

EARLY SNOWMELT AND WARMING INDEPENDENTLY DRIVE THE REPRODUCTIVE PHENOLOGY OF SUBALPINE WILDFLOWERS

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19 **Signature page**

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Abstract

Phenology—the timing of life events—determines how a species’ life cycle aligns with the abiotic and biotic environment. However, climate change has and will continue to alter, the cues that organisms use to track optimal climates through shifting phenology. Understanding the mechanisms behind these phenological shifts is critical to predicting future change. In high elevation and high latitude environments, phenological shifts are associated with both temperature and the timing of snowmelt, but the mechanism for snowmelts control of phenology remains unclear. To address this knowledge gap, we factorially crossed early snowmelt and warming to (1) disentangle the effects of snowmelt timing and warming on reproductive phenology and fitness of three subalpine plant species and (2) test whether the effects of snowmelt are accounted for by a change in temperature accumulation, or instead manifest as a distinct phenological driver. We find that snowmelt timing often acts independently of temperature to drive plant phenology. In most cases, the snowmelt treatment worked either independently or in conjunction with warming to shift phenology earlier, indicating an additional mechanism underlying the effect of snowmelt on plant phenology (e.g., soil moisture). There was only one species where snowmelt timing affected phenology through temperature accumulation. Both the timing and duration of flowering and fruiting were susceptible to shifts under climate manipulations, however timing was more sensitive to climate than duration, and flowering was more sensitive than fruiting. Despite marked responses of reproductive phenology to these climate drivers, the species studied showed little decline in reproductive output, with only one species producing fewer seeds under the warming treatment. Our results suggest that many organisms are likely dealing with changes to multiple environmental cues, and by studying

44 climatic variables in isolation we may be missing a key dimension of how species are responding
45 to climate change.

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60	Table of Contents	Page
61		
62	Title page.....	{1}
63	Signature page.....	{2}
64	Abstract.....	{3-4}
65	Acknowledgements.....	{5}
66	Table of Contents.....	{6}
67	List of Tables.....	{7}
68	List of Figures.....	{8}
69	Introduction	{9-11}
70	Methods.....	{12-17}
71	Results.....	{18-20}
72	Discussion.....	{20-26}
73	References.....	{27-31}
74	Figures and Tables.....	{32-39}
75	Supplemental Figures and Tables.....	{40-44}
76	Appendix.....	{45-46}
77		
78		
79		

80	List of Tables	Page
81	Table 1. Effect of treatments on the timing of flowering and fruiting.....	{32}
82		
83	Table 2. Effect of treatments on the duration of flowering and fruiting.....	{33}
84		
85	Table 3. Effect of treatments on the number of flowers and seeds per individual.....	{34}
86		
87	Table 4. Effect of GDD and treatments on the timing of flowering and fruiting.....	{35}
88		
89	Table 5. Effect of GDD and treatments on the duration of flowering and fruiting.....	{36}
90		
91	Table S1. Correlation between size and the timing of flowering or fruiting.....	{41}
92		
93	Table S2. Effect of climate on the GDD at the onset of flowering.....	{42}
94		
95	Table S3. Effect of climate on the GDD at the onset of fruiting.....	{43}
96		
97	Table S4. MANOVA for timing and duration of flowering and fruiting.....	{44}
98		
99		
100		

101	List of Figures	Page
102	Figure 1. Timing of flowering and fruiting, in day of year (DOY) across treatments.....	{37}
103	Figure 2. Duration of flowering and fruiting, in number of days across treatments	{38}
104	Figure 3. Number of flowers and seeds per individual across treatments	{39}
105	Figure S1. Growing degree days at flowering and fruiting across treatments.....	{40}
106		

Introduction

Virtually all organisms require specific environmental conditions to optimally complete their life history events. As such, the timing of life history events with respect to the environment is critical to their success (Forrest and Miller-Rushing, 2010). There are a wide range of environmental variables that could signal when conditions are optimal in a seasonal environment. Failure to respond to changing seasonal conditions can have considerable consequences for the survival and reproduction of species, and climate change is rapidly altering these seasonal cues (Cleland et al., 2012; IPCC, 2014; Moller et al., 2008). In theory, the timing of life history events – phenology – should closely track climatic fluctuations through time by following changes to these environmental signals. Similarly, the duration of phenological events may change as a result of climate fluctuation, and the length of events such as flowering and fruiting can affect interactions with mutualists, antagonists, and therefore reproduction (Augspurger and Zaya, 2020; Ettinger et al., 2018; Inouye et al., 2003; Li et al., 2016; Semenchuk et al., 2016). If phenological changes are accurately tracking optimal climatic conditions, there should be minimal negative consequences for fitness, yet, if changes in phenology expose an organism to suboptimal conditions, fitness could decline (Høye et al., 2007a; Inouye, 2008).

For plants, temperature and precipitation are important climatic cues for phenological events (*reviewed in* Rathcke, 1985). Temperature catalyzes the onset of phenological events through the accumulation of heat (growing degree days), and rising temperatures due to climate change are associated with earlier life cycle events (CaraDonna et al., 2014; Forrest and Miller-Rushing, 2010; Parmesan, 2006; Parmesan and Yohe, 2003; Thackeray et al., 2010). Seasonal changes in precipitation have also been associated with shifts in plant phenology (Cleland et al.,

2007; Crimmins et al., 2010; Keller and Körner, 2003), but the mechanisms by which precipitation influences plant phenology remain largely unknown. Additionally, temperature and precipitation are often correlated, making it challenging to determine the underlying driver of phenological events (Iler et al., 2013). For example, warmer temperatures lead to earlier snowmelt timing. Temperature and precipitation are often studied in isolation, although they may interact with one another to affect plant phenology (Diez et al., 2012). Critically, accurate predictions of phenology depend on understanding the mechanisms that drive phenological change (Richardson et al., 2013), and teasing apart the combined and independent effects of temperature and precipitation on plant phenology will improve our understanding of these mechanisms.

It is clear that both snowmelt timing and warming affect plant phenology at high elevations and high latitudes (Dunne et al., 2003; Høye et al., 2007b; Jabis et al., 2020; Price and Waser, 1998; Saavedra et al., 2003; Wipf and Rixen, 2010) and disentangling the contributions of these environmental factors is especially important because climate change is having disproportionately large effects on plant phenology in these ecosystems (Ziello et al., 2009). One possible mechanism by which snowmelt timing drives phenology is that earlier snowmelt allows temperatures to begin to accumulate at earlier dates (assuming that temperatures are above organism-specific threshold values). If snowmelt timing is shifting phenology via temperature accumulation alone, then snowmelt would not be an independent driver of phenology and instead may be acting as temperature accumulation in disguise. A second, and non-mutually exclusive, possible mechanism is that snowmelt affects phenology via changes in soil moisture. There is evidence for this from studies in which the advancement or delay of snowmelt 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). Yet, to fully understand whether snowmelt timing cues plant phenology independently from temperature, a factorial manipulation of early snowmelt and warming is necessary. To our knowledge this approach has not yet been applied to reproductive phenology (but see Wang et al., 2018 for germination and Livensperger et al., 2019 for leaf senescence).

Here, we assess the phenology and reproduction of three species in a field experiment that factorially crossed warming with early snowmelt timing in a subalpine meadow to answer the two following questions. 1) *How does snowmelt timing and warming affect the timing, duration, and reproductive output?* We predicted that both early snowmelt and warming would lead to earlier flowering and fruiting, with the earliest timing in the combined treatments. Because duration depends to some extent on the timing of events, we also expected changes to the duration of flowering and fruiting. If plants are tracking their preferred environments by shifting their phenological events, we predict that flower and seed production should not be affected by early snowmelt and warming. Alternatively, if phenological shifts expose plants to new environmental conditions then flower and seed production may instead decrease. (2) *Does snowmelt timing affect reproductive phenology through temperature accumulation, or is snowmelt timing an independent cue?* We predicted that if the effects of snowmelt timing and warming date driven by the same mechanisms, snowmelt timing will simply affect phenology through the accumulation of temperature. however, if instead the effects of snowmelt timing and warming are independent, then snowmelt timing will affect phenology beyond the accumulation of temperature.

Methods

Study site. This study was conducted in a subalpine meadow at 3,000 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 snowmelt in this area is variable year to year, but there is a trend towards earlier snowmelt 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).

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*. All three species are common long-lived perennial forbs commonly found near the Rocky Mountain Biological Laboratory. *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 and Price, 1981). *Valeriana* is dioecious and thus obligately outcrossing (Meurman, 1925). *Potentilla* is capable of autonomous self-pollination but sets more seed with outcross pollen (Burkle and Irwin, 2010; Vail, 1983).

Experimental design

Climate treatments. This study implemented a factorial design of warming and early snowmelt treatments to disentangle the potentially independent effects that snowmelt timing and temperature have on flowering and fruiting phenology. We used four climate treatments: control, early snowmelt, warming, and combined warming plus early snowmelt. There were 14 7 × 7 m plots in total, and treatments were arranged in a split plot design. Seven plots received an early snowmelt manipulation, and seven were snowmelt-control plots. Warming and control sub plots

were placed within each of the 14 plots (3 of each per plot). Ambient air temperatures were increased via passive warming open-top-chambers (OTC), made out of plexiglass (*sensu* Marion et al. 1997). The chambers were hexagonal in shape and *ca.* 1 m² and 0.5 m tall. Each control sub plot was also *ca.* 1 m². Unlike the other two species, controls for *Valeriana* were not in sub plots and instead were scattered individuals within the plot (these plants were already tagged as part of a pre-existing demographic study). Warming chambers were deployed after the snow had melted in all plots to avoid affecting the date of snowmelt. The OTCs were set-up on 17 – 19 June 2019 and remained in place through 22 August 2019. Early snowmelt treatments used a 9 x 9 m black shade cloth to advance spring snowmelt timing within the plot, plus a 1 m buffer on all sides to reduce edge effects. Snowmelt timing was manipulated by placing black shade cloths directly on the snow surface, thereby decreasing albedo and increasing heat absorption. Snowmelt treatments were initiated in the early spring (27 April), and were removed over the course of one week as the snow melted in each plot (4 June – 10 June).

Tracking climate. Mounted timelapse cameras recorded snowmelt timing for four quadrants within each plot. Snowmelt timing was defined as at least 50% visible bare ground within the quadrant. The largest variation in snowmelt 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 sub plots within each plot.

A data logger was mounted in the center of each plot from 3 July–22 August, recording the air temperature every 15 min (HOBO data loggers, Onset Computer Corporation, USA). Additional data loggers rotated between *Valeriana* individuals for one week at a time throughout

the season. To calculate growing degree days, we used an interpolation model with early season temperature data from a weather station *ca.* 4 km away (billy barr, unpublished data) to fill in temperatures between snowmelt timing (early to mid-June, depending on the plot) and the date on which we began collecting temperature data (3 July), as well as temperatures for weeks when there was no data logger stationed at an individual *Valeriana* (detailed in Appendix). For each species and phenophase, the accumulated growing degree days (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). Temperatures were summed from date of snowmelt for each plot to the date of onset of each phenophase (*i.e.*, the onset of flowering for peak flowering date and flowering duration or the onset of fruiting 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 sub plot-level as the GDD of the closest *Valeriana* individual, or the mean of the closest *Valeriana* individuals if the nearest individuals were equidistant.

Tracking phenology. At the beginning of the season before reproductive structures had emerged, five individuals from *Delphinium* and five from *Potentilla* were tagged in each sub plot. *Valeriana* was part of a larger demographic study, thus numbers of *Valeriana* individuals per plot varied. As the season went on, only individuals that flowered were followed, resulting in 144 *Delphinium*, 385 *Valeriana*, and 231 *Potentilla* individuals. *Delphinium* had 34 individuals in the control, 44 in early melt, 32 in warming and 34 in the combined treatment. *Valeriana* had 141 individuals in the control, 97 in early melt, 61 in warming and 86 in the combined treatment. *Potentilla* had 60 individuals in the control, 71 in early melt, 52 in warming and 48 in the combined treatment. Individual plants within each plot were tagged and followed throughout the

growing season to determine the timing and duration of two phenological events: flowering and fruiting. Flowering was recorded when flowers were fully open and when the reproductive structures were mature. The number of open flowers were counted on each individual three days per week. For *Valeriana*, the number of flowering stalks was counted because *Valeriana* produces many small flowers within each inflorescence. Fruiting was recorded when fruits became fully ripe, indicated by a change in fruit color or in fruit drying. Flowering duration and fruiting duration were defined as the length of time (in days) between the first and last flower or fruit, respectively. Peak flowering and peak fruiting were defined as the day on which 50% of flowers or fruits were counted on an individual plant (following Høye et al., 2007; Iler et al., 2013).

Measuring reproduction. There are well-established effects of plant size on reproductive output, and size can also affect phenology (Forrest, 2014; Ollerton and Lack, 1998). We therefore accounted for plant size when considering how climate change affects plant phenology and reproductive output. The size of all individuals was measured after flowering started, under the assumption that plants were finished growing for the season once they started allocating resources to reproduction. 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*. Mature fruits for *Delphinium* and *Potentilla* were collected, and seeds per individual were counted in the lab. At the end of the season, some individual *Potentilla* plants still had immature fruit, so we did not include fruit duration for *Potentilla* in our analysis because the end fruiting date was unknown. For *Valeriana*, seed counts were estimated in the field

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.

Analysis

Sequential phenological events may not be independent of one another (Li et al., 2016). Therefore, we started by testing whether peak flowering and fruiting date responded independently to the treatments using a Multivariate Analysis of Variance (MANOVA). For this analysis the response variables were averaged across plot (or sub plot) because the individual-level data violated assumptions of normality; treatment was analyzed as a categorical variable with four levels. We also tested whether flowering and fruiting duration responded independently to the treatments following the model structure above. In all three species, both the timing and duration of fruiting was not driven by that of flowering (Table S4), so we analyzed all the response variables separately.

To answer how snowmelt timing and warming affect the timing, duration, and output of reproductive events, we used linear mixed effects models (LMMs) and generalized linear mixed effects models (GLMMs). In all mixed effects models, plot was a random intercept term (sub plot for *Delphinium* and *Potentilla* and plot for *Valeriana*). For each response variable, we conducted hypothesis testing with models that had the early snowmelt treatment and warming treatment as categorical predictors, in addition to an interaction between the warming and early snowmelt treatment. If the interaction term was significant, it indicated that the predicted effect of the combined treatment was either larger or smaller than expected under the assumption that the warming and early snowmelt treatments were additive. The warming treatment and snowmelt treatment each had two levels: control and treatment. For *Valeriana*, peak flowering and peak fruiting date were averaged across plot because mixed models violated assumptions of normality.

LMMs were used to analyze the dates of peak flowering and peak fruiting in *Delphinium* and *Potentilla* (Bates et al., 2015). GLMMs were used to analyze flower duration, fruit duration, seed count, and flower count (Brooks et al., 2017); these four responses are based on count data and were analyzed with a Poisson error distribution (log link), unless they were overdispersed, in which case a negative binomial error distribution (log link) was used.

Our initial analysis can determine if the two treatments are changing our response variables, but to determine if snowmelt timing was affecting phenology beyond the accumulation of growing degree days, we conducted an additional analysis including growing degree days (GDD). Again, we used a hypothesis testing approach with LMMs and GLMMs. For these models both the early snowmelt treatment and warming treatment were included as additive categorical variables and GDD was included as an additive as a continuous predictor. We included GDD at flowering or fruiting, depending on whether the response pertained to flowering or fruiting. If the early snowmelt treatment was still significant after accounting for effects of GDD, this suggests that the treatment was not just GDD in disguise. If early snowmelt was no longer significant after accounting for GDD, and GDD was significant, this suggests that snowmelt was simply GDD in disguise.

In every model size was included as an additive predictor in order to isolate the effects of climate on phenology from the potentially confounding effect of size. We determined which size measurements explained the most variation in phenology for each species by conducting simple linear regression models with each plant size measurement as a continuous predictor and peak flowering and peak fruiting dates as a continuous response (in separate models). The measurement with the highest R^2 value was chosen to represent plant size for each species (Table S1). The best size measurement for each species were: tallest stem for *Valeriana*, length of

longest leaf for *Potentilla*, and leaf number for *Delphinium*. Sex was also included as a categorical predictor for *Valeriana* when analyzing flowering timing and duration, because it is dioecious, and sex-specific responses to climate change have been observed in this species (Petty et al. 2016).

Results

Treatment Effects

Snow melted on average 9 days earlier in the early melt treatment compared to the controls. Mean melt date for control plots was 12 June (± 0.06 days) and for early snowmelt plots was 3 June (± 0.04 days). Means are presented ± 1 SE unless otherwise specified. Open top chambers (OTC) warmed overall seasonal air temperatures an average of 2.1°C ; mean temperature for the warming treatment was $16 \pm 0.02^{\circ}\text{C}$, and mean temperature for the control treatment was $13.9 \pm 0.03^{\circ}\text{C}$. Daytime (06:00–18:00 hr) temperatures differed by 2.5°C between treatments, with mean temperatures of $24.6 \pm 0.04^{\circ}\text{C}$ and $22.1 \pm 0.03^{\circ}\text{C}$ for the warming and control treatments, respectively. Nighttime (18:00–06:00 hr) temperatures differed by 1.7°C , with mean temperatures of $10.3 \pm 0.03^{\circ}\text{C}$ and $8.6 \pm 0.02^{\circ}\text{C}$ for the warming and control treatments, respectively.

Both early snowmelt and warming treatments increased the accumulation of temperature (i.e., growing degree days, GDD) (Tables S2, S3, Fig. S1). In the early snowmelt treatment, plants gained a 9-day head start on GDD accumulation whereas the warming treatment accumulated more GDD each calendar day. For both flowering and fruiting, the two treatments had similar magnitude of GDD accumulation, with the highest GDD in the combined treatment. In all cases the accumulated GDD in the combined treatment matched the additive expectation from both treatments individually. There were three instances where the warming treatment had

a significant effect, and yet there was no effect from GDD, indicating that the warming treatment had an effect besides a change in GDD.

How do snowmelt timing and warming affect the timing, duration, and output of reproductive events in subalpine wildflowers?

Timing. In all three species the early snowmelt treatment shifted flowering earlier. In two species the early snowmelt and warming treatments both shifted flowering earlier and there was no interaction between the two treatments (Table 1, Figure 1a, b). But, for *Valeriana*, only the early snowmelt treatment shifted flowering earlier relative to controls (Table 1, Figure 1c). In all three species the early snowmelt treatment at least marginally shifted fruiting earlier. For two species only the early snowmelt treatment shifted peak fruiting earlier (Table 1, Figure 1e, f). However, for *Delphinium*, both the early snowmelt and warming treatments shifted fruiting earlier (Table 1, Figure 1d).

Duration. Only for *Delphinium* did size affect flowering duration, with larger plants flowering for a longer period of time (Table 2). For *Valeriana*, the early snowmelt 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). For *Delphinium* and *Valeriana*, only the early melt treatment lengthened (or marginally lengthened) fruit duration (Table 3, Figure 2d, 2e).

Reproduction. For two species plant size was the only variable that significantly affected the number of flowers and the number of seeds, with larger plants having more flowers and seeds (Table 3). However, for *Delphinium* the warming treatment increased the number of flowers per individual and decreased the number of seeds per individual (Table 3, Fig. 3a, d). There also was an interaction between the treatments such that the combined treatment did not see as large of a

decline in seed production as expected if the effects of snowmelt and warming were additive. Additionally, there was a marginal interaction in *Potentilla* such that the combined treatment had more flowers than expected if the effects of snowmelt and warming were additive. *Does snowmelt timing affect reproductive phenology through temperature accumulation, or is snowmelt timing an independent cue?*

In our first analysis we found no sub-additive interactions between the two treatments in the phenological responses (the only interaction was for seed production in *Delphinium*), which we would have expected if the snowmelt treatment was masking the effect of temperature and acting through temperature accumulation in disguise. To further investigate if snowmelt timing was acting through GDD we ran additional analysis explicitly looking at the effect of GDD.

The effect of the snowmelt treatment on the timing of flowering persisted even after accounting for GDD in all three species, suggesting snowmelt date acts through a mechanism other than GDD to drive the timing of flowering (Table 4). The effect of the warming treatment also persisted after accounting for GDD for *Potentilla* (Table 4). For the timing of fruiting the effect of the snowmelt treatment was no longer significant after accounting for GDD in two species (*Delphinium* and *Potentilla*). The timing of fruiting appears to be completely driven by GDD for *Delphinium*, because the snowmelt treatment was no longer significant once GDD was included in the analysis (Table 4). However, for *Potentilla*, GDD was not significant in the second analysis, suggesting some mechanism besides GDD and snowmelt timing was driving the timing of fruiting (Table 4). For *Valeriana*, the effect of the snowmelt treatment persisted after accounting for GDD, suggesting a mechanism besides GDD is driving the timing of fruiting (Table 4).

The effects of the snowmelt treatment on flower duration persisted after accounting for GDD for *Valeriana* (Table 5). In the other two species the snowmelt treatment was not significant in the first analysis. Neither climate treatment effected *Delphinium* in either analysis and for *Potentilla* the effect of the warming treatment persisted after accounting for GDD. The effects of both the snowmelt and warming treatments on fruit duration persisted after accounting for GDD for *Valeriana* (Table 5). However, for *Delphinium* the effect of the snowmelt treatment was no longer significant after GDD was included in the model, indicating GDD was driving the longer fruiting duration (Table 5).

Discussion

Although previous experiments have examined the combined effects of early snowmelt and warming on plant reproductive phenology (Dunne et al., 2003; Price and Waser, 1998), distinguishing the effects of earlier snowmelt from warming has proven elusive. Here, we factorially crossed warming with early snowmelt in a subalpine meadow to disentangle how temperature and snowmelt date influence the timing, duration, and success of reproductive events. We find that snowmelt timing is consistently an important driver of plant phenology, both on its own (as with the timing of flowering in *Valeriana*) or in conjunction with warming (as with the timing of flowering in *Delphinium* and *Potentilla*). When the early snowmelt and warming treatments did act together to affect phenology their effects were always additive. Having only additive effects of multiple climate drivers could make predictions of future phenological responses straightforward, as interactive effects can be difficult to predict. Additionally, we find that the timing of snowmelt can drive plant phenology through mechanisms other than temperature accumulation (*e.g.*, soil moisture). In fact, growing degree days was only an important driver of phenology for one out of our three study species.

As expected, earlier snowmelt and warmer temperatures lead to earlier flowering, consistent with previous observational and experimental research (Bjorkman et al., 2015; Iler et al., 2013; Inouye, 2008; Price and Waser, 1998). There were no cases where early snowmelt did not at least weakly shift the timing of reproductive events earlier, supporting other findings that suggest snowmelt timing as the driving cue of phenology in high-elevation and high-latitude environments (Bjorkman et al., 2015; Forrest et al., 2010; Høye et al., 2007b).

We provide novel experimental evidence that snowmelt can act independently of growing degree days, by examining whether effects of experimentally advanced snowmelt persist after statistically accounting for the effects of growing degree days. We observed that snowmelt timing can act independently from the warming treatment, when early snowmelt and the combined treatment advance phenology but warming does not (*e.g.*, peak flowering in *Valeriana*), however, this does not preclude the possibility that snowmelt timing is still simply temperature accumulation in disguise. In 6 out of 9 cases where the snowmelt treatment shifted phenology, either alone or in conjunction with the warming treatment, the effect of the snowmelt treatment persisted after growing degree days were included in the model, supporting the hypothesis that snowmelt affects phenology independent of temperature accumulation. It has been previously suggested that the influx of soil moisture after snowmelt likely helps to 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 snowmelt on phenology. There is also observational evidence that rainfall and soil moisture affect flowering phenology in other, arid ecosystems (Crimmins et al., 2010; Gordo and Sanz, 2010; Peñuelas et al., 2004).

Certain species may be driven by growing degree days (in tandem with other drivers), while other species may not use growing degree days to cue phenology at all. We found that in

the remaining three out of nine cases, the effect of the snowmelt treatment disappeared after growing degree days was included in the model. Thus, when GDD was significant, it indicated temperature accumulation was the driver of these changes. Two of these cases were for the timing and duration of fruiting in *Delphinium*. Flowering in *Delphinium*, while not solely driven by growing degree days, was the only instance of growing degree days and the snowmelt treatment working together to drive phenology. *Delphinium* is the earliest flowering species we studied, and its sensitivity to a change in growing degree days is consistent with the finding that early season species are more sensitive to warming, as previous studies have suggested (Pau et al., 2011; Wolkovich et al., 2012).

The duration of life history events are 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. We found that flowering duration was influenced by the climate treatments in two out of our three study species (consistent with Dunne et al., 2003; Li et al., 2016). Neither of the shifts in flowering duration were driven by temperature accumulation, despite the fact that the warming treatment affected flowering duration in both cases. This result suggests that other unintended effects of the warming chambers, such as dryer soils and reduced wind, may be driving these changes to flower duration instead of temperature (*e.g.*, Marion et al., 1997). We did not find any effects of the climate treatments on the duration of flowering in one species, following other studies that show flowering duration may not be as susceptible to changes in climate (Jabis et al., 2020; Price and Waser, 1998; Semenchuk et al., 2016), and instead may be driven by biotic factors such as pollination (Arroyo et al., 2013). If climate change causes the duration of flowering to lengthen in some species, but shorten, or remain unchanged in others, this may lead to changes in co-

flowering overlap, potentially shifting competition for resources, such as pollinators (Forrest et al., 2010; Mitchell et al., 2009, Faust & Iler, unpublished).

We found little evidence for effects of warmer temperatures and early snowmelt on reproductive output, potentially because phenological shifts in the study species allowed them to track optimal abiotic conditions for flowering and fruiting. Both the warming treatment and the snowmelt treatment gave rise to climatic changes on par for previous climate changes in subalpine ecosystems (Anderson et al., 2012; IPCC, 2014; Ogilvie et al., 2017). However, 2019 was a relatively late snowmelt year, occurring 18 days later than the long-term average at the RMBL (1975–2018; barr, 2020). Therefore, the early snowmelt treatment was more reflective of current conditions, whereas the control treatment was more reflective of historic climatic conditions. Plants in the early snowmelt only treatments were perhaps not exposed to climatic conditions outside of their physiological limits. Previous studies found decreased flowering under early snowmelt due to increased frost damage (Gezon et al., 2016; Høye et al., 2007a; Inouye, 2008; Thomson, 2010), but *Delphinium* and *Potentilla* are not particularly sensitive to frost damage (frost sensitivity is unknown in *Valeriana*) (CaraDonna and Bain, 2016, CaraDonna and Bain, unpublished data). Our experiment provides a rigorous method for disentangling the effects of early snowmelt and warmer temperatures under realistic climate change conditions, however if climate change creates more extreme conditions, effects to reproductive output may unfold differently.

Delphinium was the only species in which the climate manipulations affected reproductive output. Although we cannot distinguish between the effects of the *treatments* on reproductive output versus the effects of the *phenological change* on reproductive output, understanding their consequences together is still an important step toward understanding the

ecological consequences of phenological shifts (Iler *et al.*, in prep). Early snowmelt and warmer temperatures did not have a significant effect on reproductive output, with the exception of *Delphinium*. 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 much more than passive warming, and reduced soil moisture can lead to higher rates of flower abortion (Saavedra *et al.*, 2003). We also found a decrease in the number of seeds per plant under the warming treatment in *Delphinium*, which may be due to decreased flower visitors inside the warming chambers. A study at the same site found that OTCs reduced visitation rates by 96% in *Delphinium* and 81% in *Potentilla*. The same study also found OTCs 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 autonomously self-pollination (Adamson and Iler, in review). Although reduced pollination could explain the decrease in seeds under the warming treatment, there was not a similar decrease under the combined warming x snowmelt 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 the expected additive effect of the two treatments. This suggests that warming, or at least warming induced by an open top chamber, exerted a direct negative effect on seed production in *Delphinium* that was counteracted by the snowmelt treatment when they were combined, because the plants in the combined treatment produced more seeds than those in the warming chambers alone.

Montane environments have a short growing seasons and as a result, thus there is likely a tradeoff 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 and Lack, 1998; Stinson, 2004). If plants benefit from early season conditions (*e.g.*, high soil moisture, reduced biotic competition) or a longer reproductive time period, larger plants should flower earlier, but if it is more beneficial for plants to have time to grow *before* reproducing, then larger plants should flower later. We found that in *Potentilla*, larger plants flowered later and produced more flowers and seeds, suggesting this 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 size was the only variable driving flower duration in this species. (We did not examine the effect of plant size in *Valeriana* because we analyzed peak flowering and fruiting at the plot-level.) Although larger plants seem to have a reproductive advantage across species, and it is clear that 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 between species.

Shifts in phenological events are occurring in all kinds of ecosystems across the globe, but climate change encompasses more than just rising temperatures and organisms may be responding to more than one environmental signal when they shift their phenology. Here we exemplify how a single climatic signal can have multiple mechanisms for driving phenology. Although there is ample experimental and observational evidence that the timing of snowmelt affects flowering phenology (Bjorkman et al., 2015; Høye et al., 2007a; Price and Waser, 1998; Steltzer et al., 2009), it has remained unclear whether snowmelt simply acts as temperature accumulation in disguise or whether it can cue phenological events independently from temperature. This distinction is important because it improves our mechanistic understanding of

519 how snowmelt timing acts as a phenological cue. We find support for snowmelt acting via both
520 mechanisms: temperature accumulation in disguise and independent of temperature
521 accumulation. Thus, snowmelt timing should *not* be exclusively viewed as a proxy for
522 temperature accumulation—instead, snowmelt is also likely affecting phenology via changes in
523 the timing or pulse of soil moisture, providing avenues for future research on the mechanistic
524 role of snowmelt timing (and precipitation in general) as a phenological cue. Accurate
525 predictions of phenology depend on understanding how different climatic cues interact and
526 understanding the mechanism behind climate effects on phenology, both of which require further
527 study.

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Table 1. Summary tables from LMMs for *Delphinium* and *Potentilla* and LM for *Valeriana* for the effect of climate manipulations (warming and early snowmelt) and plant size on the timing of flowering and fruiting (peak flowering date and peak fruiting date). Sub plot was a random effect in LMMs.

Response	Species	Predictor	Estimate	Std. Error	df	t value	P
Peak Flowering	Delphinium	Intercept	193.6	0.9	108.8	209.9	<0.0001
		Warming	-2.0	0.8	68.0	-2.4	0.02
		Early Melt	-6.4	0.8	56.5	-7.8	<0.0001
		Size	-0.1	0.2	122.9	-0.4	0.70
		Warming x Early Melt	-0.5	1.2	63.0	-0.5	0.64
	Potentilla	Intercept	211.9	1.8	207.2	115.5	<0.0001
		Warming	-4.8	1.3	67.2	-3.7	<0.001
		Early Melt	-6.3	1.2	59.7	-5.1	<0.0001
		Size	1.0	0.3	200.8	3.3	0.001
	Valeriana	Warming x Early Melt	-0.6	1.9	66.8	-0.3	0.73
		Intercept	212.0	0.7	49.0	293.2	<0.0001
		Warming	-0.2	1.1	49.0	-0.2	0.85
		Early Melt	-4.2	1.0	49.0	-4.0	<0.001
		Warming x Early Melt	-0.7	1.5	49.0	-0.5	0.63
Peak Fruiting	Delphinium	Intercept	212.8	1.5	49.2	137.7	<0.0001
		Warming	-4.6	1.6	36.2	-3.0	0.005
		Early Melt	-4.8	1.4	30.7	-3.4	0.002
		Size	-0.2	0.3	45.9	-0.6	0.55
		Warming x Early Melt	1.9	2.2	34.7	0.9	0.38
	Potentilla	Intercept	231.8	1.4	93.8	165.7	<0.0001
		Warming	-0.5	0.9	41.6	-0.6	0.58
		Early Melt	-1.5	0.9	28.8	-1.7	0.09
		Size	0.2	0.2	104.8	0.9	0.37
		Warming x Early Melt	-0.1	1.3	39.3	-0.1	0.94
	Valeriana	Intercept	219.5	0.4	23.0	505.3	<0.0001
		Warming	-0.7	0.6	23.0	-1.1	0.27
		Early Melt	-2.0	0.6	23.0	-3.2	0.004
		Warming x Early Melt	-0.1	0.9	23.0	-0.1	0.92

Table 2. Summary tables from GLMMs for *Delphinium*, *Potentilla* and *Valeriana* for the effect of climate manipulations (warming and early snowmelt) and plant size on the duration of flowering and fruiting. Plot and sub plot were a random effect in GLMMs.

Response	Species	Predictor	Estimate	Std. Error	z value	P
Flower Duration	Delphinium	Intercept	1.7	0.2	9.1	<0.0001
		Early Melt	0.2	0.1	1.3	0.19
		Warming	0.0	0.1	0.1	0.94
		Size	0.2	0.0	3.9	<0.0001
		Early Melt x Warming	-0.2	0.2	-0.7	0.46
	Potentilla	Intercept	2.3	0.2	10.7	<0.0001
		Early Melt	-0.1	0.1	-0.9	0.39
		Warming	-0.3	0.1	-2.4	0.02
		Size	0.2	0.0	4.2	<0.0001
		Early Melt x Warming	0.1	0.2	0.4	0.67
	Valeriana	Intercept	3.3	0.1	60.9	<0.0001
		Early Melt	0.1	0.0	4.1	<0.0001
		Warming	0.1	0.0	2.6	0.01
		Size	0.0	0.0	5.4	<0.0001
		Sex	0.1	0.0	3.8	0.001
		Early Melt x Warming	0.0	0.0	-0.8	0.41
Fruit duration	Delphinium	Intercept	-0.6	0.4	-1.4	0.16
		Early Melt	0.9	0.4	2.7	0.01
		Warming	0.3	0.4	0.8	0.45
		Size	0.2	0.1	3.3	0.001
		Early Melt x Warming	-0.1	0.5	-0.3	0.78
	Valeriana	Intercept	3.2	0.1	59.4	<0.0001
		Early Melt	0.1	0.0	1.9	0.06
		Warming	0.0	0.0	0.3	0.80
		Size	0.0	0.0	5.8	<0.0001
		Early Melt x Warming	0.0	0.0	-1.0	0.310

Table 3. Summary tables from GLMMs for *Delphinium*, *Potentilla*, and *Valeriana* for the effect of climate manipulations (warming and early snowmelt) and plant size on the number of flowers and seeds per individual. Plot and sub plot were a random effect in GLMMs.

Response	Species	Predictor	Estimate	Std. Error	z value	P
Flower count	Delphinium	Intercept	0.5	0.2	3.6	<0.001
		Early Melt	0.0	0.1	0.3	0.77
		Warming	0.3	0.1	2.0	0.05
		Size	0.1	0.0	4.2	<0.0001
		Early Melt x Warming	0.0	0.2	0.0	1.00
	Potentilla	Intercept	0.8	0.2	4.3	<0.0001
		Early Melt	0.2	0.1	1.6	0.11
		Warming	-0.1	0.1	-0.5	0.59
		Size	0.1	0.0	4.2	<0.0001
		Early Melt x Warming	-0.3	0.2	-1.7	0.09
	Valeriana	Intercept	0.5	0.2	2.9	0.004
		Early Melt	0.1	0.1	0.6	0.52
		Warming	0.1	0.1	0.9	0.39
		Size	0.0	0.0	3.9	<0.001
		Sex	0.1	0.1	1.4	0.17
		Early Melt x Warming	-0.1	0.1	-0.6	0.57
Seed Count	Delphinium	Intercept	3.6	0.3	13.2	<0.0001
		Early Melt	-0.2	0.2	-1.0	0.32
		Warming	-0.8	0.2	-3.5	<0.001
		Size	0.2	0.1	3.2	0.001
		Early Melt x Warming	0.7	0.3	2.0	0.04
	Potentilla	Intercept	4.6	0.3	13.3	<0.0001
		Early Melt	0.1	0.2	0.5	0.59
		Warming	-0.3	0.2	-1.4	0.17
		Size	0.2	0.1	3.5	<0.001
		Early Melt x Warming	-0.3	0.3	-1.2	0.25
	Valeriana	Intercept	3.7	0.4	10.6	<0.0001
		Early Melt	0.3	0.2	1.4	0.18
		Warming	-0.2	0.2	-0.9	0.39
		Size	0.0	0.0	10.0	<0.0001
		Early Melt x Warming	-0.3	0.3	-1.3	0.21

Table 4. Summary tables from LMMs for *Delphinium* and *Potentilla* and LM for *Valeriana* for the effect of growing degree days (GDD), climate manipulations (warming and early snowmelt), and plant size on the timing of flowering and fruiting (peak flowering date and peak fruiting date). Sub plot was a random effect in LMMs.

Response	Species	Predictor	Estimate	Std. Error	df	t value	P
Peak Flowering	Delphinium	Intercept	202.1	2.3	68.4	88.2	<0.0001
		Warming	-1.0	0.6	56.5	-1.7	0.10
		Early Melt	-4.6	0.8	61.0	-5.8	<0.0001
		GDD	0.0	0.0	62.8	-3.9	<0.001
		Size	-0.1	0.2	114.4	-0.3	0.74
	Potentilla	Intercept	211.0	5.3	84.6	39.7	<0.0001
		Warming	-4.9	1.2	68.3	-4.0	<0.001
		Early Melt	-6.7	1.1	61.9	-6.1	<0.0001
		GDD	0.0	0.0	67.8	0.2	0.87
		Size	1.1	0.3	193.0	3.4	0.001
	Valeriana	Intercept	213.8	3.1	48.0	69.5	<0.0001
		Warming	-0.5	0.8	48.0	-0.6	0.58
		Early Melt	-4.1	1.0	48.0	-4.3	<0.0001
		GDD	0.0	0.0	48.0	-0.5	0.59
Peak Fruiting	Delphinium	Intercept	235.5	7.1	27.3	33.0	<0.0001
		Warming	-1.3	1.3	29.0	-1.0	0.34
		Early Melt	0.1	1.4	27.3	0.1	0.94
		GDD	0.0	0.0	27.3	-3.3	0.003
		Size	-0.2	0.3	45.0	-0.6	0.57
	Potentilla	Intercept	239.2	5.2	46.0	45.8	<0.0001
		Warming	-1.1	0.8	31.5	-1.4	0.17
		Early Melt	0.7	1.0	37.1	0.6	0.52
		GDD	0.0	0.0	38.0	-1.5	0.15
		Size	0.2	0.3	95.7	0.7	0.46
	Valeriana	Intercept	217.0	2.4	23.0	89.3	<0.0001
		Warming	-1.1	0.5	23.0	-2.0	0.05
		Early Melt	-2.3	0.5	23.0	-4.4	<0.001
		GDD	0.0	0.0	23.0	1.0	0.32

Table 5. Summary tables from GLMMs for *Delphinium*, *Potentilla* and *Valeriana* for the effect of growing degree days (GDD), the climate manipulations (warming and early snowmelt), and plant size on the duration of flowering and fruiting. Plot and sub plot were a random effect in GLMMs.

Response	Species	Predictor	Estimate	Std. Error	z value	P
Flower Duration	Delphinium	Intercept	1.6	0.4	3.7	<0.001
		Early Melt	0.1	0.2	0.6	0.56
		Warming	-0.1	0.1	-0.8	0.41
		GDD	0.0	0.0	0.2	0.85
		Size	0.2	0.0	4.1	<0.0001
	Potentilla	Intercept	1.5	0.7	2.3	0.02
		Early Melt	-0.2	0.1	-1.3	0.20
		Warming	-0.4	0.1	-2.5	0.01
		GDD	0.0	0.0	1.2	0.23
		Size	0.2	0.0	4.1	<0.0001
	Valeriana	Intercept	3.6	0.0	150.8	<0.0001
		Early Melt	0.1	0.0	3.2	0.001
		Warming	0.1	0.0	2.2	0.03
		GDD	0.0	0.0	1.1	0.29
		Size	0.1	0.0	4.9	<0.0001
		Sex	0.1	0.0	3.6	<0.001
Fruit Duration	Delphinium	Intercept	0.2	0.5	0.4	0.72
		Warming	0.3	0.3	1.1	0.29
		Early Melt	-0.5	0.3	-1.4	0.17
		GDD	0.5	0.2	2.3	0.02
		Size	0.2	0.1	3.2	0.001
	Valeriana	Intercept	3.3	0.1	56.7	<0.0001
		Warming	0.1	0.0	2.6	0.009
		Early Melt	0.0	0.0	0.0	0.986
		GDD	0.0	0.0	-1.4	0.158
		Size	0.0	0.0	5.1	<0.0001

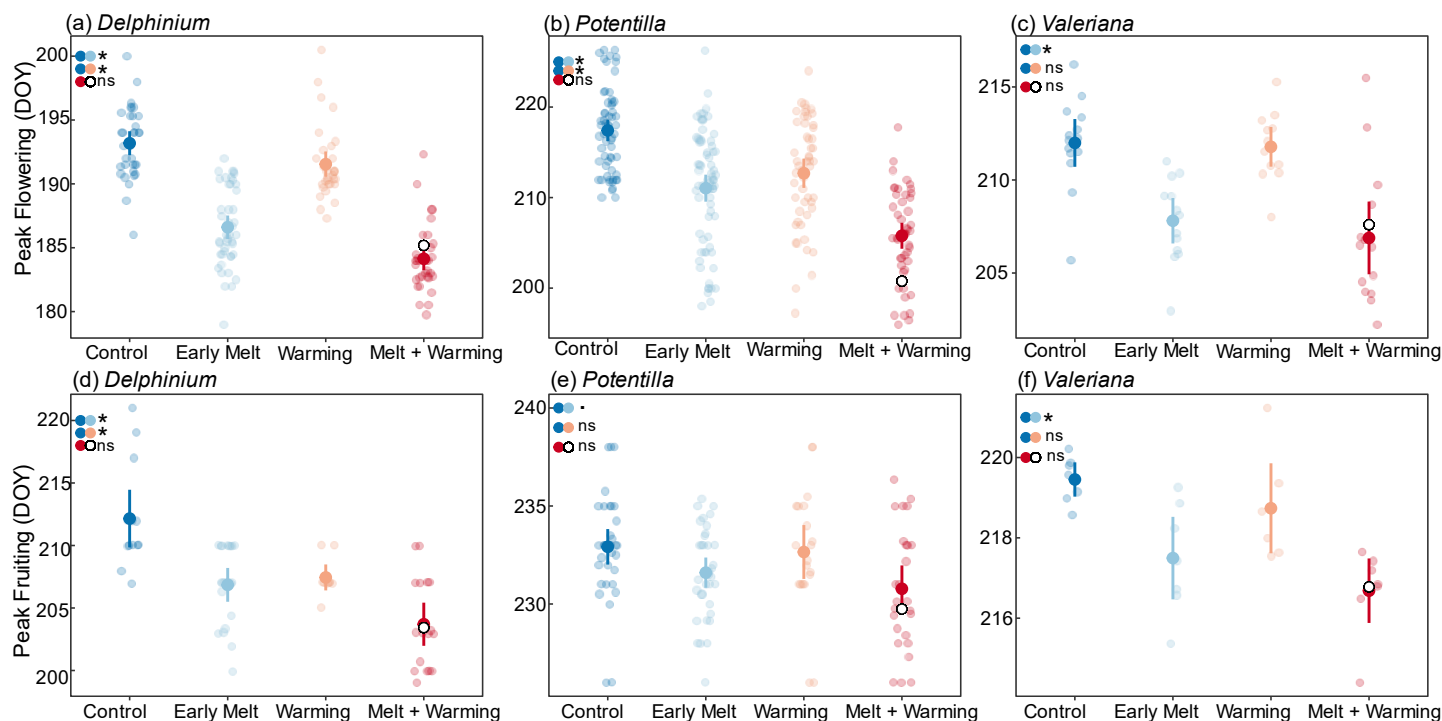
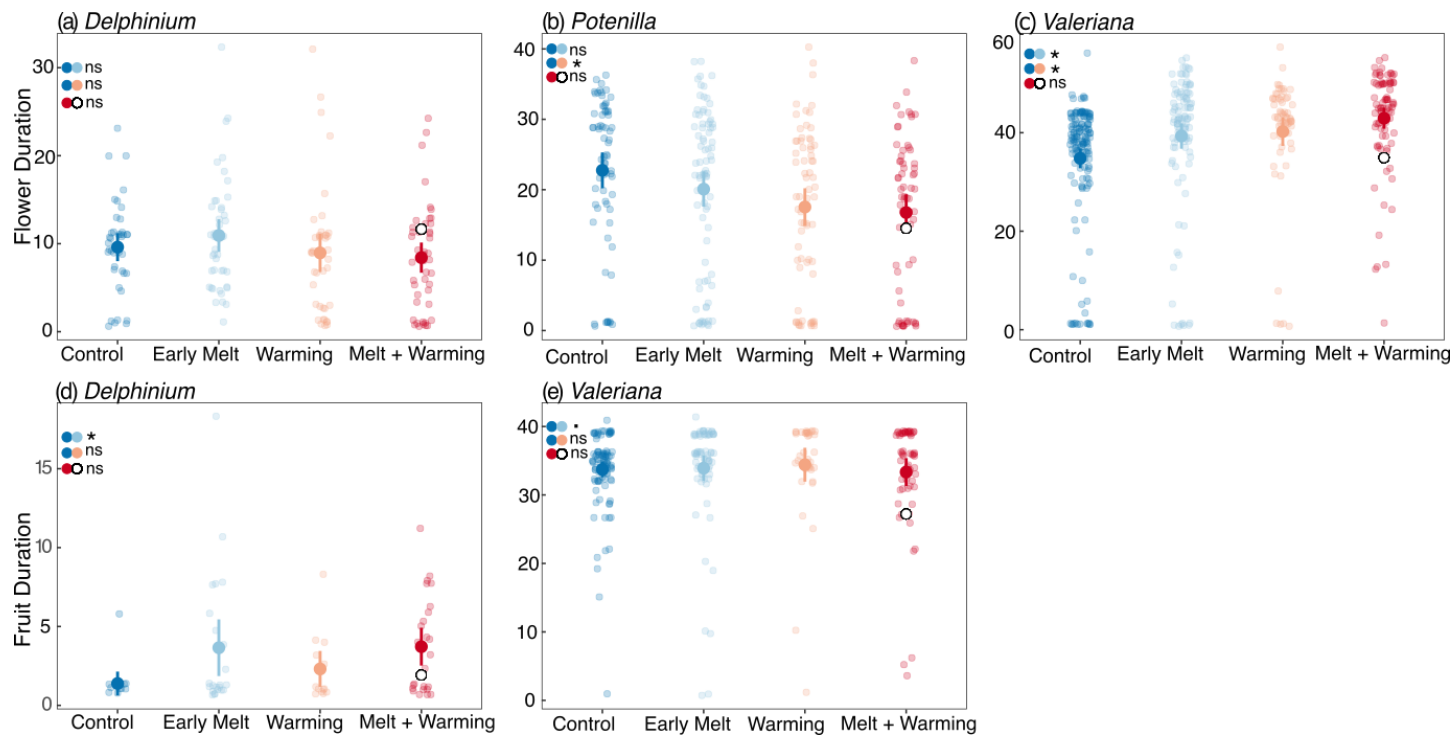


Figure 1. Timing of flowering and fruiting, shown in day of year (DOY) across four treatments: control, early melt, warming, and a combination of early melt and warming. Solid dots are means, and error bars represent 95% confidence intervals. Open circles represent the additive expectation when the warming 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 non-significant comparisons. Note that y-axes are on different scales because species flower and fruit on different dates.

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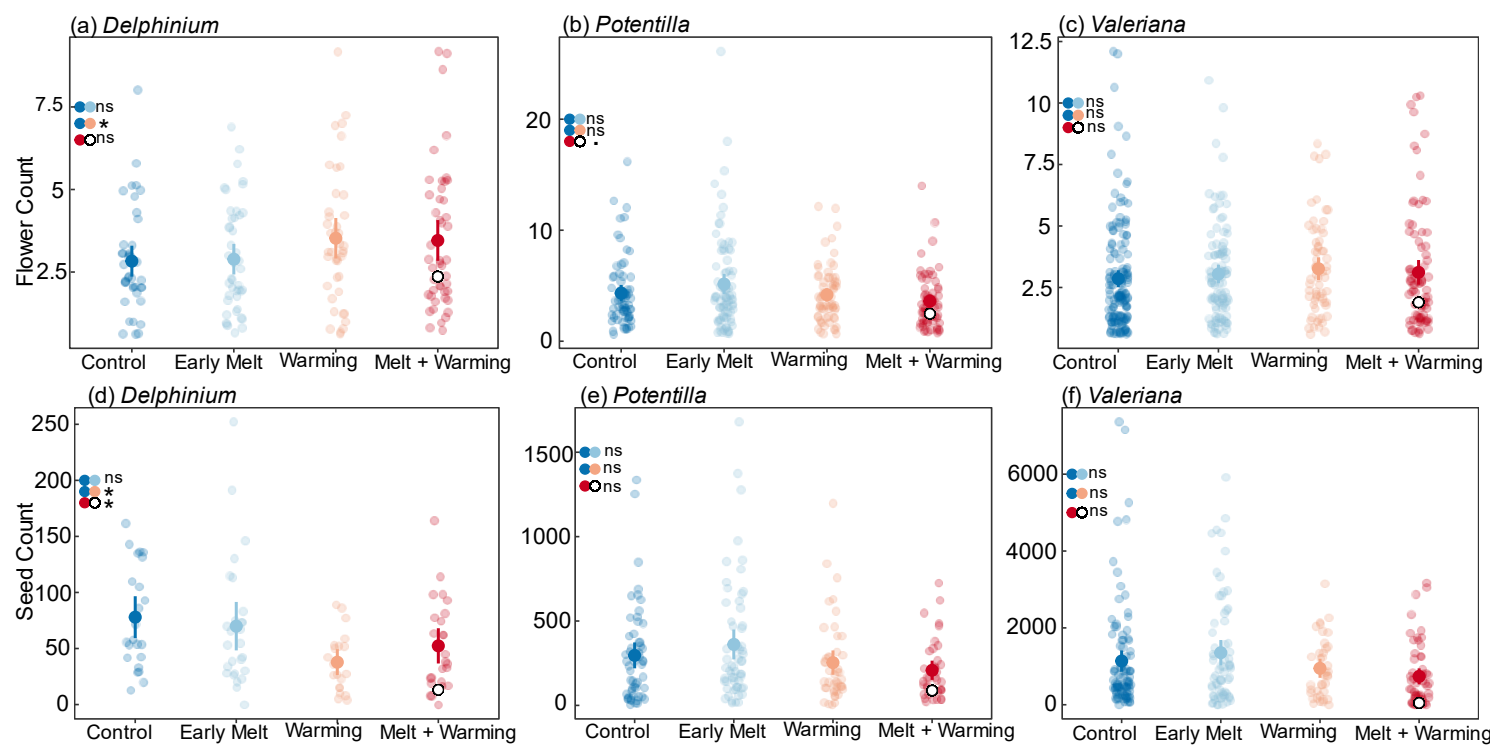
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Figure 2. Duration flowering and fruiting, shown in number of days across four treatments: control, early melt, warming, and a combination of early melt and warming. Solid dots are means, and error bars represent 95% confidence intervals. Open circles 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 non-significant comparisons. Note that y-axes are on different scales because species flower and fruit on different dates.

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788 Figure 3. Number of flowers and seeds per individual, across four treatments: control, early melt,
789 warming, and a combination of early melt and warming. Solid dots are means, and error bars
790 represent 95% confidence intervals. Open circles represent the additive expectation when the
791 warming and melt treatment effects are combined. In the legends, asterisks indicate significant
792 differences at $p < 0.05$, dots indicate marginally significant comparisons at $0.05 < p < 0.10$, and
793 “ns” indicates non-significant comparisons. Note that y-axes are on different scales because
794 species have varied amounts of flowers and seeds.

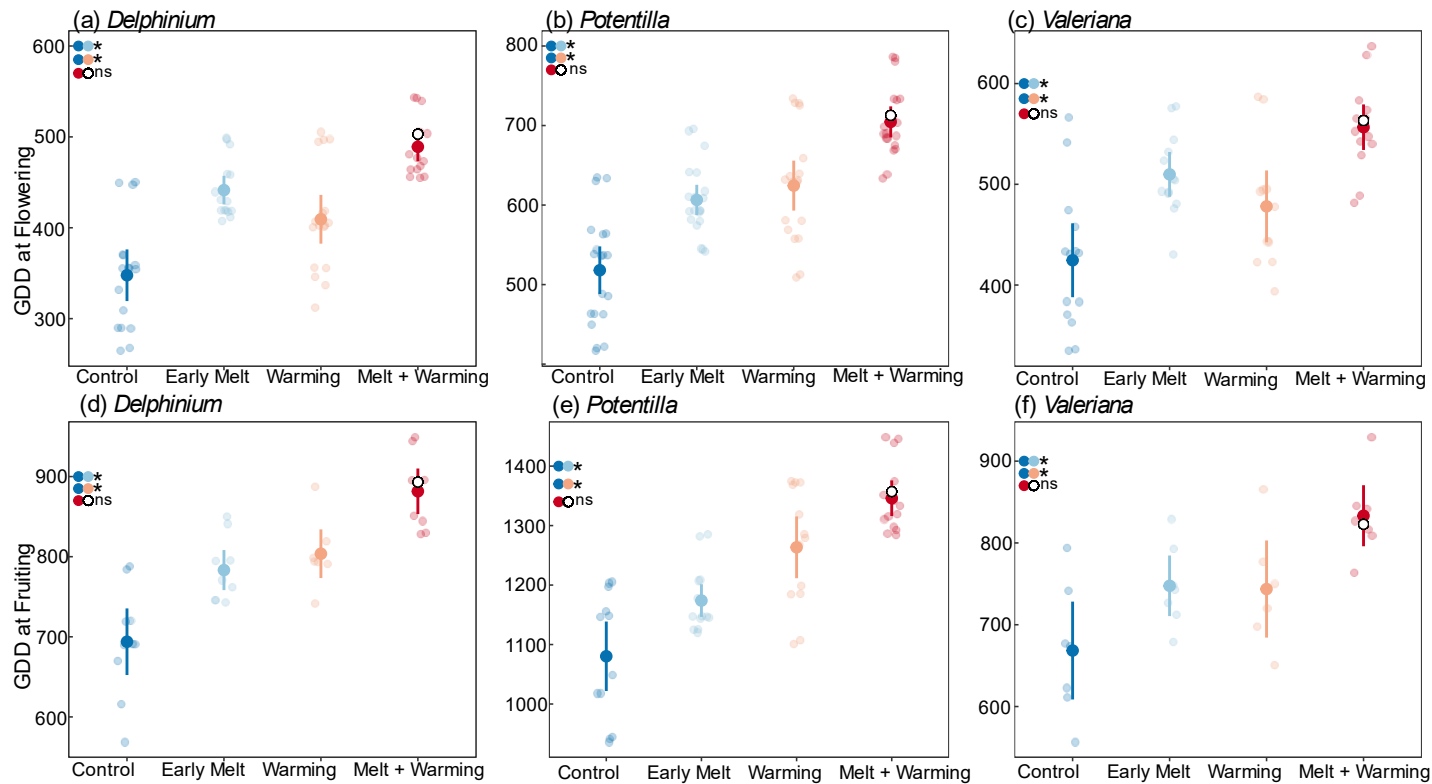


Figure S1. Growing degree days at flowering and fruiting, across four treatments: control, early melt, warming, and a combination of early melt and warming. Solid dots are means, and error bars represent 95% confidence intervals. Open circles represent the additive expectation when the warming and melt 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 non-significant comparisons. Note that y-axes are on different scales because species flower and fruit at different GDD.

Table S1. R^2 values from LM for *Delphinium*, *Potentilla* and *Valeriana* for the relationship between each size measurement on the timing of peak flowering or peak fruiting. Crown diameter A is the diameter at the widest part of the plant and crown diameter B is the diameter perpendicular to that. The measurement used in our analysis is in bold.

Species	Size Measurement	Flowering R^2	Fruiting R^2
Delphinium	Leaf number	0.02	0.04
	Leaf width	0.02	0.00
	Leaf length	0.00	0.00
Potentilla	Leaf length	0.01	0.01
	Leaf number	0.01	0.01
Valeriana	Tallest stem	0.11	0.02
	Crown diameter A	0.01	0.00
	Crown diameter B	0.01	0.00
	Perimeter	0.00	0.00

Table S2. Summary tables from LMs for *Delphinium*, *Potentilla* and *Valeriana* for the effect of climate manipulations (warming and early snowmelt) on the growing degree days at the onset of flowering.

Species	Predictor	Estimate	Std. Error	t value	P
<i>Delphinium</i>	Intercept	618.1	13.2	46.9	<.0001
	Early Melt	88.3	18.7	4.7	<.0001
	Warming	106.4	19.2	5.6	<.0001
	Early Melt x Warming	-8.2	26.9	-0.3	0.76
<i>Potentilla</i>	Intercept	-88.3	18.7	-4.7	0.0001
	Warming	-106.4	19.2	-5.6	<.0001
	Early Melt	-186.5	18.9	-9.9	<.0001
	Warming x Early Melt	-18.1	19.2	-0.9	0.78
<i>Valeriana</i>	Intercept	424.6	14.8	28.7	<.0001
	Early Melt	85.2	21.4	4.0	<0.001
	Warming	53.4	22.3	2.4	0.02
	Early Melt x Warming	-6.6	30.9	-0.2	0.83

Table S3. Summary tables from LMs for *Delphinium*, *Potentilla* and *Valeriana* for the effect of climate manipulations (warming and early snowmelt) on the growing degree days at the onset of fruiting.

Species	Predictor	Estimate	Std. Error	t value	P
Delphinium	Intercept	693.9	16.3	42.7	<0.0001
	Early Melt	89.4	23.6	3.8	0.001
	Warming	109.9	25.3	4.3	<0.001
	Early Melt x Warming	-11.5	35.0	-0.3	0.75
Potentilla	Intercept	1080.3	23.7	45.7	<0.0001
	Warming	183.2	32.8	5.6	<0.0001
	Early Melt	93.7	32.2	2.9	0.006
	Warming x Early Melt	-11.1	45.1	-0.2	0.81
Valeriana	Intercept	668.5	24.5	27.3	<0.0001
	Early Melt	79.2	34.7	2.3	0.03
	Warming	75.2	36.1	2.1	0.05
	Early Melt x Warming	10.5	50.1	0.2	0.84

824 Table S4. Model outputs for the MANOVA for timing of flowering and fruiting and duration of
825 flowering and fruiting.

Response	Response	Species	Df	Pillai	F	Df den	Df	P
Timing	Delphinium	Treatment	3	0.8	10.9	6	100	<0.0001
		Residuals	50					
	Potentilla	Treatment	3	0.5	11.1	6	212	<0.0001
		Residuals	106					
	Valeriana	Treatment	3	0.8	58.5	6	554	<0.0001
		Residuals	277					
Duration	Delphinium	Treatment	3	0.2	2.6	6	134	0.022
		Residuals	67					
	Valeriana	Treatment	3	0.2	12.7	6	574	<0.0001
		Residuals	287					

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Appendix: Interpolation model to calculate growing degree days

We had fewer temperature loggers than subplots (see Methods), and these loggers were deployed shortly (but not immediately) after snowmelt. As such, the daily temperature timeseries at each subplot had a short-duration gap at the beginning of the growing season and additional gaps occurring throughout in the season as loggers were rotated among nested plots. To fill these gaps in the temperature record, we constructed and parameterized a spatio-temporal Bayesian hierarchical model. Specifically, we predicted the joint posterior distribution of daily temperature highs and lows, using these to calculate GDD in a way that accounts for our uncertainty in the ‘true’ value of these extremes.

Model structure

The central intuition of the GDD model rests on the notion that “everything is related to everything else, but near things are more related than distant things” (Tobler, 1970). First, the model expected that spatially-adjacent subplots should have more similar temperatures than subplots that are farther away from one another (all else being equal). During fitting, the model ‘learned’ about the strength and spatial pattern of these associations across our study site without needing to identify *why* a pair of subplots had similar conditions (e.g., slope, aspect, vegetation density). To implement this, we included a two-dimensional finite Gaussian process term ($k = 20$) that used GPS coordinates to describe the spatial locations of subplots (UTM 13N projection). Extending this to temporal ‘distances,’ the model expected that temperature extremes measured on adjacent days should be more similar than for days separated by long intervals. These temporal associations come from a combination of short-term weather fluctuations and systematic warming as the growing season progressed from spring into summer, but again we focused on the pattern rather than the mechanism causing it. To add temporal associations to the model, we included a 1st order autoregressive term with moving average (ARMA) for each of the nested plots. Thirdly, we expected that the high and low temperatures at each subplot would be correlated with one another. We allowed the model to accommodate this by estimating a correlation term between the residuals of the high and low temperature responses.

We expected that the warming chamber manipulation itself would also cause systematic increases in the high and low temperatures observed at each nested plot. Therefore, we included separate high and low temperature intercepts for the warmed and control treatment levels. We accounted for snowmelt timing and other plot-level effects with a single group-level intercept term. Because plot-level effects were unlikely to affect just one response temperature; therefore, we allowed the model to share information about the effect of a given plot on high and low temperatures through a correlation term.

Finally, to enable prediction during the period between snowmelt and temperature logger deployment, we included the high and low temperatures observed at a nearby long-term weather station (4km S; billy barr, unpublished data) as predictors for the high and low temperature responses, respectively. Effectively, this allowed us to model nested plot-level temperatures as *deviations* from the nearby weather station rather than absolute temperature values. By assuming that the spatial pattern of these deviations was the same prior to logger deployment as it was

during the rest of the growing season, we were able to reconstruct the expected high and low temperatures in all subplots using only the nearby weather station observations.

Model fitting

We sampled the joint posterior distribution of the high and low temperatures using Hamiltonian Monte Carlo implemented in Stan (Carpenter et al., 2017) and interfaced via the R package ‘brms’ (Bürkner, 2017). We used weakly informative priors on all parameters, and the size of our temperature dataset (>6800 high/low temperature observations) ensured that these choices had little influence on the posterior distribution. We drew 1000 post-warmup samples on each of four chains, ensured that there were no divergences (Betancourt and Girolami, 2013), and checked for convergence across chains using Vehtari et al.’s (2020) modified Gelman-Rubin convergence diagnostic ($\hat{R} < 1.01$).

Predicting temperatures and GDD from the fitted model

Because the model was fit to high and low temperatures rather than GDD, filling the gaps in the GDD timeseries required (i) predicting the temperature extremes at each unobserved timepoint then (ii) using these temperature extremes to calculate the GDD. We provided the fitted model with the independent variables needed to predict the joint posterior distribution of high and low temperature for each missing timepoint. These included information about the subplot (GPS coordinates, enclosing plot identifier, level of warming treatment imposed), the day of year, and the high and low temperatures observed at the nearby weather station. We then drew 1000 predictive samples for each gap from the joint posterior distribution of high and low temperatures. Because the temperature extremes are correlated in our model, we can’t simply calculate GDD (see Methods) using the mean high and mean low temperatures. Instead, we calculated GDD for each joint posterior sample, estimated the mean GDD across all 1000 samples, then filled the GDD timeseries gap with this mean.