LETTER

Accelerating flowering phenology drives community-wide negative effects on plant fecundity

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Abstract

Anthropogenic changes to the timing of life history events can have functional consequences. Numerous studies have examined how changes in flowering phenology affect the fecundity of individual plant species, yet simultaneous phenological changes among multiple species could affect coexistence and community composition. To understand how multi-species phenological change shapes plant community fecundity, we conducted a large-scale snowmelt acceleration experiment (10 m x 14 m plots) to advance flowering phenology in montane meadow communities in the Colorado Rocky Mountains, USA. In six snowmelt-accelerated plots and their paired control plots, we measured how induced phenological change altered the fecundity of eight plant species, evaluating pollen limitation in five species using hand pollination treatments. Early flowering resulted in lower overall fecundity and greater pollen limitation, with significant changes to the proportions of seeds produced by different species in a community. Our results underscore the importance of studying phenological change at a community level.

Introduction

Changes in plant flowering time are a well-established manifestation of global change (Wolf *et al.* 2017; Pearson 2019) but we know little of their impact on wild plant communities. Several studies focused on individual plant species have shown that earlier flowering phenology can decrease short-term fitness (Thomson 2010; Kudo & Cooper 2019; Sritongchuay *et al.* 2021). As with other types of global change such as increased temperatures (Ma *et al.* 2015), nitrogen deposition (Wainwright *et al.* 2019) or altered trophic interactions (Descombes et al. 2020), species-specific responses to phenological change potentially affects communities by altering species' relative fitness, coexistence and diversity. Moreover, under global climate change scenarios we are likely to see simultaneous changes in multiple species, which has the potential to alter a range of interactions. Phenological change should thus be examined at the community

level to understand its potential effects on the fecundity of multiple, naturally co-occurring species.

Various anthropogenic factors such as introduced species (Tadey 2020) and urbanization (Fisogni *et al.* 2020) can trigger plant flowering times that deviate significantly from their seasonal optima, with climate change receiving significant attention (Inouye 2008; Bartomeus *et al.* 2011; Thackeray *et al.* 2016; Renner & Zohner 2018; Zohner *et al.* 2020). In temperate ecosystems, a warming climate typically advances flowering time (Parmesan & Yohe 2003). One of the most apparent abiotic challenges to precocious flowering is exposure to freezing temperatures. Shifts towards earlier blooming may increase the risk of frost damage to flowers and reduce fitness (Inouye 2008; Wheeler *et al.* 2015; Pardee *et al.* 2019). Conversely, earlier blooming may benefit species that are sensitive to late summer droughts (Franks 2011; Iler *et al.* 2019) or extend favorable growing conditions (Giménez-Benavides *et al.* 2011).

The effect of plant phenological change on biotic drivers of fitness is likewise species-dependent. Differences in climate change sensitivity across taxa (Thackeray *et al.* 2016; Olliff-Yang & Mesler 2018; Kehrberger & Holzschuh 2019) can potentiate phenological mismatches between plant bloom time and the active period of their antagonists or mutualists, changing the frequency and intensity of such interactions. For example, in some species, earlier flowering increases the risk of herbivory (Brody 1997; Waterton & Cleland 2016). Phenological mismatches between plant blooming and pollinator seasonal activity have received substantial attention (Hegland *et al.* 2009; Miller-Rushing *et al.* 2010; Renner & Zohner 2018, Visser & Gienapp 2019). While many flowering plant species benefit from animal pollination (Ollerton *et al.* 2011), empirical evidence that plant-pollinator phenological mismatches reduce plant seed set is limited (but see Thomson 2010; Kudo & Cooper 2019; Sritongchuay *et al.* 2021). This may be because 1) imperfect synchrony with pollinators is adaptive for plants due to trade-offs with

other aspects of fitness such as seed quality or dispersal (Bolmgren & Eriksson 2015), 2) that plant-pollinator relationships are robust to change in partner identity (Bartomeus *et al.* 2011), and / or 3) that the fitness losses from plant-pollinator mismatch are overwhelmed by abiotic changes (Gezon *et al.* 2016; Campbell *et al.* 2022; Faust & Iler 2022). Experiments are needed to isolate the effects of phenologically-driven biotic change from the effects of abiotic change for various taxa (Forrest 2015).

To our knowledge, research that directly tests the effects of community-level phenological change on the fecundity of co-occurring species is lacking. Among correlational studies, a few have examined long-term interannual species phenology (e.g., Gordo & Sanz 2009; CaraDonna *et al.* 2014, Rafferty et al. 2020, Fisogni et al. 2022) but complementary long-term data on interannual species fecundity measured in seed set are rare (but see Thomson 2019). Correlations have been found between species distributions and spatial variations in environmental phenological triggers (Winkler *et al.* 2018). Experimental field studies that manipulate flowering phenology have used potted plants (e.g., Waters *et al.* 2020) or small-scale snow removal treatments for species whose phenology is linked to snowmelt time (Gezon *et al.* 2016; Sherwood *et al.* 2017; Pardee *et al.* 2019). Due to the intense labor required, snow removal treatments have only been feasible with fairly small plots (< 3 square meters) in close proximity, which limits the taxonomic breadth and spatial independence of findings. Finally, it is challenging to disentangle the abiotic stress of flowering early from the biotic effects, such as pollen limitation caused by plant-pollinator phenological mismatch. To date, studies that have manipulated flowering phenology and examined pollen limitation are rare (Pan *et al.* 2017; Bogdziewicz et al. 2020; Gallagher & Campbell 2021; Faust & Iler 2022; de Manincor et al. 2023).

In this study, we measured how experimentally induced early flowering (henceforth 'precocious flowering') affects the fecundity of eight co-occurring montane plant species with diverse phenology, floral morphology and dependence on pollinators for seed set. We accelerated snowmelt in eight 10 m x 14 m treatment plots, spatially replicated across a mountain landscape—to our knowledge, an endeavor unprecedented at this scale. For six of these plots, we examined whether changes in flowering phenology affected species fecundity compared to adjacent control plots (12 plots total) by comparing counts of seed or fruit. The mechanisms for why early snowmelt influences plant fecundity are poorly understood but may include longer growing seasons despite limited water availability (Iler *et al.* 2019), growing degree days (Jerome *et al.* 2021), pollination success (Campbell 2019) and interactive effects (Faust & Iler 2022). Here we focus on one of these mechanisms, pollination success, measured using pollen limitation experiments on five species.

We hypothesized that the effects of precocious flowering on fecundity are highly species-dependent, given the differences in species life histories and ecology (e.g., seasonal flowering time, dependence on pollinators, types of pollinators, frost tolerance, etc.). We expected increased pollen limitation with precocious flowering due to potential timing mismatches with pollinators. Across the community of plants, we also expected precocious flowering to reduce seed set at the community level (i.e. when seed set is pooled across species). Finally, we expected that the proportions of seed produced by different species would change between the accelerated snowmelt versus control plots.

Methods

Study location
This study was conducted in montane meadows around the Rocky Mountain Biological Laboratory located in Gunnison National Forest, Colorado, United States (38°57.5′ N, 106°59.3′

W, 2900 m above sea level). Snowfall in this system typically begins in September and persistent snowpack lasts from November to late May. The growing season occurs when the ground is snow-free from May to September, with snowmelt timing being a major determinant of herbaceous plant phenology (CaraDonna *et al.* 2014). Occasional frost can occur into June. Precipitation is minimal early in the growing season until the North American Monsoon in July. Following snowmelt, pollinator abundance and diversity increases with daily maximum temperature (Gezon *et al.* 2015), declining rapidly in mid-August to September. The vast majority of montane meadow plant species are long-lived perennials.

Experimental design and phenology manipulation

We established eight montane meadow study sites, spaced at least 800 m apart, in the spring of 2019 (Figure 1). Snowpack this year was within one standard deviation from the 30-year average based on long-term data at the field station (https://www.gothicwx.org/). In each site, we set up a pair of 10 m x 14 m plots at least 5 m apart (Figure S1, Table S1), of similar slope, aspect and plant community composition (eight pairs, 16 plots). We randomly assigned one of the two plots to receive the accelerated snowmelt treatment, while the other was unmanipulated in terms of snowmelt and served as a control. We accelerated snowmelt using a tested solarization technique (Steltzer *et al.* 2009), which was applied two to five weeks before the anticipated natural snowmelt date - based on the long-term snowmelt data available from the Rocky Mountain Biological Laboratory, our pilot study in a previous year, and constrained by spring weather conditions and avalanche risk. For each manipulated plot, we spread a 10 m x 14 m sheet of woven black plastic 50% shade cloth over each designated snowmelt plot. We removed the shade cloth when we observed >80% of the ground was snow-free.

When each plot was snow-free, we established a 1 m-wide U-shaped region concentric to, and 1 m away from, the plot edge (Figure S1). We further divided this region equally into 1 m

squares in which we tagged plants, tracked fecundity, and performed hand pollination. In addition, we marked three evenly spaced 1 m x 10 m transects in the center of each plot, where we recorded community flowering phenology.

Estimating snowmelt date

We took weekly measurements of snow depth at all study plots until they were snow-free. Starting in early May, we used an avalanche probe to determine snow depth at three points along the two lengths of each study plot (6 points per plot, Figure S1). Because we were unable to visit plots daily due to time and logistical constraints (visiting sites multiple kilometers apart in deep snow), we estimated snowmelt date by running linear regressions on the available snow depth data at each plot. Nevertheless, we ground-truthed snowmelt date estimates with visual inspection of satellite images from the database Planet (Planet Team 2017) in five of our seven sites for which satellite data were available.

Tracking phenology

To measure the advancement of precocious flowering caused by our snowmelt treatment, we tracked community flowering phenology in each plot. Once a week for the entire field season, we counted and recorded all open flowers of every non-graminoid species in the three transects of every plot. We visited 2-3 sites per day, so that all 6 sites could be visited twice a week (for hand pollinating flowers). Phenology was collected during one weekly visit and spaced 6-8 days apart for consistency.

Selection of focal species and individuals

The plant communities at each site comprise 25-40 species. We chose eight focal species (Figure 1, supplementary table S2), five known to produce fewer seeds without pollinator visitation (pollinator-limited) and three capable of autonomous seed set (wind-pollination, selfing, apomixis, etc.). These species were among the most abundant at each site and were

also present in both of the paired plots (censused the previous year during site scouting). This resulted in 3 – 7 focal species being represented at each site. For every focal species at a site, we tagged 16 individuals, evenly divided between the accelerated snowmelt and control plots. To select individuals to tag, we first performed an exhaustive survey of focal species in each plot (identified by foliage), then used a stratified random approach to ensure selected individuals were well-spaced so as to capture within-plot variation in microhabitats if present. We counted the number of flowers (capitulums for one species, *Taraxacum officinale*) each tagged individual produced during the studied season ('flower number'), and collected and counted seeds (fruits for one species, *Lathyrus lanzwertii*) per individual ('per capita fecundity') at the end of the season.

Measuring pollen limitation

To understand a potential biotic cost to precocious flowering—mismatches between plants and their pollinators—we performed pollen limitation experiments. Three of the focal species have high seed set without external pollination. For the remaining five focal species, we tagged an additional 16 individuals evenly divided between the accelerated snowmelt and control plots to receive hand pollination. Pollen supplementation by hand is a standard method used to isolate the effects of pollen limitation from other non-pollination limitations to plant fecundity (Kearns & Inouye 1993), most notably resource limitation. If pollen supplementation significantly increases the fecundity of plants relative to those receiving only natural pollination, then naturally-received pollen quality or quantity is limiting population fecundity (i.e., pollen limitation). We used a clean paintbrush to transfer pollen from 2-4 conspecific pollen donor individuals onto the stigmas of individuals tagged for the pollen limitation experiment. Pollen donors were untagged individuals from within the recipient's plot and multiple donors were used to increase likelihood of pollen compatibility. Because many focal species produce a succession of flowers over several days, we revisited plots twice a week to hand-pollinate all the flowers produced on each plant until the

end of flowering. We counted the number of flowers each pollen-supplemented individual

produced during the studied season ('flower number'), and collected and counted seeds or fruits

per individual ('per capita fecundity') at the end of the season. Fecundity was measured in terms

of seed set (number of developed seeds per individual) for all but one species, the legume *L.*

lanzwertii, in which fecundity was measured in fruitset (number of enlarged legume pods per

flowering stem). In Fabaceae, expanded ovules often indicate successful fertilization (Cooper &

Brink 1940; Johansson & Walles 1993; Martin & Lee 1993; Jiang *et al.* 2019). In *L. lanzwertii*

individuals found in and around the Rocky Mountain Biological Laboratory, pods typically contain

1-3 seeds (Keeler & Rafferty 2022), of which usually only one is viable (Keeler, *personal*

communication, November 11, 2022), making *L. lanzwertii* fruit counts comparable to seed

counts of the other focal species.

Data analysis

We conducted all statistical analyses in R (R Core Team 2022); a fully reproducible analysis

report is included in the supplemental materials.

Accelerated snowmelt and phenological change

To quantify the bloom time for focal species at different locations, we calculated the weekly

mean number of open flowers for every species in each transect. Based on these weekly

means, we determined when each focal species reached its highest number of recorded flowers

at every study plot. Time of peak flowering is less biased by extreme early- or late- flowering

individuals and performs well against other more complex phenology metrics (Taylor 2019). To

measure the effect of accelerated snowmelt on species flowering time at each site, we

subtracted each species' peak flowering week in the snowmelt-accelerated plot from the peak

flowering week of its conspecifics in the adjacent control plot. The snowmelt acceleration never

delayed peak flowering time in this study, hence all values for phenological change were either

negative (phenological acceleration) or zero (no change). We visualized the magnitude of

precocious flowering in accelerated snowmelt plots by plotting 95% confidence intervals around the mean phenological acceleration of all focal species relative to zero. We used the presence or absence of precocious flowering for each species at the plot level (phenological acceleration greater than 6 days) in analyses of fecundity.

Overall community fecundity

To understand whether precocious flowering changed community-level fecundity, we ran a generalized linear mixed-effects model examining per-capita fecundity of multiple focal species simultaneously, using only data from naturally pollinated (no hand-pollinated) individuals. We were primarily interested in whether plant fecundity was altered by phenological acceleration, i.e., the presence/absence of precocious flowering for each species at the plot level (phenological acceleration, treated as discrete due to the resolution of the measured response, see Table 1). This is a species- and plot-specific factor that allows for instances where a species responded to accelerated snowmelt treatments at some sites but not others. We also wanted to know whether the effect of phenological acceleration on fecundity differed among species. We accounted for per-plant flower counts in models to isolate the effects of phenological acceleration on per-capita fecundity. We removed sites where no phenological change was detected from per-week surveys, because the effect of phenological acceleration on seed set was analyzed as a binary factor (i.e., with or without acceleration) and an absence of any phenological acceleration at a site would result in a factor of only one level for the pair of plots within a site.

We modeled plant fecundity using the 'glmmTMB' package (Brooks *et al.* 2022), and included three explanatory variables: (a) phenological acceleration, (b) species identity and (c) flower number. These factors interact to influence plant fecundity in several ways that are critical to interpreting their effects. First, we were interested in whether the effect of precocious flowering

on fecundity was species-dependent; hence, we needed to analyze the interaction between (a) phenological acceleration (categorical, yes vs. no) and (b) species identity. Second, our model considered the interaction between (b) species identity and (c) flower number on fecundity. This is because species differ in the number of ovules per flower (e.g., *Mertensia fusiformis* usually has < 5 ovules per flower while *Boechera stricta* can have up to 200), so the effect of an increase by a single flower unit on per capita fecundity is species-specific. As such, we designed our model to include a three-way interaction to evaluate whether (a) phenological acceleration significantly changes the two-way interaction between (b) species identity and (c) flower number. To maximize our statistical power and allow model convergence, we prioritized maintaining the evaluation of these interactions and estimated only one main effect: phenological acceleration. Our final model allowed the interpretation of 1. the main effect of phenological acceleration (a), 2. the isolated interaction (without main effects) between phenological acceleration and species identity (a : b) and 3. the isolated three-way interaction among all three main effects (a : b : c). We included 'plot' nested within 'site' as random effects and used a negative binomial error model (count data overdispersed relative to a Poisson distribution) with zero inflation, as there were more zero-counts than expected relative to the negative binomial distributions fit by our initial models. We evaluated statistical significance using the 'Anova' function in the 'car' package (Fox & Weisberg 2019), and conducted model validation using the 'DHARMa' package (Hartig & Lohse 2022).

Pollen limitation

We assessed whether precocious flowering mediated the effect of pollen limitation across the plant community on per capita fecundity in pollinator-limited species. We focused on whether phenological acceleration altered the fecundity difference between plants that were hand-pollinated and those that were open pollinated. Thus, we analyzed how the per capita fecundity of each focal species changed with (a) phenological acceleration (presence/absence

of precocious flowering for species at the plot-level), (b) presence/absence of supplemental hand pollination on the individual and (c) plant species, because different plant species inherently differ in seed production and pollen limitation. As with the models of fecundity discussed above, we focused on the interactions of those variables and estimated only the main effect of phenological acceleration to allow for model convergence. We followed up on this base model (with a 3-way interaction) to analyze a second model that included an interaction with flower number (4-way interaction), to assess whether phenological acceleration changed the slope of accumulation of developed seeds (relative to flower number) with and without pollen supplementation, in different focal plant species. We analyzed these data using 'glmmTMB' generalized linear mixed-effects models, including 'plot' nested within 'site' as random effects and specifying negative binomial errors. We evaluated statistical significance and conducted model validation as explained above.

Species fecundity

We examined whether accelerated snowmelt caused the seed or fruit set of any species to change more than other species in its community. We analyzed these changes between accelerated snowmelt and control plot pairs using mixed-effects conditional logistic regression models with the 'mclogit' package (Elff 2022). These are modified standard multinomial GLM models which compare proportions among user-defined 'choice sets'. Here the 'choice sets' are the plant species compositions at each site (which differ between sites) and the proportions are the number of seeds of each focal species divided by the total summed seed set for all species represented in a plot. This allowed us to examine changes in the fecundity of co-occurring focal species relative to one another within each accelerated snowmelt and control plot pair, which by design contains identical co-occurring focal species per site ('choice sets'). Importantly, this method also allowed us to compare between sites with differing plant community composition

(distinct 'choice sets'). We included 'plot treatment' (snowmelt acceleration vs. control) as a fixed effect and 'site' as a random effect in these models.

Results

Overview

Our snowmelt treatment advanced snowmelt in treatment plots relative to controls by a mean of 8.29 ± 2.01 days (± SE, Fig 2A). The greatest effect of snowmelt acceleration was 17 days (site PF) and the smallest was one day (site BB). We used linear regressions to estimate snowmelt dates (Fig 2A, Fig S3). As measurements of snow depth occurred only weekly, and snowmelt rate may not be linear, reported snowmelt dates are coarse estimations but are not incorporated into any other analysis in this study. Early snowmelt generally caused focal species communities to bloom earlier (Fig 2B). Flowering phenology was not measurably changed for any species at the sites 'BB' or '403B'.

Accelerated snowmelt and phenological acceleration

At most sites, focal species in the accelerated snowmelt plots bloomed significantly earlier than in control plots (Fig 2B) based on 95% confidence intervals largely not overlapping with zero. At a plot level, focal species did not always accelerate their phenology by more than a week, in which case we were unable to detect any phenology change during weekly phenology surveys. The phenological acceleration ranged from 0 - 2 weeks (Table 1), which was sometimes greater than the amount of snowmelt acceleration.

Community fecundity

Phenological acceleration significantly changed community fecundity in at least two ways. We found statistically significant three-way interactions among phenology acceleration, focal species identity, and flower number ($p < 0.001$, supplemental table S3), indicating that even after accounting for the relationship between number of flowers a species produces and its seed or fruit production, the effects of phenological change on fecundity are still species-specific. There was a significant and negative main effect of phenology acceleration on mean whole-plant fecundity ($p < 0.001$, supplemental table S3, Figure 3A). However, this effect differed significantly among species (phenology acceleration x species two-way interaction $p < 0.001$; supplemental table S3, Figure 3B). For example, precocious flowering tended to increase fecundity of *L. lanzwertii* but reduce fecundity in *B. stricta*, ('Lala' and 'Bost,' Figure 3B).

Pollen limitation

We found evidence that accelerating flowering phenology affected community-level pollen limitation. All significant interactions in the 3-way interaction model were found to be significant in the 4-way interaction model.

In the 3-way interaction model, there was a significant interaction among phenology acceleration, hand pollination, and plant species ($p < 0.0001$, supplemental table S4). We also found a significant two-way interaction between pollen limitation and phenological acceleration ($p < 0.0001$, Fig 4A). Figure 4B shows that the directionality of response to accelerated snowmelt was different in different species—consistent with the 3-way interaction—with *D. nutallianum* showing a trend toward increased pollen limitation (reduced fecundity) and *L. lanzwertii* trending toward reduced pollen limitation (increased fecundity) with experimentally induced phenological advancement. In the other three species, there were no clear trends graphically.

In the 4-way interaction model, we found that the effect of phenological advancement on pollen limitation was also influenced by the number of flowers on a plant (interaction among phenological acceleration, hand pollination, plant species, and flower number, $p < 0.0001$, supplemental table S5). In other words, phenological advancement affected pollen limitation distinctly in different species in terms of the relationship between number of flowers and fecundity. The model with 2- and 4-way interactions, however, showed significant quantile deviations when comparing residuals vs. predicted values in a combined adjusted quantile test using the DHARMa package in R. Therefore, we put more stock in the previously described model (with 2- and 3- way interactions), though both models yielded qualitatively identical results.

Species fecundity

We found that the fecundity of focal species relative to one another changed significantly in plots where snowmelt was accelerated relative to control (est. = 0.16, SE = 0.007, $p < 0.001$, Figure 5).

Discussion

We used a large-scale controlled, replicated snowmelt acceleration treatment to accelerate flowering in multiple co-occurring plant species from montane meadow communities, and assessed how this impacted community-level seed production. Three major findings stand out from our analyses. Accelerating snowmelt 1) significantly reduced pooled plant fecundity across all species; and 2) significantly increased community-level pollen limitation. Different species showed different directional trends for both fecundity and pollen limitation. These

species-specific differences underpinned our third finding, that accelerating snowmelt changed the proportions of seeds produced by co-occurring species relative to non-accelerated controls.

Effects of phenological acceleration on plant communities

The three major findings from this study are consistent with phenological advancement potentially altering future plant community composition (Rudolf 2019). Fitness differences — including fecundity, a vital component of fitness — are important in determining coexistence and the intensity of competition in a changing world (Valladares *et al.* 2015). Differential responses to environmental changes across species can reduce the potential for species to coexist. For example, extreme drought conditions can reduce the likelihood of species coexistence by reducing seed production in ways that increase species sensitivity to interspecific competition (Ma *et al.* 2015; Wainwright *et al.* 2019). A long-term, longitudinal study on forests of the southeastern United States also suggests that environmental change can alter the competitive abilities of different tree species to shape future forest composition (Clark *et al.* 2011). However, the nature of interspecies interactions, from competition to facilitation, is highly dependent on the environmental context (Bimler *et al.* 2018). Changes to relative fitness may promote plant diversity, if they act to equalize fitness differences by boosting the fecundity of rarer species (Tilman & Lehman 2001). Even if fitness differences widen, several coexistence mechanisms can act to stabilize community diversity, including niche differences and intransitivity (Bimler *et al.* 2018; Matías *et al.* 2018; Wainwright *et al.* 2019). In our study system, any such changes on plant community composition are likely to be buffered due to the long-lived nature of the perennial plants. While this buffering is likely to be positive, it also underscores the importance of long-term monitoring to understand how plant communities may already be changing under global climate change.

Phenological advancement reduces overall seed production

An overall reduction in seed production in response to accelerated flowering phenology could have more immediate and direct impacts on seed consumers. Because it represents the direct loss of a primary food resource, this effect has the potential to be more impactful over short time scales than changes to plant community composition. At the same time, it is difficult to predict the specific impacts of this effect on seed consumers, because plant species differed in their responses to accelerated snowmelt in terms of plant fecundity, and seed consumers vary in their preferences in seed types (Kerley & Erasmus 1991; Radtke 2011). Still, such changes have the potential for community-wide impacts on seed consumers (e.g., anecdotal evidence of seed parasitic fly larvae and mice in our study system) and their food webs.

Phenological acceleration and pollen limitation

At the whole-community level we found greater pollen limitation in accelerated-snowmelt plots relative to controls. This indicates that the fecundity differences between control and snowmelt accelerated plots are driven at least in part by interactions with pollinators, in addition to potential abiotic effects of early snowmelt and precocious flowering, such as minor frost damage to flowers. To our knowledge, this is the first evidence of community-level pollen limitation following simultaneous manipulation of flowering time in multiple plant species. A community-wide reduction in animal-mediated pollination success may lead to the decline of animal-pollinated plants in favor of species that autonomously or wind- pollinated (Ehlers et al. 2021). Nevertheless, our study also shows that precocious flowering can have contrasting effects on reproductive success even among insect-pollinated species. We see an overall reduction in pollination success (especially pronounced in *Delphinium nuttallianum*) but improved pollination in one focal species (*L. lanzwertii*). While this study does not reveal the precise drivers of changes in pollen limitation, the pollen limitation we observed may be driven by some combination of temporal mismatches with pollinators and/or alteration of pollinator foraging behavior, for example with alteration of co-flowering patterns (e.g. Gordo & Sanz 2009;

Forrest *et al.* 2010; CaraDonna *et al.* 2014, Rafferty et al. 2020, Fisogni et al. 2022) leading to changes in allocation of pollinator foraging effort among plant species. The potential impacts on pollinator populations and communities is unknown.

Caveats and study limitations

Like all field experiments, there are limitations that are important to consider in interpreting our results. We highlight two such caveats here. First, although our snowmelt acceleration treatments are the largest in area that we know of, treatment plots are still "islands" within a larger, unmanipulated landscape. Precocious flowering individuals in our isolated plots may have experienced unnatural levels of pollen donor density (either high or low) and/or concentrated pollinator movement within accelerated snowmelt plots (Forrest 2015). Thus, our results cannot be interpreted as necessarily reflecting what would happen under climate change when snowmelt impacts would be spread more evenly across the landscape. Second, this analysis focused only on plant fecundity, and while we demonstrated negative effects of accelerated flowering time on pollen limitation, we cannot attribute the differences to change in pollinator temporal mismatches, visitation intensity, or identity. Understanding how changes in flowering phenology impact plant-pollinator interactions and the resulting effects on plant fecundity at a community level is a key need for future research.

Conclusion

Anthropogenic environmental changes continue to alter the timing of life history events in a wide range of species. Several studies have shown that both within species and interspecific phenological mismatches can have dramatic fitness consequences. Such concerns are heightened in groups of mutually dependent organisms, such as plants and pollinators. Still, nearly all work on plant-pollinator phenological mismatches has focused on single species — or in a few cases, a handful of species — despite the fact that species are embedded in diverse

interacting biological communities. We manipulated flowering time across entire plant

assemblages via controlled, spatially replicated snowmelt acceleration experiments. We found

that community-wide flowering advancement led to an overall reduction in seed production and

pollination success, but critically, the direction of fitness changes was species-specific,

suggesting that community-wide changes in phenology have the potential to alter future plant

community composition. This work underscores the critical need for more work using

community-level approaches to assess the effects of phenological acceleration driven by

anthropogenic environmental change.

Acknowledgements

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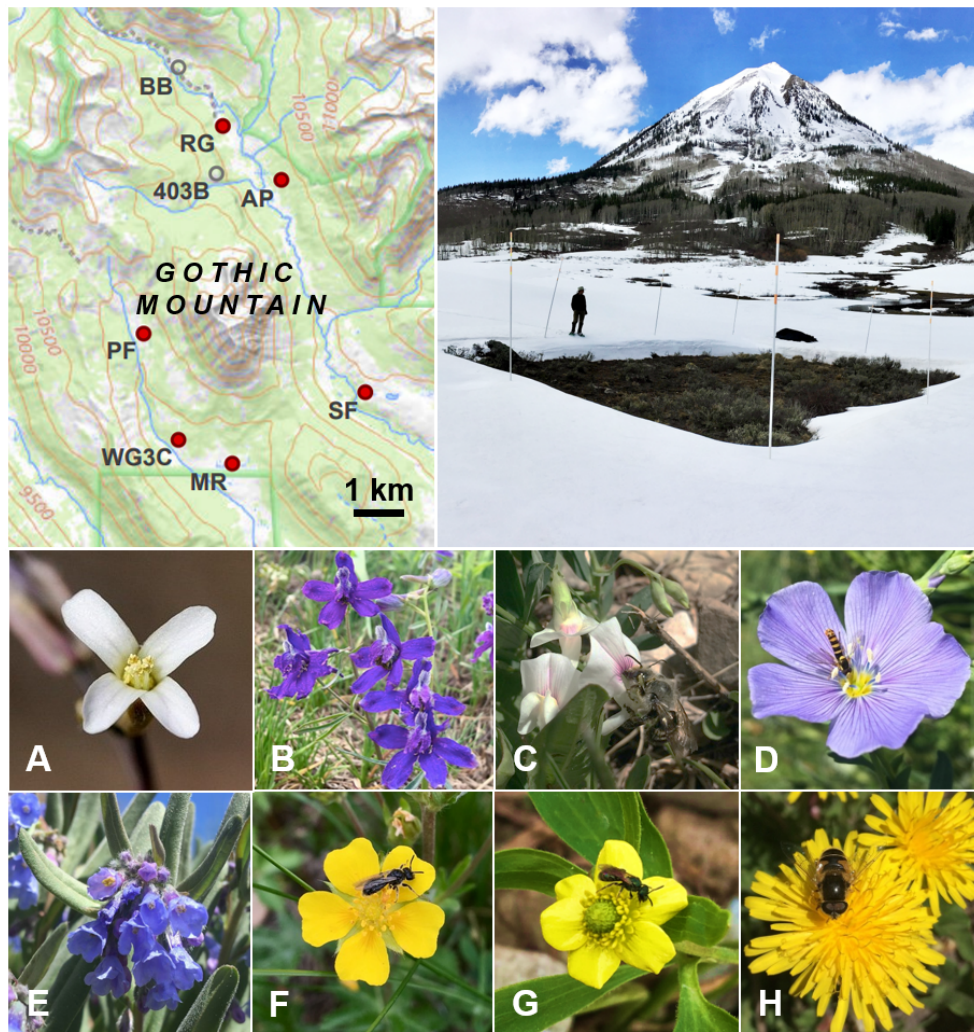
Figure 1. Site map of eight study sites, photo of accelerated snowmelt plot at MR site and photos of eight focal species. Only six of the sites, indicated by red filled circles, were included in fecundity analyses (see *Results - Overview*). These six sites were spaced at least 1 km apart and each contained accelerated snowmelt and control paired plots. Focal species: A - *Boechera stricta*, B - *Delphinium nuttallianum*, C - *Lathyrus lanzwertii*, D - *Linum lewisii*, E - *Mertensia fusiformis*, F - *Potentilla pulcherrima*, G - *Ranunculus inamoenus*, H - *Taraxacum officinale*. Photo of *B. stricta* in Saguache County, Colorado by Patrick Alexander; photos of other species in Gunnison County, Colorado by Loy Xingwen.
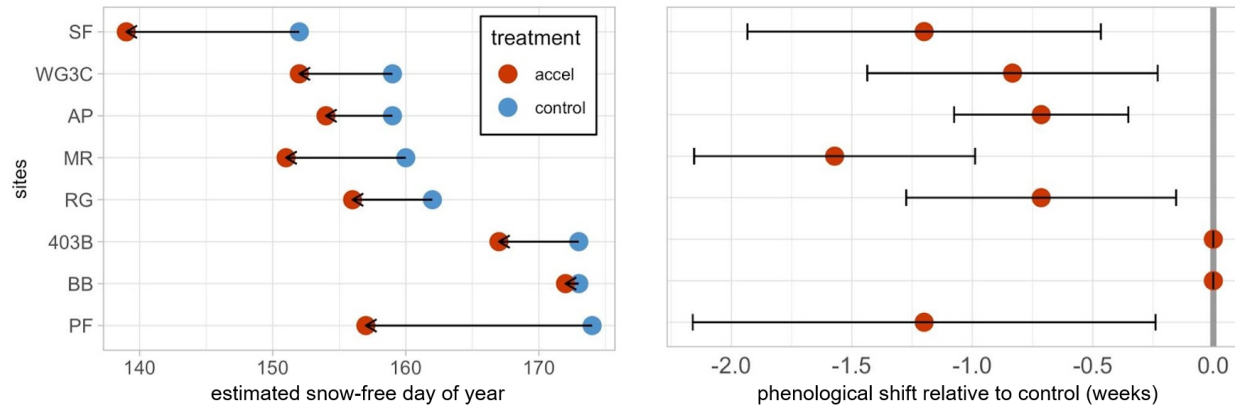
Figure 2. Estimated snow-free day of year for accelerated snowmelt and control plot-pairs (A), alongside effect on focal species phenology (B), at all seven sites. Sites are sorted by meltout date of control plots. Panel A shows estimated snowmelt dates of all plots based on linear regressions, with colors representing accelerated snowmelt and control plots. Panel B shows the mean change in pooled peak flowering time for all focal species for each site, with 95% confidence intervals.
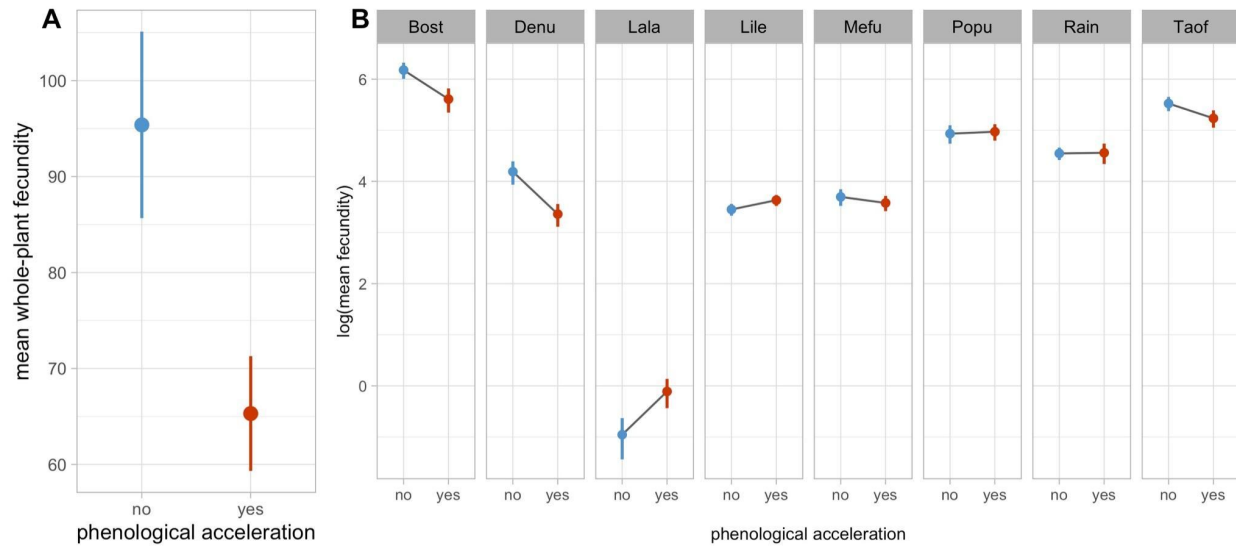
Figure 3: Phenological acceleration and whole-plant fecundity. Panel A shows the significant main effect of phenological acceleration on whole-plant fecundity, with mean whole-plant fecundity data pooled across species. Data are not transformed to show raw effect size. Panel B shows the significant two-way interaction between phenological acceleration and species identity, depicting different directions of species-level responses. Data are log-transformed to aid in the visualization of the inherently large differences in per-capita fecundity among species. Error bars depict standard errors, which include variation across species, sites, and individuals in Panel A; and across sites and individuals in Panel B. As in any mixed-effects modeling context, because of these sources of variation, overlap in standard errors cannot be interpreted to indicate absence of statistically significant differences. Species abbreviations: Bost - *Boechera stricta*, Denu - *Delphinium nuttallianum*, Lala - *Lathyrus lanzwertii*, Lile - *Linum lewisii*, Mefu - *Mertensia fusiformis*, Popu - *Potentilla pulcherrima*, Rain - *Ranunculus inamoenus*, Taof - *Taraxacum officinale*.
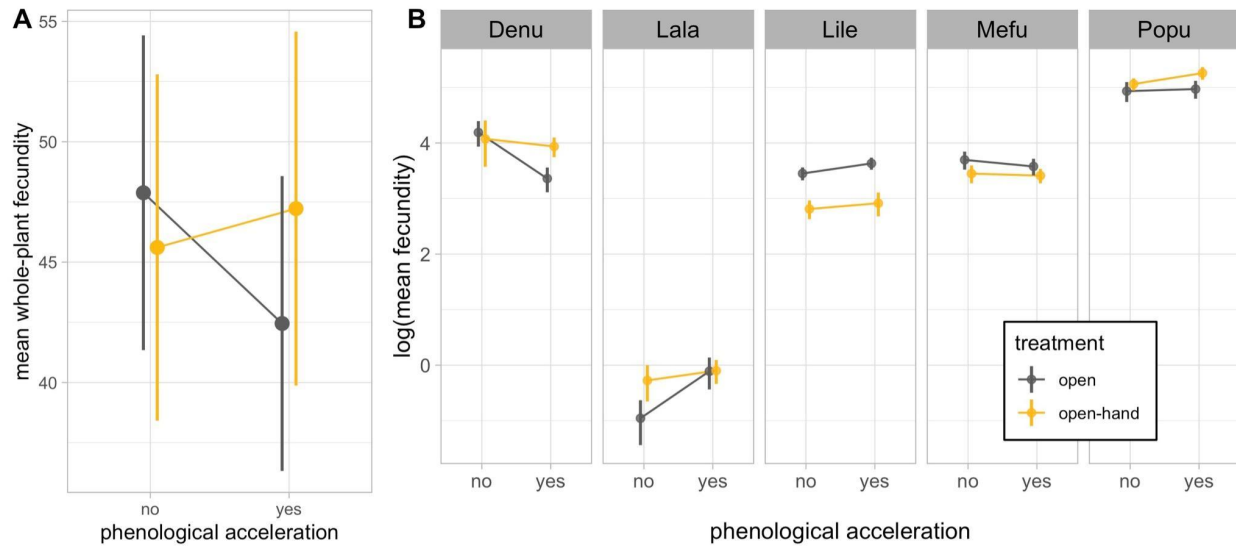
Figure 4: Phenological acceleration and pollen limitation. Pollen limitation occurs when hand-pollinated seed set (yellow) is greater than open seed set (gray). Panel A depicts the significant interaction between phenological acceleration and hand pollination treatment on whole-plant fecundity. Data are not transformed to show raw effect size. Panel B shows the significant three-way interaction among phenological acceleration, hand pollination treatment, and species identity, showing different directions of species-level responses. Data are log-transformed to cope with the inherently large differences in per-capita fecundity among species. Error bars depict standard errors, which include variation across species, sites, and individuals in Panel A; and across sites and individuals in Panel B. As in any mixed-effects modeling context, because of these sources of variation, overlap in standard errors cannot be interpreted to indicate absence of statistically significant differences. Species abbreviations: Denu - *Delphinium nuttallianum*, Lala - *Lathyrus lanzwertii*, Lile - *Linum lewisii*, Mefu - *Mertensia fusiformis*, Popu - *Potentilla pulcherrima*.
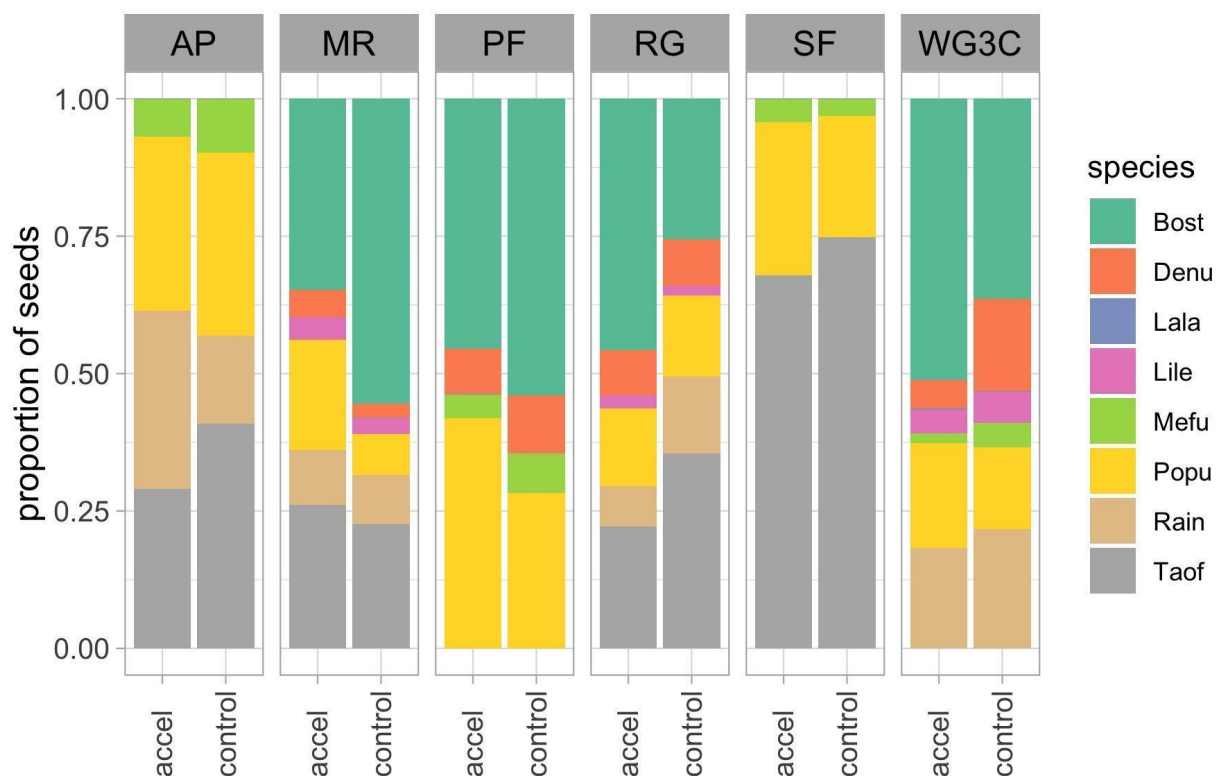
Figure 5: Snowmelt acceleration and relative seed proportions. Fecundity of eight focal species in six sites, comparing accelerated snowmelt plots with control plots. Colored bars show the individual mean whole-plant fecundity for each species (fruitset for "Lala", *Lathyrus lanzwertii*) as a proportion of the total summed individual mean seed set for species represented at each plot. Because *L. lanzwertii* fruitset is small relative to seed set in other species, it is not easily visible in this plot; we chose to depict non-transformed data to directly show effect sizes. Species abbreviations - Bost - *Boechera stricta*, Denu - *Delphinium nuttallianum*, Lala - *Lathyrus lanzwertii*, Lile - *Linum lewisii*, Mefu - *Mertensia fusiformis*, Popu - *Potentilla pulcherrima*, Rain - *Ranunculus inamoenus*, Taof - *Taraxacum officinale* .

Table 1. Number of sites for each focal species where early snowmelt plots showed zero-, one- and two-week advancements in peak flowering time relative to adjacent control plots. Phenology was tracked weekly by counting all open flowers within three transects at every snowmelt and control plot. While we had 6 plots, each species was represented at a variable number of sites due to site conditions.

focal species	Number of sites with peak flowering earlier than control			
	no shift	1 week shift sites	2 week shift sites	total shift sites (%)
Boechera stricta	2	2	1	3 (60%)
Delphinium nuttallianum	3	1	1	2 (40%)
Lathyrus lanzwertii	2	3	2	5 (71%)
Linum lewisii	1	3	0	3 (75%)
Mertensia fusiformis	3	3	0	3 (50%)
Potentilla pulcherrima	3	4	1	5 (63%)
Ranunculus inamoenus	3	1	1	2 (40%)
Taraxacum officinale	2	2	1	3 (60%)