Effects of individual variation in leaf emergence phenology on subalpine perennial plant performance

Abstract

As snowmelt timing continues to shift earlier due to climate change, many studies have focused on population level effects of earlier snowmelt on plant flowering phenology, but there are other aspects of phenology, and phenology also varies within a population. Another important aspect of phenology is leaf emergence, which is the process of a plant putting up new leaves at the beginning of the growing season. In high altitude environments, snowmelt is the primary cue for plants to begin this process. This study will focus on whether individual variation in leaf emergence phenology has an effect on plant fitness, and if that relationship changes in the presence of early snowmelt.

I used historical data (2023-2026) from an ongoing experiment conducted by Drs. Amy Iler and Dylan Simpson on *Delphinium nuttallianum, Geum triflorum, Delphinium barbeyi* and *Linum lewisii* to compare leaf up date to a series of demographic measurements between control plots and experimental plots treated to advance snowmelt. Leaf up date, size, reproductive traits (attempt to flower and fruit set), growth and survival were recorded each year. This data was used to see if there is an ideal time for plants to emerge within a population and if that time changes in early snowmelt conditions.

Species varied in their leaf up timing and treatment tended to delay leaf up timing. Leafout timing affected at least one vital rate in all four species. *Delphinium nuttallianum* was the only species to experience significant effects of leaf emergence timing on all four vital rates: growth, survival, probability of flowering and probability of fruiting. Later emergence increased the probability of fruiting in all species and growth in *D. nuttallianum*, while earlier emergence increased the probability of survival and flowering in *D. nuttallianum.* Of the eight instances where leaf up timing affected vital rate success, treatment altered the effect that leaf up timing had on success in five instances.

Introduction

Phenology is the timing of life history events in plants and animals. For herbaceous perennials these life events are spring leaf emergence, growth, reproduction and senescence. A plant's ability to survive and reproduce is dependent in part on when these life events happen, and thus variation in phenology could have an effect on plant fitness (Forrest & Miller-Rushing, 2010). Often phenology is studied at a population level (i.e., population first or average), but phenology can vary on an individual level as well. Individual variation in phenology refers to the variation in the timing of life events among individuals in the same population. Individual variation in phenology could affect variation in performance among individuals within populations.

Many studies have focused on flowering phenology due to its importance in plant-pollinator interactions, but much less is known about the effects of variation in leaf emergence timing. Leaf emergence or leaf up is the biological process by which new leaves break the soil surface at the beginning of the growing season. It initiates the photosynthetic period in which plants can produce energy and invest that energy into growth and reproduction (Inouye 2008).

Leaf up timing could be important to plant performance because it influences a plant's access to resources. Stationary organisms such as plants rely on local environmental conditions and resource availability for growth, survival and reproduction (Bratton 1976; Silvertown, 2004). Resource availability varies through time and plants must be active while these resources are available to utilize them (Forrest & Miller-Rushing, 2010). Plants that experience different leaf emergence timing may have differences in the ability to access temporally fluctuating resources such as soil moisture, soil nutrients and sunlight. Leaf up timing also influences the environmental conditions a plant is subject to, which could affect plant fitness. In the early growing season, plants could experience overnight freezing temperatures and late season frost events (Inouye 2000). Additionally, plants that emerge early could become drought stressed while waiting for later season precipitation (Iler et al, 2019).

Climate change could change a plant’s optimal phenology. In high altitude mountain environments, leaf emergence is triggered by the melting of the snowpack (Inouye 2008). Long term trends of lower snowpack and earlier snowmelt due to climate change-induced warming may affect the relationship between intraspecific phenology and plant performance (Inouye and McGuire 1991; Arft et al 1999). While many plants have been shifting their phenology earlier to track temperature and snowmelt timing (Springate and Kover, 2014), other conditions like freezing overnight temperatures, late season frost, and drought may not shift at the same rate, resulting in exposure to harsher conditions and potentially a reduction in fitness (Frank, Sims & Weis, 2007; Inouye 2008). As a result, effects of early snowmelt timing observed under normal snowmelt conditions could be altered when plants are faced with more extreme conditions present with early snowmelt.

There have been many studies investigating the relationship between snowmelt timing and population level shifts in phenology (e.g, Inouye 2008; Kiel et al,2025), but fewer studies have examined how individual variation in phenology affects plant performance. This study aims to understand if intraspecific leaf emergence phenology has an effect on plant fitness. As climate change continues to affect snowpack and snowmelt timing, it is important to understand how plants are shifting their phenology to predict future survival and performance (Kiel et al, 2025). To address this, I will test the effect of leaf up timing on perennial plant performance. I will ask, 1) Is there a relationship between an individual plant's leaf up timing and its demographic vital rates (survival, growth, reproduction)? And 2) Does that relationship change under more extreme early snowmelt conditions?

Methods

Study Site

This study was conducted south of Copper Creek in the research meadow at the Rocky Mountain Biological Laboratory (RMBL). The RMBL is in the East River Valley of the West Elk Mountains and sits at 2886 m elevation. Eight blocks, each containing a control and a treatment plot, were established in 2020-2022 by Dr. Amy Iler. The individual plots are 5m x 5m and divided into three 1.2 m x 5m subplots.

Study Species

This study reports on data for *Delphinium nuttallianum* , *Geum triflorum* , *Delphinium barbeyi* and *Linum lewisii*, which are all perennial herbs. They vary in size from small rosettes to tall, multi-stalked plants. They also vary in phenology from early spring to mid-summer. These species were chosen due to their differences in phenology, convenient location, and availability of historical data. Individual plants (n *D. nuttallianum* = 682, n *G. triflorum* = 349, n *L. lewisii*

= 1373, n *D. barbeyi* = 393) were tagged with a number so that individual plants could be tracked through time .

Experiment Design

Early Snowmelt Treatment

In each of the eight blocks, one of the plots was manipulated to advance snowmelt. In the spring when there was approximately 1 m of snow left, a black shade cloth was attached to rebar outside the corners of the plot in a 7-m x 7-m square. The cloth heated in the sun and accelerated snowmelt under the tarp via simple heat conduction. When bare dirt was exposed beneath the tarp the cloths were removed. The snowmelt treatment was applied each year 2023-2026. Across years, the treatment effect ranged from a difference of 6 days (2023) to 14 days (2025).

Leaf Out Surveys

Leaf out surveys were conducted by other members of the lab as soon as possible after bare ground was exposed. These surveys consisted of visiting each tag and seeing if the plant put up any leaves or stalks. Plants were considered up when green vegetation was visible above ground. Surveys were conducted 2-3 days per week, and the date of leaf emergence was recorded for each individual plant. These surveys were conducted each spring 2024-2026.

Demography Surveys

Demography surveys were taken once per year when plants switched from growth to reproduction. The surveys consisted of size and reproductive measurements. Size measurements included the estimated area of the largest leaf, calculated with length and width (*D. nuttallianum*), the product of the number of leaves and length of longest leaf (*G. triflorum*), and teh tallest stalk height (*L. lewisii*, *D. Barbeyi*). Reproductive measurements included whether the plant tries to flower, number of flowers, number of fruits and the number of seeds per fruit which was estimated via a subsample. Survival was recorded as whether a plant present in year t was still present in year t+1. Growth was measured as the proportional change in plant size from year to year. Demographic surveys were conducted each year 2023-2026. I participated in the 2026 survey for my field work, while previous years were conducted by other members of the lab.

Leaf up timing can be associated with within-year measures (flowering, fruiting) for each year 2024-2026, and can be associated with annual transitions between 2024-25 and 2025-26.

Analysis

I used linear models to test for changes in size, reproductive traits, growth and survival (*performance*) as a function of leaf up timing (*timing*). I tested for a change in that relationship under early snowmelt conditions (*treatment*) by testing for an interaction between treatment and timing. Because perennial plants tend to increase in size with age, and plant performance increases with size, I controlled for size (*size*) in my analysis of growth. Additionally, because plant performance might vary across space or through time, I also controlled for variation among blocks and years using random intercepts. The general model formula for my analysis is *performance ~ size + (timing x treatment) + (1|year) + (1|block)*.

Results

Summary

Species varied in their leaf up timing and treatment tended to delay leaf up timing. The average day of leaf up for all four species in the control plots occurred before day ten since snowmelt (*D. nuttallianum: 4.8 dss; G. triflorum: 1.0 dss; L. lewisii: 3.5 dss; D. barbeyi: 8.1 dss*). In contrast, average leaf up in the treatment plots occurred *after* day ten (*D. nuttallianum: 14.4 dss; G. triflorum: 12.9 dss; L. lewisii: 12.9 dss; D. barbeyi: 19.7 dss*). Leafout timing affected at least one vital rate in all four species. *Delphinium nuttallianum* was the only species to experience significant effects of leaf emergence timing on all four vital rates: growth, survival, probability of flowering and probability of fruiting. Later emergence increased the probability of fruiting in all species and growth in *D. nuttallianum*, while earlier emergence increased the probability of survival and flowering in *D. nuttallianum.* Of the eight instances where leaf up timing affected vital rate success, treatment altered the effect that leaf up timing had on success in five instances.

Growth

There was a significant effect of leaf out timing on the growth of *D. nuttallianum* ($p = 0.02$) . Plants that emerged later grew larger by the next year than plants that emerged earlier. Treatment did not change the effect of leaf out timing on growth, but overall plants in the treatment plot grew less than plants in the control plots ($p = .0005$) (Figure 1). There was no significant effect of leaf out timing on growth or treatment of *G. triflorum, L. lewisii,* and *D. barbeyi*.

Survival

There was a significant effect of leaf out timing on the survival of *D. nuttallianum* (Figure 2). In the control plots, plants that emerged the earliest had the highest probability of survival ($p=.008$), and probability of survival decreased with time. In the treatment plots, probability of survival increased moderately with time ($p=.005$). There was no significant effect of leaf out timing or treatment on *G. triflorum, L. lewisii* or *D. barbeyi*.

Probability of Flowering

There was a significant effect of leaf out timing on the probability of flowering in *D. nuttallianum* and *G. triflorum.* In *D. nuttallianum*, probability of flowering decreased significantly with time, with most plants emerging after 20 dss not likely to flower at all ($p = .0006$). Treatment did not affect the overall probability of flowering on day 0, but it did change how probability of flowering is influenced by leaf out timing. While probability of flowering decreases with time in the control plots, probability of flowering does not change with time in the treatment plots ($p = .0002$) (Figure 3).

Probability of flowering in *G. triflorum* increases with time with time in both control and treatment plots ($p=.002$). Plants in treatment plots were less likely overall to flower, and treatment did not change the effect of leaf out timing on probability of flowering (Figure 3).

There was no significant effect of leaf up timing or treatment on *L. lewisii* or *D. barbeyi*. In both species, size had a significant effect on probability of flowering with larger plants being more likely to flower.

Probability of Fruiting

There was a significant effect of leaf out timing on the probability of fruiting (Figure 4). In the control, probability of fruiting increased with time for all four species ($p < .05$). In *D. nuttallianum* and *G. triflorum*, treatment changed how leaf out timing affects the probability of fruiting. In *D. nuttallianum*, fruit set increases with dss in treatment plots, but reaches an asymptote in the control. In *G. triflorum*, fruit set increases with dss in the control, but did not change with dss in the treatment. In *D. barbeyi* control plots, probability of fruiting increased moderately with time ($p=.008$). In treatment plots, leaf out timing had little effect on the probability of fruiting($p=.04$).

In *L. lewisii* control plots, probability of fruiting increased moderately with time ($p=.02$). The treatment did not change the effect of leaf out timing on probability of fruiting, but overall, plants in the treatment plots were less likely to produce fruits.

Discussion

In this study I investigated the potential effects of leaf emergence timing on plant fitness, and whether or not that effect changes under early snowmelt conditions. I found that leaf up timing had a significant effect on the success of at least one vital rate across all four study species and that this effect did change with early snowmelt treatment.

Delphinium nuttallianum was the only species to experience significant effects of individual variation in leaf up timing on all four vital rates measured in this study, while the other later season species only experienced an effect on probability of flowering *(D. nuttallianum, G. triflorum)* and fruiting (*D. nuttallianum, G. triflorum, L. lewisii, D. barbeyi)*. This partially supports my first hypothesis that there is a relationship between individual leaf emergence timing and plant fitness. The disparity in effect of leaf up timing on the different species could be explained by their differing phenologies. Previous studies have shown that the correlation between snowmelt date and first flowering date of early spring plants like *D. nuttallianum* is highly significant (Inouye 2008). That same study found that *D. barbeyi*, a late flowering plant, did not experience significant variation in flowering time when the snow melted out before day 140 of the year (snowmelt occurred on day 140 or earlier for all years encompassed by my study). It is possible that the level of sensitivity to snowmelt timing could apply to the other vital rates measured in this study.

Contrary to my expectations, not all vital rates performed better with earlier emergence. The increase of growth with later emergence could be attributed to the warmer later season temperatures and avoidance of drought stress. Cold-adapted subalpine and alpine plants have been shown to experience more growth under warmer temperatures given that water stress is not an issue (Dolezal et al, 2020; Meineri et al, 2013; Springate and Kover, 2014). Once temperature reaches a certain threshold, precipitation becomes a significant limiting factor for plant growth (Dolezal et al, 2020). In Colorado, plants that emerge following snowmelt rely almost entirely on soil moisture for the typically dry late spring and early summer months until the monsoon season begins around July (Sloat et al, 2015). Later plants experience a relatively smaller window between emergence and the monsoon season than early plants. It is possible that late emergence allows plants to experience the maximum amount of growth and investment into reproductive structure due to warmer temperatures without experiencing significant drought stress.

Leaf up timing had a significant effect on the probability of fruiting in all four species, and in all four species, probability of fruiting increased with later emergence. There are multiple possible explanations for these results. Reproductive structures are more vulnerable to frost damage than vegetative structures (Ladinig et all, 2013; Inouye, 2008; Inouye 2002), so it makes sense that probability of fruiting would increase with later emergence after the danger of frost events has passed. Additionally, phenological synchrony with pollinators could explain why plants that emerged later were more likely to fruit. One study showed that early flowering of *Corydalis ambigua* led to a phenological mismatch with pollinators which was strongly related with a less successful seed set (Kudo and Cooper, 2019). In contrast, another study conducted at the Rocky Mountain Biological Lab did not find strong evidence of early flowering causing a phenological mismatch or a less successful seed set (Gezon et al, 2016). There is not enough evidence from the present study to determine the reason later emergence increases the probability of fruit set, but further investigation could be the focus of a future study.

The majority of control plants across all species emerged before 20 dss, with the average day of leaf up occurring before day 10 dss in all species. Survival and the probability of flowering of *D. nuttallianum* was higher for the earliest plants, whereas growth was higher for later plants. It makes sense that actual leaf up timing and optimal phenology for survival match considering survival is a key vital rate for population dynamics of long-lived species (Iler et al, 2021). However, there could be consequences in other vital rates like growth where the leaf up timing and optimal phenology do not match (Figure 5). The mismatch of average leaf emergence and optimal phenology for fruiting could be less concerning at a population level, as reproduction losses are not a significant cause of population decrease in long lived perennials (Iler et al, 2019).

Treatment altered the effect that leaf up timing had on plant success in five of the eight vital rates significantly affected by leaf up timing in control plots. This partially supports my hypothesis that the effect of leaf emergence timing on plant fitness changes under early snowmelt conditions. In most cases, leaf up timing in treatment plots had little to no effect on the success of those vital rates, as opposed to the control plots where either earlier or later emergence was favored. This is likely due to a threshold effect, where plant growth in the early treatment is limited regardless of emergence date due to suboptimal temperatures in the early season. A similar effect was observed in a high alpine study where leaf emergence and flowering were delayed in advanced snowmelt plots until temperatures climbed above 0 C (Steltzer et al, 2009). Another study of Arctic plants found that advancing snowmelt without warming resulted in a decrease in plant production, further suggesting that temperature is a significant limiting factor of plant growth that outweighs the benefits of a longer photoperiod (Livensperger et al, 2016).

Surveys did not always start immediately after snowmelt, and as a result, the leaf up date is imprecise for some species. The early treatment was especially affected by this as there is not as much variation as there should be. As a result, many plants have been recorded as up on the first day of the survey when they likely emerged earlier. Additionally, it became clear throughout the study that *G. triflorum* does not fully senesce its green leaves from the previous year, which could have caused an inaccurate record of leaf up date for some individuals. This study did not include data from a year with late snowmelt and therefore the effects of leaf up timing on later season plants were not fully investigated.

It would be interesting to repeat this study with more very early spring plants to see if the higher sensitivity to snowmelt timing exhibited by *D. nuttallianum* is consistent across different species. Including another later season plant would be interesting to affirm the weak effect of leaf up on late season species.

Phenology studies have largely focused on flowering phenology, but this study shows that leaf emergence timing can influence plant fitness. Studies also often compare phenology at a population level, but variation within a population also matters. As snowmelt timing shifts earlier, so do the environmental conditions. Given that leaf emergence timing dictates the environmental conditions a plant is exposed to, understanding the relationship between actual leaf emergence timing and optimal phenology, and whether that relationship is changing with climate warming will be critical to understanding the future health of plant populations.

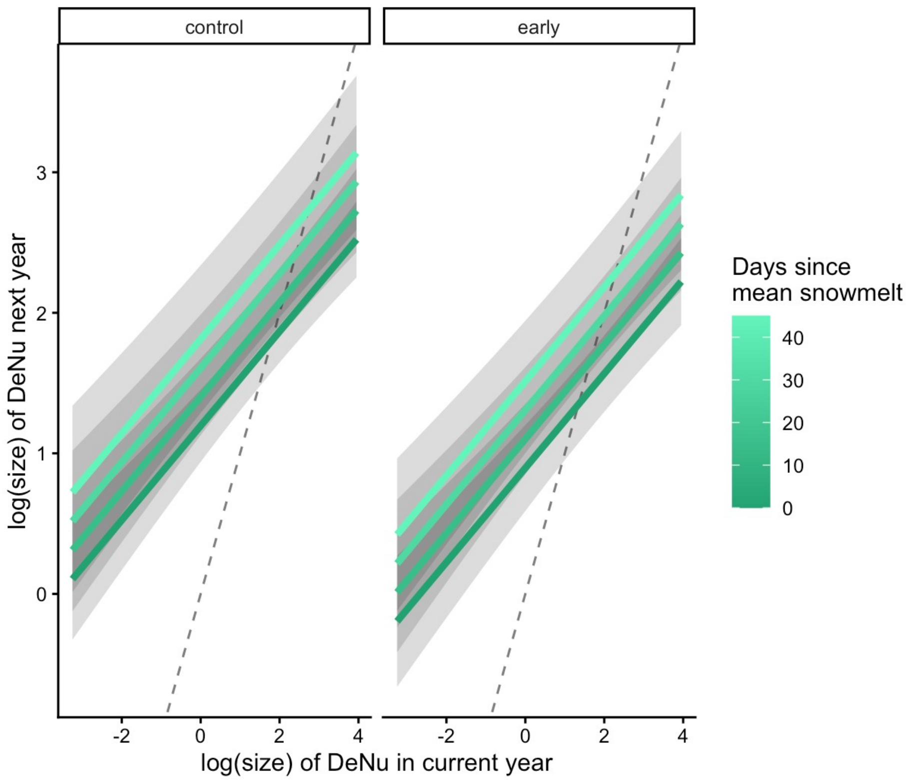

Figure 1: Leaf up timing and treatment each affected interannual growth. Solid, colored lines show size of a plant in year *t* vs size in year *t+1*, and the gray dashed lines are the 1:1 line (along which a plant remains the same size). Later plants and those in the control each had higher intercepts, meaning higher interannual growth rates regardless of their size.

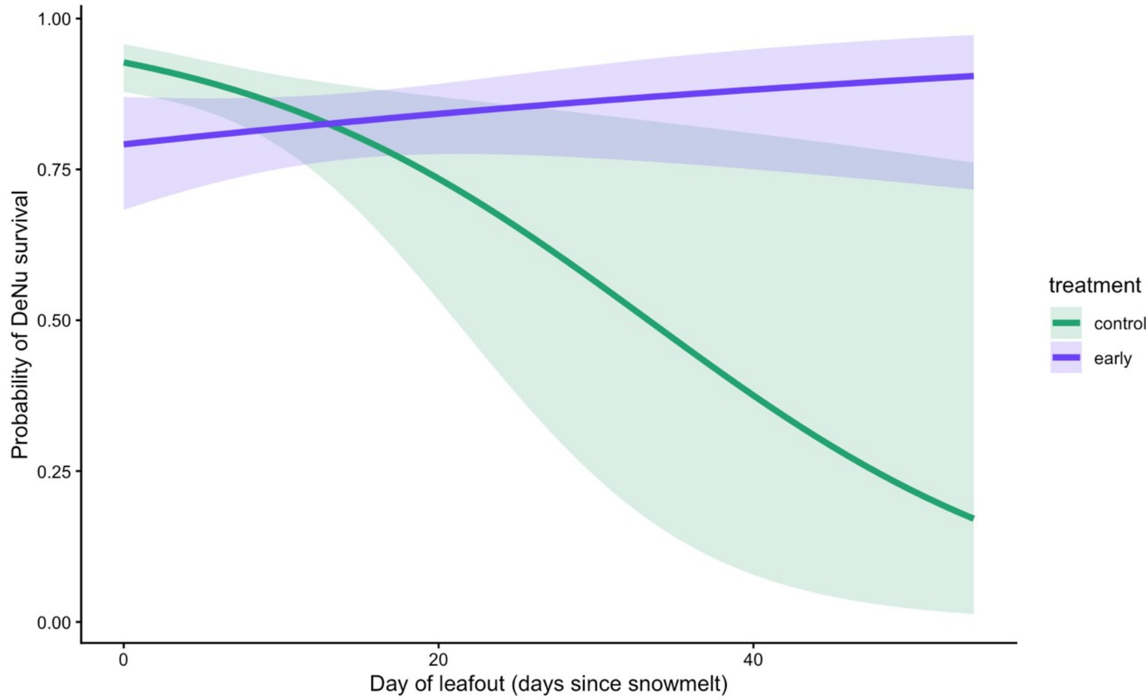

Figure 2: In the control plots, survival probability decreases with later emergence, but this effect goes away or maybe reverses in the early snowmelt treatment. Transparent bands represent 95% confidence intervals.

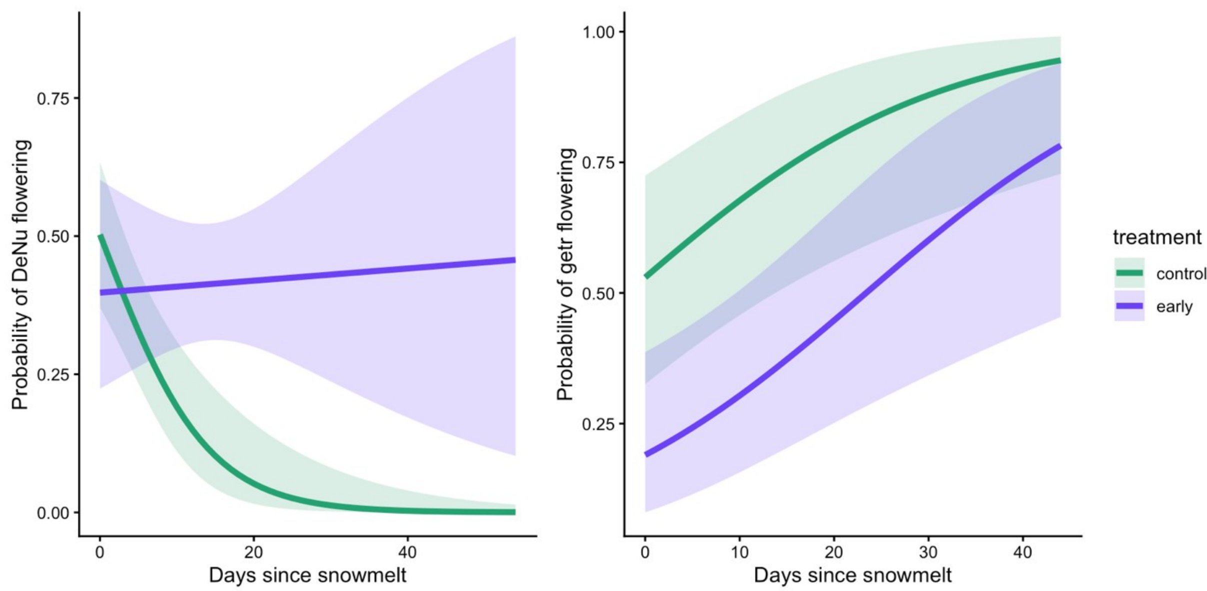

Figure 3: Probability that *D. nuttallianum* (left) flowers decreases with later emergence, but this effect goes away or maybe reverses in the early snowmelt treatment. Probability that *G. Triflorum* (right) flowers increases with late emergence, with a similar effect in the early snowmelt treatment. Transparent bands represent 95% confidence intervals.

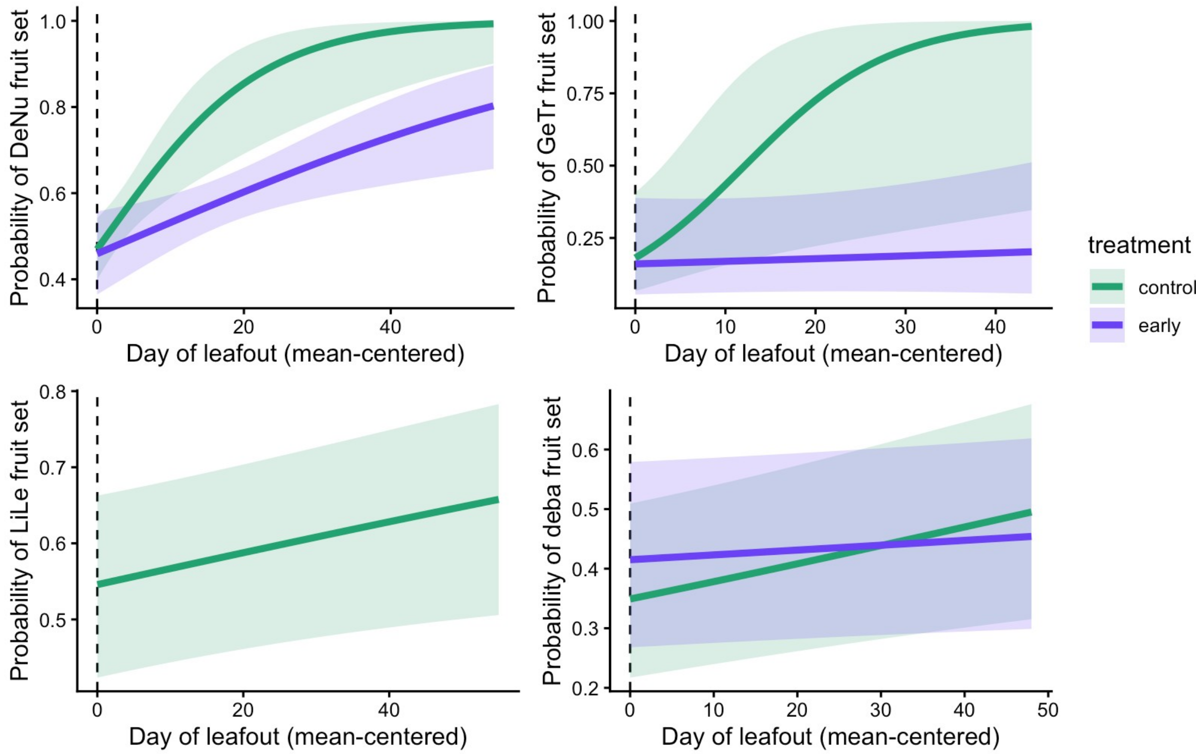

Figure 4: Probability of fruit set per flower increases with later emergence, but this effect becomes less significant or goes away with early snowmelt treatment. Transparent bands represent 95% confidence intervals.

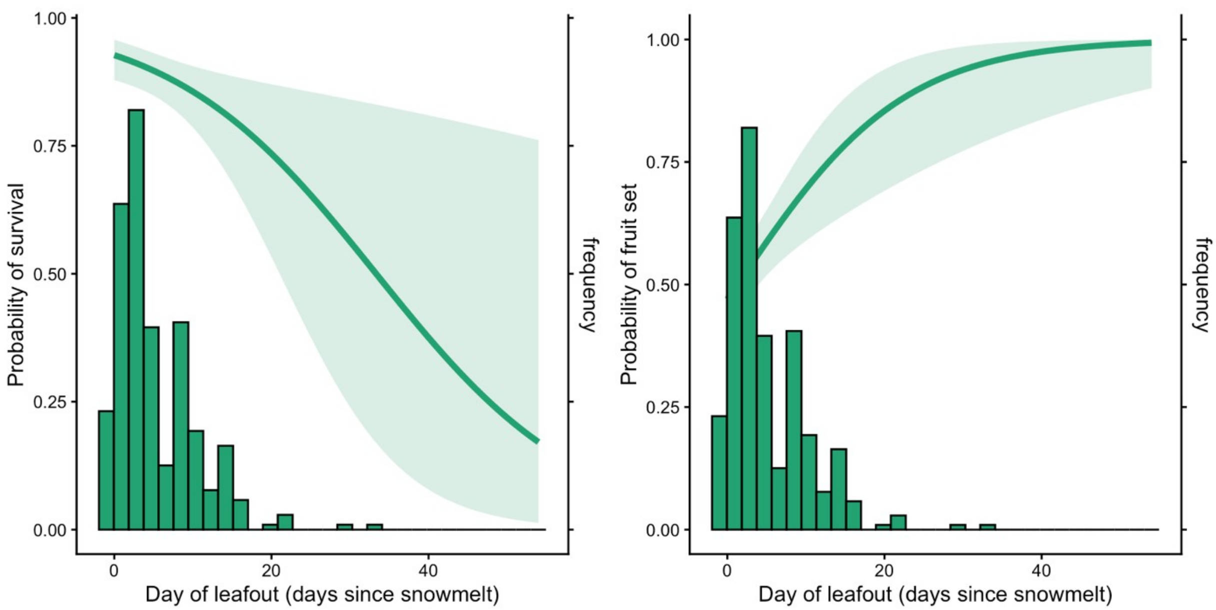

Figure 5: Most *D. nuttallianum* plants emerged before day 20 dss, which aligns with the optimal phenology for probability of survival (left) but is in contrast to the optimal phenology for probability of fruiting (right). The histogram shows the number of new plants that emerged on a given day. The linear graph shows the probability of survival and fruit set on a given leaf up day. Transparent bands represent 95% confidence intervals.

Julia Blatz Map

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