

ARTICLE

Climate Ecology

Earlier spring snowmelt drives arrowleaf balsamroot phenology in montane meadows

J. Simone Durney  | Arden Engel | Diane M. Debinski  | Laura A. Burkle 

Department of Ecology, Montana State University, Bozeman, Montana, USA

Correspondence

J. Simone Durney

Email: simone.durney@gmail.com

Funding information

Iowa State University, Department of Ecology, Evolution, and Organismal Biology; Montana State University; Disney Conservation Fund; the Xerces Society; University of Wyoming NPS Research Station; the Center for Global and Regional Environmental Research; Iowa State University Department of Ecology

Handling Editor: Theresa M. Crimmins

Abstract

Climate change is shifting phenology globally, altering when and how species respond to environmental cues such as temperature and the timing of snowmelt. These shifts may result in phenological mismatches among interacting species, creating cascading effects on community and ecosystem dynamics. Using passive warming structures and snow removal, we examined how experimentally increased temperatures, earlier spring snowmelt, and the poorly understood interaction between warming and earlier spring snowmelt affected flower onset, flowering duration, and maximum floral display of the spring-flowering montane species, arrowleaf balsamroot (*Balsamorhiza sagittata*), over a 7-year period. Additionally, potential cumulative effects of treatments were evaluated over the study duration. The combination of heating with snow removal led to earlier flower onset, extended flowering duration, and increased maximum floral display. While there was year-to-year variation in floral phenology, the effect of heating with snow removal on earlier onset and maximum floral display strengthened over time. This suggests that short-term studies likely underestimate the potential for climate change to influence phenological plant traits. Overall, this research indicates that *B. sagittata*'s flowering onset responded more strongly to snow removal than to heating, but the combination of heating with snow removal allowed plants to bloom earlier, longer, and more profusely, providing more pollinator resources in spring. If warming and early snowmelt cause similar responses in other plant species, these patterns could mitigate phenological mismatches with pollinators by providing a wider window of time for interaction and resiliency in the face of change. This example demonstrates that a detailed understanding of how spring-flowering plants respond to specific aspects of predicted climatic scenarios will improve our understanding of the effects of climate change on native plant–pollinator interactions in montane ecosystems. Studies like this help elucidate the long-term physiological effects of climate-induced stressors on plant phenology in long-lived forbs.

This is an open access article under the terms of the [Creative Commons Attribution](https://creativecommons.org/licenses/by/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2022 The Authors. *Ecosphere* published by Wiley Periodicals LLC on behalf of The Ecological Society of America.

KEYWORDS

arrowleaf balsamroot, climate change, flower duration, flower onset, Greater Yellowstone Ecosystem, maximum floral display, montane meadows, phenology, snowpack manipulation, temperature manipulation

INTRODUCTION

Climate change is a growing issue, leading to species declines and influencing species interactions globally (Valiente-Banuet et al., 2015). Environmental cues, such as temperature and the timing of spring snowmelt, initiate species behaviors and physiology patterns. Alteration in the timing of environmental cues associated with climate change can induce deviations in a species' typical life cycle pattern (i.e., shift in phenology) and affect onset and duration of biological events for both flora and fauna (Parmesan & Yohe, 2003; Walther et al., 2002). Phenological shifts may have detrimental effects on plant communities and those species with which they interact. Even minute shifts in the timing, magnitude, and spatial extent of these environmental cues can have cascading effects on community dynamics via species abundance and distribution shifts (Parmesan & Yohe, 2003) and have the potential to lead to phenological mismatch between species (Visser & Both, 2005). Phenological shifts and mismatches can impact species fitness, abundance, and persistence in a community, creating lasting effects on overall ecosystem structure and function (Burkle & Alarcon, 2011).

Previous studies have examined the separate effects of warming and snowmelt on flowering phenology and flower production in montane systems. Earlier flowering has been documented under warmer temperatures (Arft et al., 1999; Fitter & Fitter, 2002; Jabis et al., 2020; Kehrberger & Holzschuh, 2019) and advanced spring snowmelt, with spring-flowering plants being particularly sensitive to the timing of snowmelt (Gezon et al., 2016; Steltzer et al., 2009; Wadgymar et al., 2018; Wipf, 2010). Increased flower production has been observed with experimental warming in tundra ecosystems spanning the Arctic (Arft et al., 1999) and with experimentally advanced snowmelt in Colorado subalpine meadows (Gezon et al., 2016). Conversely, a study conducted on the Tibetan Plateau reported decreased flower production with simulated warming (Liu et al., 2012). A yearlong glasshouse warming experiment resulted in shortened flowering duration due to earlier plant senescence following typical flowering onset (Nagahama et al., 2018). These studies highlight that montane and alpine plant species experience altered phenology in response to warming and/or early snowmelt.

A few studies have observationally or experimentally examined the separate and combined effects of warming and advanced snowmelt on plant individuals in montane environments over a period of time longer than 4 years. These studies in the Rocky Mountains of Colorado found earlier flowering onset with warming and advanced snowmelt (Dunne et al., 2003; Jabis et al., 2020; Wadgymar et al., 2018), increased floral displays with earlier snowmelt (Inouye, 2008), and extended flowering duration in response to earlier melt (Dunne et al., 2003; Jabis et al., 2020; Price & Waser, 1998), indicating that the phenologies of plant species in this montane ecosystem are tracking climate change. By contrast, Inouye (2008) found reduced floral abundance for three early-spring-flowering perennials (i.e., *Delphinium barbeyi*, *Erigeron speciosus*, and *Helianthella quinquenervis*) associated with earlier snowmelt in a 32-year observational study. The reduction in floral abundance was due to convective frost events (i.e., cold air masses) with trending lower air temperatures after snowmelt, which damaged flower buds (Inouye, 2008). In the same montane ecosystem, extended flowering duration, especially for spring-flowering species, was observed over a 4-year period in response to a naturally occurring and experimentally manipulated earlier snowmelt and warmer spring soil temperatures (Dunne et al., 2003). Thus, phenological responses to temperature-related climate change were detected within a 4-year study period, which could lead to longer term asynchronies in interspecific interactions. For the early-spring-flowering perennial, *Delphinium nuttallianum*, experimental warming reduced floral abundance (i.e., the number of quadrats in which *D. nuttallianum* was present) and the number of flowers per plant over a 6-year period, suggesting that global warming could affect the fecundity of montane-flowering species and floral resources available for pollinators (Saavedra et al., 2003). Jabis et al. (2020) detected earlier flower onset of forbs in response to experimental heating and heating-induced earlier snowmelt, with the timing of snowmelt date driving the pattern, especially for early-season species. This 4-year study uncovered that forbs respond more strongly to changes in temperature that are beneficial for reproduction and local plant-pollinator communities.

Arrowleaf balsamroot (*Balsamorhiza sagittata*) is a vital early-spring floral resource for pollinators in montane regions just after snowmelt. In addition to its role as

a nectar source for generalist pollinators, *B. sagittata* is a valuable source of nectar for the butterfly *Parnassius clodius* (Sherwood et al., 2017), a spring butterfly species known to interact with *B. sagittata*. Additionally, it serves as a critical nectar source for some specialized bee species in the genus *Osmia*, which forage exclusively on *Balsamorhiza* and *Wyethia* species (Cane, 2011). Therefore, *B. sagittata*'s demography, phenology, and flower production are important for the stability of pollinator community dynamics in montane regions in parts of the western United States in early spring. We experimentally investigated the effects of warming, advanced snowmelt, and their less-examined interactive effects in a factorial design on phenology and floral production of the perennial plant *B. sagittata* in a montane meadow in Wyoming, USA, over 7 years. Specifically, we investigated treatment effects on flower onset, flowering duration, and maximum floral display, the cumulative treatment effects over time, and the correlations among plant responses to treatments to understand how flower onset, flowering duration, and maximum floral display are associated. The following expectations and predictions are based on previous research. We expected earlier flowering onset with all non-control treatments with the earliest onset occurring in the heating and snow removal treatment in response to earlier light access and warmer spring temperatures (Arft et al., 1999; Fitter & Fitter, 2002; Gezon et al., 2016; Jabis et al., 2020; Kehrberger & Holzschuh, 2019; Steltzer et al., 2009; Wadgymar et al., 2018). We predicted extended flowering durations with snow removal in response to earlier onset and access to light (Dunne et al., 2003; Price & Waser, 1998), but no change with heating and snow removal, as the two treatments could counteract each other (Nagahama et al., 2018). We expected increased maximum floral display with snow removal in response to earlier

onset and extended flowering duration, which allows plants to flower longer and potentially produce more flowers (Gezon et al., 2016). However, we predicted a decrease in maximum floral display in response to the combination of heating and snow removal due to temperature and soil moisture stress (Saavedra et al., 2003). Further, we expected that the effects of each treatment on *B. sagittata* flowering onset, flowering duration, and maximum floral display would strengthen over the course of the study. All the above hypotheses are listed in Table 1. This study contributes unique insights to the potential for advanced snowmelt to interact with warming to influence flowering phenology and the degree to which these treatment effects strengthen over time.

MATERIALS AND METHODS

Study site

This study was conducted from 2013 to 2019 in a flat montane meadow near Pilgrim Creek at an elevation of 2100 m in Grand Teton National Park, Wyoming, USA (43.914977°; -110.578072°). Meadow vegetation composition consists of various sagebrush species (*Artemisia* spp.) and herbaceous flowering plants and grasses but is dominated by bare ground (about 50% cover). The soil surface is highly permeable, consisting of gravel glacial outwash deposited by the Pinedale glaciers (Martin, 2008). The regional climate is characterized by mean annual precipitation of 60 cm with most of that falling as snow (Western Regional Climate Center, Moran, WY, USA). The mean snow depth (i.e., all-season snow accumulation) is 6.4 m, with snow cover beginning in October and ending in May (NRCS SNOTEL: Base Camp). Mean monthly temperatures ranged

TABLE 1 Hypotheses about how *Balsamorhiza sagittata* flower onset, flowering duration, and maximum floral display may respond to decreased spring snowmelt via removal, warming via passive heating, and warming with decreased spring snowpack.

Predictions	Flower onset	Flowering duration	Maximum floral display
Decreased spring snowpack via snow removal (SR)	Earlier in response to earlier access to light	Extended in response to earlier flower onset with earlier light access	Increase due to earlier flowering onset and extended flowering duration
Warming via passive heating (H)	Earlier in response to gradually increasing winter and spring temperatures	Shortened due to asymmetrical shift in flowering onset and senescence	Decrease in response to higher temperatures and decreased soil moisture causing stress
Warming with snow removal (H + SR)	Earlier due to the interactive effect of increasing temperatures and access to light	Similar to control in response to interactive effect of warming and snow removal canceling each other out	Decrease in response to higher temperatures and decreased soil moisture causing stress
SR × year, H × year, and H + SR × year	The effect of treatment will strengthen over the 7-year study	The effect of treatment will strengthen over the 7-year study	The effect of treatment will strengthen over the 7-year study

from -32 to 21°C from 1988 to 2019; December and January are the coldest months, and July and August are the warmest (NRCS SNOTEL: Base Camp). The growing season typically begins in mid-May with snowmelt and extends to the end of August or early September (Debinski et al., 2000).

Experimental methods and design

Twelve 2.4-m^2 ($8\text{ ft} \times 8\text{ ft}$) plots were established on existing native plant communities in this meadow in 2010 and monitored annually. Across the 12 plots, the number of *B. sagittata* plants in a plot ranged from 6 to 26 plants across the study duration. Heat and snow removal were manipulated in a factorial design to create four treatments ($N = 3$ replicates/treatment): decreased spring snowpack via snow removal (SR: not heated, snow removal), warming via passive heating (H: heated, no removal), heating and snow removal (H + SR: heated, snow removal), and control (C: not heated, no removal) (Sherwood et al., 2017). Within each of the three blocks (east, central, and west), treatments were randomly assigned to plots, with one treatment replicate per block (Appendix S1: Figure S1). Treatments assigned to plots remained the same for the duration of the study. Plots were regularly spaced at 4.9 m (16 ft) apart from one another. Decreased spring snowpack, simulating early snowmelt, was achieved by manually removing snow from designated plots in late April or early May prior to the growing season leaving about 2 cm of snow to prevent vegetation damage. Snow removal was accomplished in all except for 2 years (2015 and 2016) when snowpack was too low to allow for removal. Snow depths removed ranged from 55 to 80 cm for the years when snow was removed. Heating was accomplished by constructing a 2.4-m^2 ($8\text{ ft} \times 8\text{ ft}$) passive warming structure. The top of the structure was 59 cm from the ground as to not impede plant growth. During 2010–2015, these structures were made of wood and plexiglass (Sherwood et al., 2017). From 2016 to 2018, the structures were made of wood with a glasshouse plastic roof with perforations to allow precipitation to fall through. In 2019, these structures were made of polyvinyl chloride pipe with a glasshouse plastic roof with small perforations. All warming structures enhanced the downward reflectance of infrared radiation on the ground and increased the daily minimum temperatures of plant and soil surfaces by 2°C (Sherwood et al., 2017). Mean surface temperatures in western North America are projected to increase by $1\text{--}7^{\circ}\text{C}$ by 2100 (IPCC, 2014). The passive warming structures used here increase surface temperature on the low end of regional climate projections; therefore, resulting

responses to warming are a conservative response. Passive warming structures were installed on designated plots at the time of snow removal (i.e., late April and early May) prior to the growing season and remained in place until late September or October after the growing season was completed (Sherwood et al., 2017). Soil and surface temperatures for each plot were recorded every hour throughout the growing season using a soil temperature probe buried 25 cm below the surface and HOBO loggers placed on the soil surface in the center of the plot. The ambient air temperature was recorded for the set of plots every hour throughout the growing season using an air sensor placed 1 m above the soil surface.

All individual *B. sagittata* plants 10 cm or taller growing within each of the 12 plots were measured every 3 days from emergence (mid-May) to senescence (mid-July). A *B. sagittata* individual takes 3–5 years to flower and remains reproductively active for up to 40 years (Gucker & Shaw, 2018; Tilley et al., 2012). Individual plants were numbered and monitored across years using plot maps and metal identification tags (Appendix S1: Figure S2). Measurements, which occurred ca. every 3 days during the growing season, included whether the individual was dead or alive and, if alive, flower phenology (i.e., buds, fully flowering, senescing, and senesced). Flowering heads were considered fully open once at least one disk flower opened, senescing once ray flowers withered but open disk flowers remained, and senesced once disk flowers withered and seed maturity was observed. We distinguished among these stages because fully open and senescing flowers are the only stages that provide nectar resources for pollinators (Potts et al., 2003) that feed on *B. sagittata* in montane meadows, and we wanted to quantify this window of time for each treatment. Within an individual *B. sagittata* plant, buds and flowers often co-occur with blooming occurring sequentially, where the bloom and senescence of an individual flower is followed by another, across primarily solitary floral heads (Tilley et al., 2012, personal observations).

Statistical analysis

Statistical analyses were performed to determine whether flowering onset (i.e., date of first flower), flowering duration, or maximum floral display of individual plants differed among treatments across the 7-year study and whether the effect of treatment grew stronger over time. A four-level categorical variable that incorporates the main effects of heating and snow removal along with their interaction was created using the *interaction* function in R. The four levels are described in the *Experimental methods and*

design. This variable was included as a predictor variable in all models and statistical tests. Individual plants that failed to produce flowers because they had not yet reached flowering or reproductive maturity were excluded from these analyses. Those individuals were removed in order to avoid the potential for plant age to skew maximum floral display estimates unrelated to treatment effect. A total of 88 individual plants that were alive between 2013 and 2019 and flowered at least once were included in these analyses. All analyses were evaluated at a significance level of 0.05, where $p < 0.05$ indicates significance, $0.05 < p < 0.1$ indicates marginal significance, and $p > 0.1$ indicates no significance. Missing values were removed prior to model construction. For example, plants that produced a flower one year but did not produce in subsequent years were removed from the analyses, while plants that produced a flower one year but skipped a year of flowering and continued to flower in a subsequent year remained in the analyses. Skipped years were represented with a “0” value. Mixed-effects models were used to test the effects of treatment on response variables and included individual plant identity nested within plot as random effects to account for multiple measurements of each individual across plots over the 7-year duration of this study. When testing the effect of treatment, year was included as a crossed additive random effect in each mixed-effects model to control for random year-to-year variation around the patterns of the treatments. This allowed us to assess how treatment affected each variable while accounting for year-to-year differences in weather and other conditions. Linear mixed-effects models with a Tukey’s contrast were used to test for multiple comparisons.

To test whether treatment effects on flower onset, flowering duration, and maximum floral display took time to develop (cumulative effects of treatment) or grew stronger over time, year was included as an interaction with treatment in each mixed-effects model. Initial evidence of an interaction between treatment and year was supported by an F test prior to further analysis and interpretation. Pairwise comparisons of treatment–year combinations are not shown because absolute values of treatment effects depended on year.

Flowering onset (i.e., date of first flower) was defined as the date on which an individual plant was observed to have at least one fully opened flower. Two linear mixed-effects models (described above) were used to identify whether the effects of treatment on flower onset varied across the 7-year study and whether the effects of treatment on flower onset grew stronger over the 7-year period.

Duration of flowering was defined as the number of days between observation of an individual’s first fully open flower and its last senescing flower in a given

growing season. In some instances, an individual was observed to be flowering on only one date in a particular year, prohibiting the estimation of a flowering duration for that individual in that year. Such individuals were excluded from these analyses. Linear mixed-effects models were fit to identify whether the effects of treatment on the flowering duration varied across the 7-year study and whether the effects of treatment on the flowering duration grew stronger over the 7-year period.

Maximum floral display (i.e., the maximum number of concurrent flowers) was calculated by totaling the number of fully flowering, senescing, and senesced flowers of an individual at each visit to identify the maximum number of flowers present concurrently on an individual in a given year. Buds were not included in these counts because the number of flowers produced was intended as a proxy for the quantity of available nectar, and buds that failed to flower provided no nectar. A sum of all flowers produced by an individual over the growing season would not be reliable due to the potential for the same flower to be counted multiple times on successive visits. Using the maximum number of concurrent flowers eliminates the possibility of recounting the same flowers, providing a conservative estimate for the number of flowers produced by an individual over each growing season. Additionally, disintegrated and fallen senesced flowers were excluded when using the maximum number of concurrent flower metrics. Generalized linear mixed-effects models with a negative binomial distribution to account for overdispersion were fit using these estimates to determine whether the effects of treatment on maximum floral display varied across the 7-year study duration and whether the effects of treatment on maximum floral display grew stronger over the 7-year period.

The raw data over the 7-year study were visually examined to investigate the associations between flower onset, flowering duration, and maximum floral display of *B. sagittata* within each treatment to explore potential relationships between these response variables. Models prove difficult to use in this instance due to the multicollinearity of using response variables as predictor variables for other response variables in the same study. Here, we chose to present graphed relationships using raw data collected in this study and their associated correlation values to draw attention to possible relationships. The correlation coefficient was calculated using the *cor.test* function to evaluate the association between these variables for each treatment. All raw observations in each treatment across the 7-year study were pooled.

Mixed-effects models were constructed using the *lmer* and *glmer.nb* functions in the *lme4* package (Bates et al., 2015) with the *lmerTest* package (Kuznetsova et al., 2017) to obtain p values in R and the *glmmadmb*

function in the *glmmADMB* package (Fournier et al., 2012; Skaug et al., 2016). Estimated marginal mean pairwise comparisons were completed using the *emmeans* function in the *emmeans* package (Lenth, 2020) in R to create figures with letters identifying significance between treatments. Multiple comparisons of means using a Tukey's contrast for each mixed-effects model were conducted using the *glht* function in the *multcomp* package (Hothorn et al., 2008) in R to determine relative effects of treatment. Figures were created using the *ggplot2* package (Wickham, 2016) in R (R Core Team, 2020).

RESULTS

Flower onset

Heating mediated the influence of snow removal on flowering onset (interactive effect between heating and snow removal; Table 2). There were also main effects of snow removal and heating (Table 2). Snow removal (SR) and heating with snow removal (H + SR) advanced flowering onset by 4.0 and 3.8 days, respectively, while heating alone (H) advanced onset by 1.9 days compared with the control (C) treatment, though the difference in heated effects was not significant (Figure 1). Multiple comparisons of means with a Tukey's contrast showed a significant interaction between heating and snow removal on

flower onset (Table 2), but snow removal appears to have the strongest effect on flower onset (Figure 1). The treatment effects of heating and heating with snow removal strengthened over the 7-year study duration significantly (Table 3). For instance, *B. sagittata* flowering onset occurred earlier over time with snow removal (SR) and heating with snow removal (H + SR) and occurred later over time in the heating (H) and in the control (C) treatments (Table 3, Figure 2).

Flower duration

Both heating and snow removal individually extended flowering duration, and heating with snow removal (H + SR) had a significant effect, extending flowering duration by 5.0 days compared with the control (C) treatment. The flowering duration was 3.6 days longer in the snow removal treatment (SR) and 3.4 days longer in the heated (H) treatment compared with plants in the control (C) treatment (Figure 1). These increases in the *B. sagittata* flowering duration were captured in multiple comparisons of means with a Tukey's contrast across all treatments (Table 2). For one of the treatments (heating, H), there was a discrepancy in the effects of heating on the flowering duration between the two statistical tests that we used: While heating did not affect the flowering duration according to estimated marginal means (Figure 1), heating did significantly extend the flowering duration according to the linear mixed-effects model with the Tukey test (Table 2). The latter test is more powerful because it tests for multiple comparisons (Meier, 2021), and we summarize our results based on Table 2. There was no evidence that the magnitude of treatment effects on the *B. sagittata* flowering duration changed over time (Table 3, Figure 2). The slopes of the relationships between the flowering duration and year for all treatments (i.e., control [C], heating [H], snow removal [SR], and heating with snow removal [H + SR]) are nearly zero, indicating that the strength of cumulative treatment effects was relatively consistent across the 7-year study (Figure 2).

TABLE 2 Multiple comparisons of means with Tukey's contrasts to identify whether treatment affected individual plant flowering onset, flowering duration, or maximum floral display.

Source	<i>z</i>	<i>p</i>
Flowering onset		
Heated	−2.94	0.0171
Snow removal	−6.28	<0.0001
Heated × snow removal	−5.61	<0.0001
Flowering duration		
Heated	3.43	0.0035
Snow removal	3.73	0.0011
Heated × snow removal	4.94	<0.0001
Maximum floral display		
Heated	1.89	0.2302
Snow removal	1.64	0.3570
Heated × snow removal	2.78	0.0273

Note: Each model included heated and snow removal treatments as main effects and their interaction with individual nested within plot as a random effect, and year as an additive random effect. Values in boldface indicate significant effects at $\alpha < 0.05$.

Maximum floral display (i.e., the maximum number of concurrent flowers)

Heating mediated the influence of snow removal on *B. sagittata*'s maximum floral display (interactive effect between heating and snow removal; Table 2). Maximum floral display was higher in the heating with snow removal treatment by 1.2 flowers compared with the control treatment (Figure 1). The treatment effect of heating with snow removal (H + SR) strengthened over the

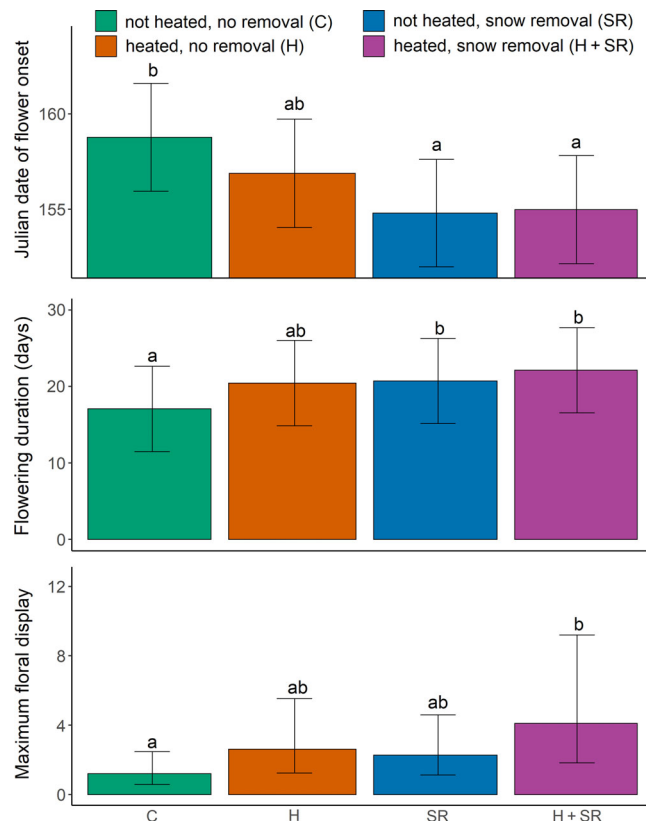


FIGURE 1 Effect of treatment on the least squares mean flower onset date, flowering duration, and maximum floral display. Treatments included the following: decreased spring snowpack via snow removal (SR: not heated, snow removal), warming via passive heating (H: heated, no removal), decreased spring snowpack and warming (H + SR: heated, snow removal), and control (C: not heated, no removal). Estimated marginal mean pairwise comparison is indicated by letters where the same letter indicates overlap and different letters indicate variation. The error bars represent the upper and lower 95% confidence levels.

7-year study significantly, with a slight increase in *B. sagittata* maximum floral display (Table 3, Figure 2). Treatment effects on maximum floral display were consistent across all years: Plants in the heating with snow removal (H + SR) treatment had the most flowers, while those in the control (C) treatment had the fewest, regardless of year (Figure 2).

Relationships between flower onset, flowering duration, and maximum floral display

Flower onset and duration were negatively associated with each other across all treatments, indicating that *B. sagittata* plants that began flowering earlier also bloomed for a longer period of time. Within treatments, heat with snow removal (correlation = -0.55 , $t = -5.66$, $df = 75$, $p < 0.0001$) and snow removal (correlation = -0.53 , $t = -5.92$, $df = 88$, $p < 0.0001$) exhibited the strongest negative correlation, while the control (correlation = -0.38 , $t = -3.76$, $df = 82$, $p = 0.0003$) and heated (correlation = -0.33 , $t = -3.40$, $df = 96$, $p = 0.0010$) treatments had the weakest negative correlation (Figure 3).

Flowering duration and maximum floral display were positively associated across all treatments, with plants that bloomed for a longer duration also having a larger maximum floral display. Within treatments, snow removal (correlation = 0.52 , $t = 5.67$, $df = 88$, $p < 0.0001$) and the control (correlation = 0.32 , $t = 3.06$, $df = 82$, $p = 0.0030$) indicated the strongest positive correlation, while heated (correlation = 0.18 , $t = 1.82$, $df = 96$, $p = 0.0718$) and heat with snow

TABLE 3 Mixed-effects models to identify whether treatment $\times$ year interactions affected individual plant flowering onset, flowering duration, or maximum floral display over time.

Parameter	Flowering onset		Flowering duration		Maximum floral display	
	<i>t</i>	<i>p</i>	<i>t</i>	<i>p</i>	<i>z</i>	<i>p</i>
Heated	4.991	<0.0001	-1.300	0.195	0.34	0.7338
Snow removal	-0.714	0.4756	-0.095	0.925	-1.72	0.0852
Heated $\times$ snow removal	-2.315	0.0213	1.151	0.250	-2.76	0.0058
Year	-0.600	0.5492	-1.698	0.090	-3.76	0.0002
Heated $\times$ year	-4.999	<0.0001	1.304	0.193	-0.33	0.739
Snow removal $\times$ year	0.717	0.4737	0.093	0.926	1.72	0.0853
Heated $\times$ snow removal $\times$ year	2.317	0.0212	-1.151	0.251	2.76	0.0057

Note: The treatment $\times$ year interactions were tested to evaluate whether treatment effects grew stronger over time. Each model included the interaction of year and heated and snow removal treatments with individual nested within plot as a random effect. Bolded *p* values indicate significant effects at $\alpha < 0.05$.

removal (correlation = 0.17, $t = 1.49$, $df = 75$, $p = 0.1404$) had the weakest positive correlations with no significant support (Figure 3).

There was a negative relationship between flower onset and maximum floral display across all treatments, with *B. sagittata* plants that began flowering later also having a smaller maximum floral display. Within treatments, the control (correlation = -0.27 , $t = -2.54$, $df = 82$, $p = 0.0128$) and heated (correlation = -0.24 , $t = -2.40$, $df = 96$, $p = 0.0183$) treatments exhibited the strongest positive correlation,

while snow removal (correlation = -0.21 , $t = -2.00$, $df = 88$, $p = 0.0512$) and heated with snow removal (correlation = -0.09 , $t = -0.79$, $df = 75$, $p = 0.4329$) had the weakest negative correlations with no significant support (Figure 3).

DISCUSSION

Climate change is affecting the phenology and flower production of flowering plants globally. Warmer

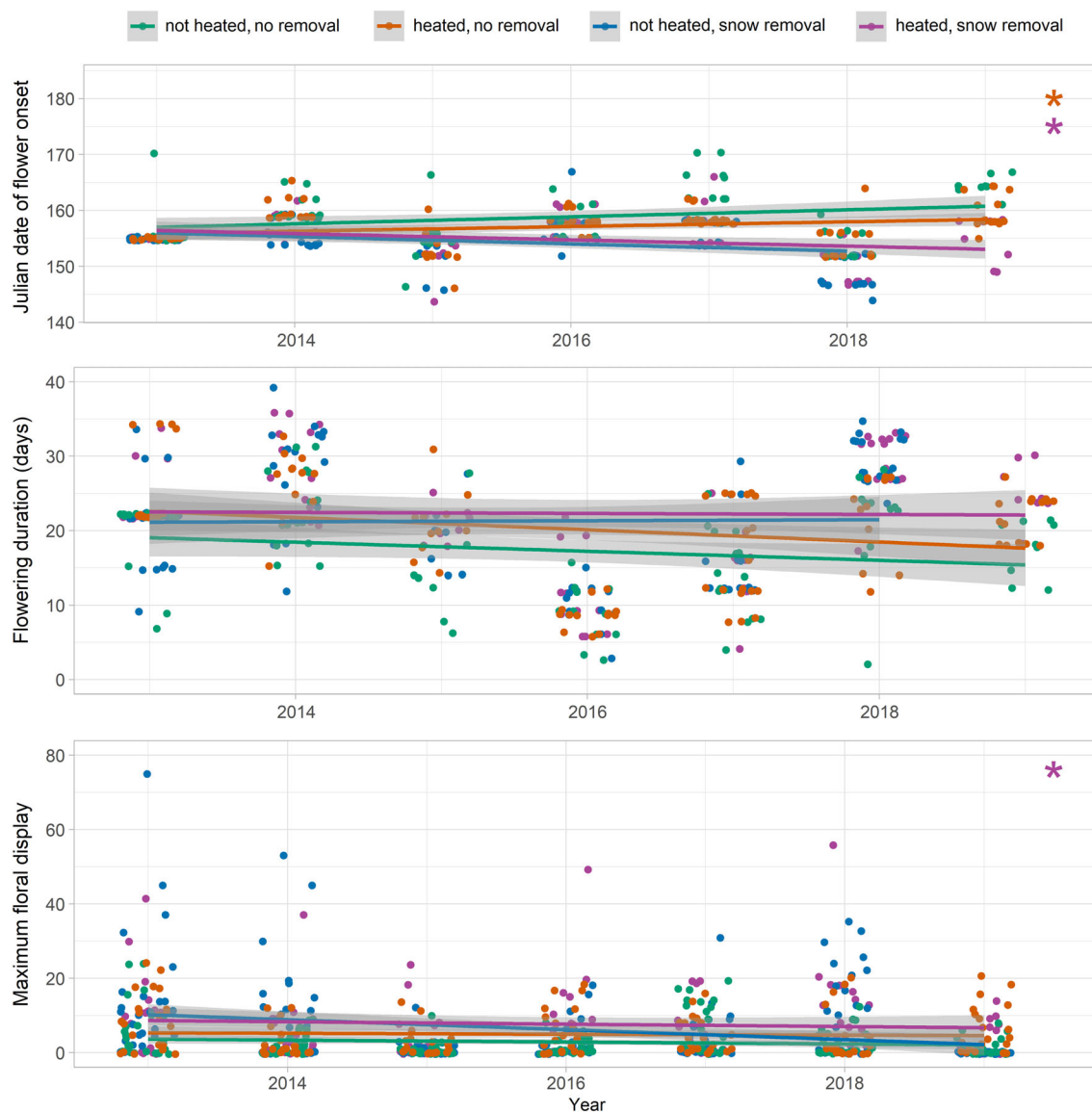


FIGURE 2 Treatment effects over time on flower onset, flowering duration, and maximum floral display. Treatments included the following: decreased spring snowpack via snow removal (SR: not heated, snow removal), warming via passive heating (H: heated, no removal), decreased spring snowpack and warming (H + SR: heated, snow removal), and control (C: not heated, no removal). The figure displays results of treatment interactions with year. Asterisks indicate a significant treatment $\times$ year interaction (indicated by treatment color) compared with the control on the response variable (i.e., flowering onset, flowering duration, and maximum floral display). The normal confidence intervals (indicated by the gray-shaded areas along each line) were constructed using generalized linear smoothing to observe a linear change in each treatment over time. Flowering onset did not occur in snow removal plots in 2019; therefore, there are no data available for that treatment and year.

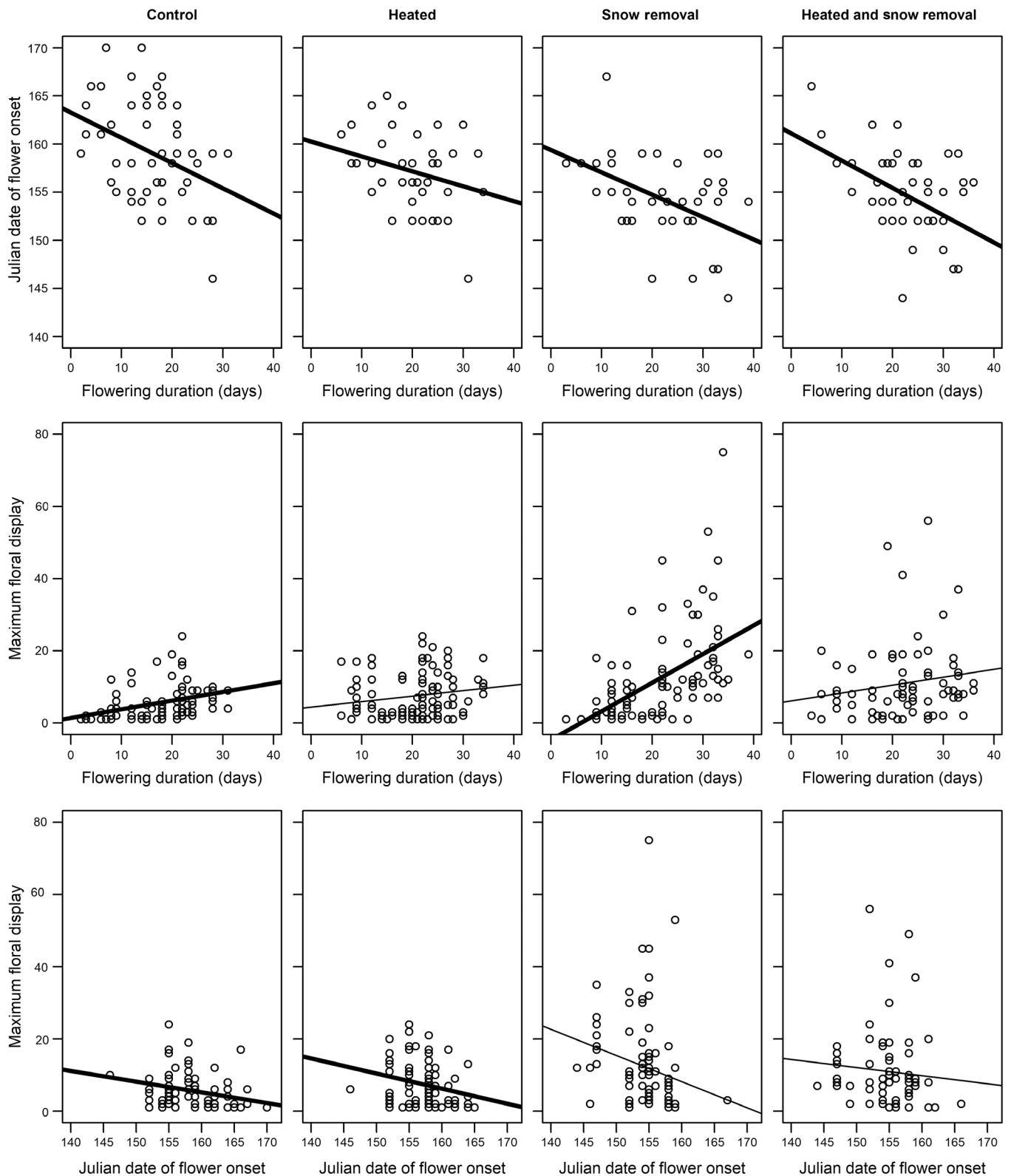


FIGURE 3 Relationships between the raw values for plant individuals of *Balsamorhiza sagittata* flower onset and flowering duration, flowering duration and maximum floral display, and flower onset and maximum floral display within each treatment across the 7-year study. Treatments included the following: decreased spring snowpack via snow removal (not heated, snow removal), warming via passive heating (heated, no removal), decreased spring snowpack and warming (heated, snow removal), and control (not heated, no removal). A best-fit line was added to display the relationship between the variables, with bolded lines indicating a significant correlation.

temperatures and earlier snowmelt individually lead to advanced flowering onset (Arft et al., 1999; Fitter & Fitter, 2002; Gezon et al., 2016; Jabis et al., 2020; Kehrberger & Holzschuh, 2019; Steltzer et al., 2009; Wadgyman et al., 2018; Wipf, 2010), extended flowering durations (Dunne et al., 2003; Jabis et al., 2020; Price & Waser, 1998), and greater maximum floral displays (Arft et al., 1999; Gezon et al., 2016), but the combined effects of warming and earlier snowmelt on flowering phenology are poorly understood, especially over many consecutive years. Consistent with our predictions, *B. sagittata* phenology and floral production varied in response to warming via passive heating with experimentally accelerated spring snowmelt across the 7-year study, suggesting that components of climate change interact to affect montane floral populations and community interactions through altered phenology. Heating with snow removal drove the patterns of earlier flower onset, extended flowering duration, and increased maximum floral display—beyond the individual effects of heating and snow removal. These results suggest that earlier springs in montane regions will likely lead to earlier and longer flowering periods with more flowers produced, thereby reducing possible phenological mismatches with interacting species. Our prediction concerning the ability of heating with snow removal treatments to counteract each other with respect to flowering duration was not supported. The effects of heating with snow removal on earlier onset and increased maximum floral displays strengthened over time, indicating that species such as *B. sagittata* may benefit from conditions of climate change and short-term experiments likely underestimate the potential impacts of warming temperatures and earlier snowmelt on flowering phenology.

Heating with snow removal leads to earlier flowering onset

Flowering onset occurred earlier under conditions of snow removal and heating with snow removal, suggesting that snow removal drives this trend. This result indicates that earlier access to light enables photosynthesis and fosters earlier growth and the onset of flowering of *B. sagittata*, rather than changes in temperature. While earlier flowering can result from higher plant productivity due to increased soil moisture in snow removal plots in some systems (Gezon et al., 2016; Lambert et al., 2010), soil moisture in these snow removal plots was significantly reduced (Sherwood et al., 2017). Therefore, earlier light availability is more likely to drive the observed responses to snow removal than changes in soil moisture.

The effect of heating and heating with snow removal on earlier flower onset strengthened over the 7-year study period, signifying that the influence of temperature on flower onset became more important with time and may eventually outweigh the effects of snow removal in the long term. Together, these results indicate that while early-spring snowmelt has a strong, consistent effect on *B. sagittata* flowering onset, the effects of warming on flowering onset have the potential to play a stronger role in directing flowering phenology over decades of climate change, especially as climate warming intensifies.

Heating with snow removal extended flowering durations

Flowering duration was prolonged under conditions of snow removal and heating with snow removal, with longer durations related to earlier flower onset. Our results are consistent with previous work linking longer forb flowering durations to earlier snowmelt (Price & Waser, 1998) and to increased soil heat (Dunne et al., 2003; Jabis et al., 2020). However, other studies have attributed shortened flower durations to warming (Kudo, 2020) resulting from earlier senescence (Nagahama et al., 2018), likely due to increasing drought stress with declining soil moisture as the growing season progresses. This study system exhibited declining soil moisture following day of year (DOY) 170 (Sherwood et al., 2017), although from 2013 to 2019, *B. sagittata* individuals completed flowering by DOY 170 regardless of treatment. Notably, we found no change in the timing of flowering senescence across all treatments, similar to another early-season forb, glacier lily (*Erythronium grandiflorum*) (Lambert et al., 2010). Research presented here combined the effects of heating with snow removal to uncover the interactive ability of these treatments to advance onset, maintain senescence date, and thereby extend flowering duration—allowing longer periods of flowering that facilitate interactions with other organisms in montane communities. It should be noted that *B. sagittata* would likely extend flowering durations in warmer years with earlier snowmelt due to its sequential flowering behavior. Research by Jabis et al. (2020) also found an interactive effect between snowmelt date and temperature, with earlier snowmelt and higher temperatures further lengthening the flowering durations of forb species. Congruent with our results, durations are dependent on snowmelt date (Dunne et al., 2003; Kudo, 2020; Price & Waser, 1998). Additionally, our research showed that the effects of all treatments on flowering duration were consistent over time, suggesting that flowering durations remain stable in their responses to advanced spring snowmelt and warming.

Maximum floral display increased under heating with snow removal

Maximum floral display (i.e., the maximum number of concurrent flowers) marginally increased under conditions of heating with snow removal, indicating that the combination of these climatic variables influences montane plant investment in floral displays and potentially impacts their fitness. Our findings were consistent with previous research that observed increased flower numbers with earlier snowmelt (Gezon et al., 2016) and warming (Arft et al., 1999). By contrast, other studies have found decreased flower numbers with earlier snowmelt (Inouye, 2008) and warming (Liu et al., 2012; Saavedra et al., 2003), suggesting that the effects of warming and advanced spring snowmelt on maximum floral display are context-dependent on the species and location. Therefore, additional research is needed to evaluate the physiological responses to warming and early snowmelt in relation to maximum floral displays of flowering species. Soil moisture affects maximum floral displays, with declining moisture leading to lower investments in reproduction, reflected in reduced flower production (Phillips et al., 2018). *B. sagittata* in our study system complete flowering prior to observed declines in soil moisture (Sherwood et al., 2017); therefore, soil moisture may be unlikely to affect *B. sagittata* floral production in a given growing season. Few other studies have investigated the potential for snow removal to interact with heating to affect maximum floral display. Our results indicate that heating with snow removal increases maximum floral display for *B. sagittata* and that this effect strengthens over time. These findings highlight the positive effect that warmer conditions and reduced snowpack could have on early-spring floral displays in montane meadows in the context of climate change.

Earlier flower onset associated with longer flowering durations and greater maximum floral displays

Our findings uncovered that flower onset was negatively correlated with flowering duration across all treatments, with the heated and snow removal treatment experiencing the strongest negative response. The consistency of this pattern across treatments, including the control, suggests that regardless of local resource availability (i.e., light and soil moisture), individuals of *B. sagittata* that flower early also flower for a long duration in this system. This pattern could also be indicative of overall cooler temperatures earlier in the spring allowing individual flower longevity to increase, therefore extending

flowering durations (Yasaka et al., 1998). In addition, flowering duration was positively correlated with maximum floral display, with an especially strong relationship in the snow removal treatment. This strong correlation suggests that *B. sagittata* plants allocate resources toward increasing flower production when flowering for longer periods in response to earlier light access. This pattern between flowering duration and floral display has been found more generally in plants as a way to evade herbivory and increase fitness (Ehrlén et al., 2015). For the heated and heated with snow removal treatments, the lack of correlation suggests that there may not be a trade-off between flowering longer and producing more flowers based on resources available. For instance, healthy and/or larger plants may bloom longer and produce more flowers, while unhealthy and/or smaller plants may bloom for shorter periods of time and produce fewer flowers. Additionally, due to *B. sagittata*'s sequential flowering behavior, extended flowering durations may occur among individuals with greater floral displays. Finally, flowering onset was negatively correlated with maximum floral display across treatments, with the control eliciting the strongest negative response. This pattern implies that the timing of flowering onset may dictate the size of *B. sagittata* maximum floral display, with individuals that flower earlier allocating resources prior to competitors and enabling the production of more flowers to attract pollinators and maximize fitness. Earlier flowering leading to increased seed production (i.e., increased fitness) has been supported by previous research on the early-spring-flowering species, *Mertensia fusiformis* (Forrest & Thomson, 2010). This relationship between earlier flowering and resource allocation to produce more flowers may indicate *B. sagittata*'s resiliency to short-term summer dry periods and a lack of pollinator interactions due to asynchrony (Forrest & Thomson, 2010). Further, it may indicate that climate change may have weaker negative effects on *B. sagittata* plant fitness, the pollinators with which *B. sagittata* interacts, and overall *B. sagittata* community dynamics than expected.

Potential implications for plant–pollinator interactions

Advancement in flowering onset in response to earlier spring snowmelt and long-term warming may result in a phenological mismatch where floral resources emerge prior to pollinators (Kudo & Ida, 2013; Parmesan & Yohe, 2003; Walther et al., 2002). Such mismatches could have cascading effects on plant reproduction, impacting populations of both plants (Kudo & Ida, 2013) and their pollinators, especially specialists (Memmott et al., 2007), in the long

term (Kehrberger & Holzschuh, 2019). Patterns of earlier flower onset and extended flowering duration could mitigate phenological mismatches with interacting pollinators because these conditions provide a wider window of time for possible interaction with floral resources. However, it would be essential to determine the degree of a temporal shift in emergence and duration for both the plants and associated pollinators to effectively establish the severity of a potential mismatch (Rafferty et al., 2015). Increased maximum floral display in response to heating and/or snow removal may have more complex impacts on interacting pollinators that warrant additional investigation. For example, in the same system as our study under heating conditions, *B. sagittata* produced more flowers, but these flowers had decreased nectar volume and increased sugar concentration (McCombs et al., 2022). A review of the physiological effects of warming on plant–pollinator interactions (Scaven & Rafferty, 2013) highlights that altered nectar production and composition can have immediate effects on pollinator visitation as reflected in pollinator energetics (Kudo & Harder, 2005). Long-term consequences for pollinator fitness have been observed with greater nectar sugar concentration associated with increased larval solitary bee growth (Bourke & Irwin, 2009) and some butterflies and wasps relying on nectar for nutrients such as amino acids and sugars (Kevan & Baker, 1983). The patterns we observed in our experiment imply that real changes in temperature and the timing of snowmelt could have long-lasting impacts on plant–pollinator interactions, community structure and function, and ecosystem dynamics.

CONCLUSIONS

This research identified that the flowering phenology of *B. sagittata* responded most strongly to the combination of heating with snow removal rather than snow removal or heating only. Responses included advancing flower onset, extending flowering duration, and increasing maximum floral display. As one of the first studies to monitor the combined effects of snow removal and heating on montane-flowering plants over a 7-year period, we observed that advanced spring snowmelt drives spring-flowering plant phenology in montane ecosystems. Further, our results show that long-term studies are needed to quantify the effects of climate change because the influences of heating with snow removal that advanced flower onset and increased maximum floral display also strengthened over time.

This study provides important insights into understanding how climatic trends may affect the phenology and floral

production of a long-lived, spring-flowering perennial plant species in montane regions. Our results indicate that the effects of climate change on floral phenology in this system could result in earlier flowering, extended flowering periods, and more flower production, which would contribute to our understanding of plant–pollinator interactions in montane ecosystems following snowmelt. This and similar montane systems are particularly susceptible to environmental cues and shifts in the timing of those cues (Cleland et al., 2007). Future research may consider using similar methodologies to determine whether the patterns observed in this study hold for other long-lived, spring-flowering, and mid-summer flowering montane perennials. Future conservation efforts to preserve native plants and their essential interactions with pollinators will benefit from the knowledge of how these species respond to changes in climate.

ACKNOWLEDGMENTS

This research was supported by grants from Decagon Devices, the Xerces Society, the Center for Global and Regional Environmental Research, Iowa State University Department of Ecology, Evolution, and Organismal Biology, Iowa State University Graduate Program in Ecology and Evolutionary Biology, Montana State University, Disney Conservation Fund, and the University of Wyoming NPS Research Station. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the US Government. The authors would like to thank Montana State University's Statistical Consulting and Research Services for their statistical advisement concerning this research. A very special thanks go to those who assisted with the field studies throughout the years: M. Germino, K. Reinhardt, members of the Reinhardt Lab in the Department of Biological Sciences at Idaho State University, J. Sherwood, K. Szcodronski, A. McCombs, T. Proscholdt, K. McCloskey, C. Gause, A. Taylor, M. Kyer, D. Nelson, A. Binder, J. Pink, H. Pritchard, L. Crees, E. McCall, and B. Sisson.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Durney et al., 2022) are available from Dryad: <https://doi.org/10.5061/dryad.bk3j9kdfd>.

ORCID

J. Simone Durney  <https://orcid.org/0000-0002-8353-7908>

Diane M. Debinski  <https://orcid.org/0000-0002-7144-4640>

Laura A. Burkle  <https://orcid.org/0000-0002-8413-1627>

REFERENCES

- Arft, A. M., M. D. Walker, J. Gurevitch, J. M. Alatalo, M. S. Bret-Harte, M. Dale, M. Diemer, et al. 1999. "Responses of Tundra Plants to Experimental Warming: Meta-Analysis of the International Tundra Experiment." *Ecological Monographs* 69: 491–511.
- Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. "Fitting Linear Mixed-Effects Models Using lme4." *Journal of Statistical Software* 67: 1–48. <https://doi.org/10.18637/jss.v067.i01>.
- Burkle, L., and R. Irwin. 2009. "Nectar Sugar Limits Larval Growth of Solitary Bees (Hymenoptera: Megachilidae)." *Environmental Entomology* 38: 1293–300.
- Burkle, L. A., and R. Alarcon. 2011. "The Future of Plant-Pollinator Diversity: Understanding Interaction Networks across Time, Space, and Global Change." *American Journal of Botany* 98: 528–38.
- Cane, J. H. 2011. "Specialist Osmia Bees Forage Indiscriminately among Hybridizing Balsamorhiza Floral Hosts." *Oecologia* 167: 107–16.
- Cleland, E. E., I. Chuine, A. Menzel, H. A. Mooney, and M. D. Schwartz. 2007. "Shifting Plant Phenology in Response to Global Change." *Trends in Ecology and Evolution* 22: 357–65.
- Debinski, D. M., M. E. Jakubauskas, and K. Kindscher. 2000. "Montane Meadows as Indicators of Environmental Change." *Environmental Monitoring and Assessment* 64: 213–25.
- Dunne, J. A., J. Harte, and K. J. Taylor. 2003. "Subalpine Meadow Flowering Phenology Responses to Climate Change: Integrating Experimental and Gradient Methods." *Ecological Monographs* 73: 69–86.
- Durney, J. S., A. Engel, D. Debinski, and L. Burkle. 2022. "Earlier Spring Snowmelt Drives Arrowleaf Balsamroot Phenology in Montane Meadows. Dryad. Dataset." <https://doi.org/10.5061/dryad.bk3j9kdfd>.
- Ehrlén, J., J. Raabova, and J. P. Dahlgren. 2015. "Flowering Schedule in a Perennial Plant; Life-History Trade-Offs, Seed Predation, and Total Offspring Fitness." *Ecology* 96: 2280–8.
- Fitter, A. H., and R. S. R. Fitter. 2002. "Rapid Changes in Flowering Time in British Plants." *Science* 296: 1689–91.
- Forrest, J., and J. D. Thomson. 2010. "Consequences of Variation in Flowering Time within and among Individuals of *Mertensia fusiformis* (Boraginaceae), an Early Spring Wildflower." *American Journal of Botany* 97: 38–48.
- Fournier, D. A., H. J. Skaug, J. Ancheta, J. Ianelli, A. Magnusson, M. Maunder, A. Nielsen, and J. Sibert. 2012. "AD Model Builder: Using Automatic Differentiation for Statistical Inference of Highly Parameterized Complex Nonlinear Models." *Optimization Methods and Software* 27: 233–49.
- Gezon, Z. J., D. W. Inouye, and R. E. Irwin. 2016. "Phenological Change in a Spring Ephemeral: Implications for Pollination and Plant Reproduction." *Global Change Biology* 22: 1779–93.
- Gucker, C. L., and N. L. Shaw. 2018. "Arrowleaf Balsamroot (*Balsamorhiza sagittata*). In *Western Forbs: Biology, Ecology, and Use in Restoration*. Reno, NV: Great Basin Fire Science Exchange. <http://greatbasinfirescience.org/western-forbs-restoration>.
- Hothorn, T., F. Bretz, and P. Westfall. 2008. "Simultaneous Inference in General Parametric Models." *Biometrical Journal* 50: 346–63.
- Inouye, D. W. 2008. "Effects of Climate Change on Phenology, Frost Damage, and Floral Abundance of Montane Wildflowers." *Ecology* 89: 353–62.
- IPCC. 2014. *Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*, edited by R. K. Pachauri and L. A. Meyer. Geneva, Switzerland: IPCC, World Meteorological Organization.
- Jabis, M. D., D. E. Winkler, and L. M. Kueppers. 2020. "Warming Acts through Earlier Snowmelt to Advance but Not Extend Alpine Community Flowering." *Ecology* 101: 1–14.
- Kehrberger, S., and A. Holzschuh. 2019. "Warmer Temperatures Advance Flowering in a Spring Plant more Strongly than Emergence of Two Solitary Spring Bee Species." *PLoS One* 14: 1–15.
- Kevan, P. G., and H. G. Baker. 1983. "Insects as Flower Visitors and Pollinators." *Annual Review of Entomology* 28: 407–53.
- Kudo, G. 2020. "Dynamics of Flowering Phenology of Alpine Plant Communities in Response to Temperature and Snowmelt Time: Analysis of a Nine-Year Phenological Record Collected by Citizen Volunteers." *Environmental and Experimental Botany* 170: 103843.
- Kudo, G., and L. D. Harder. 2005. "Floral and Inflorescence Effects on Variation in Pollen Removal and Seed Production Among Six Legume Species." *Functional Ecology* 19: 245–54.
- Kudo, G., and T. Y. Ida. 2013. "Early Onset of Spring Increases the Phenological Mismatch between Plants and Pollinators." *Ecology* 94: 2311–20.
- Kuznetsova, A., P. B. Brockhoff, and R. H. B. Christensen. 2017. "lmerTest Package: Tests in Linear Mixed Effects Models." *Journal of Statistical Software* 82: 1–26.
- Lambert, A. M., A. J. Miller-Rushing, and D. W. Inouye. 2010. "Changes in Snowmelt Date and Summer Precipitation Affect the Flowering Phenology of *Erythronium grandiflorum* (Glacier Lily; Liliaceae)." *American Journal of Botany* 97: 1431–7.
- Lenth, R. 2020. emmeans: Estimated Marginal Means, Aka Least-Squares Means. R package version 1.5.3. <https://CRAN.R-project.org/package=emmeans>
- Liu, Y., J. Mu, K. J. Niklas, G. Li, and S. Sun. 2012. "Global Warming Reduces Plant Reproductive Output for Temperate Multi-Inflorescence Species on the Tibetan Plateau." *New Phytologist* 195: 427–36.
- Martin, L. 2008. *Hydrogeology and Water Supply Wells, Grand Teton National Park. Natural Resources Technical Report NPS/NRPC/WRD/NRTR--2008/091*. Fort Collins, CO: National Park Service.
- McCombs, A., D. Debinski, K. Reinhardt, M. Germino, and P. Caragea. 2022. Warming temperatures affect meadow-wide nectar resources, with implications for plant-pollinator communities. *Ecosphere* 13: 1–9.
- Meier, L. 2021. "ANOVA and Mixed Models: A Short Intro Using R." <https://stat.ethz.ch/~meier/teaching/anova/contrasts-and-multiple-testing.html>
- Memmott, J., P. G. Craze, N. M. Waser, and M. V. Price. 2007. "Global Warming and the Disruption of Plant-Pollinator Interactions." *Ecology Letters* 10: 710–7.
- Nagahama, A., Y. Kubota, and A. Satake. 2018. "Climate Warming Shortens Flowering Duration: A Comprehensive Assessment

- of Plant Phenological Responses Based on Gene Expression Analyses and Mathematical Modeling." *Ecological Research* 33: 1059–68.
- Parmesan, C., and G. Yohe. 2003. "A Globally Coherent Fingerprint of Climate Change Impacts across Natural Systems." *Nature* 421: 37–42.
- Phillips, B. B., R. F. Shaw, M. J. Holland, E. L. Fry, R. D. Bardgett, J. M. Bullock, and J. L. Osborne. 2018. "Drought Reduces Floral Resources for Pollinators." *Global Change Biology* 24: 3226–35.
- Potts, S. G., B. Vulliamy, A. Dafni, G. Ne'eman, and P. Willmer. 2003. "Linking Bees and Flowers: How Do Floral Communities Structure Pollinator Communities?" *Ecology* 84: 2628–42.
- Price, M. V., and N. M. Waser. 1998. "Effects of Experimental Warming on Plant Reproductive Phenology in a Subalpine Meadow." *Ecology* 79: 1261–71.
- R Core Team. 2020. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing. <https://www.R-project.org/>.
- Rafferty, N. E., P. J. Caradonna, and J. L. Bronstein. 2015. "Phenological Shifts and the Fate of Mutualisms." *Oikos* 124: 14–21.
- Saavedra, F., D. W. Inouye, M. V. Price, and J. Harte. 2003. "Changes in Flowering and Abundance of *Delphinium nuttallianum* (Ranunculaceae) in Response to a Subalpine Climate Warming Experiment." *Global Change Biology* 9: 885–94.
- Scaven, V. L., and N. E. Rafferty. 2013. "Physiological Effects of Climate Warming on Flowering Plants and Insect Pollinators and Potential Consequences for Their Interactions." *Current Zoology* 59: 418–26.
- Sherwood, J. A., D. M. Debinski, P. C. Caragea, and M. J. Germino. 2017. "Effects of Experimentally Reduced Snowpack and Passive Warming on Montane Meadow Plant Phenology and Floral Resources." *Ecosphere* 8: 1–13.
- Skaug, H., D. Fournier, B. Bolker, A. Magnusson, and A. Nielsen. 2016. "Generalized Linear Mixed Models Using 'AD Model Builder.'" R Package Version 0.8.3.3. <https://glmmadmb.r-forge.r-project.org/>.
- Steltzer, H., C. Landry, T. H. Painter, J. Anderson, and E. Ayres. 2009. "Biological Consequences of Earlier Snowmelt from Desert Dust Deposition in Alpine Landscapes." *Proceedings of the National Academy of Sciences of the United States of America* 106: 11629–34.
- Tilley, D., L. S. John, and N. Shaw. 2012. *Plant Guide for Arrowleaf Balsamroot (Balsamorhiza sagittata)*. USDA-Natural Resources Conservation Service Aberdeen, Idaho: Aberdeen Plant Materials Center.
- Valiente-Banuet, A., M. A. Aizen, J. M. Alcántara, J. Arroyo, A. Cocucci, M. Galetti, M. B. García, et al. 2015. "Beyond Species Loss: The Extinction of Ecological Interactions in a Changing World." *Functional Ecology* 29: 299–307.
- Visser, M. E., and C. Both. 2005. "Shifts in Phenology Due to Global Climate Change: The Need for a Yardstick." *Proceedings of the Royal Society B: Biological Sciences* 272: 2561–9.
- Wadgymar, S. M., J. E. Ogilvie, D. W. Inouye, A. E. Weis, and J. T. Anderson. 2018. "Phenological Responses to Multiple Environmental Drivers under Climate Change: Insights from a Long-Term Observational Study and a Manipulative Field Experiment." *New Phytologist* 218: 517–29.
- Walther, G.-R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. Beebee, J.-M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. "Ecological Responses to Recent Climate Change." *Nature* 416: 389–95.
- Wickham, H. 2016. *ggplot2: Elegant Graphics for Data Analysis*. New York: Springer-Verlag.
- Wipf, S. 2010. "Phenology, Growth, and Fecundity of Eight Subarctic Tundra Species in Response to Snowmelt Manipulations." *Plant Ecology* 207: 53–66.
- Yasaka, M., Y. Nishiwaki, and Y. Konno. 1998. "Plasticity of Flower Longevity in *Corydalis ambigua*." *Ecological Research* 13: 211–6.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Durney, J. Simone, Arden Engel, Diane M. Debinski, and Laura A. Burkle. 2022. "Earlier Spring Snowmelt Drives Arrowleaf Balsamroot Phenology in Montane Meadows." *Ecosphere* 13(8): e4198. <https://doi.org/10.1002/ecs2.4198>