

The Effect of Snowmelt Timing on Pollinator Visitation to Subalpine Wildflowers

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Abstract

The plant and pollinator mutualism is under increased stress due to climate change, especially in subalpine ecosystems. Climate change is altering the timing of snowmelt in subalpine ecosystems, which changes the flowering phenology and possibly the floral abundance of subalpine plants and therefore can impact plant and pollinator interactions. Data gathered at RMBL shows that the date of earliest snowmelt and mean summer temperature are increasing at an unsustainable rate. To better understand the consequences of snowmelt timing on plant-pollinator interactions, an early snowmelt manipulation was performed and pollinator observations were conducted on four subalpine species at the Rocky Mountain Biological Laboratory. The study consists of numerous pollinator observation sessions in control and early snowmelt plots on 4 species of wildflowers: *Delphinium nuttallianum* (DENU), *Geum triflorum* (GETR), *Linum lewisii* (GETR), and *Delphinium barbeyi* (DEBA). The four species represent a gradient of phenological flower timing across the growing season beginning with DENU and ending with DEBA. This study aims to allow us to more accurately predict the changes to plant-pollinator interactions in the future as climate change accelerates plant and animal phenology. It was hypothesized that increased likelihood of frost, decreased water availability, and loss of phenological synchrony between wildflowers and pollinators would lead to a lower mean visitation rate and probability of visits in early snowmelt plots compared to the controls. I found that DENU experienced a significantly lower mean visitation rate in early snowmelt plots while LILE experienced significantly higher mean visitation rate. Only DEBA differed significantly in the probability of receiving visit, with a higher probability in early snowmelt. It is possible that as climate change becomes more severe, there will be differential impacts for subalpine plant species and therefore both positive and negative effects on plant and animal interactions. Species that are more resilient to frost and phenological mismatch like LILE may be able to outcompete other more frost and phenologically sensitive species such as

DEBA and DENU. More years of study as well as further investigation of species' reproductive efficacy is needed to support this hypothesis.

Introduction

Climate change has a variety of consequences for the natural environment and its ecosystems (Walther et al. 2002). One widespread change is shifts in the timing of life-cycle events, otherwise known as phenological shifts, in a variety of organisms (Parmesan 2007). Plants and their pollinators may be particularly vulnerable to changes in climate because they are displaying more extreme phenological shifts than organisms in lower trophic levels, especially in alpine environments (Thackeray et al 2010; McKinney et al. 2012). Data gathered at the Rocky Mountain Biological Laboratory (RMBL) shows that the date of snowmelt is moving earlier at a rate of 4.14 day/decade and that mean summer temperature is increasing by 0.4 °C/decade (Lambert et al. 2010). As the snowmelt date occurs earlier in the spring, the flowering phenology of many species, including subalpine wildflowers changes (Iler et al. 2013a). Not only is this phenomenon seen in the Rockies, but it is also known to be a global change (Høye et al. 2007).

Changes in flowering phenology due to climate change can have a number of impacts on the reproductive success of plant species. Altering flower phenology from a species' "norm" can have a negative effect on its reproductive ability (Gezon et al. 2016). When a plant species flowers at a different time than its historical average, a discrepancy can occur with the phenology of the pollinator. Some studies have indicated that there is already a significant phenological mismatch between specific plants and pollinators, but as of now, plant-pollinator interactions at the ecosystem level are still functional in many ecosystems (Kudo 2019). This is in spite of evidence that shows shifts in flowering phenology can significantly and variably affect pollinator visitation rates (Iler et al. 2013b). Though currently, most plant-pollinator interactions are still occurring at a functional rate, further assessment is needed as climate change continues to progress (Iler et al. 2021).

This study seeks to understand the consequences of climate change on plant-pollinator interactions by asking the following question: How does altered snowmelt timing, and therefore altered flowering timing, affect pollinator visitation and composition to subalpine plant species? Previous literature suggests that there will be fewer pollinators in areas with artificially melted snow (Rigby 2021). One study investigating pollinator composition in terms of phenological mismatch found that there is only a change in composition in some plants, but as a rule of thumb, pollinator composition does not change as visitation rates decrease (Rafferty & Ives 2011). With this in mind, a second hypothesis is that the pollinator community will not vary significantly between treatments.

Methods

We selected seven areas in the RMBL research meadow in Gothic, Colorado with a mix of plant species with similar elevation and abiotic conditions. Seven black shade cloths 7 m by 7 m in size were placed in the areas to melt out snow earlier. In 2022, the tarps caused a 2-3 day advance in snowmelt. The interior 5 m by 5 m of each plot was studied, to allow for a 1 m buffer around the edge of the area where snow melted early. Each melted out area was paired with a control 5 m by 5 m plot to form a block. Seven total blocks were used in this study. Each plot contains three 1.2 m by 5 m subplots with walkways in between them to allow for various plant measurements within the plots (Figure 1).

Four species were studied. The species and their associated 4-letter code are *Delphinium nuttallianum* (DENU), *Geun triflorum* (GETR), *Linum lewisii* (LILE), and *Delphinium barbeyi* (DEBA). Each species flowers sequentially in the season beginning with DENU and ending with DEBA. The primary pollinators of each species are- DENU: queen bees, worker bees, and hummingbirds (Bosch & Waser 1999), GETR: bumblebees, LILE: flies and wind (Kearns & Inouye 1994), DEBA: bees and hummingbirds (Williams 2007). The experiment was conducted from the middle of the DENU flowering season through the end of DEBA flowering.

I repeatedly conducted pollinator observations across subplots while each study species was flowering. To begin each observation, I recorded the weather conditions, including wind amount, temperature, cloud cover, and time of day. I then selected an area of subplot 1 containing the study species and counts the number of inflorescences within their cone of vision. Over the next five minutes, I recorded the species of pollinator and number of flowers visited, defining a visit as any time a part of the pollinator touches the reproductive organs of the flower (stigma or anthers). After the five minutes were up, I moved to another subplot in the block, alternating between each treatment for each observation session. I began observations of each species as they began to flower in the plots. Due to the limited activity of flies and bees in adverse weather conditions, observations were generally only performed when the temperature was above 10 °C, cloud cover was less than 70%, and wind was not high. No observations were performed in the rain. Working within these restraints, as many observations as possible were recorded.

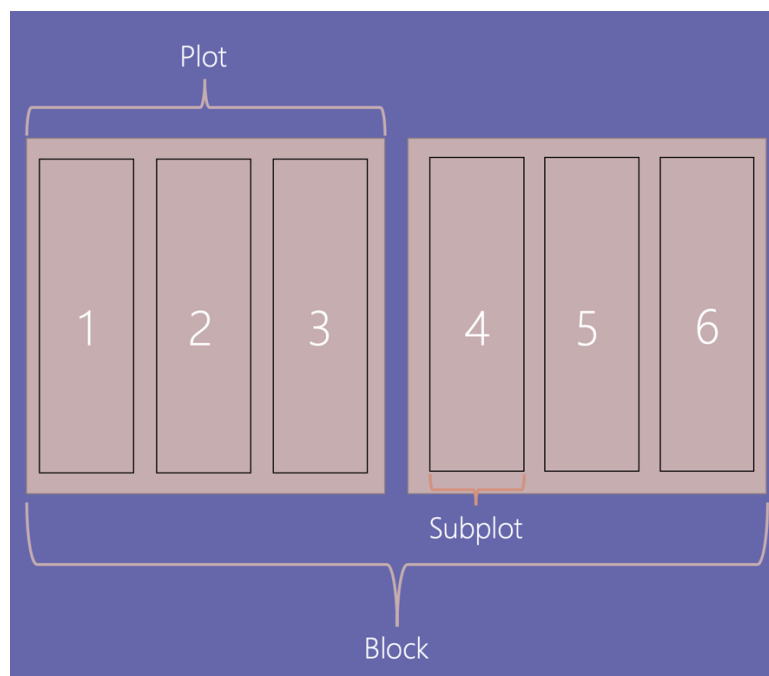


Figure 1. A diagram of a single block. Subplots 1, 2, and 3 refer to the snowmelt plot. Subplots 4, 5, and 6 refer to the control plot. Each plot has walking lanes between the subplots.

Data analysis was performed using standard R (R Core Team, 2022) and the dplyr R package. Visitation rates were averaged across dates for each subplot due to a large number of zeros in the dataset, and each species was analyzed separately. Mean visitation rate was analyzed using a generalized linear mixed effect model with a beta binomial distribution, treatment as a categorical predictor, and block and date as random intercept terms. I then ran the above model through a type 2 ANOVA to calculate a p-value. The probability of receiving a visit was calculated by converting the observations to a binomial response where 1 was a visit and 0 was an observation with no visit. It was analyzed with a similar model with, treatment as a categorical predictor and date as a random intercept term (to account for repeated observations across dates). Pollinator composition was organized by pollinator group (BEE, BEETLE, FLY, GRASSHOPPER, MOTH, or WASP). Bumble bee species were recorded as frequently as possible but were not used in analysis. Figures were made using ggplot in R. A map of the plots using GPS coordinates accurate to ~ 0.5 m was created using ArcGIS (Figure S1).

Results

In total, 624 five-minute observations were recorded across all species. Broken down by species, there were 125 observations of DENU, 103 of GETR, 225 of LILE, and 171 of DEBA. Each species is pollinated by different pollinators but bees and flies were the primary pollinators of all four studied species (Figure 2). Differences in diversity of pollinators across species are visible with LILE having the greatest diversity.

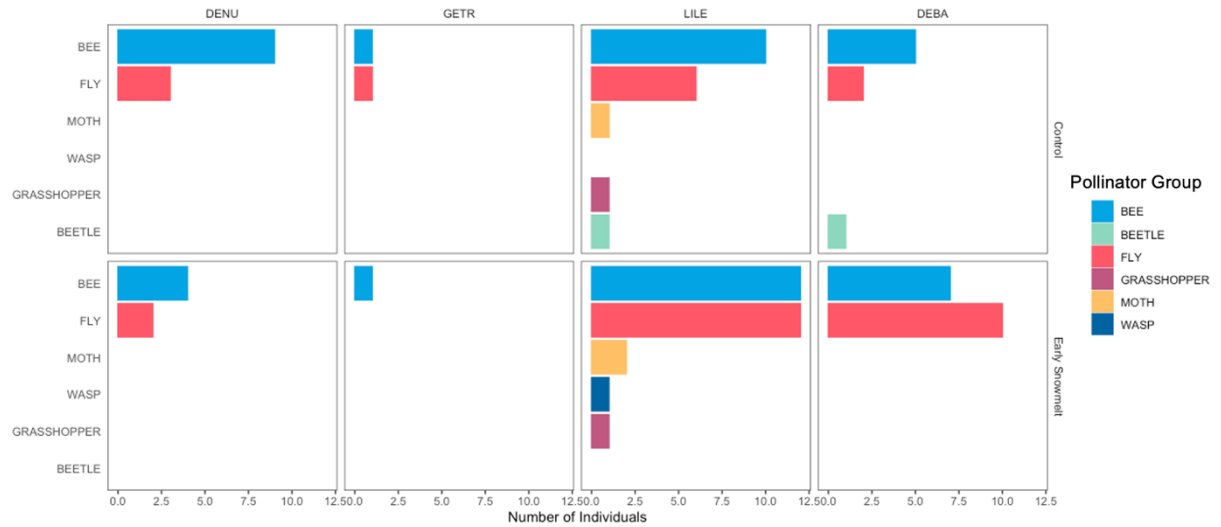


Figure 2. Composition of pollinators by group for each studied species in early snowmelt and control plots.

Observations of DENU showed a mean visitation rate of 0.0247 in early snowmelt and 0.0085 in control, differing significantly between treatments ($F = 3.85$, $p = 0.049$). LILE had a mean visitation rate of 0.0298 in early snowmelt and 0.0655 in the control plots, which also differed significantly between treatments but in the opposite direction of DENU ($F = 7.61$, $p = 0.006$). DEBA had a mean visitation rate of 0.0184 in early snowmelt and 0.0204 in control, but did not differ significantly between treatments ($F = 0.069$, $p = 0.793$). Despite having 103 observation sessions, GETR was only observed being pollinated 3 times and could not be analyzed for mean visitation rate with reasonable accuracy. Visitation rate varied widely across species (Figure 3).

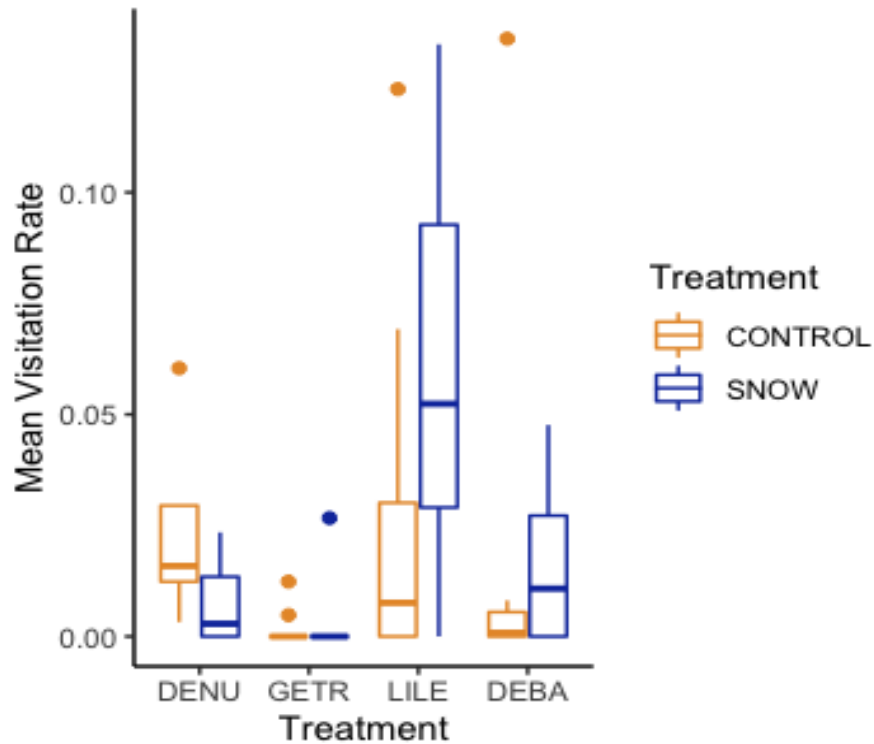


Figure 3. Mean visitation of all studied species on same scale. GETR is shown to illustrate its exceptionally low visitation rate.

DENU, GETR, and LILE probability of receiving a visit did not differ significantly between treatments (DENU: $p = 0.307$, GETR: $p = 0.588$, LILE: $p = 0.542$). There was a marginally significant difference in DEBA, with DEBA plants being more likely to receive a visit in the early snowmelt plots compared to the controls ($p = 0.061$). Probability of visit changed as the season progressed for all four studied species. Additionally, two out of the four species had trends in different directions in their early snowmelt plots and control plots. DENU had a positive trend in control and a negative one in early snowmelt as the season went on. GETR showed a negative trend in control and a positive trend early snowmelt (Figure 4).

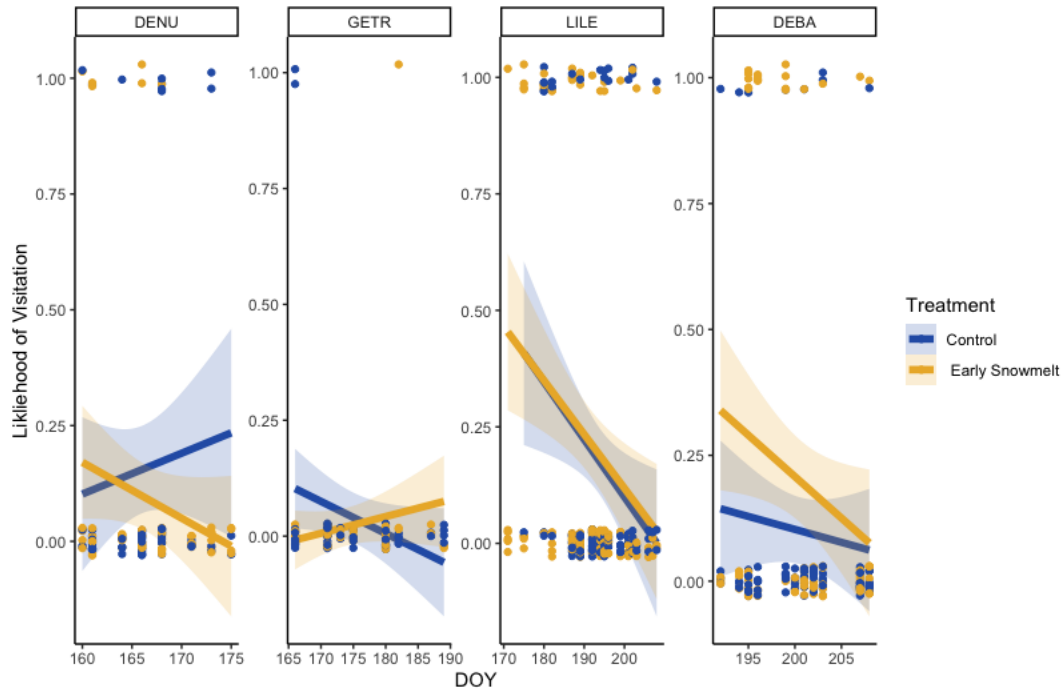


Figure 4. The change in probability of visit as the season progresses. DOY=1 is January 1.

Discussion

Trends in visitation probability in DENU show signs of advanced phenology in the early plots. Though the treatment only caused a three-day difference in snowmelt timing, it was anecdotally noted that the change in phenology was much more dramatic. The negative trend in the early snowmelt plots for DENU as shown in Figure 4 indicate that the plants in those plots likely reached peak bloom before the emerged bee population peaked. The positive trend in the control plots is an indicator of greater phenological synchrony with its pollinators.

For LILE, there were significantly more pollinator visits in early snowmelt plots than in the control plots. LILE was likely not affected by the late frost due to its frost tolerance and unique life history (Ogle et al. 2009). LILE inflorescences are very delicate and only last approximately one day, so the plant creates new flowers each morning, meaning that even in the unlikely event that a bud is frost killed, there will be a functional bud the next morning that there is not a freeze event overnight. This life history also allows LILE to create many inflorescences per day and to flower for a longer period than most other subalpine plants

(Burkle and Irwin 2009). One hypothesis is that fewer competitors for pollinators due to frost damage to other flowers could have allowed LILE to have a higher visitation rate than other wildflower species. The difference in visitation rate between control and early snowmelt plots in LILE may have been due to the plants shifting more resources toward reproduction in early snowmelt conditions (Sultan 2003). It is theorized that increased reproductive output, like increased flower size, in unfavorable conditions may be a way for plant population to remain large enough to stay viable (Sultan 2003). Flower size in each plot was measured, but has not been analyzed yet, which will provide some insight into resource allocation to reproduction.

No consistent in pollinator visitation in the early snowmelt plots was observed in 2022, in contrast to the data collected in 2021. The same experiment (including *Hymenoxys hoopesii* in replacement of GETR) was done in the summer of 2021. The results of 2021 showed a clear trend toward decreased visitation rate and lower probability of a visitor in the early snowmelt plots compared to the control plots (Rigby 2021). The difference in results may be due, in part, to the dramatic change in the magnitude of the treatment between both years. In 2021, the early plots melted an average of 17 days earlier than the control, while in 2022 they melted on average 3 days earlier. Weather conditions at the day of snowmelt show further difference between the two years. In 2021, the average high temperature for the three days before and after snowpack was measured at 0 cm as 9.5 °C. In 2022, the average temperature was 14°C (barr, unpublished data). This indicates a more rapid decrease in snowpack in 2022 than 2021, which explains why there was less of a treatment effect in 2022. Additionally, there was a much later freeze event in 2022, dropping to -3.5°C on June 21. That temperature was not reached after June 1 in 2021. DEBA buds are exceptionally vulnerable to frost damage by late June frosts (Inouye 2008). There was extensive frost damage to developing flowers in the study area (J Moloney and E Godtfredsen, personal observation). This likely explains why DEBA, which is generally known to have a high visitation rate was so sparsely visited in 2022 (Figure 5).

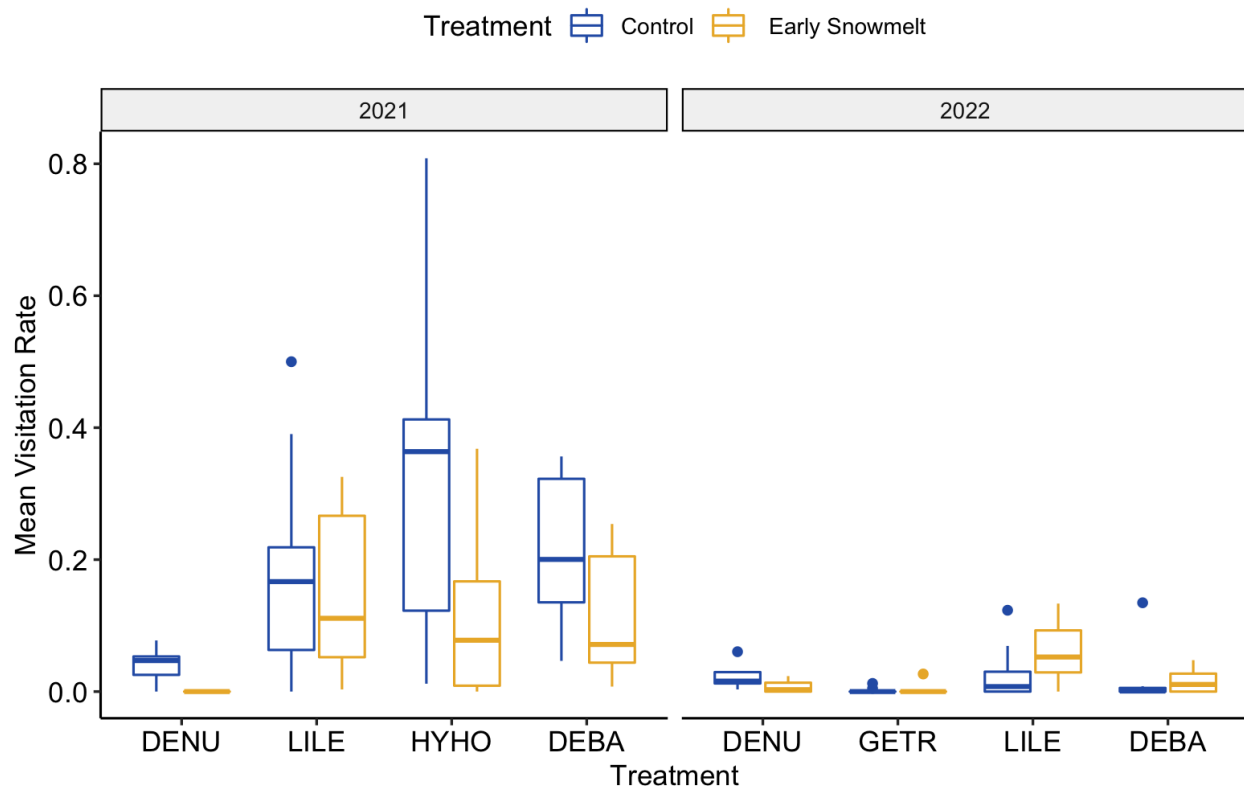


Figure 5. The mean visitation rate of each study species in 2021 (left) and 2022 (right). HYHO was replaced by GETR in 2022.

Drastically reduced pollinator visitation, as shown in Figure 5, may have had an effect on the results of this study. Though some of the results from 2022 were still significant, there may have been more significant differences between control and early snowmelt plots if visitation increased overall.

Despite the climatic difference between 2021 and 2022, there were effects of early snowmelt on some species. There was a significant difference in mean visitation rate in DENU in both 2021 and 2022, with lower visitation in the snowmelt plots compared to the controls. It is possible that this effect represents a phenological mismatch between DENU and bumble bees that pollinate it, since DENU did flower earlier in the early snowmelt plots compared to the controls. The phenological synchrony between wildflowers and bee pollinators is very important to a successful mutualism. Though the temporal overlap of pollinators and the four studied

species of wildflowers was not investigated, it is inferred that the artificial disruption of the plant-pollinator relationship by our experimental manipulation caused some level of phenological asynchrony. Alternatively, the advanced phenology of DENU in the early snowmelt plots may have caused decreased visitation because they had too low of a floral density relative to the surrounding meadow to attract pollinators at the same rate.

Bee emergence is tied closely to spring temperatures (Forrest & Thomson 2011), while wildflower bloom and syrphid fly emergence are closely tied to snowmelt timing (Kudo 2014, Iler et al. 2013b). The different cues for pollinator emergence are seen in the pollinator composition data as well. There was no significant change in the number of flies that visited DEBA in the control and early snowmelt plots. However, there was a change in the number of bees that visited (Figure 2). So, it seems plausible that as the climate continues to warm, flies will take a more significant pollination role.

Climate change, as simulated in this study, will likely continue to disrupt the phenological synchrony of subalpine wildflowers and pollinators in some cases. While climate change is associated with higher temperatures on average, it does not mean that all days will be warmer than the historical average. In fact, climate change has been shown to cause increased variability in the frost-free period and number of frost days in various simulations (Marquis et al. 2022). Earlier snowmelt and the potential for later frosts will cause more flower buds to be killed than in past years, which could affect pollinator visitation rates to remaining flowers. Results from this experiment show that some species may benefit from the changing climate while others might be harmed. Greatly reduced fruit counts have been observed in DEBA plants this year. All species in this study are long lived perennials, which may make their population less susceptible to climate fluctuations (Bemmels 2019). However, as these climate fluctuations gradually become the climate norm *Delphinium* species may be at risk unless they adapt to new climate conditions. In the future they could be out-competed by more adaptable species like LILE, causing a decrease in biodiversity and fewer available resources for long-tongued

pollinators like bees and hummingbirds. Further research into the impacts of late freeze events on subalpine ecosystems may reveal more about the complex pollinator visitation network and how it responds to climate induced stress.

Appendix

Jimmy Moloney_Snowmelt Map

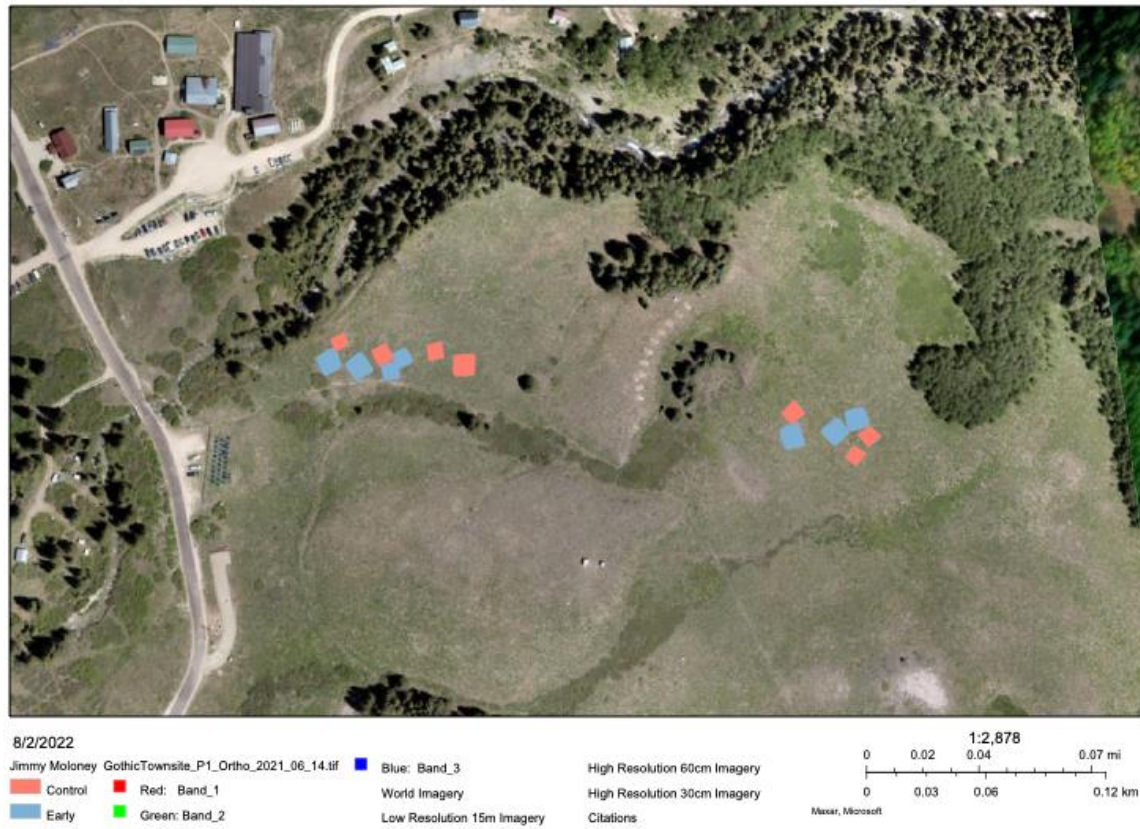


Figure S1. ArcGIS map of research sites. Control plots are in red and early snowmelt is in blue.

References

- Bemmels, J. B., & Anderson, J. T. (2019). Climate change shifts natural selection and the adaptive potential of the perennial forb *Boechera stricta* in the Rocky Mountains. *Evolution; International Journal of Organic Evolution*, 73(11), 2247–2262. <https://doi.org/10.1111/evo.13854>
- Burkle, L. A., & Irwin, R. E. (2009). The Effects of Nutrient Addition on Floral Characters and Pollination in Two Subalpine Plants, *Ipomopsis aggregata* and *Linum lewisii*. *Plant Ecology*, 203(1), 83–98. <https://doi.org/10.1007/s11258-008-9512-0>
- Bosch, M., & Waser, N. M. (1999). Effects of local density on pollination and reproduction in *Delphinium nuttallianum* and *Aconitum columbianum* (Ranunculaceae). *American journal of botany*, 86(6), 871–879.
- Gordo, O., & Sanz, J. J. (2005). Phenology and climate change: a long-term study in a Mediterranean locality. *Oecologia*, 146(3), 484–495. <https://doi.org/10.1007/s00442-005-0240-z>
- Høye, T. T., Post, E., Møllgaard, H., Schmidt, N. M., & Forchhammer, M. C. (2007). Rapid advancement of spring in the High Arctic. *Current biology : CB*, 17(12), R449–R451. <https://doi.org/10.1016/j.cub.2007.04.047>
- Iler, A. M., Høye, T. T., Inouye, D. W., & Schmidt, N. M. (2013a). Nonlinear flowering responses to climate: are species approaching their limits of phenological change?. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, 368(1624), 20120489. <https://doi.org/10.1098/rstb.2012.0489>
- Iler, A. M., Inouye, D. W., Høye, T. T., Miller-Rushing, A. J., Burkle, L. A., & Johnston, E. B. (2013b). Maintenance of temporal synchrony between syrphid flies and floral resources despite differential phenological responses to climate. *Global change biology*, 19(8), 2348–2359. <https://doi.org/10.1111/gcb.12246>
- Iler, A.M., CaraDonna, P.J., Forrest, J.R., & Post, E. (2021). Demographic Consequences of

Phenological Shifts in Response to Climate Change. *Annual Review of Ecology, Evolution, and Systematics*.

Inouye, D. W. (2008). Effects of Climate Change on Phenology, Frost Damage, and Floral Abundance of Montane Wildflowers. *Ecology*, 89(2), 353–362.
<http://www.jstor.org/stable/27651548>

Inouye, D. W. (2020). Effects of climate change on alpine plants and their pollinators. *Annals of the New York Academy of Sciences*, 1469(1), 26–37. <https://doi.org/10.1111/nyas.14104>

Kearns, C. A., & Inouye, D. W. (1994). Fly Pollination of *Linum lewisii* (Linaceae). *American Journal of Botany*, 81(9), 1091–1095. <https://doi.org/10.2307/2445470>

Kudo, G. (2014). Vulnerability of phenological synchrony between plants and pollinators in an alpine ecosystem : Winter Climate Change. *Ecological Research*, 29(4), 571–581.

Lambert, A.M., Miller-Rushing, A.J. and Inouye, D.W. (2010), Changes in snowmelt date and summer precipitation affect the flowering phenology of *Erythronium grandiflorum* (glacier lily; Liliaceae). *American Journal of Botany*, 97: 1431-1437. <https://doi.org/10.3732/ajb.1000095>

Marquis, B., Bergeron, Y., Houle, D., Leduc, M., & Rossi, S. (2022). Variability in frost occurrence under climate change and consequent risk of damage to trees of western Quebec, Canada. *Scientific Reports*, 12(1), 1–15. <https://doi.org/10.1038/s41598-022-11105-y>

McCabe, L & Cobb, N. (2021) From Bees to Flies: Global Shift in Pollinator Communities Along Elevation Gradients

McKinney, A.M., CaraDonna, P.J., Inouye, D.W., Barr, B., Bertelsen, C.D. and Waser, N.M. (2012), Asynchronous changes in phenology of migrating Broad-tailed Hummingbirds and their early-season nectar resources. *Ecology*, 93: 1987-1993. <https://doi.org/10.1890/12-0255.1>

Ogle, D.G., L. St. John, J.S. Peterson, and D.J. Tilley. 2009. Plant guide for blue flax (*Linum*

- perenne*) and Lewis flax (*L. lewisii*). USDA-Natural Resources Conservation Service, Idaho State Office. Boise, ID.
- Parmesan, C. (2007), Influences of species, latitudes and methodologies on estimates of phenological response to global warming. *Global Change Biology*, 13: 1860-1872. <https://doi.org/10.1111/j.1365-2486.2007.01404.x>
- Primack, R. B., & Inouye, D. W. (1993). Factors affecting pollinator visitation rates: A biogeographic comparison. *Current Science*, 65(3), 257–262. <http://www.jstor.org/stable/24095126>
- R Core Team (2022). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org>
- Rafferty, N. E., & Ives, A. R. (2011). Effects of experimental shifts in flowering phenology on plant-pollinator interactions. *Ecology letters*, 14(1), 69–74. <https://doi.org/10.1111/j.1461-0248.2010.01557.x>
- Rigby, C., Iler, A.M., Godtfredsen, E., (2021) The effect of early snowmelt on pollination: A study of four Rocky Mountain subalpine plant species. *RMBL Publications Database*. [https://www.rmbl.org/wp-content/uploads/2021/10/Rigby Ceci StudentPaper 2021.pdf](https://www.rmbl.org/wp-content/uploads/2021/10/Rigby_Ceci_StudentPaper_2021.pdf)
- Sultan, S. E. (2003). Phenotypic plasticity in plants: a case study in ecological development. *Evolution & development*, 5(1), 25-33
- Thackeray, S.J., Sparks, T.H., Frederiksen, M., Burthe, S.J., Bacon, P.J., Bell, J.R., Botham, M.S., Brereton, T., Bright, P.W., Carvalho, L., Clutton-Brock, T.H., Dawson, A., Edwards, M., Elliott, J.M., Harrington, R.C., Johns, D.G., Jones, I.D., Jones, J.T., Leech, D.I., Roy, D.B., Scott, W.A., Smith, M., Smithers, R.J., Winfield, I.J., & Wanless, S. (2010). Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. *Global Change Biology*, 16.
- Walther, GR., Post, E., Convey, P. *et al.* Ecological responses to recent climate change. *Nature* **416**, 389–395 (2002). <https://doi.org/10.1038/416389a>
- Williams, C.F. (2007), Effects of floral display size and biparental inbreeding on outcrossing

rates in *Delphinium barbeyi* (Ranunculaceae). Am. J. Bot., 94: 1696-1705. <https://doi.org/10.3732/ajb.94.10.1696>