Effects of early snowmelt and frost on plant-pollinator interactions

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**Abstract**

As a result of climate change, plants are experiencing shifts in flowering phenology due to early snowmelt, and thus becoming more susceptible to damage from spring frost events. These direct effects of snowmelt and frost on plants can indirectly impact plant-pollinator interactions, yet few studies have examined these indirect effects. At the Rocky Mountain Biological Laboratory, we conducted a series of experiments to answer the following questions: 1) Does variation in the phenology of flowering plants affect pollinator visitation rate? and 2) How do species and community level plant-pollinator responses to early snowmelt and frost damage compare? At our study site, we had 40 $2m^2$ plots assigned to one of four treatment types: 1) early snowmelt and frost, 2) early snowmelt no frost, 3) natural snowmelt and frost, and 4) natural snowmelt and no frost, Pollinator observations were conducted over 8 weeks and visitation rates were compared among treatment type. We found that early snow removal plots had higher pollinator visitation rates. Further, frost treatment had no effect on pollinator visitation rate overall, but affected certain early blooming flower species. Overall, we found that early snowmelt and frost affect plant species differently; some species, and therefore some plant-pollinator interactions, are more resilient to changes in flowering phenology than others.

## Introduction

Within an ecosystem, the majority of flowering plants depend entirely or at least partially on pollinators for reproductive success (Ollerton et al. 2011). Therefore, these interactions are vital to ecosystem health and function. Unfortunately, plant-pollinator interactions are becoming threatened by a variety of anthropogenic factors, prominently climate change.

Increasing temperatures due to climate change are causing earlier spring events, including earlier snowmelt, which can affect the phenology of flowering plants (Badeck et al. 2004, CaraDonna et al. 2014). When snowmelt and warmer temperatures occur earlier in the spring, some plant species will begin to bloom earlier (Hegland et al. 2009). This may result in a longer growing and flowering season (Rafferty et al. 2013). However, an earlier bloom date also makes plants more susceptible to frost damage. Though increasing spring temperatures are resulting in early snowmelt, low temperatures resulting in frost damage have not decreased in frequency (Inouye 2008). Flower buds are especially susceptible to frost damage (Inouye 2000), thus we might see fewer flowers in years with early snowmelt and high frost events.

Both shifts in flowering phenology as well as frost damage may impact pollination. When plant phenology changes due to increasing temperatures, there may be temporal or spatial mismatches on certain plant-pollinator interactions (Hegland et al. 2009, Burkle et al. 2013). Iler et. al (2013) found that early snowmelt and higher temperatures caused flowers to advance at a faster rate, while syphrid fly emergence did not advance to the same extent as the flowers. This is an example of one temporal mismatch faced by a group of pollinators. Additionally, plant species differ in their resilience to frost damage (Inouye 2008), resulting in further potential for temporal or spatial disruptions to plant-pollinator interactions. Often, there are differences in species-level and community-level plant-pollinator responses to changes in phenology, and community-level plant-pollinator interactions are likely more resilient to changes in phenology (Iler et al. 2013). In addition to directly affecting plant phenology, frost may have other negative impacts on pollination. Plants with frost damage might be less attractive to pollinators than healthy plants that were not damaged by frost.

In this study, we examined the effects of early snowmelt and frost on the abundance and diversity of plant-pollinator interactions in 40 alpine meadow field plots and asked the following questions: 1) Does variation in the phenology of flowering plants affect pollinator visitation rate? and 2) How do species and community level plant-pollinator responses to early snowmelt and frost damage compare? In order to answer these questions, we conducted pollinator observations within each plot to examine the effect of early snowmelt and frost on plant-pollinator responses at community level, pollinator family level, and plant species level.

**Methods**

Our field site was located at Marriage Meadow (Fig. 1) near the Rocky Mountain Biological Laboratory (RMBL) in Gothic, CO at an elevation of 2590 m. In April 2015, Gabriella Pardee established 40 2x2m plots within the meadow. She removed snow in April on 20 of the plots to simulate early snowmelt. The other 20 plots were left to melt out naturally. Further, 10 of the early snowmelt plots and 10 of the natural snowmelt plots were protected from frost damage by covering with tarps on cold nights when the temperature dropped below freezing. A random number generator was used to select plots for the snow and frost treatments.

Two to three times a week for eight weeks, we observed each plot for 10 minutes. A random number generator was used before each observation round to determine the order in which the plots were observed to ensure that certain plots were not observed at the same time of day or weather condition each time. The random number generator also helped account for the fact that there are different pollinators active at different times of the day.

When a pollinator entered the plot, each flower species visited, number of flowers visited per plant, and duration of each flower visit was recorded. As the pollinator left the plot, it was captured for identification. Bumblebees were captured, identified to species level, and released after identification while all other bees and flies were placed in alcohol and taken back to the lab. After every 30 min of observation, we stopped observations and netted for 10 min to capture any pollinators over the field plots. Since it was not possible to capture all of the pollinators as they were leaving the plots during the observation periods, netting helped identify the pollinators present near the plots that day.

Twice a week, we conducted flower counts in each plot. The number of flowering plant species and flowers per plot were counted to see whether plant diversity and evenness varied across the different treatments since this can influence pollinator visitation rates.

*Analyses*

The number of visitors to each plot within each treatment was used to compare overall pollinator visitation rate across all four treatments. The total number of flowers and plants visited within the plots of each treatment was also used to compare pollinator visitation rate. ANOVAs were used to test the effects of early snowmelt and frost on total number of plants visited, total number of flowers visited, and total number of pollinators that visited flowers within the plots. Generalized linear mixed models were used to examine whether treatment had an effect on individual pollinator families and on individual plant species.  Pollinators were divided into one of six families; Halictidae, Apidae, Megachilde, Andrenidae, Syrphidae or an "other flies" category.  The six most abundant flower species, *Potentilla pulcherrima*, *Claytonia lanceolata, Taraxacum officinale, Androsace septentrionalis*, *Delphinium nuttallianum*, and *Mertensia fusiformis* were used to examine the effect of treatment on individual plant species.  Distributions and overdispersion ratios were used to justify the models.  R Version 0.98.1049 was used for analysis with packages "reshape," "AICcmodavg," and "lme4."


Fig. 1.  Marriage Meadow Field Site.  The red line outlines the perimeter of the field site.

## Results

*Pollinator visitation rates across treatments*

Early snow removal plots had more pollinator visits to flowers (ANOVA, $t$= 2.210, $p$=0.0335, Fig. 2) and plants (ANOVA, $t$= 2.777, $p$=0.00865, Fig. 3) than the natural snowmelt plots. There was no significant effect of frost treatment on either the number of pollinator visits to flowers (ANOVA, $t$=-0.036, $p$=0.9711) or plants (ANOVA, $t$=-0.350, $p$=0.72843). Further, the interaction between frost and snow treatments was not significant for the number of flowers (ANOVA, $t$=-0.627, $p$=0.5347) or plants visited (ANOVA, $t$=-0.737, $p$=0.46587).

A higher number of pollinators visited flowers in the snow removal plots than natural snowmelt plots (ANOVA, $t$= 3.475, $p$=0.00135, Fig. 4), while frost treatment did not have an effect on number pollinators that visited plants (ANOVA, $t$=-1.142, $p$=0.26102). Further, the interaction between frost and snow treatments did not significantly affect the number of pollinators that visited the plants (ANOVA, $t$=-1.170, $p$=0.24959). When we sorted the pollinators to the family level, we did not find a significant effect of visitation rates for the frost and snow treatments. On plant species level, several species were significantly impacted by frost and snow treatments.

When we compared visitation rates for individual plant species, we found differences in visitation rates for three species. More pollinators visited *Potentilla pulcherrima* plants in the early snow removal plots than the natural snowmelt plots (Generalized linear mixed model, $z$=1.99, $p$=0.0463). Further, more pollinators visited *Claytonia lanceolata* (GLMM, $z$=-2.21, $p$=0.0271) and *Taraxacum officinale* plants

(GLMM, $z$=-2.17, $p$=0.0299) in the plots protected from frost events than the plots that underwent frost events.

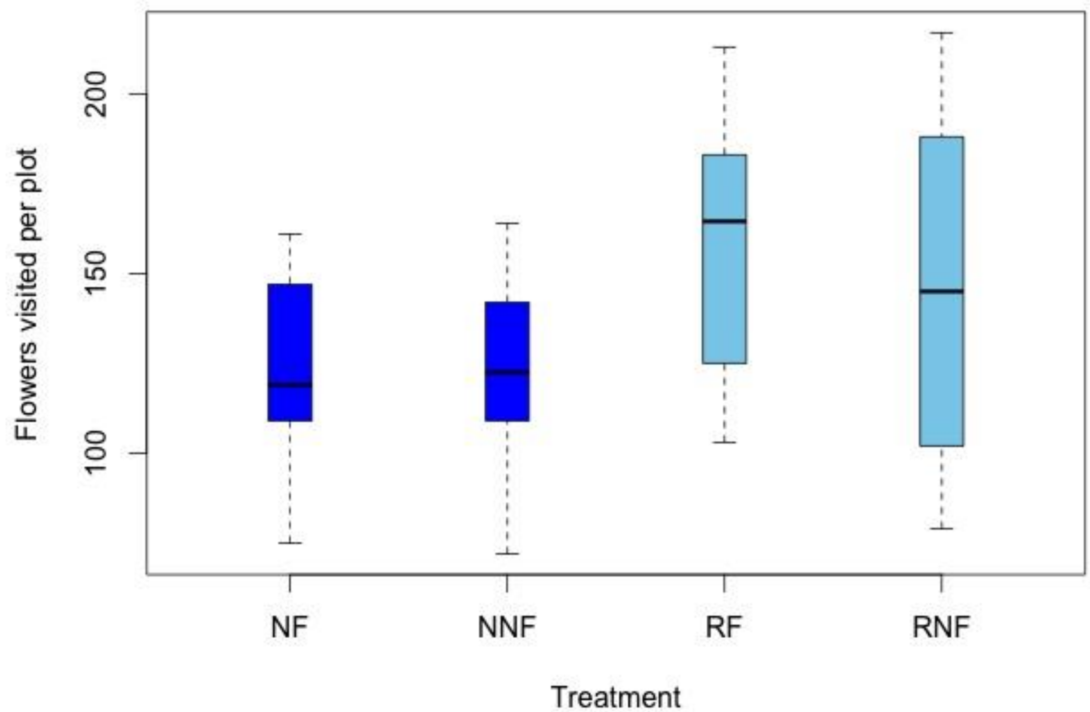


Fig. 2. Effect of treatment on total flowers visited per plot. NF indicates natural snowmelt and frost treatment. NNF indicates natural snowmelt and no frost treatment. RF indicates early snow removal and frost treatment. RNF indicates early snow removal plots without frost treatment. There was a significant effect of snow treatment on flowers visited per plot ($P$=0.0335), but there was no significant effect of frost on flowers visited per plot ($P$=0.9711).

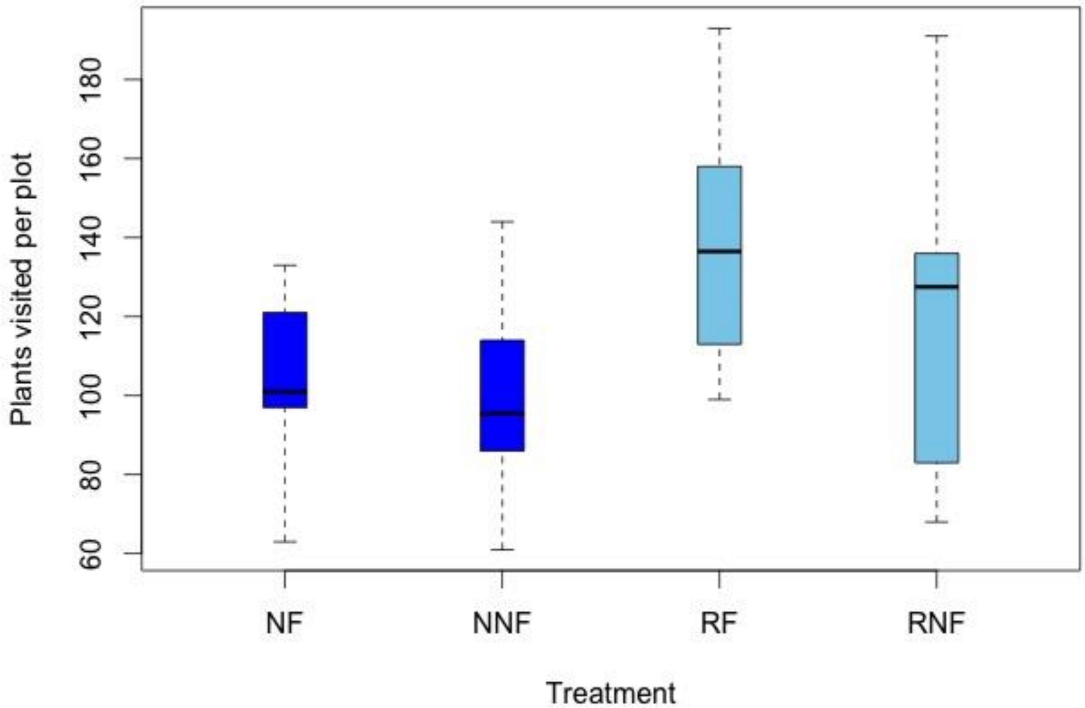


Fig. 3. Effect of treatment on total plants visited per plot. NF indicates natural snowmelt and frost treatment. NNF indicates natural snowmelt and no frost treatment. RF indicates early snow removal and frost treatment. RNF indicates early snow removal plots without frost treatment. There was a significant effect of snow treatment on flowers visited per plot (*P*=0.00865), but there was no significant effect of frost on flowers visited per plot (*P*=0.72843).

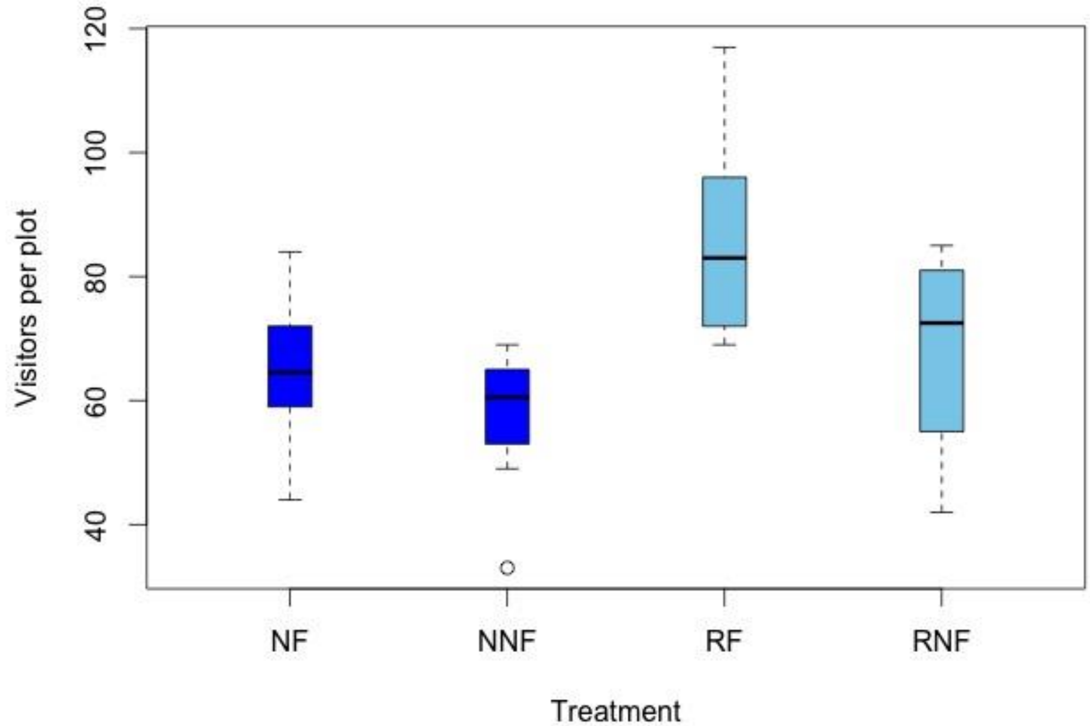


Fig. 4. Effect of treatment on total visitors per plot. NF indicates natural snowmelt and frost treatment. NNF indicates natural snowmelt and no frost treatment. RF indicates early snow removal and frost treatment. RNF indicates early snow removal plots without frost treatment. There was a significant effect of snow treatment on flowers visited per plot (*P*=0.00135), but there was no significant effect of frost on flowers visited per plot (*P*=0.26102).

**Discussion**

The early snow removal plots had significantly more flowers and plants visited, and more pollinators visited them than the natural snow removal plots. Early snow removal allowed plants to bloom earlier, creating more opportunities for pollinators to visit. Our results seem to indicate that the pollinators are still in sync with flowering time, even if the plants bloom earlier. This contrasts studies that suggest early snowmelt does not affect pollinator immergence to the same extent as it affects flower bloom time (Iler et al. 2013, Rafferty et al. 2013). However, one caveat to our study is that we only sampled through the end of July, yet some of the flowering species, such as *Potentilla pulcherrima* and *Erigeron speciosus* were still in bloom. Pollinator observations would need to be carried out through the end of the flowering season for all of the flowering species in the plots to more realistically evaluate the effect of the snow treatment on pollinator visitation rate.

When looking at visitation rates at the plant species level, we saw that early snowmelt and frost affected plant species differently. Although the frost treatment did not have an effect on pollinator visitation rate at the community level, it did have an effect on species level. The earliest blooming flower species, *Claytonia lanceolata,* was affected most strongly by the frost treatment, followed by *Taraxacum officinale,* another early blooming species. Earlier blooming species are exposed to more frost events compared with those blooming later in the summer, so these results are consistent with the expectation that the frost treatment would affect early blooming species most strongly. When considering the snow removal treatment, we found that even though plants are blooming earlier, they are still in sync with pollinators. Since there are actually more visitors to early snowmelt plots, the earlier blooming plants must have an advantage over plants that bloom later. This was the case most strongly with the *Potentilla pulcherrima*, which was visited significantly more often in the snow removal plots. These differences on the species level demonstrate that there will be some plant-pollinator interactions that are more resilient to climate driven changes in snowmelt timing and frost events, and some interactions may actually be more successful.

Frost treatment may have an even stronger effect in subsequent years because the amount of snowfall and snowmelt timing can affect the severity of frost events. Although temps dropped below freezing, there was heavy rain and snow in May. Snowfall for May 2015 was higher than the previous ten years (appendix 3), and late snowmelt can protect plants from frost damage (Inouye 2008). Since the natural snowmelt plots this summer had more snow than usual, plants may have been protected from many of the frost events.

Also evidenced by the plant species level results, there are differences in community and species level plant-pollinator responses to early snowmelt and frost damage. Since the frost treatment did not affect pollinator visitation rate overall but it did affect individual species, our findings are in support of Iler et. al (2013) which found that community-level plant-pollinator interactions are likely more resilient to changes in phenology. This information, especially if the study is continued in further years, helps predict which plant-pollinator interactions will be affected by climate change and early snowmelt most strongly as well as predict shifts in community composition that are likely to occur.

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**Appendix 1**

Generalized linear mixed model- effect of pollinator family

| | Estimate | Std. Error | z value | Pr(>\|z\|) |
|---|---|---|---|---|
| (Intercept) | -2.35e+01 | 4.24e+04 | 0 | 1 |
| snowR | -2.20e+00 | 7.92e+04 | 0 | 1 |
| frostNF | -6.64e-01 | 6.39e+04 | 0 | 1 |
| FamilyAndrenidae | 2.50e+01 | 4.24e+04 | 0 | 1 |
| Familyapidae | 2.46e+01 | 4.24e+04 | 0 | 1 |
| FamilyHalictidae | 2.60e+01 | 4.24e+04 | 0 | 1 |
| FamilyMegachilidae | 2.34e+01 | 4.24e+04 | 0 | 1 |
| Familyother_flies | 2.71e+01 | 4.24e+04 | 0 | 1 |
| FamilySyrphidae | 2.57e+01 | 4.24e+04 | 0 | 1 |
| snowR:frostNF | 4.26e+00 | 1.01e+05 | 0 | 1 |
| snowR:FamilyAndrenidae | 2.13e+00 | 7.92e+04 | 0 | 1 |
| snowR:Familyapidae | 1.96e+00 | 7.92e+04 | 0 | 1 |
| snowR:FamilyHalictidae | 2.39e+00 | 7.92e+04 | 0 | 1 |
| snowR:FamilyMegachilidae | 2.49e+00 | 7.92e+04 | 0 | 1 |
| snowR:Familyother_flies | 2.59e+00 | 7.92e+04 | 0 | 1 |
| snowR:FamilySyrphidae | 2.33e+00 | 7.92e+04 | 0 | 1 |
| frostNF:FamilyAndrenidae | 5.13e-01 | 6.39e+04 | 0 | 1 |
| frostNF:Familyapidae | 6.99e-01 | 6.39e+04 | 0 | 1 |
| frostNF:FamilyHalictidae | 4.64e-01 | 6.39e+04 | 0 | 1 |
| frostNF:FamilyMegachilidae | 1.17e+00 | 6.39e+04 | 0 | 1 |
| frostNF:Familyother_flies | 4.85e-01 | 6.39e+04 | 0 | 1 |
| frostNF:FamilySyrphidae | 7.28e-01 | 6.39e+04 | 0 | 1 |
| snowR:frostNF:FamilyAndrenidae | -4.58e+00 | 1.01e+05 | 0 | 1 |
| snowR:frostNF:Familyapidae | -4.39e+00 | 1.01e+05 | 0 | 1 |
| snowR:frostNF:FamilyHalictidae | -3.97e+00 | 1.01e+05 | 0 | 1 |
| snowR:frostNF:FamilyMegachilidae | -4.55e+00 | 1.01e+05 | 0 | 1 |
| snowR:frostNF:Familyother_flies | -4.43e+00 | 1.01e+05 | 0 | 1 |
| snowR:frostNF:FamilySyrphidae | -4.48e+00 | 1.01e+05 | 0 | 1 |

**Appendix 2**

Generalized linear mixed model- effect of flower species

| | Estimate | Std. Error | z value | Pr(>\|z\|) |
|---|---|---|---|---|
| (Intercept) | 1.1763 | 0.2299 | 5.12 | 3.1e-07 |
| snowR | -0.3547 | 0.3436 | -1.03 | 0.3019 |
| frostNF | 0.4802 | 0.3058 | 1.57 | 0.1163 |
| Scientific_plantClaytonia_lanceolata | -0.4966 | 0.3480 | -1.43 | 0.1536 |
| Scientific_plantDelphinium_nuttallianum | -0.6048 | 0.3559 | -1.70 | 0.0893 |
| Scientific_plantMertensia_fusiformis | -1.4051 | 0.4432 | -3.17 | 0.0015 |
| Scientific_plantPotentilla_hippiana | 2.7286 | 0.2714 | 10.06 | < 2e-16 |
| Scientific_plantTaraxacum_officinale | 0.6150 | 0.2957 | 2.08 | 0.0376 |
| snowR:frostNF | 0.0977 | 0.4534 | 0.22 | 0.8293 |
| snowR:Scientific_plantClaytonia_lanceolata | -0.6886 | 0.5901 | -1.17 | 0.2432 |
| snowR:Scientific_plantDelphinium_nuttallianum | -0.9163 | 0.6411 | -1.43 | 0.1529 |
| snowR:Scientific_plantMertensia_fusiformis | -0.1143 | 0.6932 | -0.16 | 0.8690 |
| snowR:Scientific_plantPotentilla_hippiana | 0.7930 | 0.3979 | 1.99 | 0.0463 |
| snowR:Scientific_plantTaraxacum_officinale | -0.1923 | 0.4476 | -0.43 | 0.6674 |
| frostNF:Scientific_plantClaytonia_lanceolata | -1.1708 | 0.5298 | -2.21 | 0.0271 |
| frostNF:Scientific_plantDelphinium_nuttallianum | -0.4203 | 0.4889 | -0.86 | 0.3899 |
| frostNF:Scientific_plantMertensia_fusiformis | -0.1557 | 0.5891 | -0.26 | 0.7916 |
| frostNF:Scientific_plantPotentilla_hippiana | -0.5976 | 0.3674 | -1.63 | 0.1038 |
| frostNF:Scientific_plantTaraxacum_officinale | -0.9013 | 0.4151 | -2.17 | 0.0299 |
| snowR:frostNF:Scientific_plantClaytonia_lanceolata | 0.4325 | 0.8600 | 0.50 | 0.6151 |
| snowR:frostNF:Scientific_plantDelphinium_nuttallianum | 0.1765 | 0.8552 | 0.21 | 0.8365 |
| snowR:frostNF:Scientific_plantMertensia_fusiformis | -0.9385 | 1.0149 | -0.92 | 0.3551 |
| snowR:frostNF:Scientific_plantPotentilla_hippiana | -0.2945 | 0.5361 | -0.55 | 0.5827 |
| snowR:frostNF:Scientific_plantTaraxacum_officinale | 0.4706 | 0.6124 | 0.77 | 0.4421 |

**Appendix 3**
May snowfall in Gothic over the past ten years.