	0.28	−1.16	0.25
		Size	0.21	0.06	3.55	**<0.001**

damage (frost sensitivity is unknown in *Valeriana*; CaraDonna & Bain, 2016, CaraDonna & Bain, unpublished data). Our experiment provides a rigorous method for disentangling the effects of early snow melt and warmer temperatures under realistic, near-term changes in average conditions; however, if climate change creates more extreme conditions, effects on reproductive output may unfold differently.

Delphinium was the only species in which the climate manipulations affected reproductive output. Warming increased *Delphinium* flower abundance, whereas previous studies found the opposite effect in the same species (Saavedra et al., 2003). This discrepancy is likely due to a difference in warming methodology. Saavedra et al. (2003) used active warming through infrared radiation, which decreases soil moisture and can lead to increased flower abortion (Saavedra et al., 2003). We also found a reduced seed count per plant in the warming treatment for *Delphinium*. A study at the same site found that OTC reduced visitation rates by 96% in *Delphinium* and 81% in *Potentilla*. The same study also found OTC reduced the mean number of pollen grains on *Delphinium* stigmas by 73%, but did not affect pollen deposition to *Potentilla*, in part because *Potentilla* is capable of autonomous self-pollination (Adamson & Iler, in review). Although reduced pollination could explain the decrease in seeds under the warming treatment, there was no similar decrease in the combined warming × snow melt treatment, suggesting that the exclusion of pollinators within the chambers was not the cause of a decrease in seeds. In fact, the combined treatment had more seeds than expected under additive effects of snow melt and warming. This suggests that warming, or at least OTC, exerted a direct negative effect on seed production in *Delphinium* that was counteracted by the snow melt treatment when they were combined.

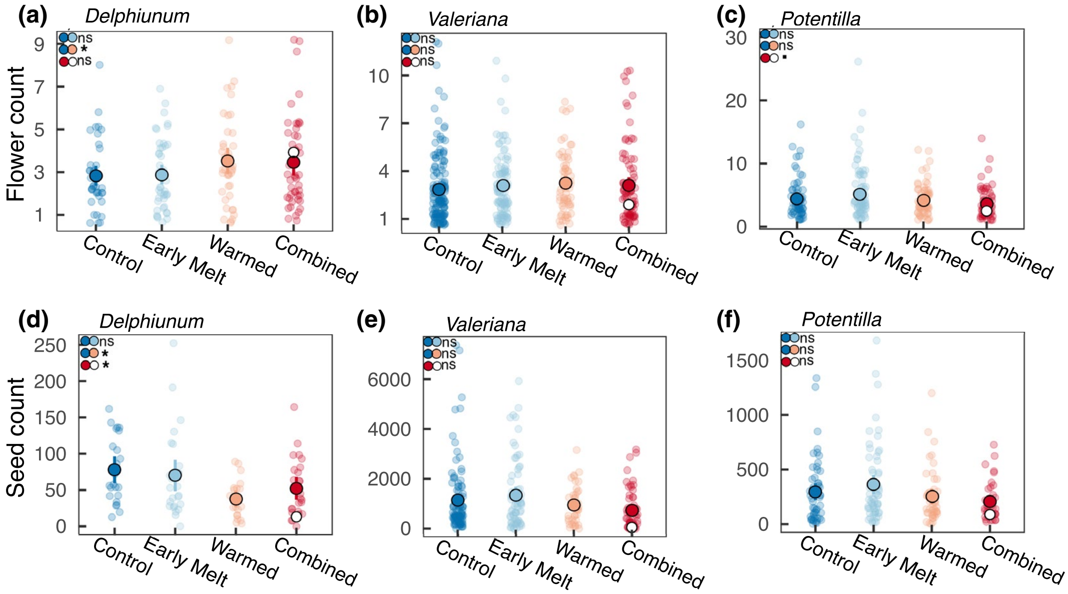


FIGURE 3 Number of flowers and seeds per individual, across four treatments: control, early melt, warming, and a combination of early melt and warming. Solid dots are means, and error bars represent 95% confidence intervals. Open circles represent the additive expectation when the warming and melt treatment effects are combined. In the legends, asterisks indicate significant differences at $p < 0.05$, dots indicate marginally significant comparisons at $0.05 < p < 0.10$, and "ns" indicates nonsignificant comparisons. Note that y-axes are on different scales because species have varied amounts of flowers and seeds [Colour figure can be viewed at wileyonlinelibrary.com]

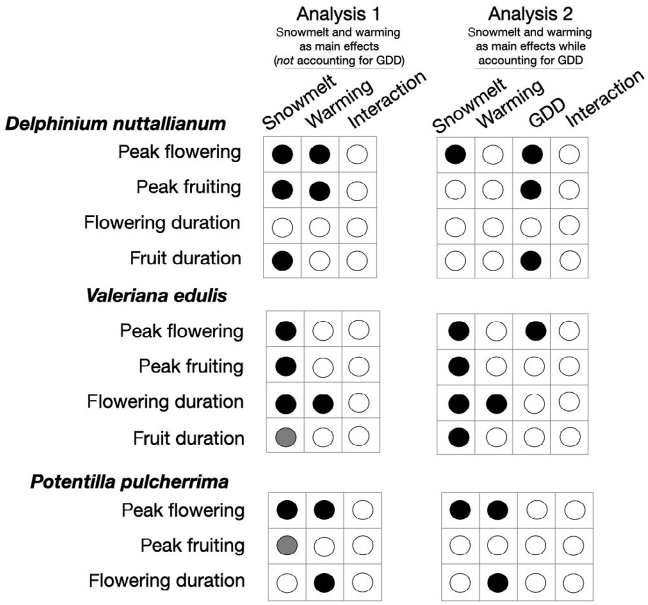
TABLE 4 Summary tables from linear mixed effects models (LMMs) for *Delphinium*, *Valeriana*, and *Potentilla* for the effect of growing degree days (GDD), climate manipulations (warming and early snow melt), and plant size on the timing of flowering and fruiting (peak flowering date and peak fruiting date). Subplot was a random effect in LMMs. Bold indicates $p < 0.05$

Response	Species	Predictor	Estimate	SE	*df*	*t* value	*p*
Peak flowering	*Delphinium*	Intercept	201.98	2.32	67.04	87.19	**<0.0001**
		Warming	−0.79	0.84	60.98	−0.94	0.35
		Early melt	−4.31	0.95	53.12	−4.53	**<0.0001**
		Warming × Early melt	−0.53	1.12	57.13	−0.48	0.64
		GDD	−0.02	0.01	61.57	−3.92	**<0.001**
		Size	−0.07	0.19	113.43	−0.34	0.73
	Valeriana	Intercept	210.50	2.49	15.65	84.43	**<0.0001**
		Warming	−0.74	0.77	165.37	−0.96	0.34
		Early melt	−3.42	0.88	15.96	−3.90	**<0.01**
		Warming × Early melt	1.26	1.03	347.87	1.22	0.22
		GDD	−0.01	0.01	13.42	−2.36	**0.03**
		Size	0.08	0.01	347.99	6.45	**<0.0001**
		Sex	1.91	0.54	330.70	3.52	**<0.001**
	Potentilla	Intercept	210.94	5.37	83.84	39.31	**<0.0001**
		Warming	−4.86	1.53	64.53	−3.19	**<0.01**
		Early melt	−6.70	1.36	56.79	−4.92	**<0.0001**
		Warming × Early melt	−0.07	1.82	66.58	−0.04	0.97
		GDD	0.00	0.01	66.77	0.17	0.87
		Size	1.07	0.31	192.15	3.44	**<0.001**

(Continues)

TABLE 4 (Continued)

Response	Species	Predictor	Estimate	SE	*df*	*t* value	*p*
Peak fruiting	*Delphinium*	Intercept	235.63	7.21	27.28	32.67	**<0.0001**
		Warming	−1.12	1.77	29.96	−0.63	0.53
		Early melt	−2.27	1.57	26.61	−1.44	0.16
		Warming × Early melt	2.32	2.02	28.37	1.15	0.26
		GDD	−0.03	0.01	27.48	−3.22	**<0.01**
		Size	−0.07	0.34	43.72	−0.22	0.83
	Valeriana	Intercept	217.96	2.15	15.54	101.43	**<0.0001**
		Warming	−0.36	0.62	116.84	−0.58	0.56
		Early melt	−1.84	0.58	18.30	−3.14	**0.01**
		Warming × Early melt	−0.50	0.81	233.92	−0.62	0.54
		GDD	0.00	0.01	227.29	0.39	0.70
		Size	0.00	0.00	14.64	0.52	0.61
	Potentilla	Intercept	239.32	5.35	46.42	44.70	**<0.0001**
		Warming	0.55	1.23	33.15	0.45	0.66
		Early melt	−1.17	0.99	24.96	−1.18	0.25
		Warming × Early melt	0.25	1.39	36.32	0.18	0.86
		GDD	−0.01	0.00	38.49	−1.47	0.15
		Size	0.19	0.26	94.62	0.74	0.46



	Analysis 1 Snowmelt and warming as main effects (*not* accounting for GDD)			Analysis 2 Snowmelt and warming as main effects while accounting for GDD			
	Snowmelt	Warming	Interaction	Snowmelt	Warming	GDD	Interaction
Delphinium nuttallianum							
Peak flowering	●	●	○	●	○	●	○
Peak fruiting	●	●	○	○	○	●	○
Flowering duration	○	○	○	○	○	○	○
Fruit duration	●	○	○	○	○	●	○
Valeriana edulis							
Peak flowering	●	○	○	●	○	●	○
Peak fruiting	●	○	○	●	○	○	○
Flowering duration	●	●	○	●	●	○	○
Fruit duration	◍	○	○	●	○	○	○
Potentilla pulcherrima							
Peak flowering	●	●	○	●	●	○	○
Peak fruiting	◍	○	○	○	○	○	○
Flowering duration	○	●	○	○	●	○	○

FIGURE 4 The combined results of the first and second analyses for phenology and duration (reproductive success was not included because growing degree days, GDD, is not expected to affect reproduction). Black indicates a significant effect ($p < 0.05$), gray indicates a marginally significant effect ($0.05 < p < 0.10$), and white indicates no significant effect ($p > 0.10$)

Montane environments have a short growing season, and as a result, there is likely a trade-off between flowering earlier to have the most time to reproduce, and growing for longer before allocating resources to reproduction (Forrest, 2014). Indeed, there is indirect evidence for both strategies: in some plant species, larger individuals flower earlier, and in others, larger individuals flower later (Forrest, 2014; Ollerton & Lack, 1998; Stinson, 2004). We found that in *Valeriana* and *Potentilla*, larger plants flowered later, suggesting these species may benefit from a longer period of growth prior to reproduction. In contrast, we found no effect of size on the timing of flowering in *Delphinium*. Although larger plants have a reproductive advantage across species and size can play a role in the timing of flowering, it remains unclear exactly how and why plant size is often related to phenology, especially because effects vary among species.

Shifts in phenological events are occurring in a variety of ecosystems across the globe, but climate change encompasses more than just rising temperatures, and organisms may be responding to more than one environmental cue when they shift their phenology. Our results highlight the importance of studying changes to phenology in response to precipitation change, in addition to how precipitation and temperature changes act in combination. Here we show that a single climatic cue—snow melt timing—can have multiple mechanisms for driving phenology. Although there is ample experimental and observational evidence that the timing of snow melt affects flowering phenology (Bjorkman et al., 2015; Høye, Mølgaard Ellebjerg, et al., 2007; Price & Waser, 1998; Steltzer et al., 2009), it has remained unclear whether snow melt simply acts through temperature accumulation or whether it can cue phenological events independently from temperature. This distinction is important because it improves our mechanistic understanding of how snow melt timing acts as a phenological cue. We find support for snow melt acting via both mechanisms: independent of temperature accumulation and through temperature accumulation. Thus, snow melt timing should *not* be exclusively viewed as a proxy for temperature accumulation—instead, snow melt is also likely affecting phenology

TABLE 5 Summary tables from generalized linear mixed effects models (GLMMs) for *Delphinium*, *Valeriana*, and *Potentilla* for the effect of growing degree days (GDD), the climate manipulations (warming and early snow melt), and plant size on the duration of flowering and fruiting. Plot or subplot was a random effect in GLMMs. GDD and size are scales to have a mean of 0 and a SD of 1 in flower and fruit duration in *Valeriana* and in flower duration in *Delphinium*. Bold indicates $p < 0.05$

Response	Species	Predictor	Estimate	SE	*z* value	*p*
Flower duration	*Delphinium*	Intercept	1.59	0.44	3.65	**<0.001**
		Warming	−0.08	0.15	−0.49	0.63
		Early melt	0.11	0.18	0.60	0.55
		Warming × Early melt	−0.04	0.21	−0.20	0.84
		GDD	0.00	0.00	0.19	0.85
		Size	0.18	0.04	4.05	**<0.0001**
	Valeriana	Intercept	3.61	0.02	145.22	**<0.0001**
		Warming	0.08	0.04	2.25	**0.02**
		Early melt	0.11	0.04	3.24	**<0.01**
		Warming × Early melt	−0.05	0.05	−0.95	0.34
		GDD	0.02	0.02	1.17	0.24
		Size	0.06	0.01	4.78	**<0.0001**
		Sex	0.09	0.03	3.54	**<0.001**
	Potentilla	Intercept	1.56	0.69	2.26	**0.02**
		Warming	−0.38	0.17	−2.31	**0.02**
		Early melt	−0.19	0.15	−1.27	0.20
		Warming × Early melt	0.06	0.19	0.33	0.74
		GDD	0.00	0.00	1.19	0.23
		Size	0.16	0.04	4.06	**<0.0001**
Fruit Duration	*Delphinium*	Intercept	0.89	0.40	2.21	**0.03**
		Warming	−0.30	0.48	−0.61	0.54
		Early melt	0.47	0.43	1.09	0.28
		Warming × Early melt	−0.21	0.49	−0.44	0.66
		GDD	0.49	0.21	2.28	**0.02**
		Size	0.32	0.11	3.05	**<0.01**
	Valeriana	Intercept	3.50	0.02	167.58	**<0.0001**
		Warming	0.01	0.03	0.38	0.71
		Early melt	0.08	0.03	2.57	**0.01**
		Warming × Early melt	−0.03	0.05	−0.57	0.57
		GDD	−0.02	0.01	−1.30	0.19
		Size	0.06	0.01	4.98	**<0.0001**

via changes in the timing or pulse of soil moisture, providing avenues for future research on the mechanistic role of snow melt timing, and precipitation in general, as a phenological cue.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the EDI Data Portal at https://doi.org/10.6073/pasta/8831719d04c94504eed6b12318ed7312.

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SUPPORTING INFORMATION

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