

# Changes in Phenology of Flowering, Correlation with Climate Variability, and Response of Honeybees

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## Abstract

*Many studies have found that the timing of flowering has shifted temporally in response to climate change, but few have ascertained the possibility of asynchrony developing between flowering and pollinator appearance. Collapses in pollination could have serious consequences for interdependent plant-pollinator networks. Five years of plant-pollinator data collected in twelve montane meadows at the HJ Andrews Experimental Forest in Oregon provided an opportunity to examine how climate variability has affected the flowering of plants and how pollinators have responded. For nearly all plant species, the timing of flowering shifted significantly earlier from 2011 to 2015. Interestingly, the timing of first flowering, peak flowering, and last flowering did not shift uniformly with each other or consistently from year to year. The timing of flowering was highly correlated with both timing of snowmelt and cumulative degree days at June 1, probably because the growing season typically cannot commence until the snowpack melts. The earlier the snow melted, the earlier the flowering season commenced. Timing of flowering was less correlated with average Antecedent Precipitation Index from May 1 to June 1 (a proxy for soil moisture), which did not change consistently from year to year. Analysis of the timing of peak number of interactions between *Apis mellifera* (honeybee) and *Eriophyllum lanatum* from 2011 to 2015 indicated that its visitations to the flowers shifted temporally in parallel with shifts in flower timing. However, *Apis mellifera* is a generalist pollinator that is perhaps more adaptable to perturbations than specialists. Analysis of specialist species would give a better indication of increasing asynchrony in plant-pollinator networks over time. These findings provide a preliminary analysis of how climate variability has affected plant-pollinator networks in montane meadows at the HJ Andrews Forest and confirm the importance of maintaining species biodiversity in meadows as a way to buffer networks against the negative effects of climate change.*

## 1 Introduction

Anthropogenic environmental changes are devastating pollination from multiple fronts: climate warming, intensive agriculture, landscape alteration, introduction of non-native species, and increasing transmission of pathogens (Gonzalez, 2013). Because 75% of the leading global food crops rely on insect pollinators for production (Rader *et al*, 2013), disturbances in pollination dynamics will place heavy stress on food production, on top of the pressures from a growing world population and

the negative responses of certain crops to warming. In plant-pollinator networks, plant species rely on pollination for reproduction while pollinator species collect pollen and nectar from the flowers as a food source (Gonzalez, 2013). Because pollination is a mutualistic interaction between the plants and the pollinators, perturbations in one population can distress the other.

Five years of plant-pollinator data collected in montane meadows of the HJ Andrews Experimental Forest in Oregon provide an opportunity to examine how climate variability has affected flowering

plant species and how pollinators have responded.

Plant reliance on environmental cues for initiation of flowering (Hegland, 2009) raises the question of how timing of flower seasons will shift in response to climate variability in the meadows. Phenology, the timing of seasonal activities such as the timing of flowering, is affected by temperature and precipitation (Walther, 2002). Many studies have found a correlation between early flowering and warming temperatures (Hegland, 2009), but fewer have examined the role of timing of spring snowmelt or soil moisture. In fact, in high altitude meadows with significant snowfall, flower timing is primarily influenced by how early the snowpack melts in spring. Typically, the growing season cannot commence until the snow melts (Inouye, 2002). If flowering begins too early in the season, early reproduction in plants may result in failure to find mates, to provide time-sensitive food resources to offspring, or to be pollinated (Inouye, 2008).

Interdependence in plant-pollinator networks necessitates the ability of pollinator species to adapt to temporal shifts in flowering. There are gaps in the literature about the effect of shifting phenology on the synchrony between plant flowering and pollinator appearance. Some studies predict that climate warming will produce asynchrony, while others predict that although individual species will suffer, overall plant-pollinator networks will be resilient and dynamic enough to withstand disturbances. The negative impacts of earlier flowering could snowball unexpectedly. For example, climate change may affect early-flowering species the most, in which case their resulting asynchrony with pollinators could fail to sustain the pollinator populations for the later-flowering species (Hegland, 2009). For pollinators, asynchrony would limit food resources necessary for survival and reproduction. For plants, asynchrony would result in decreases in the quantity and quality of pollination necessary for reproductive success. Figure 1 from Hegland *et al* summarizes the ways in which climate warming might disturb plants, pollinators, and their interactions with each other.

By examining the plant-pollinator data for the HJ Andrews meadows, we can gain a better understanding of how the timing of flowering shifted over time, how the timing related to temperature, snowmelt, and precipitation, and whether pollinators adapted in response.

## 2 Methods

### 2.1 Calculating Flower Abundances

I used data from the Eco-Informatics Summer Institute at the HJ Andrews Experimental Forest for 2011 to 2015. Data were collected in 3 complexes, each of which consisted of 4 meadows. Each meadow had ten 3x3m<sup>2</sup> plots. Typically, teams collected data from each complex for five weekly watches throughout the summer. One dataset consisted of flower surveys, which are records of each plant species and its abundance in each plot. The other dataset contained observations of the interactions between plant species and pollinator species during a 15-minute watch of each plot.

In some cases, when a field team did not finish a watch of a complex in one day, they collected the rest of the data as soon as possible afterwards. To simplify the analysis of flower abundance for a given watch, I used the date of the first day for the whole watch.

In order to analyze the flower survey data, I created a matrix with the abundances for each meadow-species at each date. To compute the matrix, I developed code in the R programming language to consider each meadow-species and take the average flower abundance across the 10 plots in that meadow for each date in which that plant was surveyed. In a few cases, the flower count for a species in a plot was N/A (because of a data collection error). To handle this missing data, I excluded that plot from the average. In the case that a plant species was not listed in the flower survey for a plot, the abundance for that species was zero. This flower abundance matrix facilitated the calculations for timing of flowering.

### 2.2 Estimating Flower Timing

Because flower timing varied depending on the plant species or meadow, I refer to the unit "meadow-species" as a particular pair of meadow and species. For an understanding of the phenology curves for each meadow-species in each year, I used the data on flower abundance over each summer to estimate three points on the curve: first flowering, peak flowering, and last flowering. Because each meadow only had about five data points for each year, I also calculated uncertainty intervals to represent the range in which that flowering event could have occurred, as described below. Figure 2 summarizes how I estimated each flower timing from the data points.

First flowering is the date at which plants begin

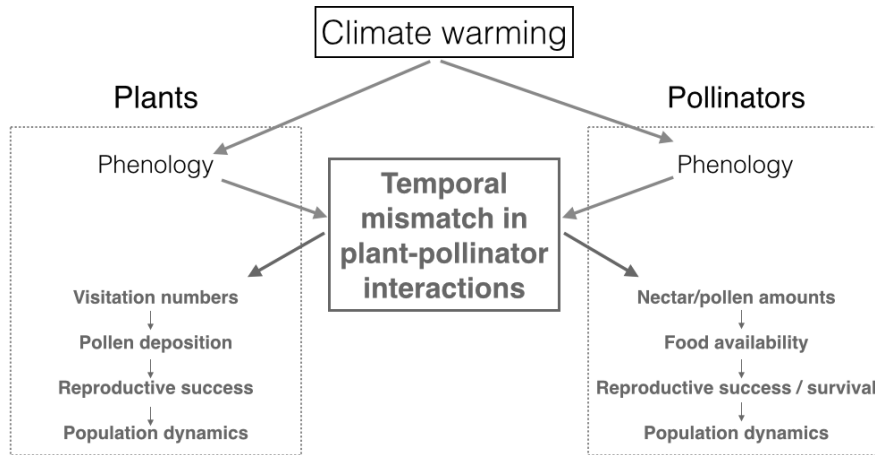


Figure 1: Diagram adapted from Hegland *et al* 2009: "Framework showing how climate warming may affect the phenology and distribution of plants (left panel) and pollinators (right panel) and thereby creating temporal or spatial mismatches in plant-pollinator interactions."

flowering. For each meadow-species, my estimate for first occurrence was the first date with positive abundance, as long as an earlier data point existed with abundance of zero. If there was not a zero-abundance data point recorded at the beginning of the season, then the first flowering was recorded as N/A. The uncertainty was the range from the zero-abundance data point to the calculated date of first occurrence.

Peak flowering is the timing of the maximum flower abundance for a given meadow-species. My estimate was the date of the maximum number of flowers. If there was not a shoulder on either side of that date, the peak flowering was recorded as N/A. This ensured that the maximum abundance was a true peak. The uncertainty interval was the range from the date of the left shoulder to the date of the right shoulder. In my estimation of peak flowering, I ignored the possibility that species could peak twice in one season.

Last flowering is the date with the last occurrence of any flowers for a given meadow-species. My estimate was the date of the last data point with positive abundance, but only if there was a later data point with abundance zero. If there was not an abundance of zero after that last occurrence, the last flowering was recording as N/A. The uncertainty was the interval from the date of last occurrence to the date of the next zero-abundance observation.

The restrictions on estimating first, peak, and last flowering allowed me to only include data points that had accurate intervals for timing of

flowering. For example, if the data point with maximum observed flower abundance is not paired with an earlier data point of lower abundance, then theoretically the uncertainty interval is infinite, which is useless for my analysis.

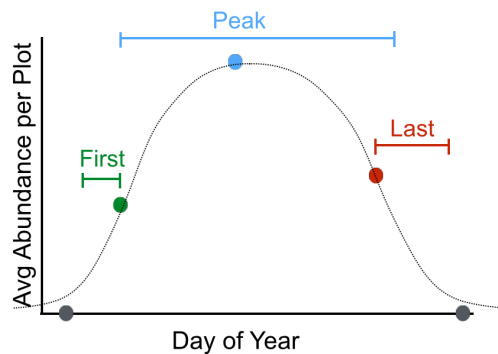


Figure 2

I narrowed the data by the top 30 plant species, calculated based on total abundance across all years and meadows. For each flower timing event, I excluded meadow-species pairs that did not have estimates for both 2011 and 2015 or did not include two of the three middle years, so that the averages for each year were not skewed by differences in flower composition. For first flowering, there were 7 unique meadow-species with estimates (4 unique species: *Eriogonum nudum*, *Erigeron foliosus*, *Hypericum perforatum*, and *Eriogonum compositum*). For peak flowering,

there were 29 meadow-species with estimates (12 species: *Achillea millefolium*, *Eriophyllum lanatum*, *Orthocarpus imbricatus*, *Erigeron foliosus*, *Potentilla gracilis*, *Eriogonum compositum*, *Eriogonum nudum*, *Rumex acetosella*, *Vicia americana*, *Montia parvifolia*, *Lupinus laxiflorus*, and *Eriogonum umbellatum*). For last flowering, there were 52 meadow-species (20 species: *Gilia capitata*, *Castilleja hispida*, *Phlox gracilis*, *Delphinium nuttallianum*, *Ligusticum grayi*, *Rumex acetosella*, *Vicia americana*, *Potentilla gracilis*, *Erysimum asperum*, *Eriophyllum lanatum*, *Lupinus laxiflorus*, *Eriogonum compositum*, *Calochortus subalpinus*, *Collinsia parviflora*, *Montia parvifolia*, *Achillea millefolium*, *Erigeron foliosus*, *Sedum oreganum*, *Penstemon procerus*, and *Mimulus guttatus*).

To develop my figures, I averaged the timings of flowering across all meadows and all species in year. The uncertainty interval of the average was the average of the uncertainties of the data points. One advantage of averaging across all meadow-species, other than to obtain a simplified summary, was that it patched together the good data from each species. For example, one species may have had data on first flowering, while another only had data on peak flowering, and another only last flowering, so combining the data provided an overall picture of how flowering shifted temporally.

In many figures, I used "Days earlier than 2011" as a measurement for how early the timing of first, peak, and last flowering shifted for each year in comparison to 2011. When calculating the uncertainty interval for this value, I combined the uncertainty for 2011 and the year being compared to capture the lower and upper bound. As a result of using the worst-case bounds, the uncertainty interval for that year amplified, but this unit allowed for easier visualization of the amplitude of temporal changes in flowering.

### 2.3 Developing Climate Indicators

To analyze the effect of climate variability on flowering phenology over the five-year period, I calculated three climate variables for each year: timing of snowmelt, average Antecedent Precipitation Index, and cumulative degree days.

To obtain data about the snowpack for each year, I downloaded the SNOTEL dataset for McKenzie station from the Natural Resources Conservation Service (NRCS, 2015). The McKenzie station is located at 1433 m elevation and 20 km from the meadows in the Andrews Forest. The study meadows range from 1331 to 1518 m in elevation. I calculated the last day of snowpack to

be the last date in spring/summer at which the snow depth (in inches) was greater than 0. The SNOTEL site provided an estimate for each year, but the date of snow disappearance at the montane meadows may have disagreed with the date at the SNOTEL site because of differences in elevation, aspect, topography, or even shading by vegetation.

I chose to use Antecedent Precipitation Index (API) as a proxy for soil moisture. Based on prior work in literature, I calculated the API for a given day  $d$  to be:

$$API_d = API_{d-1} * K + P_d$$

where the coefficient  $K$  discounts the impact of precipitation on soil moisture over time. I used a  $K$  value of 0.9, informed by the results of recession analysis on coastal Oregon storm hydrographs (Fedora and Beschta, 1989). In this way, the API gave an estimate for the amount of moisture remaining in the soil at a given time. Because the API calculation for a particular day was heavily swayed by rainfall on or near that day, I decided to take the average API from May 1 to June 1 as a measure for the soil moisture leading up to flowering. Using an averaged API over a fixed interval instead of the API on each year's date of flowering also allowed for more accurate comparison across years, because flowering dates were different for each year and rainfall patterns varied throughout the summer season. To calculate the APIs, I obtained precipitation data for the study meadows from a database at the HJ Andrews Experimental Forest (Daly and McKee, 2015). I used data from three met stations closest to the area (CENmet, UPLmet, and PRIMet) and averaged the three values for precipitation. These three meteorological stations are located at 1000 (CENmet), 1300 (UPLmet) and 430 (PRImet) m elevation. The stations are within 1 km of at least one of the meadow complexes in the study. No meadow-specific data on precipitation were available.

Next, I calculated cumulative degree days (CDD) for each year. Cumulative degree days are a measure of heat accumulation at a given time, and are frequently used to estimate timing of phenology in crops. First I calculated the degree days for each day  $d$  to be:

$$DD_d = \frac{(T_{max} - T_{min})}{2} - T_{base}$$

where I chose  $T_{base} = 5^\circ$ . Then, my CDD measurement for each year was the sum of the non-negative degree days from March 1 to June 1. The calculation for CDD was informed by previous years' calculations for this dataset (Helderop, 2015) and by similar work in the literature (McMaster, 1997).

Using the CDD at June 1 for each year allowed for standardized comparison across years. I obtained the temperature data from the same database at the HJ Andrews Experimental Forest (Daly and McKee, 2015). I used data from the PRImet station because it was the closest one with 2015 data, although PRImet is location at 430 m elevation and the study meadows range from 1331 to 1518 m elevation. However, temperatures at the study meadows do change predictably with elevation in the spring and summer months when the air is well-mixed, so PRImet is a good reference point. I also used the 2011-2014 CENmet data (closer in elevation to the study meadows) as a comparison.

## 2.4 Measuring Pollinator Responses

After observing how plant species responded to changes in climate, I also tested whether pollinators adapted to shifting timings of flowering. I chose to look at the activity of *Apis mellifera* (honeybee) because it is the most common pollinator and it was the only insect we already had identified in the 2015 data. I examined its interactions with the plant *Eriophyllum lanatum*, which was one of the most common interactions in the meadows. I measured how the timing of peak number of visitations to *Eriophyllum lanatum* matched up temporally with the timing of peak flowering for the plant. Comparison across years offered a portrayal of how well *Apis mellifera* adjusted to the climate variability, whether directly or indirectly through changes in flowering phenology.

# 3 Results

## 3.1 Shifts in Timing of Flowering

For all the meadow-species with sufficient data on flower abundance, the timing of flowering varied over the years, with a significant difference between the 2011 and 2015 seasons (Figure 3).

Individual plant species varied in the uncertainty of the data points and in the types of flower timings (first, peak, and last) able to be estimated (Figure 4). When averaged across all meadows, the timings of flowering for each species showed a tendency to shift earlier over time.

Similarly, when averaged across all species, the timing of flowering shifted earlier in each meadow, though to differing degrees for first, peak, and last flowering (Figure 5).

The similarities between temporal shifts in flowering for different meadows and species justified the

averaging across all meadow-species. The averaged results give further evidence that first, peak, and last flowering shifted earlier over time (Figure 6).

Interestingly, first, peak, and last flowering did not shift in synchrony, nor did they shift uniformly from one year to the next.

## 3.2 Correlation to Climate Variability

Timing of snowmelt seemed to be a significant factor in flower timing. The last day of snowpack shifted earlier over time, and the earlier the snowpack disappeared, the earlier flowering commenced (Figure 7).

By contrast, the average Antecedent Precipitation Index from May 1 to June 1 (a proxy for soil moisture) did not change as uniformly over time (Figure 8). However, some correlation did exist between dryness of soil and earliness of flowering.

There is a strong relationship between cumulative degree days and flower timing, suggesting that a combination of cumulative degree days and snowmelt affect flowering phenology (Figure 9).

After evaluating the correlations for these climate variables individually, I performed a multiple regression to see if an interaction of the three variables is a better indicator for timing of flowering. I used data for all meadow-species combinations in a year. With terms for day of snowmelt, average API, cumulative degree days, and the interaction of each, the model predicted first, peak, and last timing to be:

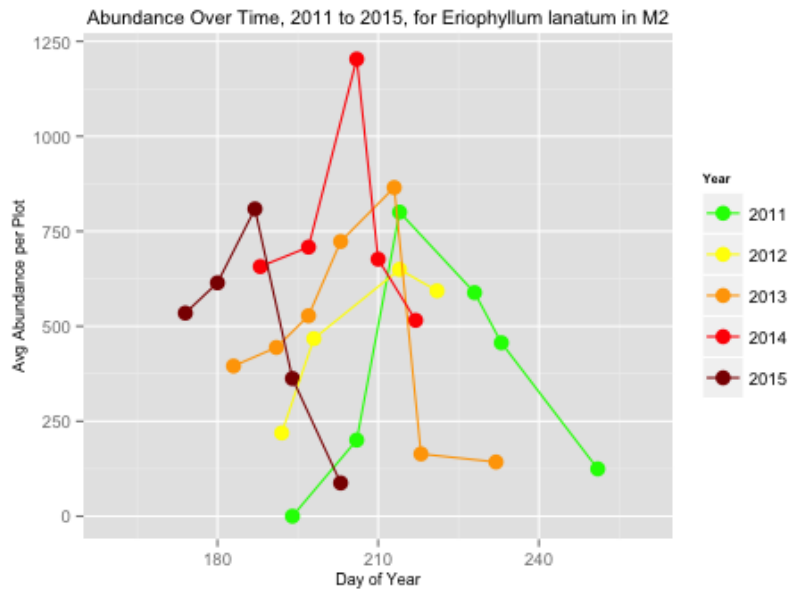
$$16 - 0.3 * snow - 1.3 * api + 0.03 * cdd + 0.008 * snow * api$$

The  $R^2$  value was 0.78 and the p-value was  $< 0.0001$ . For first, peak, and last flowering separately, the  $R^2$  values were 0.88, 0.73, and 0.78, respectively. When I removed API from the regression, the  $R^2$  value was the same, implying that flower timing was less dependent on soil moisture.

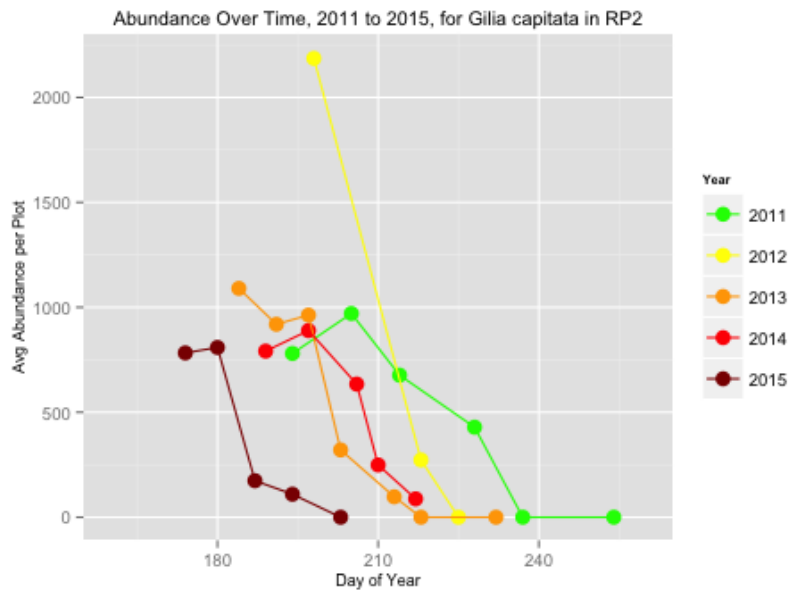
## 3.3 Response of Honeybees to Shifts in Flower Timing

*Apis mellifera* interacted with *Eriophyllum lanatum* whenever the flowers appeared in abundance, regardless of the time during the summer (Figure 10). Both the timing of peak flower abundance and the timing of peak number of interactions shifted earlier over time. This suggests that at least the honeybees shifted in response to changes in flowering phenology or to changes in climate.

Figure 3: Trends in flower abundance over the summer from 2011 to 2015 for two common meadow-species pairs: a) *Eriophyllum lanatum* in Frissell M2 and b) *Gilia capitata* in Frissell RP2. a) provides an example of clear peaks in abundance for each year but less clear timing of first and last flowering. b) provides an example with unclear timing of peak abundances but more clear timing of last flowering.



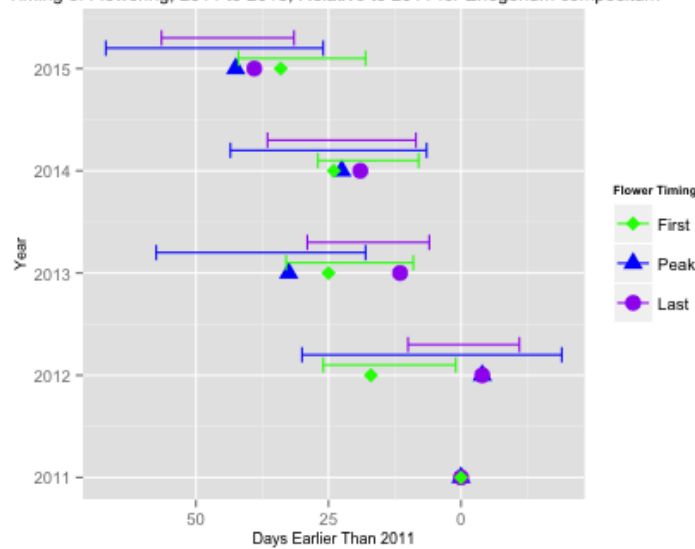
(a)



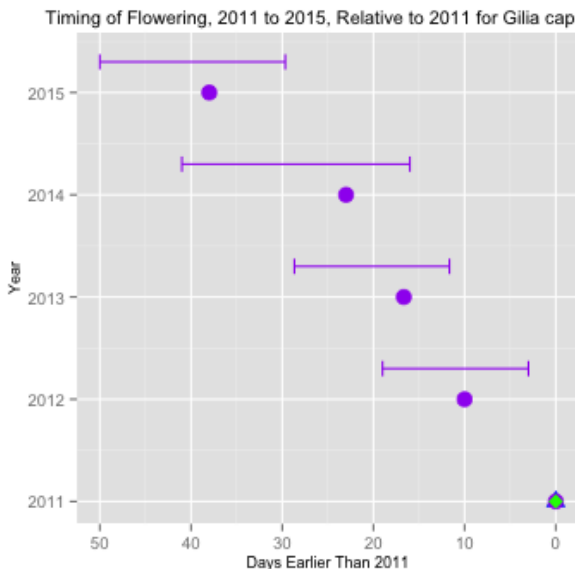
(b)

Figure 4: Trends in timing of first, peak, and last flowering from 2011 to 2015 for three different example plant species, averaged across meadows. The horizontal range bars represent the uncertainty in the measurements of flower timing relative to 2011. a) *Eriogonum compositum*, an example of a plant species with a strong signal for shifts in timing of flowering. The timing of flowering in 2015 for *Eriogonum compositum* was on average 34.0, 42.5, and 39.0 days earlier than 2011 for first, peak, and last flowering respectively. The uncertainty intervals for these estimates were 18 to 42, 26 to 67, and 31.5 to 56.5. A linear regression produced an  $R^2$  value of 0.77 and a p-value  $\leq 0.0001$  (not taking into account the uncertainty bars). b) *Gilia capitata*, an example of a species with a strong signal but poor data for first and peak flowering. c) *Eriogonum umbellatum*, an example of a species with both high uncertainty and poor data. The timing events (first, peak, and last) did not shift in synchrony. For example, peak flowering in 2015 shifted earlier by a larger number of days than did first flowering, whereas the opposite was true for 2012 (a).

Timing of Flowering, 2011 to 2015, Relative to 2011 for *Eriogonum compositum*

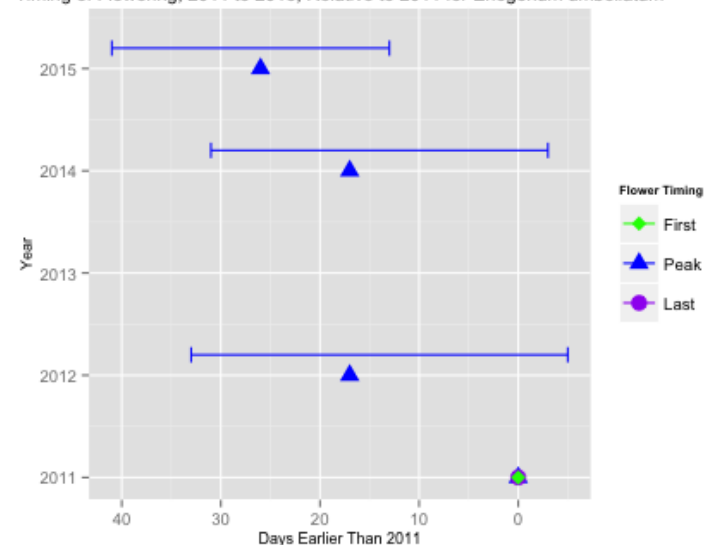


(a)



(b)

Timing of Flowering, 2011 to 2015, Relative to 2011 for *Eriogonum umbellatum*



(c)

Figure 5: Trends in timing of first, peak, and last flowering from 2011 to 2015 for two different example meadows, averaged across plant species. The horizontal range bars represent the uncertainty in the measurements of flower timing relative to 2011. a) Lookout Outcrop (LO) meadow, an example with data for all flowering events and a decent signal but with a fair amount of uncertainty. The timing of flowering in 2015 for this meadow was on average 36.3, 29.0, and 39.5 days earlier than 2011 for first, peak, and last flowering respectively. The uncertainty intervals for these estimates were 18 to 44.3, 14 to 46.3, and 32 to 52.2. ( $R^2 = 0.79$ ,  $p < 0.0001$ ). b) Frissell M2 (M2) meadow, an example with a strong signal for last flowering, a poorer signal for peak, and no data for first. The downward trends in these graphs suggest that flowering has shifted earlier over the years. This trend appears in all the meadows that had sufficient data for timing of flowering, but with varying strengths of signal.

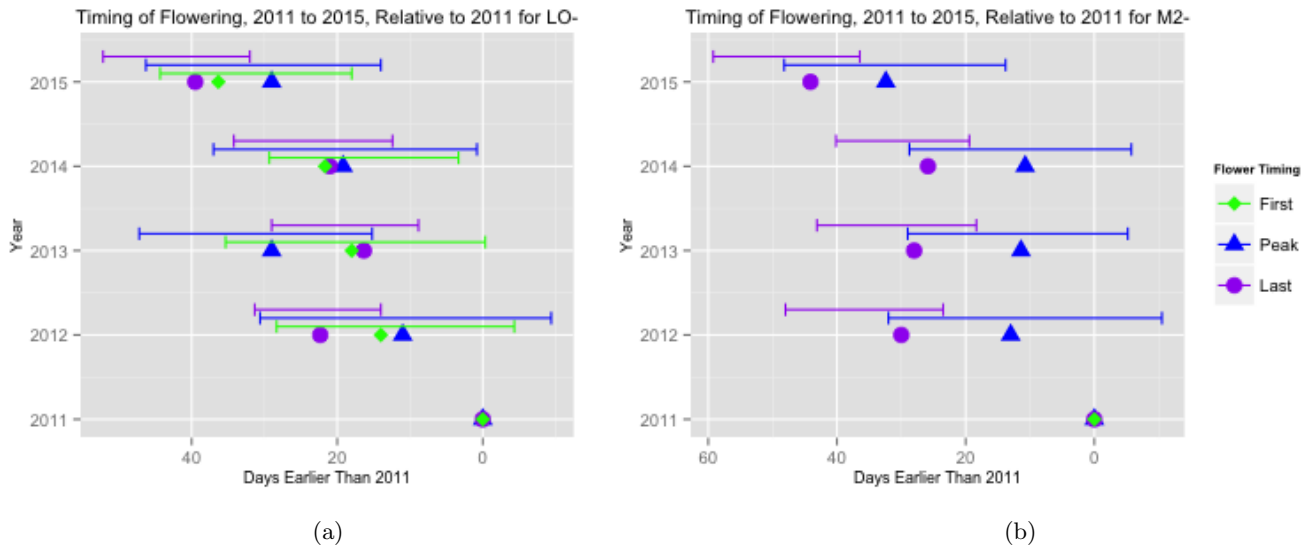
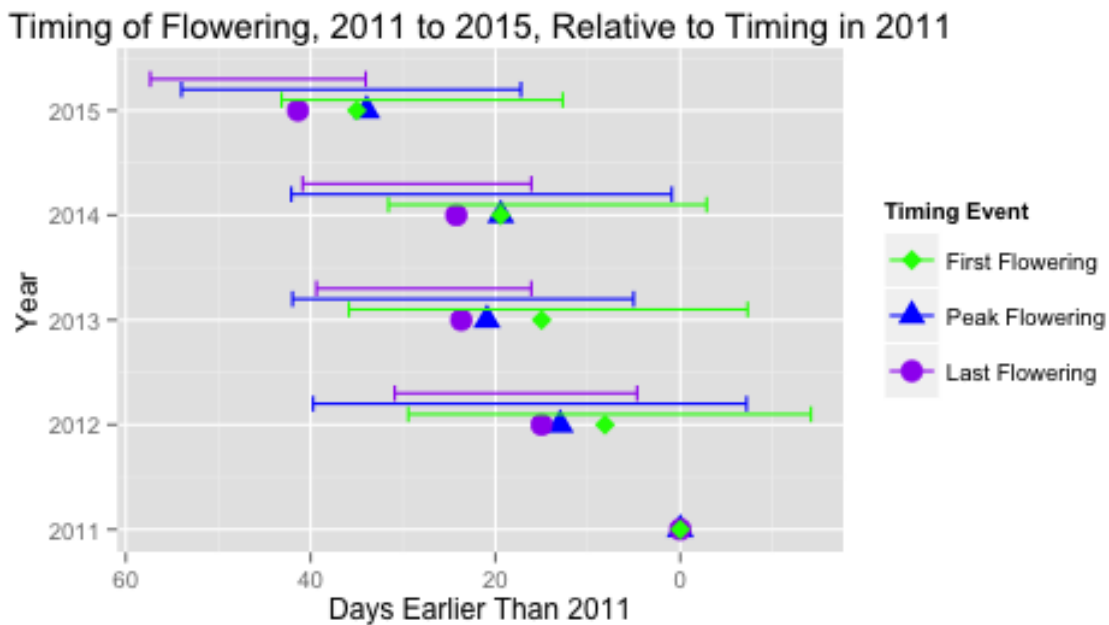




Figure 6: a) Trends in timing of first, peak, and last flowering from 2011 to 2015, averaged across all meadow-species combinations. The horizontal range bars represent the uncertainty in the measurements of flower timing relative to 2011. On average, flowering in 2015 shifted earlier by 35.0, 33.9, and 41.4 days compared to 2011 for first, peak, and last flowering, respectively. The uncertainty ranges for these three estimates were 12.7 to 43.1, 17.2 to 54.0, and 34.0 to 57.3. Without taking into account the uncertainty intervals, the  $R^2$  value was 0.89 and the p-value was  $< 0.0001$ . The downward trend indicates that flowering shifted earlier over the years, although first, peak, and last flowering did not shift in synchrony with each other or uniformly from year to year. For example, the graph indicates that the timing of last flowering shifted by more days than that of first flowering does.

b) Trends in timing of first, peak, and last flowering from 2011 to 2015 for all meadow-species combinations (that have data points). The uncertainty bars are not shown in this graph. The  $R^2$  value was 0.78 and the p-value was  $< 0.0001$ , suggesting a consistent trend across all meadows and species in which flowering shifted earlier over time.



(a)

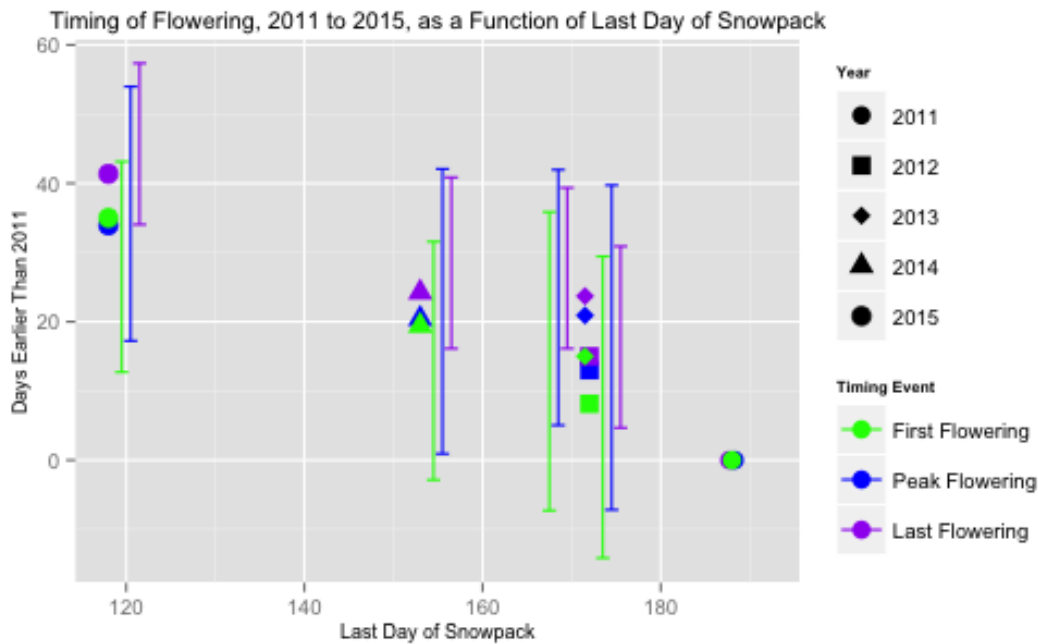


(b)

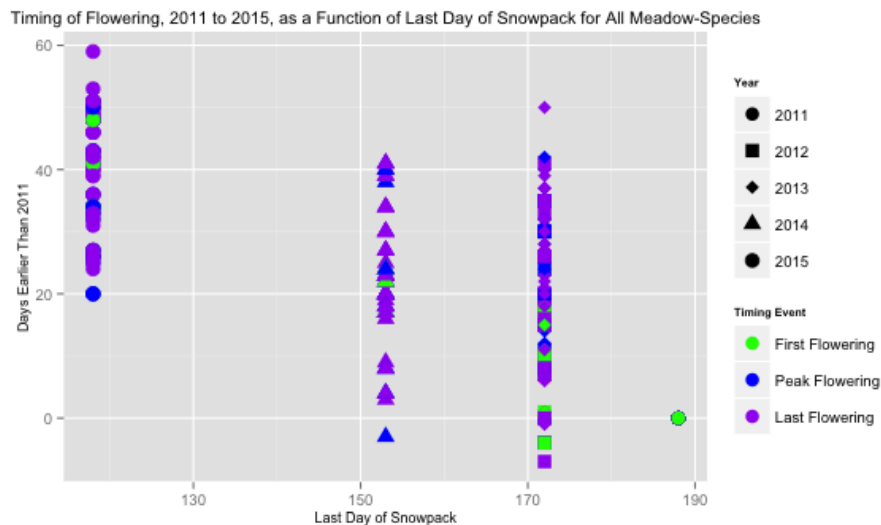
Figure 7:

a) Shifts in timing of flowering in response to timing of snowmelt, from 2011 to 2015. The horizontal range bars represent the uncertainty in the measurements of flower timing relative to 2011. A strong effect is seen in 2015: on average, the timing of peak flowering shifted 33.9 days earlier than 2011 (with an uncertainty range from 17.2 to 54.0 days earlier) while the last day of snowmelt for 2015 was 70 days earlier than 2011. The trend indicates that as snowpack melted earlier over time, the timing of flowering also shifted earlier ( $R^2 = 0.85$ ,  $p < 0.0001$ ). Note: 2012 and 2013 had the same last day of snowpack, but the 2013 points and uncertainty bars show slightly to the left for visual clarity.

b) Timing of first, peak, and last flowering from 2011 to 2015 as a function of last day of snowpack for all meadow-species combinations (that have data points). The uncertainty bars are not shown in this graph. The graph indicates a consistent trend across most meadows and species, in which flowering shifted earlier, although the degree of shift varied across meadows and species ( $R^2 = 0.69$ ,  $p < 0.0001$ ). Although the  $R^2$  value was lower when looking individually at all meadow-species than in a), it is expected to see different degrees and timings of shifts for different species.



(a)

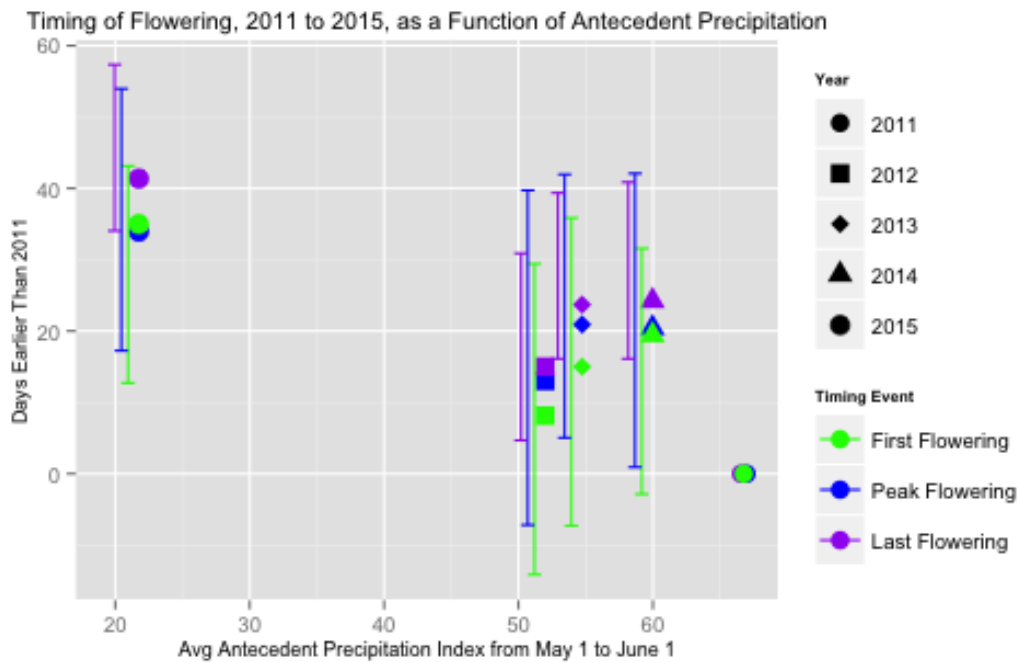


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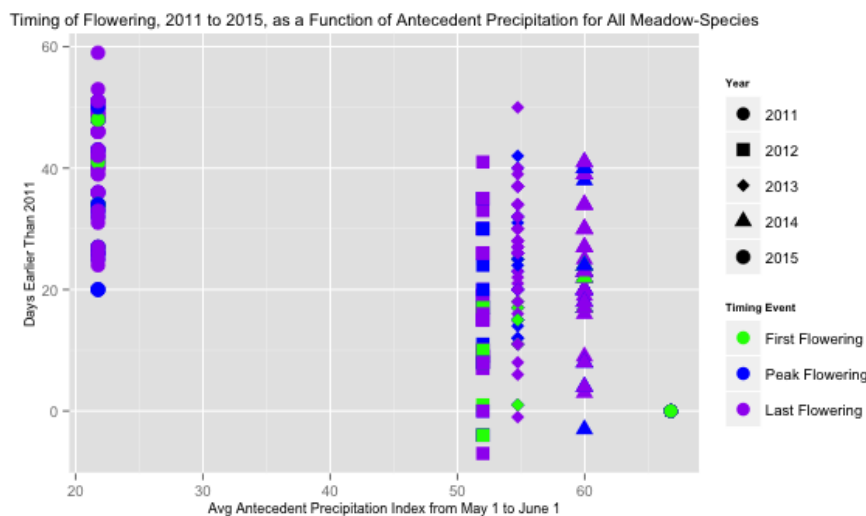
Figure 8:

a) Shifts in timing of flowering in relation to year-to-year variation in the Antecedent Precipitation Index (API) averaged from May 1 to June 1. Antecedent precipitation serves as a proxy for soil moisture. The horizontal range bars represent the uncertainty in the measurements of flower timing relative to 2011. Average API did not decline consistently over time. The graph suggests that generally as the soil got drier over time, the timing of flowering shifted earlier ( $R^2 = 0.70$ ,  $p < 0.0001$ ). However, the timing of flowering in 2014 shifted earlier by more days than that of 2012, even though 2014 experienced a higher API. Looking back at Figure 7, the last day of snowpack for 2014 was significantly earlier than that of 2012, which could explain this result.

b) Timing of first, peak, and last flowering from 2011 to 2015 as a function of average API for all meadow-species combinations (that have data points). The uncertainty bars are not shown in this graph. The graph indicates a consistent trend across most meadows and species, although the degree of shift varies across meadows and species ( $R^2 = 0.6193$ ,  $p < 0.0001$ ). This  $R^2$  was probably smaller than a) because of variations in how particular species respond to climate variability.

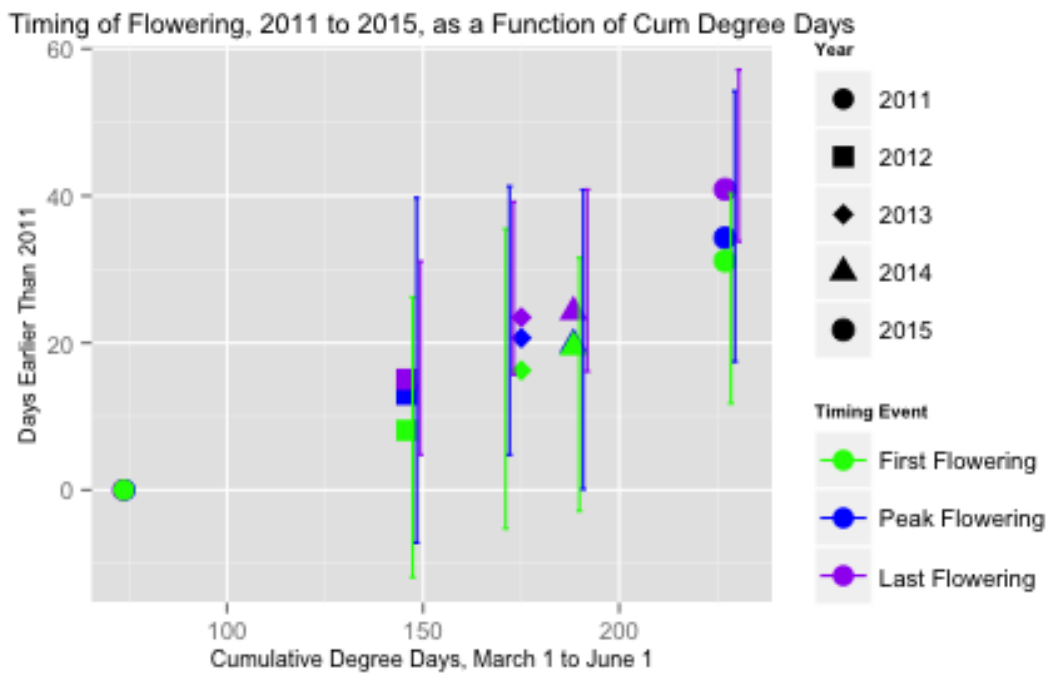


(a)

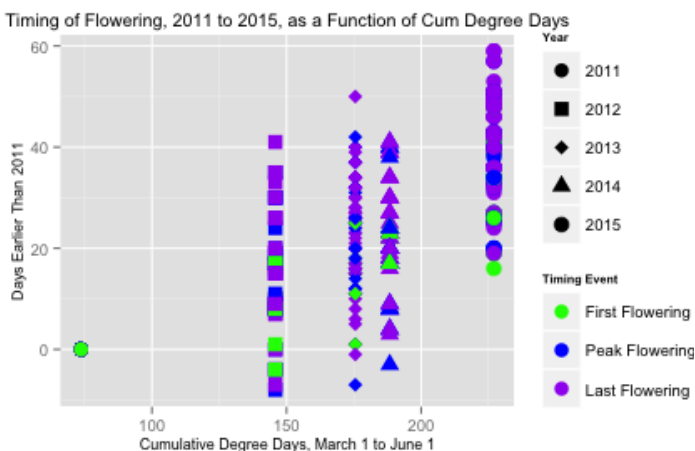


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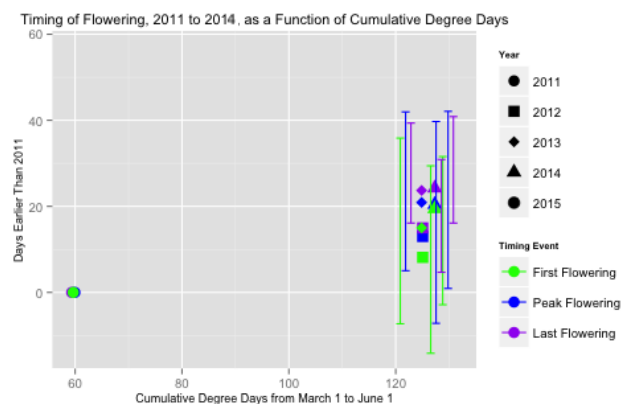
Figure 9: a) Shifts in timing of flowering in relation to cumulative degree days from March 1 to June 1 for 2011 to 2015 (using PRImet station data). The horizontal range bars represent the uncertainty in the measurements of flower timing relative to 2011. The cumulative degree days increased each year. A positive association exists between the timing of flowering and the cumulative degree days ( $R^2 = 0.91$ ,  $p < 0.0001$ ). b) Shifts in timing of flowering in relation to CDD for all meadow-species pairs (without uncertainty bars). The flowering shifted earlier over the years, but to varying degrees for different meadows and species ( $R^2 = 0.76$ ,  $p < 0.0001$ ). c) Shifts in timing of flowering for 2011 to 2014 in relation to CDD, using temperature data from the CENmet station, which is closer in elevation to the study meadows than PRImet (Figure a). There was less variation in the CDD from 2012 to 2014 and the correlation was not as clear, but perhaps the trend would be more visible with 2015 data.



(a)

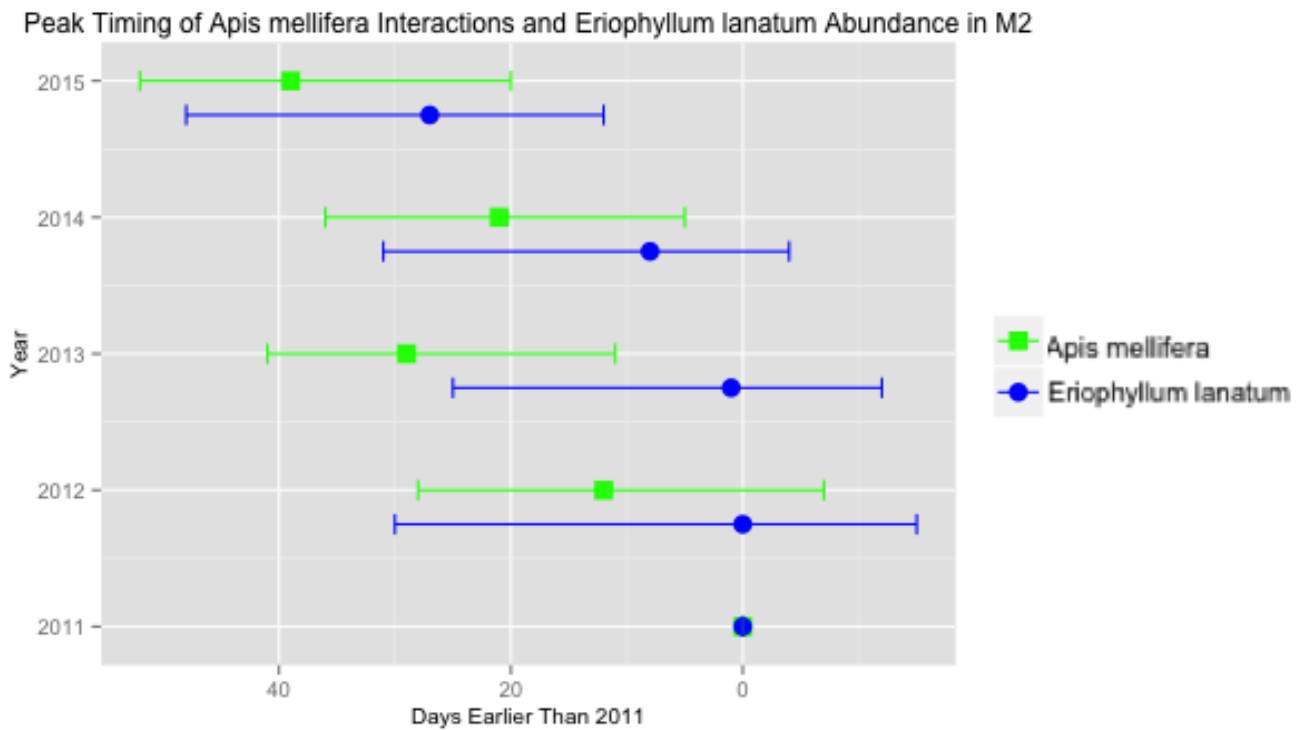


(b)



(c)

Figure 10: Trends in the timing of peak number of pollinator interactions in relation to the timing of peak flowering, for 2011 to 2015 for the common plant-pollinator pair *Apis mellifera* and *Eriophyllum lanatum*. *Apis mellifera* was active during the peak flowering for each year. The timing of peak visitations by *Apis mellifera* shifted by 39 days from 2015 to 2011, with an uncertainty range of 20 to 52 days. The timing of peak flower abundance for *Eriophyllum lanatum* shifted by 27 days from 2011 to 2015, with an uncertainty range of 12 to 48 days. It seems that peak *Apis mellifera* visitations shifted by more days than peak flower abundance, although this could be a product of the uncertainty.



## 4 Discussion

### 4.1 Errors and Effects of Methods

The main limitations on analysis of changes in phenology at the HJ Andrews meadows were inadequacy in the quantity of data. The dataset only covers five years, which is too short of a time frame to make conclusions about long-term trends, particularly in relation to climate change. Furthermore, because the 2015 flowering season started so early, the data collection did not capture as many first (or peak) abundances as it did in 2011. While the data included 140 estimates of peak flowering in 2011, there were only 67 for 2015. The table below summarizes the number of estimates for each year.

Year	First	Peak	Last
2011	92	140	156
2012	71	110	111
2013	71	122	182
2014	55	114	149
2015	31	67	114

In addition, many meadow-plant pairs were excluded from analyses if their data were insufficient to estimate a particular timing of first, peak, or last flowering for multiple years and for both 2011 and 2015. This data trimming not only reduced the number of data points, but also limited the number of species for which the results applied to. For example, there were few data collected at the start of flowering, so my analysis did not necessarily address changes in phenology for early-flowering species. The few number of estimates for first flowering also means that the trends were not as tangible as they were peak and last flowering. The table below gives the number of meadow-species pairs (i.e. number of data points) used in the final analysis after data-trimming for each of first, peak, and last flowering for each year. The sample size for last flowering was the largest because the tail end of the flower season was almost always captured in data collection.

Year	First	Peak	Last
2011	7	29	52
2012	7	22	37
2013	7	23	50
2014	7	24	43
2015	7	29	52

To improve the quantity and quality of estimates for first, peak, and last flowering, flower surveys could be conducted more frequently and include the earliest times of flowering.

For the data points that I did use for timing of first, peak, or last flowering, the calculated intervals quantified the uncertainties in the estimates.

However, the intervals were at least as long as the time between data collection for that meadow (typically about a week) because of how I estimated the timings, so uncertainties were an inherent component of the data points. When I averaged across meadows and species to obtain the number of days that flowering shifted in comparison to 2011, the uncertainty intervals amplified. The new intervals were the lower and upper bounds calculated from the combination of the intervals for 2011 and the year being compared.

Limitations on evaluating correlations between flower timing and climate variability stemmed from the poor spatial resolution of data on degree days, precipitation, and date of springtime snowmelt. Frequently, I could only use data from one weather station for a climate variable and so had one shared value for all meadows for each year, even though meadows varied by location, elevation, and aspect.

### 4.2 Changes in Phenology Over Time

The results confirm my hypothesis that the timing of first, peak, and last flowering shifted earlier over the years. However, the results also introduce a new question about how first, peak, and last flowering shift in relation to each other. The figures indicate that on average, last flowering shifted by the most days, whereas first flowering did not shift as rapidly, at least initially. Many studies only evaluate the timing of first flowering as a measure for changes in phenology, but this ignores other important properties of phenology, such as how soon flowering terminates in the summer. A study by CaraDonna *et al* using 39 years of phenology data from the Colorado Rocky Mountains found that first, peak, and last flowering rarely shifted uniformly with each other (CaraDonna, 2014). Figure 11 is a diagram from the study that summarizes the variability in how a phenology curve for an individual species can shift over time.

I hypothesized that changes in the timing of first, peak, and last flowering relate to changes in snowmelt timing, soil moisture, and temperature. The results indicate that flowering phenology did depend on the timing of snow disappearance, on cumulative degree days, and on soil moisture. However, snowmelt and degree days seemed to be more significant explanatory variables than soil moisture, most likely because snowmelt is dependent on temperature and the majority of plants begin to grow as soon as the snowpack disappears from the ground, at least for high-altitude meadows (Inouye, 2008). Although many studies focus solely on the relationship between rising tempera-

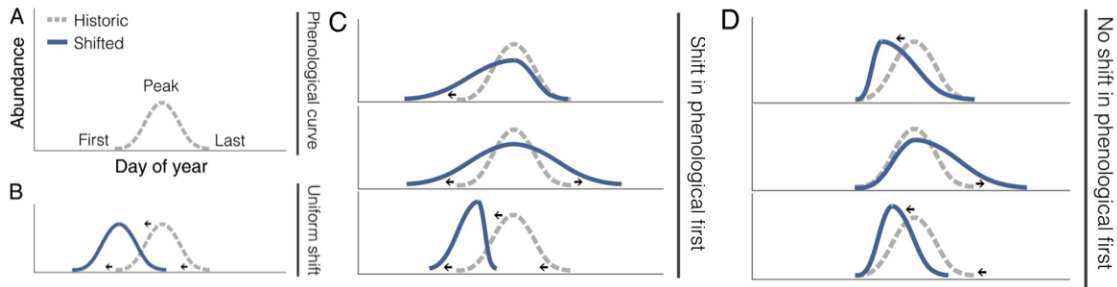


Figure 11: Diagram from CaraDonna *et al* 2012: "Conceptual representation of shifts in multiple phenological measures for individual species through time. (A) Multiple measures of flowering phenology available for 60 species from a 39-y study of a plant community in the Colorado Rocky Mountains, USA." (B-D) provide examples of the variability in how a phenology curve can shift over time.

tures and shifts in phenology (Hegland, 2009), perhaps snowmelt could explain part of this correlation, since warmer springs mean earlier snowmelt. The strong fit produced by the multiple regression analysis indicates that some combination of the climate factors significantly affected the flower timing.

Because flowering phenology is shifting earlier over time, the pollinator species that rely on the flowers will need to adapt in response. The results show that *Apis mellifera* shifted the timing of its pollination activity in parallel with the flower species, so no asynchrony was apparent. This agrees with a study in Spain from 1952 to 2014 that found that *Apis mellifera* populations have reacted quickly to warmer springs and shifting flower seasons by appearing earlier (Gordo and Sanz, 2006). However, *Apis mellifera* is a generalist species that can pollinate many different species of plants and so can more easily adjust its behavior than a specialist. For example, if late-flowering plants start flowering at times when early-flowering plants used to, generalist pollinators could switch to pollinating the late-flowering plants. By contrast, asynchrony might affect specialist species more negatively. Specialists are expected to experience the worst damage from climate change (Memmott, 2007; Gonzalez, 2013), so a more conclusive analysis of pollinator response would need to address the effects on specialist and non-native species. Furthermore, the behavior and health of *Apis mellifera* could be responding to changes in climate, or to changes in flowering phenology, or to both, so predictions about responses in *Apis mellifera* populations are difficult.

## 5 Conclusion

This analysis of the five years of plant-pollinator data for the HJ Andrews meadows serves as a preliminary report about changes in flowering and pollination. The data showed an initial trend in flowering shifting earlier over time, primarily in correlation with timing of snowmelt and cumulative degree days. Hopefully, more concrete conclusions can be made once additional years of data have been collected. In addition, future work could produce hierarchical linear regression models for flower timing in order to see how the climate variability affects individual meadow-species differently. For example, plant species might vary in their response to climate variability based on their perennation (perennial or annual). Some studies have shown that the timing of flowering in annual plants shifts more than perennials do, perhaps because annuals prefer timings with less competition over pollinators and still favorable weather conditions (Calinger, 2013). In the study meadows, the majority of the plants used for my analysis were perennials, so I could not evaluate this possibility. Furthermore, future analysis could examine whether perennials with underground bulbs that are usually insulated by snowpack are more vulnerable to earlier snowmelt than perennials with above-ground bulbs are.

The activity of the pollinator *Apis mellifera* shifted temporally in parallel with changes in flowering phenology, but the data did not allow for analysis on population abundance, population health, or quality of pollination. More data on pollinator populations in particular would facilitate investigations into how climate variability directly affects the development and activity of pollinator species. Furthermore, future work should consider the impact of climate variability on less-resilient specialist pollinator species. This would paint a more com-

plete picture of how plant-pollinator networks are transforming over time.

Analyses of how climate variability negatively affects plant-pollinator interactions can inform policies that seek to preserve the networks. Most importantly, pollinator biodiversity serves as a buffer against negative changes in climate. For example, honeybees (*Apis mellifera*) and bumblebees (*Bombus* sp.) have generalist diets, wide spatial movements, and long foraging seasons that are beneficial for adapting to changes in flowering phenology (Gonzalez, 2013). On the other hand, wild bee species are sometimes less affected by certain environmental changes than honeybees are. For example, Brittain *et al* found that when honeybees moved away from a location because of increased wind speeds, the native bees easily filled their place (Brittain, 2012). In fact, Radar *et al* predicted that, under the most extreme IPCC scenario for climate warming, honeybee pollination would decline by about 15% but native, wild bee pollination would increase in response, producing a net increase in pollination of about 4.5% by 2099 (Radar, 2013). These results suggest that plant-pollinator networks need a diverse and healthy balance of pollinator species that have differential responses to climate variability. Policies that seek to sustain

plant-pollinator networks should focus on maintaining biodiversity.

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