

The Effect of Climate Change on Pollinators and the Implications for Global Agriculture

A Case Study in the H.J. Andrews Experimental Forest, Oregon



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Abstract

More than one-third of global food crops depends on commercial bees for pollination, but over 30% of domesticated honey bee colonies collapse each year due to poor nutrition, spread of pathogens, exposure to pesticides, and transportation stress. To avoid a pollination crisis that would cripple global agriculture, farmers can introduce diverse populations of wild bees by simply planting pollen-rich wildflowers near the cropland. Diverse bee populations not only supply higher crop yields and larger fruit set (compared to single-species management), but the differential responses among species to climate change and other perturbations provide a buffer against disastrous declines in any one species. In this essay, I analyze the effect of climate change on wild pollinators in montane meadows at the H.J. Andrews Experimental Forest in Oregon. Globally, warming temperatures have confused plants into flowering earlier each spring, which can cause temporal mismatches with pollinator species. Asynchronies can hinder plant reproduction and limit the food resources necessary for pollinator survival. At the study site, springtime temperatures rose significantly from 2011 to 2015, and the snowpack melted from the ground consistently earlier over the five years. In response to this climate variability, the median date of peak flower abundance and the median date of peak plant-pollinator interactions both shifted earlier by about five weeks from 2011 to 2015. Despite sustained synchrony between the plants and pollinators, the median flower abundances declined by 68% and the median number of interactions declined by 73%. Although the data suggest that the wild pollinators are trying to adapt to shifts in timing of flowering, the dwindling interaction counts indicate that the populations are still suffering. These findings reinforce the importance of cultivating a diverse set of wild bee species for agriculture. Even if a few individual species decline as a result of climate change and harmful agricultural practices, pollinator biodiversity can mitigate systemic crop pollination failures.

I. Introduction

The white bulbs of bear grass glowed against the dark shadows of the Douglas-fir forest. I brushed aside these stalks to pass, only for them to whip back and release a plume of pollen in my face. Swimming



through a sea of bear grass that reached my eyes, I escaped, coated in pollen, to a meadow. The flowers and bees thrived in an environment so steep that trees took their roots elsewhere. Tucked in acres of forest and accessible solely by devoted bushwhacking, these meadows rewarded me with the perspective that only high elevation affords. Not a single person specked the mountainous landscape except for my four team mates, yet human impacts reached even here. The flowers



surrendered to the record-high heat so early in the summer that my bug-catching net lay untouched on the bare ground. My data sheet craved the touch of a pen recording observations of bees pollinating flowers. The verdant meadows with spots of scarlet paintbrush flowers and violet lupine blossoms faded to silent brown as if looking at a sepia photograph. A few buzzing bees searched for pollen before giving up and seeking refuge from the heat.

During my field work last summer, I questioned the role of warming temperatures on changes in the behavior of bees and flowering plants. In this essay, I will analyze how climate variability has negatively affected wild plant and pollinator populations inhabiting the montane meadows in the H.J. Andrews Experimental Forest in Oregon. Because agricultural crop production currently faces its own pollination crisis, the health of wild pollinators grows increasingly vital.

Importance of pollinators for global agriculture

Just a few hundred miles away in homogenous, carefully manicured farmlands, industrial agriculture struggles to prevent massive losses of domesticated bees. Every winter, paid beekeepers pack over 30 billion European honeybees into overcrowded boxes on thousands of trucks, where the bees spend months surviving on nutrient-poor sugar syrup and pollen patties. These trucks come from all over the country to deliver honeybees to the 90 million almond



Figure 1. Image of a truck carrying honeybee hives. Source: Glacier County Honey Co.

trees scattered across 810,000 acres in California's Central Valley (USDA, 2013; Jabr, 2013). Once February arrives, the blushing almond flowers start to blossom. Each flower on the almond trees blooms for only five days, during which time the honeybees must deposit pollen from a

different variety of almond tree onto the flower in order for a nut to grow (McGregor, 1976).

These honeybees pollinate upwards of 2.5 trillion almond flowers and reward the farmers with



Figure 2. Aerial photographs of blooming almond orchards in California. Source: Anthony Dunn Photography.

some 700 billion individual almonds. However, the surviving bees then face acres and acres of now flowerless almond tree fields, with no other pollen in sight to consume. To make matters worse, many bees are simply carted off in another migratory journey to pollinate other food crops (Jabr, 2013).

The forced mass migration of honeybees for intensive, monocrop agriculture does not embody sustainable practices. Similar to the spread of flu in an airport, the gathering of such large numbers of honeybees from all over the nation provides the perfect environment for viruses, mites, and fungi to spread and ravage the populations. In fact, many beekeepers

experience average wintertime losses of over 30% of their honeybee colonies due to an unusual phenomenon called colony collapse disorder (CCD). These collapsed colonies are characterized by the mysterious disappearance of the adult honeybees (with no dead bodies found), leaving behind immature bees and the queen bee (Johnson & Corn, 2015). CCD most likely stems from a combination of problems associated with agricultural beekeeping, including pathogens, nutritional deficiencies and lack of a varied diet, exposure to neonicotinoid insecticides and other pesticides, lack of genetic diversity, habitat loss, and transportation stress. Pesticides, stress, and lack of diversity can actually exacerbate the vulnerability of bees to pathogens (Potts *et al.*, 2010; Lu *et al.*, 2011). In particular, neonicotinoids, a new class of insecticide, are strongly attributed to pollinator declines. Neonicotinoids are persistent neurotoxins that permeate the entire plant, including the pollen and nectar that bees ingest, and cause death, paralysis, and impaired learning and foraging ability in bees (Goulson *et al.*, 2015). In California alone, CCD threatens to wipe out 50-80% of the worldwide production of almonds (Jabr, 2013).

As bee colonies collapse, so too could many fragile agricultural systems. Over 75% of the global food crops consumed by humans depend on insect pollination to some degree, and pollinators are absolutely essential for one-third of them (Klein *et al.*, 2007). These highly dependent crops include almonds, apples, blueberries, cherries, oranges, squash, vegetable seeds, and legume seeds (Calderone, 2012). Without honeybees, the almond trees in California, for example, cannot rely on wind for pollination, and the native wild bees, if any, could only pollinate a small fraction of the flowers (Jabr, 2013). Furthermore, many crops indirectly depend on insect pollinators because they grow from seeds that resulted from pollination. Production of sugar beets, legume hay, broccoli, carrots, onions, asparagus, and other vegetables relies on insect pollinators for seeds (Calderone, 2012). Estimates place the value of insect pollination for

food production at \$168 billion, 9.5% of the total value of global food production (Gallai *et al.*, 2009). Honeybees are the most widely used pollinators for agriculture and can increase yields in 96% of animal-pollinated crops (Klein *et al.*, 2007). However, the United States lost 59% of domestic honeybee colonies between 1947 and 2005 (NRC, 2007), and bee populations continue to dwindle in the face of human-caused environmental pressures. Drastic bee declines would cripple global agriculture, especially in the face of a 60% increase in world food demand by 2050 (FAO, 2012). If pollinator conditions do not improve, we may lose the capacity to produce certain valuable food crops, such as almonds, at an economic scale.

Wild bee populations can buffer industrial agriculture against pollination gaps resulting from declines in honeybees and the few other domesticated pollinators used. About 25,000 species of bees exist in the world, and some of these pollinators can be managed for agriculture (Kearns *et al.*, 1998). For example, the hornfaced bee was successfully introduced into U.S. agriculture a few decades ago to supplement honeybee pollination of apple trees (Parker *et al.*, 1987). Studies have found that wild bee biodiversity can provide “biological insurance” for crop pollination, as long as the native bees have not already dwindled because of nearby agricultural intensification, a problem in California’s Central Valley (Winfrey *et al.*, 2007). Tapping into wild bee populations whenever the domesticated colonies collapse may provide a short-term solution, but what if wild native bees face extinctions from an invisible cause: climate change? Will we lose our back-up plan?

The effect of climate change on plant-pollinator networks

Although the wild bees seem a world away from human exploitation, anthropogenic climate change threatens the survival of even these populations. Climate change most likely harms bees through disruptions in plant-pollinator networks. Interactions in these networks

consist of mutually beneficial pollination of flowering plants by pollinator species. While plant species rely on pollinators to inadvertently drop off pollen from other compatible plants so that they can reproduce (Ollerton *et al.*, 2011), the pollinator species require pollen and nectar as a food resource (Memmott *et al.*, 2007). Because of the interdependency between plants and pollinators, perturbations in one population can distress the other.

Consider the following metaphor, where bees are hungry customers at a buffet-style restaurant and flowers are the food items that need to be eaten so that more food can be made. The bees come to the buffet three times per day for breakfast, lunch, and dinner. One day, the restaurant opens for breakfast a couple hours earlier than usual because warmer morning temperatures confused the owner's sense of time. As a result, the bees arrive at the normal time only to discover that they missed the breakfast food items. The restaurant tosses out the uneaten breakfast food. Meanwhile, the bees are so hungry that some of them die before they make it to lunch. Then, only some of the lunch food is eaten and replenished. In addition, the time-confused owner mistakenly put out the pasta entree for breakfast instead of dinner, in which case the meager dinner then fails to attract enough bees to come eat the food. Furthermore, if some of the bees have restricted diets such as vegetarianism, they will have even fewer options to eat. Likewise, the meat dishes will have fewer opportunities to be eaten. The confusion from the warming temperatures caused a temporal mismatch between the bees and plants that left the bees malnourished and the flowers discarded without having reproduced.

Current climate change entails increasing global average temperatures as a result of human emissions of the greenhouse gases carbon dioxide, methane, and nitrous oxide. Carbon dioxide emissions come primarily from fossil fuel use and land use change, while methane and nitrous oxide emissions result from agriculture. Because of the long half-life of the gases, past

and current greenhouse gas emissions will continue to warm the planet for over a millennium (IPCC, 2014). One of the uncertainties surrounding climate change is how various ecosystems and species, such as plants and pollinators, will respond to changes in climate.

Increased temperatures threaten to disrupt the environmental cues upon which flowering plants rely for the initiation of growing. Phenology refers to the annual timing of seasonal activities of plants and animals, usually influenced by weather and climate. For flowering plants, primarily temperature affects the phenology (timing) of flowering (Walther *et al.*, 2002), and not elevated carbon dioxide levels or nitrogen deposition from climate change (Cleland *et al.*, 2006). In montane meadows that experience winter snowpack, the timing of flowering depends predominantly on when the snowpack melts in the spring. Because warming temperatures from climate change cause more precipitation to fall as rain than as snow, the snowpack will disappear sooner in the spring. Snowmelt allows the ground to warm up and thus the plants to begin growing (Inouye, 2008; Dunne *et al.*, 2003). Snowmelt could either be a cue for plant phenology or a threshold for when plants can begin growth, after which temperatures determine the rate of growth (Forrest & Thomson, 2011).

Numerous studies have found that the phenology of flowering has shifted earlier in response to warming and/or earlier snowmelt (Fitter & Fitter, 2002; Ahas *et al.*, 2002; Inouye *et al.*, 2002; Bradley *et al.*, 1999). For example, from 1852 to 2006, 2.4 degrees C warming in Concord, Massachusetts correlated with an average shift in timing of flowering by seven days (Miller-Rushing *et al.*, 2008). Another dataset of flowering plants in the southeastern USA from 1951 to 2009 indicates that early-flowering species advance about 4 days for each degree C increase in mean March temperatures (Park & Schwartz, 2015). To isolate the various climate effects, Dunne *et al.* (2003) tested flowering responses to snowpack manipulation and

experimental warming on 12 meadows in the Colorado Rocky Mountains. The experiment showed that the timing of flowering advances about 11 days for every two weeks of earlier snowmelt or for every two degrees warming of growing season soil temperatures. Furthermore, the majority of these phenological studies may even under-predict plant responses to climate change. The plants that flower earlier in the growing season typically advance more in response to warming than do later-flowering species, so the averaging of phenological changes will not accurately reflect the full range of responses (Fitter & Fitter, 2002; Wolkovich *et al.*, 2012; Hegland *et al.*, 2009).

Shifts in the timing of flowering can result in reproductive failure in plant species. Not only could early flowering align with an absence of pollinators to pollinate the plant, but the plant could also flower at a different time than nearby mates with compatible pollen for reproduction (Hegland *et al.*, 2009). Furthermore, if flowering initiates too early, plants may be unable to provide time-sensitive food resources to offspring. Because growth and reproduction occur much earlier than the time when offspring need food, plants use environmental cues to predict when the peak food resources will be available and thus determine when to start growing. The preference of cues developed via natural selection, so changes in climate may cause these cues to no longer accurately predict food availability. As a result, plants may fail to acquire adequate food for offspring to survive (Visser *et al.*, 1998).

Pollinator species also respond to climate warming. Most insect pollinators are small and poikilothermic (literally “varied temperature”), meaning they can only regulate their body temperature through behavior. As a result, temperature can significantly affect their activity and life cycle development (Hegland *et al.*, 2009; Memmott *et al.*, 2007). For example, one study showed that the spring timing of flight activity in bumble bees advanced by about 2 weeks from

2001 to 2007 (Sparks & Collinson, 2007). The warmer soil temperatures most likely caused the young bumblebee queens, the only ones that live through the winter, to emerge from hibernation earlier in the spring (Alford, 1969). Another study conducted in Spain from 1952 to 2014 found that honeybee (*Apis mellifera*) populations also have reacted quickly to warmer temperatures by appearing earlier in the spring since the mid-1970's (Gordo & Sanz, 2006). However, climate change most likely affects pollinator species in multiple ways, including physiological impacts on the individuals, changes in cues for emergence, and the temporal shifts in flowering of the plants that they rely on. If temperatures rise too much, insect pollinators in some locations may even reach an upper thermal limit that they cannot tolerate (Bale & Hayward, 2010).

Asynchrony between the timing of flowering and the activity of pollinators as a result of climate change could compromise plant reproduction and the food resources necessary for pollinator survival and reproduction (Boggs & Ross, 1993). Because flowering plants and pollinators co-evolved to synchronize their activities (Donnelly *et al.*, 2011), the species could be affected even more by the indirect impact of warming on the mutualistic interactions than by individual thermal tolerance (Berg *et al.*, 2010). Temporal mismatches between flowering and pollinator activity result from the differential sensitivities to warming among plant and pollinator species (Berg *et al.*, 2010). Most likely, the phenology of flowering and pollinators both shift earlier but to different extents. Sufficient data do not exist to conclusively determine how declines in pollinator populations relate to shifts in flowering. Interestingly, a 30-year dataset of the activity of butterflies indicated that the appearance date of butterflies actually shifted later while flowering shifted earlier because of differing reliance on environmental cues. In this case, the timing of flower emergence depended on the prior month's temperatures, whereas the butterflies were influenced by temperatures during the 15 days prior to appearance, although to a

less extent. As a result, the plants that flowered earliest were not pollinated by the butterflies (Doi *et al.*, 2008). So although most pollinators will likely emerge earlier in spring, some may even appear later. The differential responses to climate variability will produce a web of unpredictable mismatches.

In particular, temporal mismatches will likely cause certain plant-pollinator pairs to no longer interact at all. Phenological records from the southern Rocky Mountains for 1974-2009 showed periods of low flower abundance in the middle of the summer, which could harm the active pollinator species if they cannot find sufficient pollen and nectar (Aldridge *et al.*, 2011). Asynchrony could affect the plant-pollinator network in other subtle ways. For example, many plant species share the same pollinator species and have evolved to flower sequentially in order to sustain the pollinator populations throughout the summer (Waser & Real, 1979). In the study meadows, honeybees (*Apis mellifera*) pollinate the lavender-blue puffs of *Gilia capitata* early in the summer before transitioning to pollinating yellow sunflowers (*Eriophyllum lanatum*) and later the cream-colored clouds of heartleaf buckwheat (*Eriogonum compositum*). On the other hand, the fuzzy-horned, orange-striped bumblebee (*Bombus mixtus*) pollinates the delicate, deep-violet flowers of *Delphinium nuttallianum* early in the summer and the blushing-pink branched flowers of *Orthocarpus imbricatus* later on. These two bee species rely on the presence of various plants throughout the summer for a steady supply of food. A disruption in the sequence of flowering might also harm the plants themselves. Because climate change affects the phenology of early-flowering plant species the most, the resulting asynchronies could cascade and cause a lack of pollinators for the later-flowering species. For instance, failure of queen bumblebees to obtain nutrition to build nests in the early part of the season would negatively

impact the pollination of later-flowering species (Waser & Real, 1979; Dunne *et al.*, 2003; Hegland *et al.*, 2009).

Another way some plant species facilitate each other is to synchronize flowering so that the higher availability of pollen and nectar attracts more pollinators. In that case, temporal mismatches between these plant species would disrupt the amount of pollinator attention (Tachiki *et al.*, 2010). For example, the honeybees at the study site have a diverse and colorful display of flowers to pollinate throughout the summer. The lofty, pale flowers of *Ligusticum grayi* accompany the lavender inflorescences of *Gilia capitata* in the earlier part of the season, while maroon flowers snaking up the stems of *Rumex acetosella* and the bursting, sunshine-like flowers of *Eriophyllum lanatum* join soon after. Honeybees would be remiss to miss out on this colorful reception.

Pollinators may face worse impacts from asynchrony than plants will. Some plants can self-fertilize or clone if they are not pollinated, although not as a permanent solution because self-pollinated seeds experience worse survival and fecundity than do cross-pollinated seeds. By contrast, pollinators hold an absolute dependence on pollen and nectar for survival (Memmott *et al.*, 2007). In one study, plant-pollinator data from Illinois for 1884-1916 was used to predict that 17-50% of all pollinator species will suffer a disruption in food resources as a result of climate change. Pollinators can be affected by a complete lack of food, by food-less periods at the tail ends of the season, or by other temporal gaps in food availability. The study notes that specialist pollinators may be at more risk than generalist species. Because specialist pollinators rely on one or a few plant species for pollen, a mismatch could result in a scarcity of food available for the pollinator (Memmott *et al.*, 2007; Donnelly *et al.*, 2011). In the study meadows, the skinny, dark bee *Dufourea calochorti* primarily pollinates only one or two plant species and so could be

particularly susceptible. (Unfortunately, as a result, the data lack sufficient observations of this bee's activity.) By contrast, generalist pollinators like honeybees have broad diets, wide spatial movements, and long foraging seasons that are beneficial for adapting to changes in flowering phenology (Gonzalez-Varo, 2013; Hegland *et al.*, 2009). At the same time, generalists may still suffer because of a reduction in diet breadth (Memmott *et al.*, 2007). Plant species face low risk from the decline of specialist pollinators. Typically, specialist pollinators selectively visit generalist plants, which can be pollinated by many different pollinator species. In addition, specialist plants are typically visited by generalist pollinators, who are better equipped to adapt to climate change (Bascompte *et al.*, 2003). So, plants will likely suffer less than pollinator species will because of their ability to self-reproduce in the short-term and their lack of absolute dependence on susceptible specialist pollinators.

Climate change affects plant-pollinator networks in a myriad of subtle ways. Figure 3 summarizes some of the mechanisms by which shifts in phenology can disrupt these networks. In this essay, I will analyze changes in the interactions between plants and pollinators in the montane meadows of the H.J. Andrews Experimental Forest in the Western Cascades of Oregon. I will use data from 2011 to 2015 on flower abundances and on observed interactions between plants and pollinators, which were collected by the NSF-funded Eco-Informatics Summer Institute of Oregon State University. I was a member of the field crew that collected data for the summer of 2015. Although this dataset does not span enough years for conclusions about the long-term interweaving consequences of changes in flowering and bee activity, I can examine how the phenologies and abundances of the plant and pollinator species respond to local climate variability.

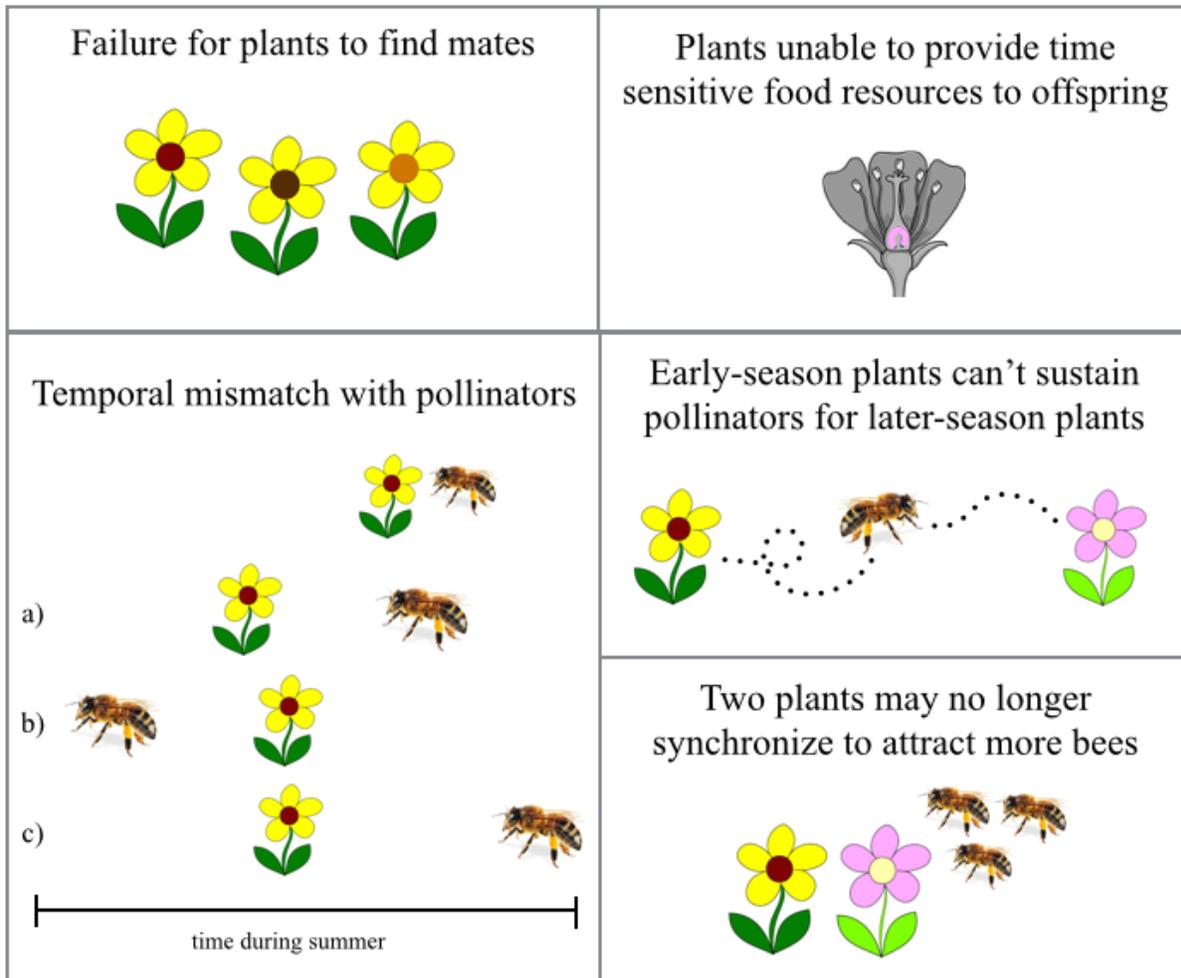


Figure 3. Some of the ways in which shifting phenology of plants and pollinators as a result of climate change can disrupt plant-pollinator networks. These consequences may result in reproductive failures in plants and reduced food resources for pollinators.

II. Methods

Study Site

The H.J. Andrews Experimental Forest is a Long-Term Ecological Research site situated in the Willamette National Forest in the Western Cascades mountain range of Oregon. The study site is a set of 12 montane meadows grouped into 3 proximity-defined complexes within this coniferous forest (Figure 4). These meadows range from 1331 to 1518 meters in elevation, 0.6 to 11 acres in size, and 11 to 36 degrees in slope. Any two meadows are at most 8680 m (5.4 miles)

away from each other (Helderop, 2015). This site experiences a climate of wet winters with snowpack, dry summers, and mild temperatures.

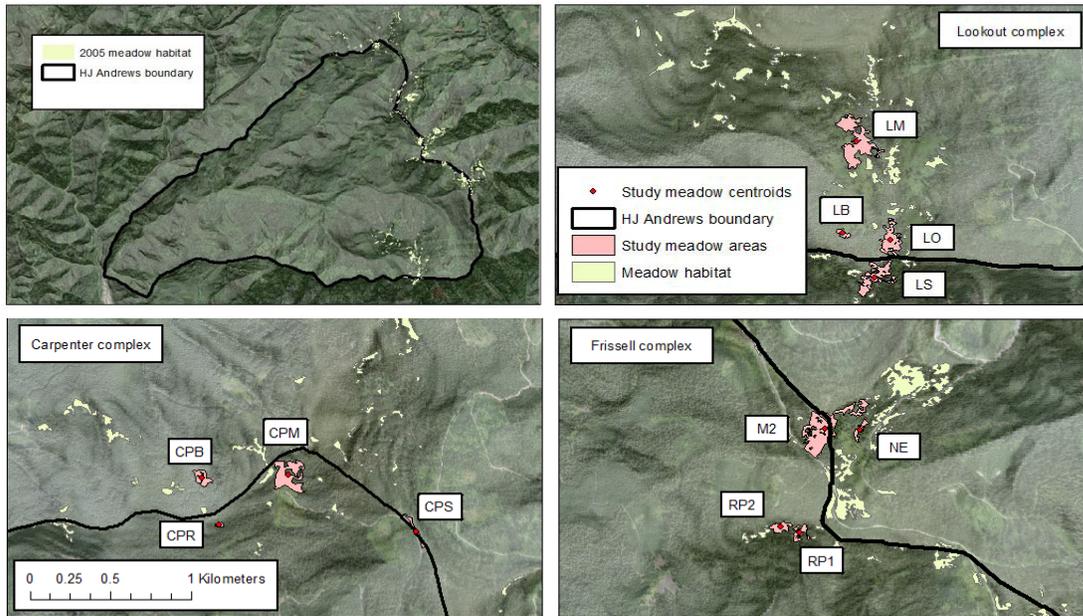


Figure 4. Geospatial images of the H.J. Andrews Forest boundaries and of the locations of the 12 study meadows in the 3 complexes. The three complexes are Lookout, Carpenter, and Frissell. Source: Helderop, 2015

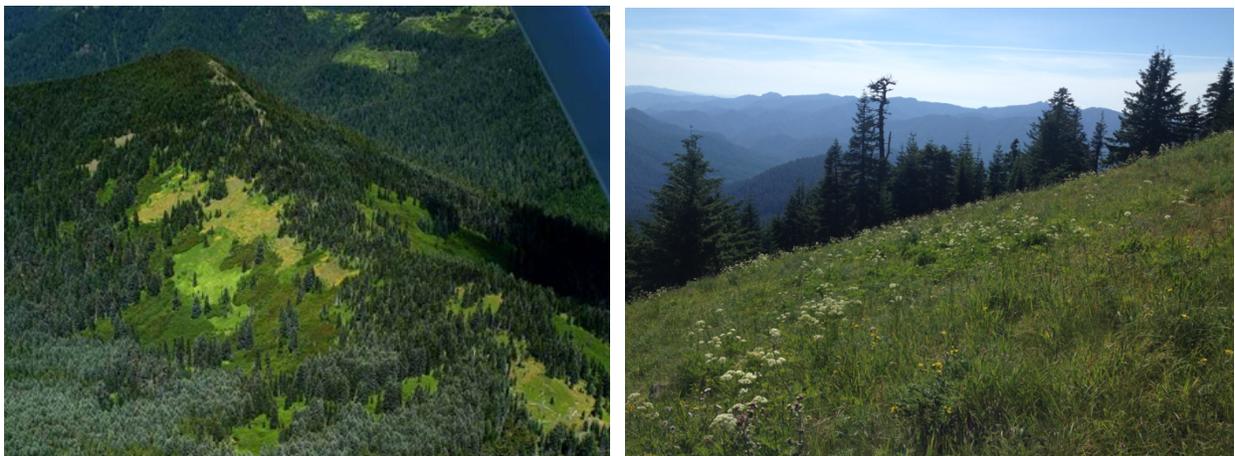


Figure 5. Images of some of the study meadows. a) Aerial photograph of Lookout Complex (Source: Al Levno). b) Image of meadow M2 in Frissell Complex.

Montane meadows such as these are increasingly rare because of forest encroachment and suppression of forest fires. In fact, the meadows in the H.J. Andrews Forest experienced a 45% habitat loss between 1948 and 2005 (Helderop, 2015).

Analysis of climate data

To analyze how climate has changed in the study meadows, I calculated the following variables for each year: average annual temperatures, cumulative degree days, and date of springtime snowmelt. I used the average annual temperatures to look at climate as a whole over recent decades, while cumulative degree days and timing of snowmelt are better biological predictors of flowering phenology.

To examine the variability in climate since 1989, I calculated monthly averages of temperature for each year and then used a 12-month moving average of these monthly values. This moving average allowed for a smooth visualization of temperature variability over time.

Next, I calculated the cumulative degree days (CDD) on June 1 for each year. Cumulative degree days are a measure of heat accumulation at a particular time and are frequently used to estimate phenology of crops. As such, they are a useful indicator for how much the ground has warmed up during spring and thus when the plants will begin growing. The degree days on a given day d are calculated as:

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

where I chose $T_{base} = 5^{\circ}$ C. Then, the CDD for each year is the sum of the non-negative degree days from March 1 to June 1. My calculation was informed by prior work on this study site (Helderop, 2015) and by similar work in the literature (McMaster, 1997). The CDD indicator serves as a predictor for when plants will flower that year.

For springtime snowmelt, I downloaded daily data from 1982 to 2015 on snow depth at the McKenzie Station from the Natural Resources Conservation Service (NRCS, 2015). The weather station is located 20 km from the study meadows and at 1433 m in elevation, similar to the meadows. I calculated the date of snowmelt to be the last date in spring or summer with snow

on the ground. The meadows may have slightly disagreed with the date of snow disappearance because of differences in elevation, aspect, topography, or shading by vegetation, but the weather station provides a consistent estimate.

To visualize these climate indicators, I created plots of the 12-month moving average of temperatures, the cumulative degree days on June 1, and the date of springtime snowmelt over time. Because temperature and snowmelt are likely highly correlated, I also developed scatterplots of CDD against snowmelt and performed linear regression. All my data analysis was performed using the R programming language.

Plant and pollinator data collection

Data were collected by the Eco-Informatics Summer Institute for five summers from 2011 to 2015 (Figure 6). Each of the 12 meadows were surveyed on five different days, separated by about a week, each summer between June and August. Typically, the field crew completed one complex (four meadows) in a day. The meadows were divided into two parallel transects 20 m apart, each with five 5x5 m² plots separated by 15 m. In total, an area of 90 m² comprising 10 plots was surveyed for each meadow.

On a given meadow visit, the field team first collected data on flower abundances. For each of the 10 plots within the meadow, the plant species were identified. Only the plants in anthesis, the flowering period in which the reproductive parts of the plant are available for pollination, were considered. If the species could not be identified, photographs and samples were taken for later identification. Then, the number of flowers in the plot for each plant species was recorded. The observer first recorded the number of stalks of that species and then recorded



Figure 6. Images of data collection in the HJ Andrews Experimental Forest.

the number of flowers per stalk. If there were more than ten stalks for a species, then the number of flowers per stalk was estimated as the average number for ten randomly chosen stalks. The total number of flowers for that plant species is then the number of flowers per stalk multiplied by the number of stalks. Inflorescences, groups of flowers clustered together on one stem, were counted as one flower. For example, what looks like a single flower on a woolly sunflower plant actually has many miniscule flowers packed into the center discoid, but we counted this discoid as one flower. Table 1 shows an example of what the data spreadsheet looks like.

Year	Date	Meadow	Plot	Species	# Stalks	# Flowers per stalk
2015	7/1	Lookout Main	4	Achillea millefolium	1	7
2015	7/1	Lookout Main	4	Eriophyllum lanatum	53	8.6
2015	7/1	Lookout Main	5	Ligusticum grayi	4	2.25
2015	7/22	Lookout Main	1	Orthocarpus imbricatus	53	8.6
2014	7/10	C. Ridge	7	Delphinium nuttallianum	1	1
2014	7/29	C. Ridge	4	Castilleja hispida	2	2.5
2014	7/29	C. Ridge	8	Phlox gracilis	1	4
2014	7/29	C. Ridge	8	Sedum oreganum	1	11
2011	8/02	C. Ridge	6	Castilleja hispida	1	4
2011	8/02	C. Ridge	6	Lupinus laxiflorus	2	10
2011	8/02	C. Ridge	6	Sedum oreganum	9	6

Table 1. Example of what the data on flower abundances look like.

During the same visit to each plot in each meadow, observations of interactions between plants and pollinators were also recorded. A crew member conducted a 15-minute “watch” of the plot. These watches could only occur between 9 am and 5 pm on sunny or partly cloud days with little wind, so that the pollinators would be active. During a timed 15-minute watch, the person paused the stopwatch upon observing an interaction between a pollinator and a plant. An interaction was defined as a visit by a pollinator to the reproductive parts of a flower in anthesis. If the pollinator species was not identifiable by sight, they caught the insect using a bug net and placed it in a jar with ammonium carbonate and a wet paper towel to euthanize it. Later, the pollinator would be identified by an expert entomologist at Oregon State University, Andy Moldenke. After the pollinator and the plant species were recorded, the watch would continue. If the same pollinator individual was seen pollinating many different flowers of the same plant, the number of interactions was recorded in a separate column instead of as a new row for each. Throughout the watch, variables for time, cloud cover, wind, temperature, and presence of shade were noted on the data sheet. Table 2 gives an example of this data spreadsheet.

Year	Date	Meadow	Plot	Time	Temp, Weather	Minute	Plant Species	Pollinator Species	# Interactions
2015	6/30	M2	1	14:15	29, sunny	1	<i>E. lanatum</i>	<i>Apis mellifera</i>	18
2015	6/30	M2	1	14:15	29, sunny	4	<i>L. laxiflorus</i>	<i>Bombus bifarius</i>	1
2015	6/30	M2	1	14:15	29, sunny	9	<i>G. capitata</i>	<i>Apis mellifera</i>	2
2015	6/30	M2	1	14:15	29, sunny	12	<i>L. laxiflorus</i>	<i>Megachile melanophaea</i>	1
2015	6/30	M2	1	14:15	29, sunny	13	<i>G. capitata</i>	<i>Apis mellifera</i>	1
2015	6/30	M2	1	14:15	29, sunny	15	<i>E. lanatum</i>	<i>Apis mellifera</i>	2
2015	6/30	M2	3	14:55	29, windy	11	<i>A. millefolium</i>	<i>Epicauta puncticollis</i>	1
2014	7/03	C. Ridge	2	13:00	25, sunny	2	<i>E. asperum</i>	<i>Bombus bifarius</i>	2
2014	7/03	C. Ridge	2	13:00	25, sunny	2	<i>E. asperum</i>	<i>Bombus mixtus</i>	1
2014	7/03	C. Ridge	2	13:00	25, sunny	11	<i>E. asperum</i>	<i>Bombus flavifrons</i>	4
2014	7/28	C. Ridge	2	10:55	29, sunny	12	<i>E. asperum</i>	<i>Bombus mixtus</i>	1

Table 2. Example of the data for plant-pollinator interactions.

In sum, data were collected for (5 years) x (12 meadows per year) x (10 plots per meadow) x (5 watches per plot) x (many species and interactions per watch). Over the five years, 102 unique plant species and 492 unique pollinator species were identified. Eleven of the pollinator species were social bees (bumblebees and European honeybees) and as many as 100 were solitary bees. About 2970 unique interactions between plants and pollinators were observed. Figure 7 shows the most abundant plant species and the most active pollinator species at the study site. The most common interaction was *Apis mellifera* (honeybee) pollinating *Gilia capitata*, followed by *Apis mellifera* pollinating *Eriophyllum lanatum*.



Figure 7. The top five most abundance plant species and top five most active pollinator species. Top row (left to right): *Achillea millefolium*, *Eriophyllum lanatum*, *Orthocarpus imbricatus*, *Gilia capitata*, *Castilleja hispida*. Bottom row: *Apis mellifera*, *Bombus mixtus*, *Bombus bifarius*, *Epicauta puncticolis*, *Bombylius major*.

Calculation of estimates for flowering phenology

First, I made small adjustments to the data so that I could calculate estimates for the timing of flowering. Very occasionally, a field team did not finish the watch of a meadow in one day. In that case, they collected the rest of the data as soon as possible afterwards, usually the next day. To simplify the analyses of flower abundance for a given watch of an entire meadow, I used only the first date for the whole watch. This only occurred 13 times in 5 years. For my data analysis, I used the meadows as the spatial scale, since the plot labels were not kept consistent from year to year. My code calculated the average flower abundance of a particular plant species across the 10 plots in each meadow for each date. In a few cases, the flower count for a species in a plot was recorded as N/A because of a data collection error. To handle this missing data, I excluded that plot from the average. When a plant species was not listed in the flower survey for a plot, that meant the abundance was zero. Because some species were rare and did not appear consistently across meadows or years, I only examined data for the 100 most frequently observed plant-pollinator pairs.

For each plant species in each meadow in each year, I calculated three phenological measures: first flowering, peak flowering, and last flowering. First flowering is the first date at which plants of that species begin flowering in late spring/early summer. My estimate for first occurrence was the first date recorded with positive flower 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 I could not be sure that the first data point with positive abundance was an accurate reflection of first flowering occurrence. In that case, the timing of first flowering was noted as N/A for that species.

Peak flowering for a given plant species in a given year is the day of the year with maximum flower abundance. I estimated peak flowering as the date with the highest recorded number of flowers. If there was not a shoulder on either side of the peak, i.e. a neighboring data point on each side with a lower abundance, the timing of peak flowering was recorded as N/A. This ensured that the estimated timing of peak flowering was a true peak. Occasionally, a species would peak twice in one season, either because of natural phenology or because of variability in data collection. I ignored this possibility, and used the first peak as the estimate.

The timing of last flowering for a species is the last date with a recorded occurrence of flowers. I estimated last flowering to be the day of year of the last data point with positive abundance. If there was not a later data point with zero abundance, I classified the estimate as N/A since there was no indication of how soon after that date the flowering actually stopped.

Using the 100 most common plant-pollinator pairs, there were a total of 225, 401, and 473 estimates for first, last, and peak flowering, respectively, across years, species, and meadows (Table 3). There are generally more estimates for timing of last flowering than of first flowering because the later part of each summer was better sampled.

Timing of Flowering	Year	N	# Unique Species
<i>First</i>		225	19
	2011	78	16
	2012	54	15
	2013	49	15
	2014	29	10
	2015	15	5
<i>Last</i>		401	19
	2011	110	18
	2012	36	9
	2013	109	15
	2014	54	11
	2015	92	12
<i>Peak</i>		473	27
	2011	110	25
	2012	80	23
	2013	104	25
	2014	109	25
	2015	70	23
<i>Total</i>		1170	21

Table 3. Summary of the number of data points and number of unique plant species by year for the estimates of first, last, and peak flowering. N in a given year is also the number of unique plant-meadow pairs.

There is inherent uncertainty in these estimates of phenology. Data points for a particular species in a season are typically a week apart. As a result, the estimate for first flowering could be as much as one week off, because the true first flowering could be any time between the date of zero abundance and the next date of positive abundance. Similarly, the estimate for last flowering could be at most one week off. The estimate for peak flowering could have a

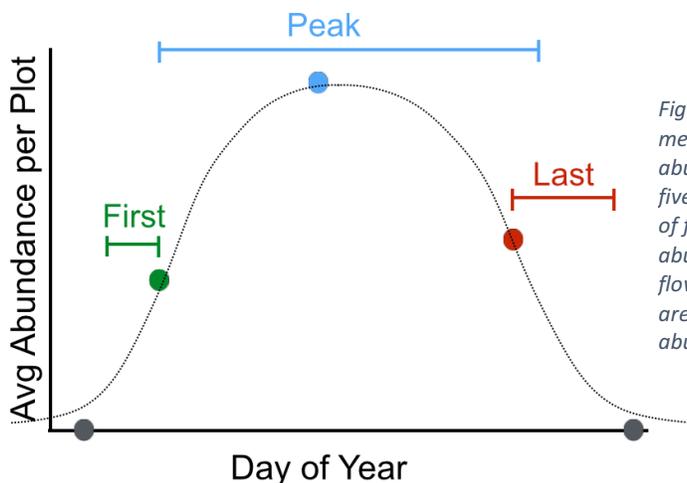


Figure 8. A typical phenological curve for one plant species in one meadow location in one year. The graph plots the average flower abundance in the meadow against the time during summer. There are five data points on the graph that correspond to the five watches. Timing of first flowering is estimated to be the first date of positive flower abundance, as long as there is an earlier date of zero abundance. Peak flowering is the first date of maximum flower abundance, as long as there are two shoulder points. Last flowering is the last date of positive flower abundance, as long as there is a later data point of zero abundance.

maximum error of one week because the peak truly occurs some time between the two neighboring data points. However, because the day of data collection during a week was more or less random, the uncertainty should not significantly skew the results. We can simply acknowledge that any shifts in flowering could be a few days off. Figure 8 illustrates the calculations of the estimates and the uncertainty.

Analysis of flowering phenology

To investigate how the timing of first, peak, and last flowering changed over time, I first developed descriptive visualizations in the form of boxplots. A boxplot is a graph that summarizes the distribution of data. The central box spans from the first quartile to the third quartile (called the interquartile range, IQR), providing a display of the range of the middle 50% of the data. The middle line within the box represents the median value. The whiskers extend to the maximum and minimum values that are within $1.5 \times \text{IQR}$ above the third quartile or below the first quartile. Values outside of that range are potential outliers, shown as asterisks. I included boxplots for the timing of first, peak, and last flowering, grouped by year and across all meadows and plant species.

Then, to conclude whether significant shifts in flowering occurred over the five years, I used a One-Way Analysis of Variance (ANOVA) test. One-Way ANOVA is a hypothesis test used to see how mean values compare across a category with more than two levels. For my analysis, the test compares the mean timing of flowering across the five years. I could assume equal variances for first, peak, and last flowering because among the five years, the largest standard deviation divided by the smallest was less than 2. The distributions of first, peak, and last flowering were all approximately normal. I did a separate ANOVA test for each flowering

event. The Tukey pairwise comparisons provide a mechanism to see which pairs of years experience a significant difference in mean timing of flowering. The hypothesis tests gave 95% confidence intervals for the mean difference in timing of flowering between a pair of years, which provide a sense of the degree of shift in flowering. These tests report a p-value to measure the significance of the difference in means between years. In this case, a p-value is a measure of the likelihood that we would see the difference in means (or a more extreme difference) if we assume that there is no difference between the two years.

Finally, I also plotted the median timings of first, peak, and last flowering over the five-year period in one graph in order to compare how each has shifted over time. For this plot, the medians only encompassed the plant-meadow pairs that had estimates for all of first, peak, and last flowering.

Analysis of pollinator phenology

Next, I examined how pollinator activity has shifted temporally over time. I estimated the timing of the peak number of interactions between plant-pollinator pairs as a proxy for peak pollinator activity. I only looked at the peak because capturing the true first or last interaction of a plant-pollinator pair in the data is inherently more skewed by human observation and the amount of time spent observing than is the recording of static flower abundances. I estimated the timing of the peak number of interactions using the same methods as for timing of peak flowering. Again, I used data from the 100 most common plant-pollinator pairs. There were a total of 767 data points with estimates for the peak (Table 4), encompassing 33 unique pollinator species.

To visualize the estimates, I graphed a boxplot of the timing of peak interactions by year. The data were approximately normally distributed and I was able to assume equal variances

across years, so I performed One-Way ANOVA with Tukey multiple comparisons to analyze the difference in mean timings of peak interactions between each pair of years.

Timing of Peak Interactions	Year	N	# Unique Species
	2011	216	23
	2012	122	23
	2013	168	24
	2014	168	21
	2015	93	14
<i>Total</i>		<i>767</i>	<i>33</i>

Table 4. Number of data points and number of unique species for estimates of timing of peak interactions.

Plant-pollinator synchrony

To evaluate whether temporal mismatches have occurred between plants and pollinators, I compared the shifts in peak flowering and in peak interactions with a plot of the median values from 2011 to 2015. For accurate comparison of medians, I only used the data points for the plant-meadow pairs that had estimates for both peak flowering and peak interactions.

I then calculated a linear regression model relating the timing of peak interactions to the timing of peak flowering. How well the model fits the data shows the degree to which the timing of interactions and flowering match up, even as they shift over the years. The R-Squared value is the percent of variability in the data that is explained by the model, so can be a measure of plant-pollinator synchrony. I also fit models that included variables for year, plant species, pollinator species, and meadow.

Furthermore, I created a variable for the difference (“mismatch”) between the day of peak flowering and the day of peak interactions, by plant species, pollinator species, and meadow. A negative value means that peak flowering occurred earlier than peak interactions. I produced a boxplot to visualize the mismatches over the years and then conducted a One-Way ANOVA test

with 95% confidence intervals of the difference in mean mismatches between years. I could assume equal variances between years. This boxplot describes the distribution of individual plant-pollinator mismatches instead of just comparing the median timing of peak flowering with the median timing of peak interactions.

Changes in flower and interaction counts

I also analyzed the effect of potential mismatches on the abundances of flowers and the number of plant-pollinator interactions. For each pair of years 2011-2012, 2012-2013, 2013-2014, 2014-2015, and 2011-2015, I calculated the percent changes in flower and interaction counts. To do this, I calculated the natural logarithm of the count in one year divided by the count in the previous (baseline) year. For example, for the pair of years 2011-2012, I took the log of the value in 2012 divided by the value in 2011. When either value was zero, I replaced it with 1 so that calculated values of infinity were avoided. The logarithm served to normalize the distributions more. I then created boxplots of these changes for each pair of years. To translate these boxplots to a median percent decrease in the flower abundances or interaction counts, I raised the number e to the median value and then subtracted 1. I also used one-sample t-tests for 95% confidence intervals for the percent decrease in counts from 2011 to 2015.

Examples of specific plant-pollinator responses

In addition, I provide a few examples of how interactions between specific plant-pollinator pairs have changed over time, as a more in-depth look at what is actually going on at an individual level. For a few plant-pollinator-meadow combinations, I created two plots: one of the timing of peak flowering and timing of peak interactions over the five years, and one of the

abundances of both flowers and interactions at the peaks over the five-year period. The chosen pairs exemplify the range of different responses among species.

Multiple regression analysis

I fit multiple regression models to the data to see how all the variables correlated with each other. First, I modeled the relationship between the timing of peak interactions and the following variables: timing of peak flowering, snowmelt, cumulative degree days, flower abundance at peak (for that year), number of interactions at peak (for that year), meadow, plant species, and pollinator species. Then I developed a model to predict the timing of peak flowering based on snowmelt, cumulative degree days, flower abundance, number of interactions, meadow, plant species, and pollinator species. I did not include the timing of peak interactions in this model because flowering starts before interactions do and thus should not be a predictor for timing of flowering.

I also developed models to predict the percent change in number of interactions and the percent change in abundances of flowers (for the periods 2011-2012, 2012-2013, 2013-2014, and 2014-2015). The predictor variables were the difference in timing of peak between those two years, the difference in CDD between those two years, the difference in snowmelt timing, the pollinator species (for number of interactions only), the plant species, and the meadow.

Summary graphs

Finally, I created two summary graphs of my results. For the first graph, I plotted the changes in timing of peak flowering, timing of peak interactions, interaction counts, and flower abundances for consecutive years from 2011 to 2015. I next graphed the changes for each year 2012-2015 relative to 2011 as a baseline.

III. Results

Climate variability over time

Average annual temperatures have gradually increased from 1989 to 2015 (Figure 9). In 2014, 12-month average temperatures surpassed the previous maximum temperature of 5.72 degrees Celsius in 1989. The maximum was 6.67 degrees in 2015.

There has not been a steady increase in cumulative degree days (on June 1) over time, but they have risen dramatically and consistently since 2011 (Figure 10). The year 2011 actually experienced the lowest value of CDD.

Similarly, there is not a clear trend in the timing of snowmelt over the past three decades, but snowmelt has shifted much earlier since 2011 (Figure 11). The minimum value for the day of year of snowmelt occurred in 2015, at day 117 (April 27). Before then, the earliest snowmelt was on day 132 (May 12) in 1987.

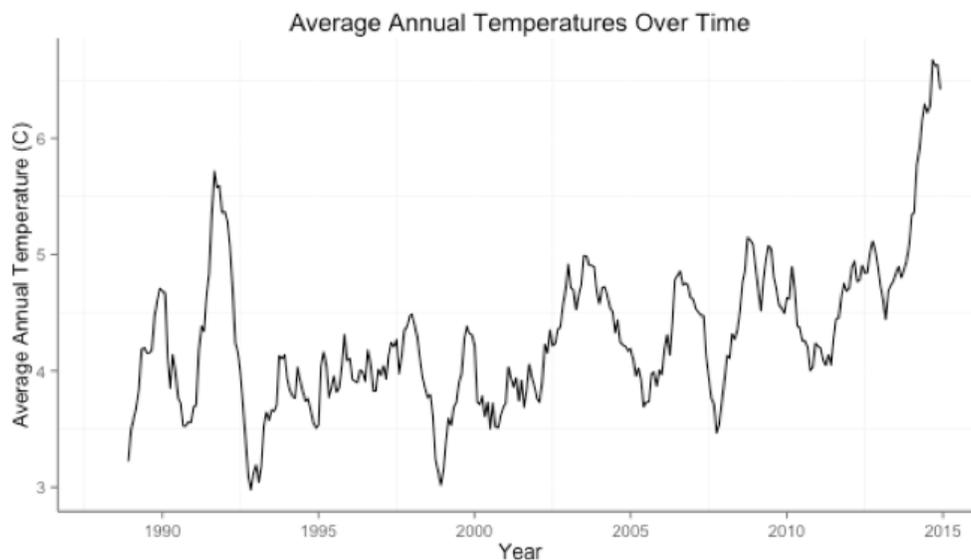


Figure 9. 12-month moving average of average monthly temperatures from 1989 to 2015. The maximum value occurred in 2015 at 6.67 degrees Celsius.

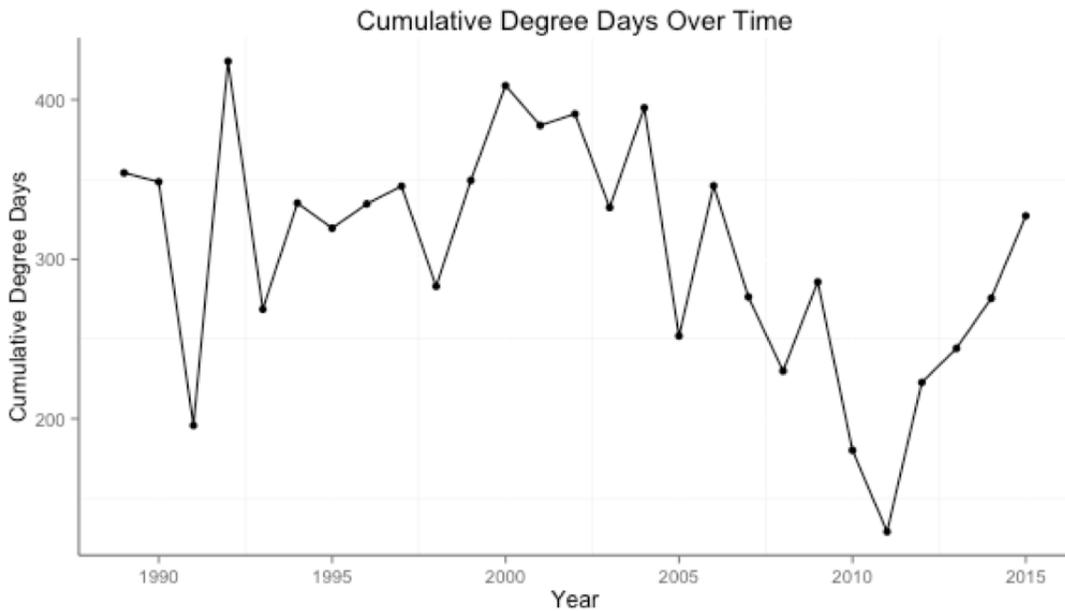


Figure 10. Cumulative degree days on June 1 for each year from 1989 to 2015. The lowest CDD value occurred in 2011 at 129.2 degrees. There is not a clear increase in CDD over time, but CDD have increased consistently from 2011 to 2015.

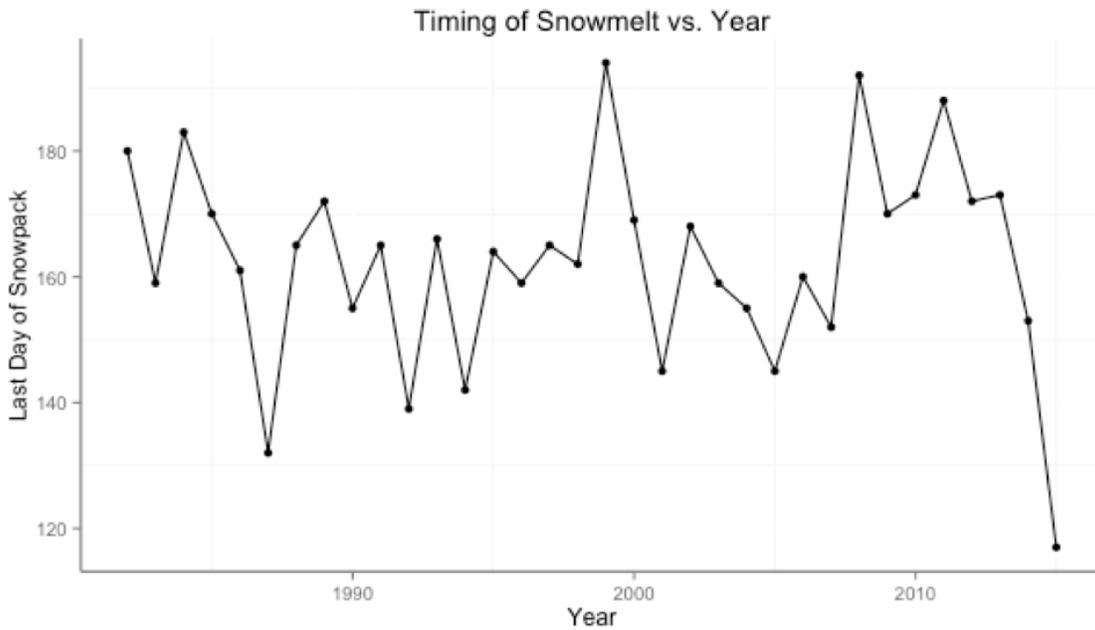


Figure 11. The last day of the year in springtime at which there is snow on the ground, from 1982 to 2015. There is not a clear trend over time, but the timing of snowmelt has shifted earlier from 2011 to 2015. Prior to 2015, the earliest snowmelt occurred on day 132 (May 12) in 1987.

From 2011 to 2015, both cumulative degree days and timing of snowmelt have shifted approximately linearly (Figure 12; Table 5). The change in CDD from 2011 to 2015 was +198

degrees C. The change in timing of snowmelt was -71 days. A linear regression relating CDD and snowmelt gave an R-squared value of 0.819 and a p-value < 0.05. So, the two variables are highly correlated.

Year	CDD	Day of Snowmelt
2011	129.2	188
2012	222.8	172
2013	244.2	173
2014	275.6	153
2015	327.2	117

Table 5. Values for Cumulative Degree Days on June 1 and for Day of Snowmelt for each year from 2011 to 2015.

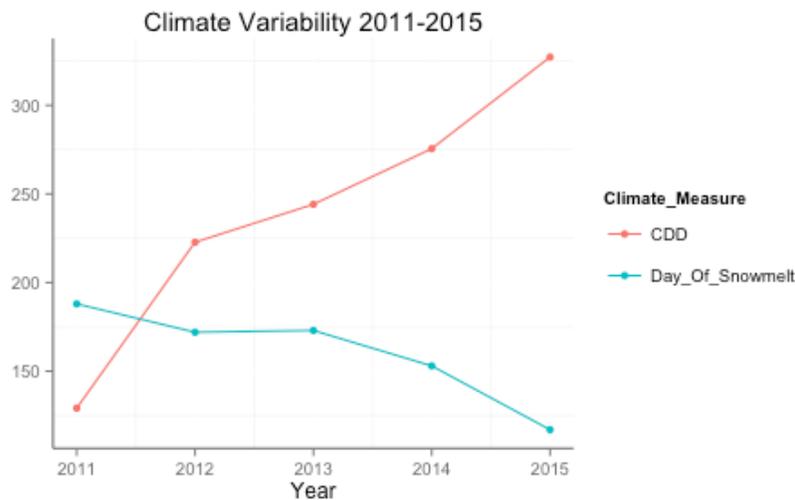


Figure 12. Cumulative Degree Days (top red line) and Timing of Snowmelt (bottom blue line) from 2011 to 2015. CDD have increased approximately linearly over time, while day of snowmelt has decreased approximately linearly. The change in CDD from 2011 to 2015 was +198 degrees C. The change in day of snowmelt was -71 days. The two variables are highly correlated ($R\text{-squared} = 0.82, p < 0.05$).

Flowering phenology

The flower-abundance curves of plant species over each summer differed in how well the timing of first, peak, and last flowering could be estimated (Figure 13). For example, the flower abundances of *Eriophyllum lanatum* in meadow M2 have clear peaks each year, but last flowering could not be estimated for any year and first flowering could only be estimated for one year. By contrast, the abundance curves of *Gilia capitata* in meadow RP2 allowed for estimates

of last flowering for each year, but not of first flowering and only for a few estimates of peak flowering. The differences likely result from interspecific variation in normal flowering timing, for example, *G. capitata* is an early-flowering species compared to *E. lanatum*.

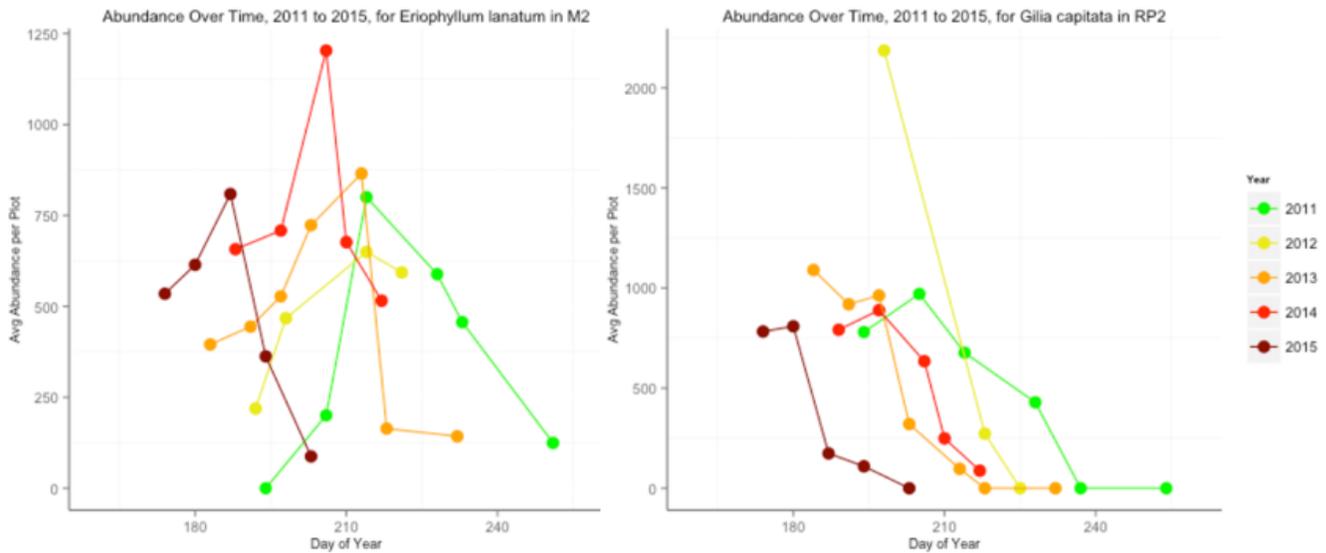


Figure 13. Examples of flower-abundance curves for two plant species, with the flower abundances over each summer from 2011 to 2015. These examples show that plant species differ in how well the timing of first, peak, or last flowering could be estimated. Left: Plant *Eriophyllum lanatum* in meadow M2, which has estimates for peak flowering for all five years but not for first or last flowering.. Right: *Gilia capitata* in meadow RP2, which has estimates for last flowering for all years but no estimates for first flowering.

Across all species, the availability of flowering estimates and the patterns of shifts in flowering vary by meadow location and by first, peak, or last flowering (Figure 14). For example, the plant *Lupinus laxiflorus* has much fewer estimates of first flowering and across only nine of the twelve meadows, while there are more estimates of last flowering across all twelve meadows. In addition, the degree of temporal shifts in last flowering for this plant are not the same across meadows.

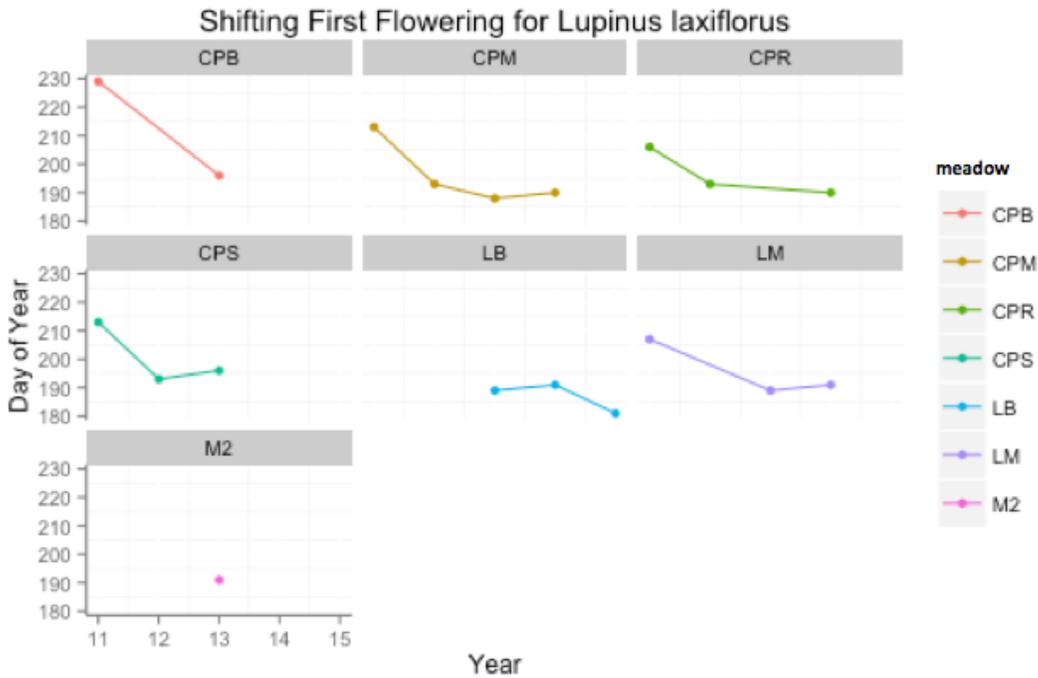
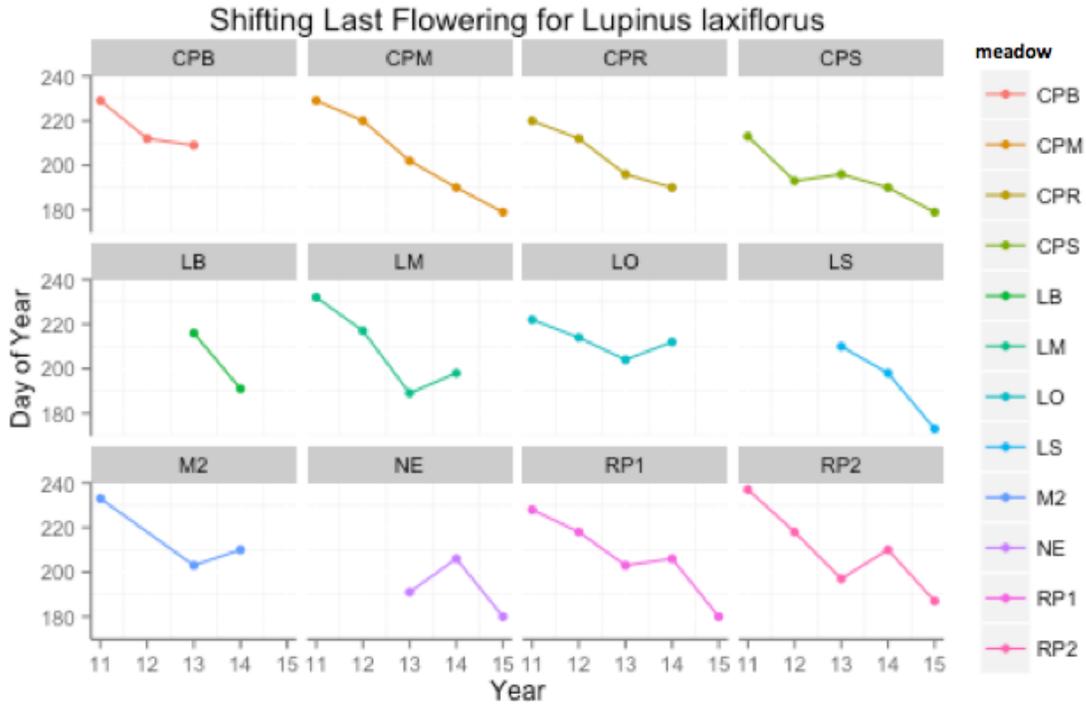


Figure 14. The shifts in timing of flowering and the availability of flowering estimates vary within an individual plant species by meadow location and by first, peak, or last flowering. Here, the plant *Lupinus laxiflorus* experiences changes in timing of last flowering that do not exactly match the changes in timing of first flowering. For example, in the meadow CPM, last flowering shifts by more days than does first flowering, and in a more linear fashion. Furthermore, there are much fewer estimates for first flowering for this plant than there are for last flowering.

The timings of first, peak, and last flowering have all shifted earlier over time (Figure 15). For first flowering, the difference in the median timing between 2011 and 2015 was -29.5 days. For peak flowering, the difference in the median between 2011 and 2015 was -29 days. For last flowering, the difference in the median was -42 days. The One-Way ANOVA tests with Tukey multiple comparisons for each of first, peak, and last flowering showed that there is a statistically significant difference (p -value < 0.05) in the mean timing between years, except for 2013-2014. For first flowering, the 95% confidence interval for the true difference between 2011 and 2015 is -35.6 to -23.6 days. For peak flowering, the 95% confidence interval for the difference between 2011 and 2015 is -35.7 to -28.4 days. For last flowering, the 95% confidence interval for the difference between 2011 and 2015 is -41.6 to -33.9 days.

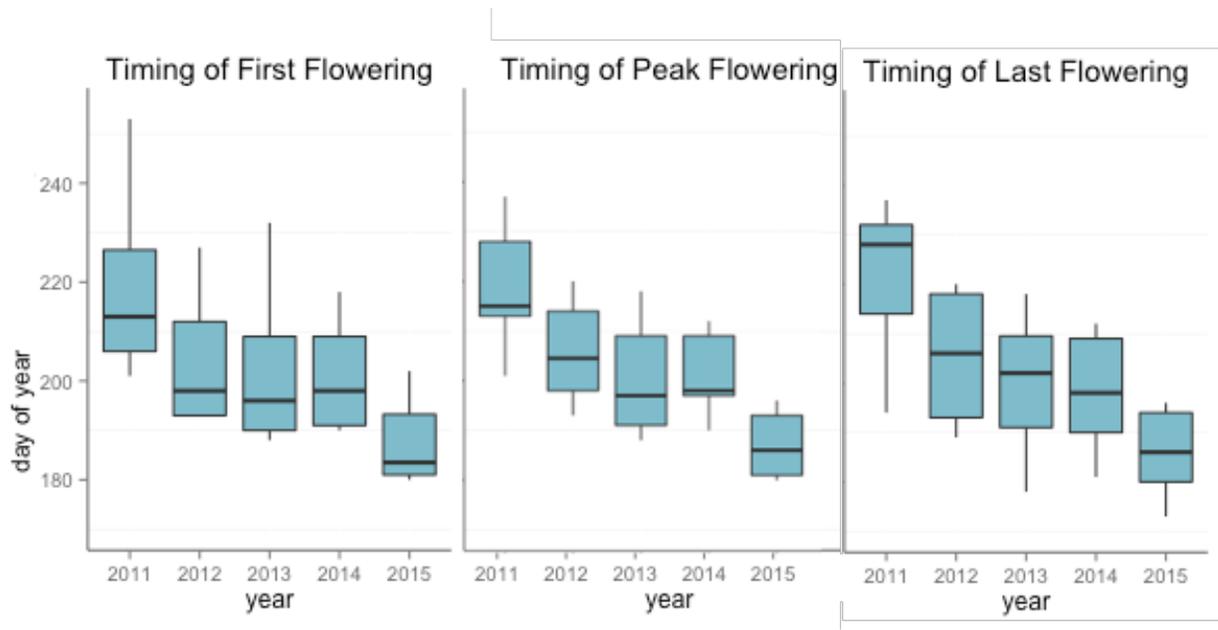


Figure 15. Day of year of first flowering (left), peak flowering (middle), and last flowering (right). All three timings of flowering shifted earlier over the five-year period. For first flowering, the median values from 2011 to 2015 were 213, 198, 196, 198, and 183.5, chronologically. For peak flowering, the median values from 2011 to 2015 were 215, 204.5, 197, 198, and 186. For last flowering, the median values were 228, 206, 202, 198, and 186. The difference in the medians between 2011 and 2015 was 29.5 days for first flowering, 29 days for peak flowering, and 42 days for last flowering.

Although the median timing of first, peak, and last flowering all shifted earlier over time, they did not shift consistently with each other over the entire five years (Figure 16). Unlike the

above boxplots (Figure 15), this figure only includes plant-meadow data points that are common to first, peak, and last flowering estimates. From 2011 to 2012, last flowering shifted earlier by more days than did peak flowering or first flowering. In fact, in 2014 the median timing of peak flowering and of last flowering occurred on the same day. Over the five years, the median timings of first, peak, and last flowering grew temporally closer to each other.

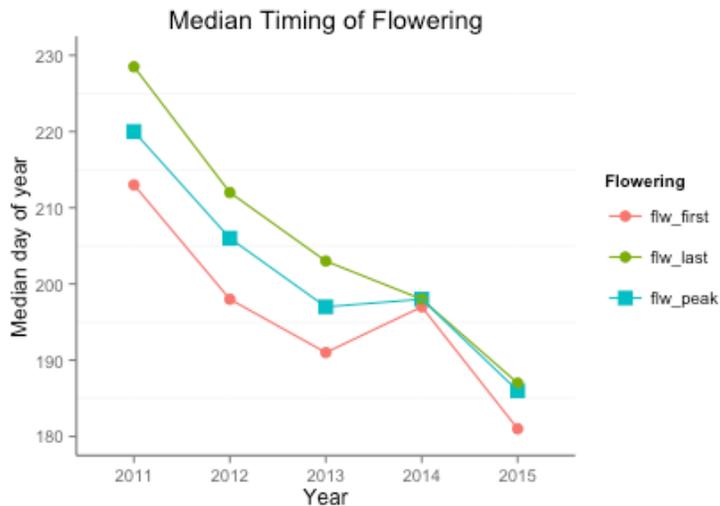


Figure 16. Median timing of first flowering, peak flowering, and last flowering from 2011 to 2015. Each shifts earlier over time, but the three measures of timing of flowering do not shift uniformly or consistently with each other.

Pollinator phenology

The timing of peak interactions between plants and pollinators has also shifted earlier over time (Figure 17). The median value of the day of peak interactions from 2011 to 2015 decreased by 39 days (from August 7 to June 29). The One-Way ANOVA test with Tukey multiple comparisons showed that there is a statistically significant difference (p -value < 0.05) in the mean timing between years except for 2013-2014. The 95% confidence interval for the true mean difference between 2011 and 2015 is -36.8 to -31.2 days.

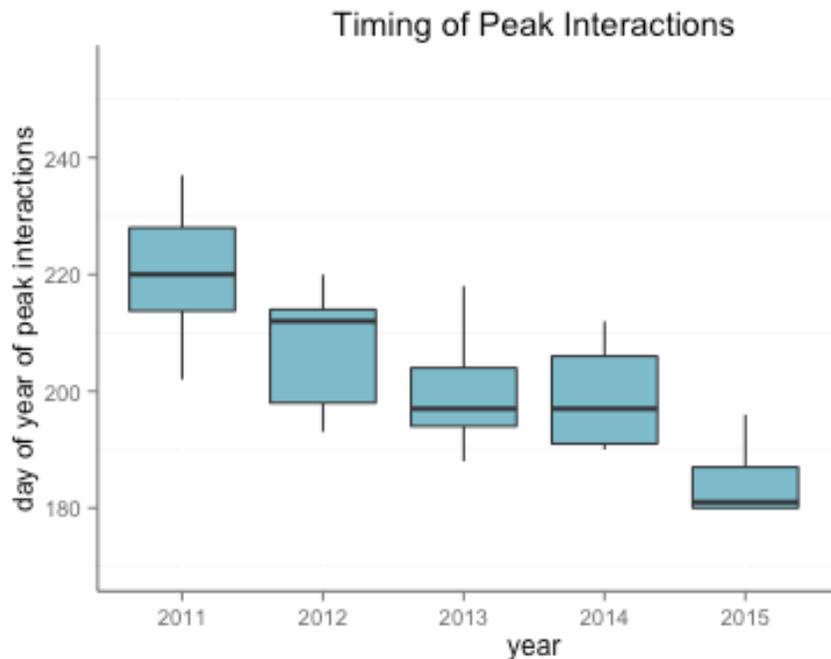


Figure 17. The day of year at which the number of interactions peaks, from 2011 to 2015, summarized for all plant-pollinator-meadow data points. The median values from 2011 to 2015 were 220, 212, 197, 197, and 181. The timing of peak interactions shifted earlier over time, with a difference of -39 days in the median between 2011 and 2015..

Plant-pollinator synchrony

The median timing of peak interactions matched exactly with the median timing of peak flowering in 2011, but then diverged (Figure 18). In 2014, the median dates did match up within one day of each other, but separated again in 2015. The median timings differed by 6 days in 2012 and by 5 days in 2013 and in 2015. Note that this figure only includes the data points of plant-meadow pairs that have estimates for both peak flowering and peak interactions.

The linear regression model relating the timing of peak interactions to the timing of peak flowering had an R-squared value of 0.30 and an equation of: $(\text{Day of Peak Interactions}) = -0.32 + 0.41 * (\text{Day of Peak Flowering})$. The coefficient had a p-value < 0.001 . So, the timing of peak flowering explains about 30% of the variability in timing of peak interactions. The equation tells us that for every increase of one day in timing of peak flowering, there is an increase of 0.41

days in the timing of peak interactions. Including a variable for year did not improve the fit of the model. A model with variables for year, plant species, pollinator species, and meadow yielded an R-squared value of 0.37 with the coefficient on timing of peak flowering as 0.39 and a p-value < 0.001.

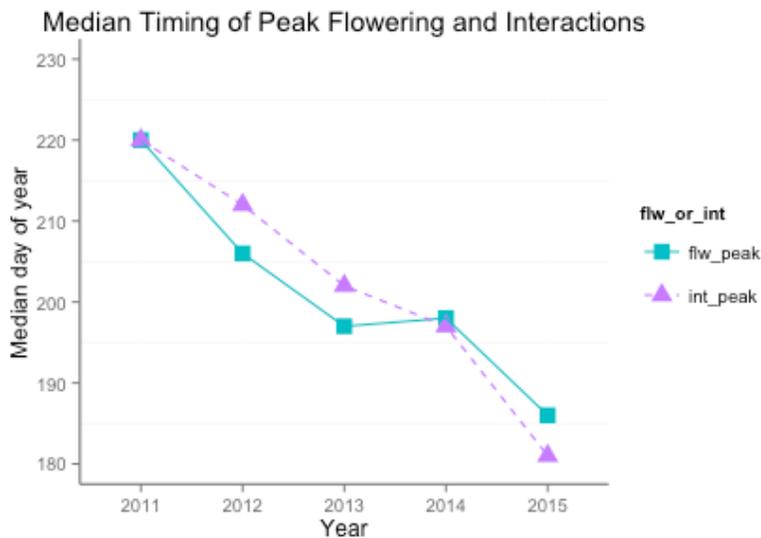


Figure 18. Median day of year of peak flowering and of peak interactions, from 2011 to 2015. Both timings shifted earlier over the five-year period and matched up closely in only 2011 and 2014. The median dates of peak flowering and peak interactions lined up exactly in 2011 and within one day of each other in 2014. The timings differed by 6 days in 2012 and by 5 days in 2013 and in 2015.

Finally, the boxplot of temporal mismatches between peak flowering and peak interactions across the years did not show clear asynchronies (Figure 19). The median mismatch was zero for all five years. However, the mismatches in 2011 were concentrated more in the negative region, indicating that peak interactions occurred later than peak flowering did. By contrast, the mismatches in 2013 were more concentrated in the positive region, with peak interactions occurring earlier than peak flowering. Although the median timing of peak interactions was 5-6 days earlier than the median timing of peak flowering in 2012 (Figure 18), the median mismatch is zero in 2012. Median mismatch is perhaps a better measure because it

looks at the specific mismatches across plant-pollinator-meadow data points instead of taking the difference between the median timing of flowering and median timing of interactions. The results of the ANOVA test showed that the only pair of years with a statistically significant difference in mean mismatch was 2011-2013, with a 95% confidence interval of 0.0 to 4.7 days.

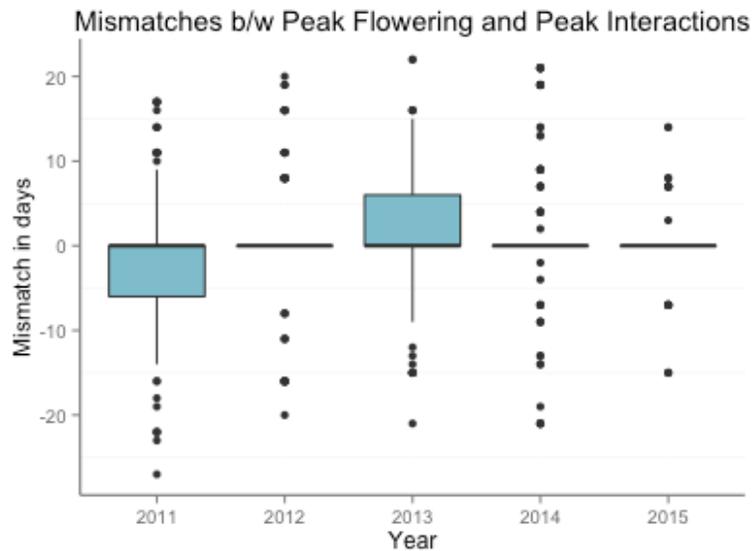


Figure 19. Boxplot of mismatches (difference in day of year) between peak flowering and peak interactions, across all plant-pollinator-meadow data points. Positive mismatches mean that peak flowering occurred later than peak interactions. The median mismatch was zero for all five years. The mismatches were more negative in 2011 and more positive in 2013.

Changes in flower and interaction counts

There was a decline in the flower abundances at the timing of peak flowering over the five-year period (Figure 20). The median values for the log fractional change in abundance show that from 2011 to 2015, the flower abundances decreased by 67.8%. Year-to-year, the abundances decreased by 25% from 2011 to 2012, increased by 12% from 2012 to 2013, increased by 6% from 2013 to 2014, and then decreased by 23% from 2014 to 2015. The 95% confidence interval for the true mean fractional change in abundance from 2011 to 2015 is a decline of 50 to 77%. The mean absolute change in flower abundance per species from 2011 to 2015 was -166.4 to -71.3 (95% confidence interval).

Similarly, the number of interactions at the timing of peak interactions decreased over time (Figure 21). Based on the median values, the number of interactions decreased by 73% from 2011 to 2015, calculated from the median in Figure 25. Year-to-year, interactions decreased by 75% in the first year, then increased by 99.9%, increased by 8%, and then decreased by 50% for 2015. The 95% confidence interval for the true mean change in interaction counts from 2011 to 2015 is a decline of 53 to 76%. The mean absolute change in interaction counts per species from 2011 to 2015 was -61.2 to -5.5 (95% confidence).

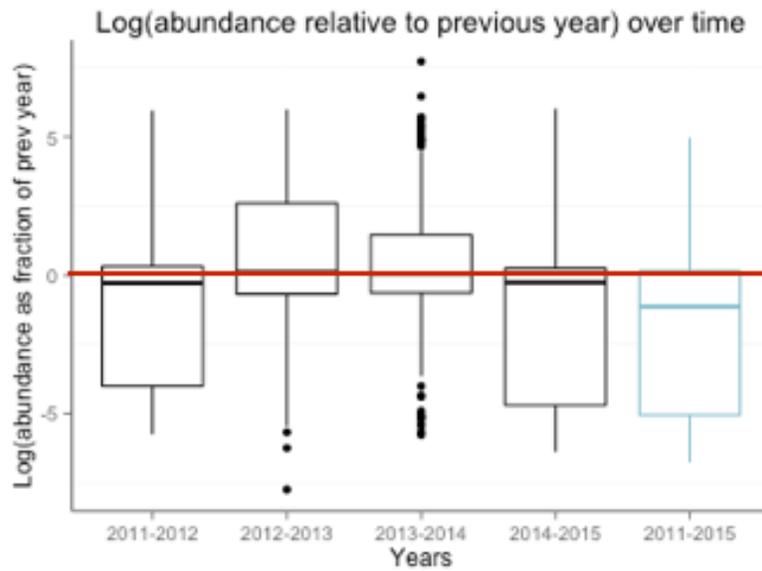


Figure 20. For sequential pairs of years, the log of the flower abundance of the later year divided by the flower abundance of the baseline year. This is a measure of how the abundances are changing over time. The median values were -0.29 for 2011-2012, 0.11 for 2012-2013, 0.06 for 2013-2014, -0.27 for 2014-2015, and -1.13 for 2011-2015. These values corresponded to percent changes in abundances of -25%, +12%, +6%, -23%, and -68%, respectively.

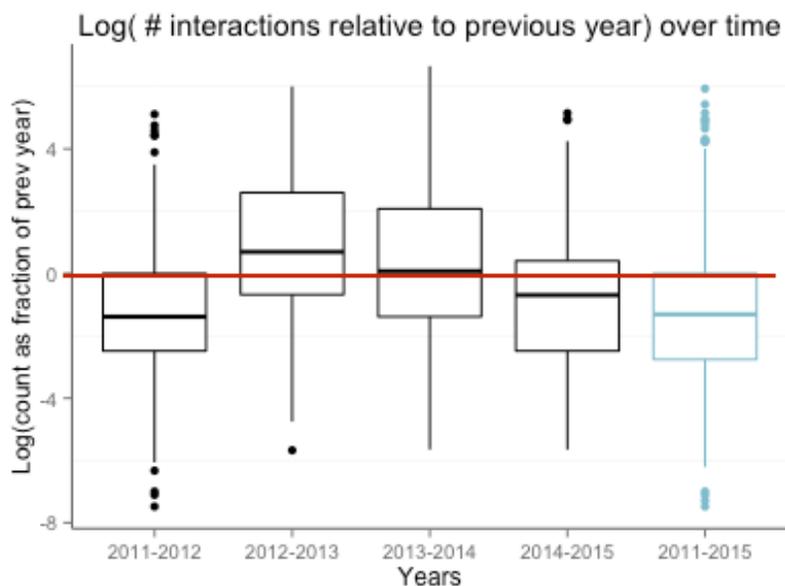


Figure 21. For sequential pairs of years, the log of the number of interactions of the later year divided by the number of interactions of the baseline year. This is a measure of how the interaction counts are changing over time. The median values were -1.4 for 2011-2012, 0.69 for 2012-2013, 0.08 for 2013-2014, -0.69 for 2014-2015, and -1.31 for 2011-2015. These values corresponded to percent changes in counts of -75%, +99.9%, +8%, -50%, and -73%, respectively.

Examples of specific plant-pollinator responses

The following are a few examples of plant-pollinator pairs that experience different responses over the five-year-period.

For instance, the number of interactions between the plant *Eriophyllum lanatum* and the honeybee *Apis mellifera* increased over time, by 632% from 2011 to 2015 (the counts in 2011 are 14% of the counts in 2015) (Figure 22). The flower abundances increased from 2012 to 2014 and decreased in 2015, but the abundance in 2011 was about the same as in 2015. The timing of peak flowering seemed to diverge from the timing of peak interactions in 2011 and 2013, but returned to synchrony in 2014 and 2015, although some degree of asynchrony might be inherent to the ecological system (such as the 2011 mismatch).

Similarly, the interactions between *Boykinia major* and *Apis mellifera* increased by 128% from 2013 to 2015, after no recorded interactions in 2011 and 2012 (Figure 23). The flower

abundances increased by 36% from 2013 to 2015. The timing of peak interactions matched the timing of peak flowering in 2013 but was about two weeks apart in 2014 and 2015.

On the other hand, the interactions between *Gilia capitata* and *Apis mellifera* decreased by 96% from 2011 to 2013, the only years with estimates (Figure 24). The flower abundances also declined slightly, by 45% from 2011 to 2014. Interestingly, the timing of peak flowering and timing of peak interactions occurred in synchrony from 2011 to 2013. So even with apparent synchronies between plants and pollinators, the populations could still be suffering. In 2014, peak flowering seemed to shift much later to day 206, but it's important to note from the raw data that on day 188 (which is earlier than the peak day in 2013) of that year there was a high flower abundance that was almost as high as on day 206, so perhaps natural observational error prevented an accurate estimate of the peak timing. Such possibly inaccurate estimates could cause under-predictions of shifts in overall flowering phenology. The raw data also show that peak flowering in 2015 occurred no later than day 174 (the actual date could not be estimated for this year), so the flowering is definitely shifting earlier over time. The plant *Gilia capitata* appears to be an earlier-flowering plant than *Eriophyllum lanatum*.

The interactions between *Potentilla gracilis* and *Apis mellifera* decreased by 73% from 2011 to 2015 (Figure 25). The timing of peak flowering and peak interactions matched up in 2011, differed by 16 days in 2012, differed by 6 days in 2013, and then matched up exactly in 2015. Although the plant-pollinator pair was synchronized in 2015, the interaction counts were much lower.

The interactions between *Sedum oreganum* and *Apis mellifera* are an example of complex changes over the five-year period (Figure 26). The number of interactions increased, decreased, increased, and then decreased again, while the flower abundances also varied year-to-year. This

plant-pollinator pair could exemplify a one-year lag between changes in quantity of interactions and changes in flower abundances. After low interaction counts in 2011, the flower abundances decreased in 2012. After higher interaction counts in 2012, the flower abundances increased in 2013. With lower interaction counts in 2013, flower abundances decreased in 2014 to a new low. Despite the changes in counts, the timings of peak flowering and peak interactions matched up for all years except 2013 when the honeybees were out much earlier than the flowers. (In 2015, there is not an estimate for timing of peak flowering or timing of peak interactions but the raw data suggest both are ≤ 179). Because of the variability in counts for this plant-pollinator pair, quantifying population health proves difficult.

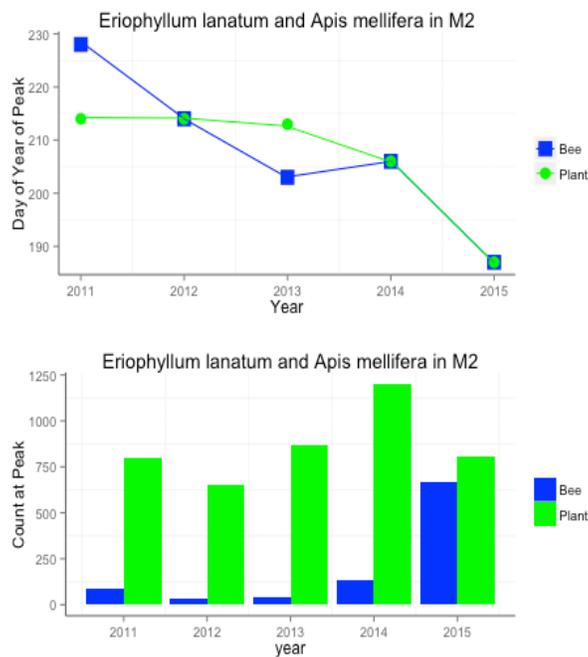


Figure 22. Day of year of peak flowering for *Eriophyllum lanatum* and of peak interactions between *E. lanatum* and *Apis mellifera* from 2011 to 2015 in meadow M2 (top). Flower abundance of *E. lanatum* at timing of peak flowering and number of interactions at timing of peak interactions for *A. mellifera* and *E. lanatum*, from 2011 to 2015 (bottom). The day of year of peak flowering from 2011 to 2015 is 214, 214, 213, 206, and 187, chronologically. The day of year of peak interactions is 228, 214, 203, 206, and 187, from 2011 to 2015. The corresponding flower abundances are 800, 650, 865, 1203, and 809. The corresponding interaction counts are 91, 31, 37, 130, and 666.

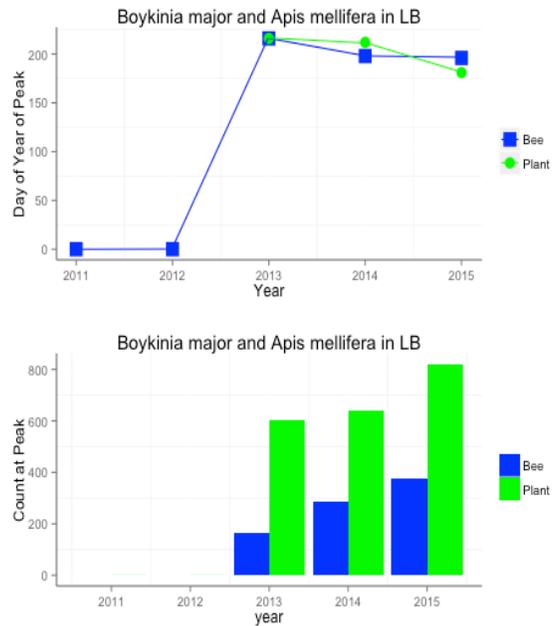


Figure 23. Day of year of peak flowering for *Boykinia major* and of peak interactions between *B. major* and *Apis mellifera* from 2011 to 2015 in meadow LB (top). Flower abundance at timing of peak flowering and number of interactions at timing of peak interactions, from 2011 to 2015 (bottom). The zero values for day of peak interactions indicates that no observations of these interactions were recorded the entire summer. The day of year of peak flowering from 2013 to 2015 is 216, 212, and 181. The day of year of peak interactions is 216, 198, and 196, from 2013 to 2015. The corresponding flower abundances are 602, 639, and 821. The corresponding interaction counts are 165, 286, and 377.

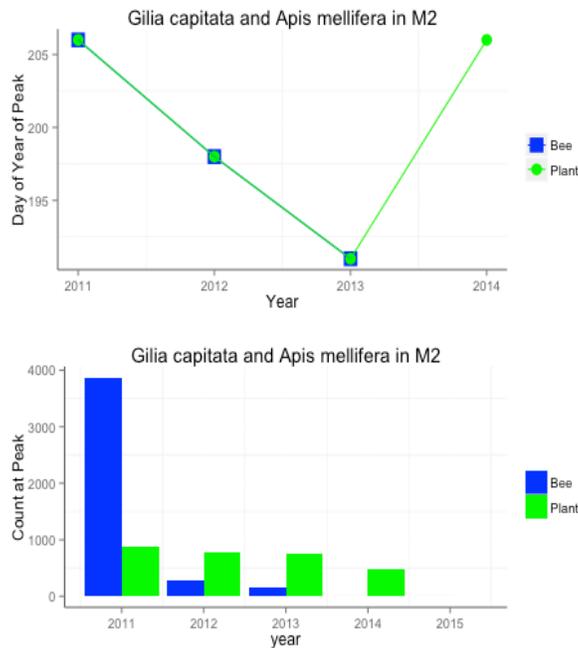


Figure 24. Day of year of peak flowering for *Gilia capitata* and of peak interactions between *G. capitata* and *Apis mellifera* from 2011 to 2015 in meadow M2 (top). Flower abundance at timing of peak flowering and number of interactions at timing of peak, from 2011 to 2015 (bottom). The timing of flowering and interactions match up from 2011 to 2013. The days of peak flower abundance, chronologically from 2011 to 2014, are 206, 198, 191, and 206. The days of peak interaction accounts are 206, 198, and 191, from 2011 to 2013. The corresponding flower abundances are 876, 766, 749, and 482. The corresponding interaction counts are 3872, 268, and 158.

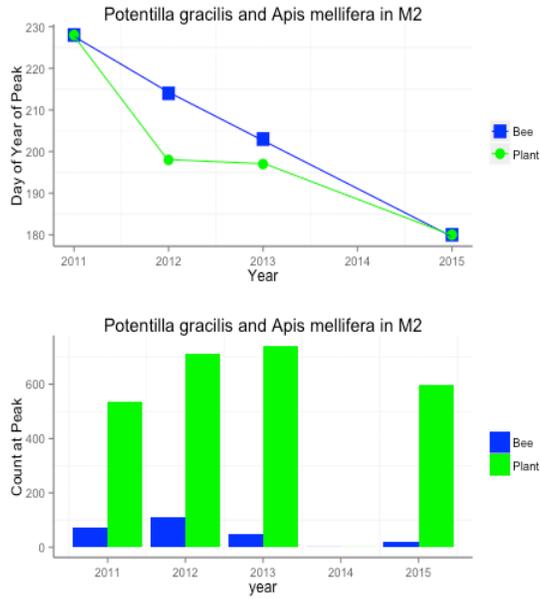


Figure 25. Day of year of peak flowering for *Potentilla gracilis* and of peak interactions between *P. gracilis* and *Apis mellifera* from 2011 to 2015 in meadow M2 (top). Flower abundance at timing of peak flowering and number of interactions at timing of peak interactions, from 2011 to 2015 (bottom). The timing of flowering and interactions matched up in 2011, diverged in 2012 and 2013, and then matched up again in 2015. The peaks in 2014 could not be estimated. The days of peak flower abundance, chronologically, are 228, 198, 197, and 180. The days of peak interaction counts are 228, 214, 203, and 180, chronologically. The corresponding flower abundances are 538, 709, 742, and 596. The corresponding interaction counts are 74, 110, 49, and 20.

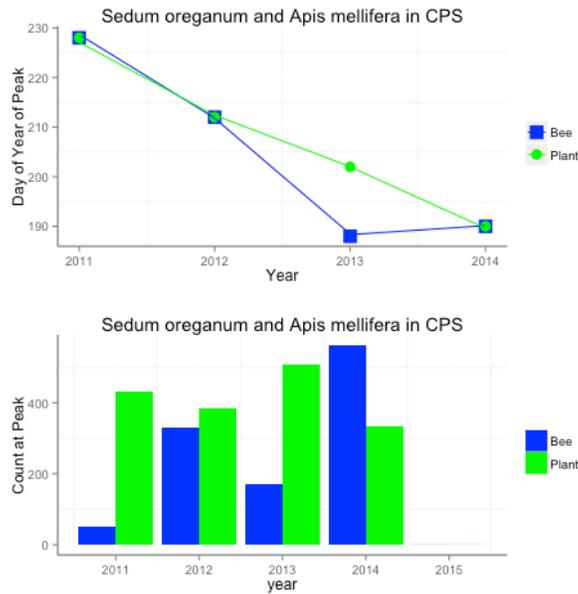


Figure 26. Day of year of peak flowering for *Sedum oreganum* and of peak interactions between *S. oreganum* and *Apis mellifera* from 2011 to 2015 in meadow M2 (top). Flower abundance of *S. oreganum* at timing of peak flowering and number of interactions at timing of peak interactions for *A. mellifera* and *S. oreganum*, from 2011 to 2015 (bottom). The day of peak flower abundance from 2011 to 2014 is 228, 212, 202, and 190, chronologically. The corresponding flower abundances are 432, 385, 508, and 333. The day of peak interaction counts from 2011 to 2014 is 228, 212, 188, and 190. The corresponding interaction counts are 50, 330, 171, and 563.

Multiple regression models

The model for predicting the timing of peak interactions produced an R-squared value of 0.82 with a p-value < 0.001. With backward stepwise modification of the model to eliminate any insignificant variables ($p > 0.05$), the significant predictors were cumulative degree days, timing of peak flowering, and plant species. The insignificant predictors were snowmelt (probably because of the high correlation to CDD), number of interactions at peak, meadow, and pollinator species. The equation was: (Day of Peak Interactions) = $139.9 - 0.1 * \text{CDD} + 0.45 * (\text{Day of Peak Flowering}) + k * (\text{Plant})$, where k is a coefficient that varies depending on the plant species.

The model for predicting the timing of peak flowering produced an R-squared value of 0.75 with a p-value < 0.001. The significant predictors were cumulative degree days, snowmelt, and plant species. The insignificant predictors were flower abundance at peak, number of interactions at peak, meadow, and pollinator species. The equation was: (Day of Peak Flowering) = $205 - 0.12 * \text{CDD} + 0.17 * \text{snowmelt} + k_1 * (\text{Plant})$.

These two models with high R-squared values explain a significant amount, about three-quarters, of the variability in timing of peak flowering and timing of peak interactions.

The models for predicting the counts of flowers and interactions did not fit quite as well. The model for predicting the percent change in number of interactions between years using variables for the difference in timing of peak between those two years, the difference in CDD between those two years, the difference in snowmelt timing, the pollinator species, the plant species, and the meadow had an R-squared value of 0.40 and $p < 0.001$. By contrast, the model for predicting the fractional change in abundance of flowers between years using equivalent variables (except for pollinator species) had an R-squared value of 0.23 and a p-value of 0.1. With backward stepwise modification, only meadow was a significant predictor for the percent

change in number of interactions, while there were no significant predictors for flower abundances. The model for change in interaction counts did improve when instead predicting the log fractional change in number of interactions (R-squared = 0.59, $p < 0.001$), with significant predictors of CDD and meadow (R-squared = 0.27, $p < 0.001$). The model did not improve for the log fractional change in flower abundances (R-squared = 0.07).

Summary

Figure 27 provides a summary of the changes in timing of peak flowering, timing of peak interactions, number of interactions, and number of flowers from 2011 to 2015. Generally, the timing of peak flowering and timing of peak interactions shifted earlier each year, although at varying rates. The largest shifts occurred 2014-2015, while there was not much of a shift from 2013 to 2014. The counts of flowers and interactions followed approximately the same trend, with decreases from 2011 to 2012, large increases from 2012 to 2013, slight increases from 2013 to 2014, and decreases again from 2014 to 2015.

Figure 28 shows a similar summary but of the changes in each year 2012-2015 relative to 2011. This figure illustrates that although there were large increases in interaction counts from 2012 to 2013, the counts never actually surpassed 2011 levels. The counts of flowers and interactions had lower levels in all years compared to 2011, but slightly recover in 2014 before declining significantly again. It's important to note that this "recovery" in 2014 could actually be a sign of population suffering if the pollinators were simply more active because they struggled to find sufficient pollen.

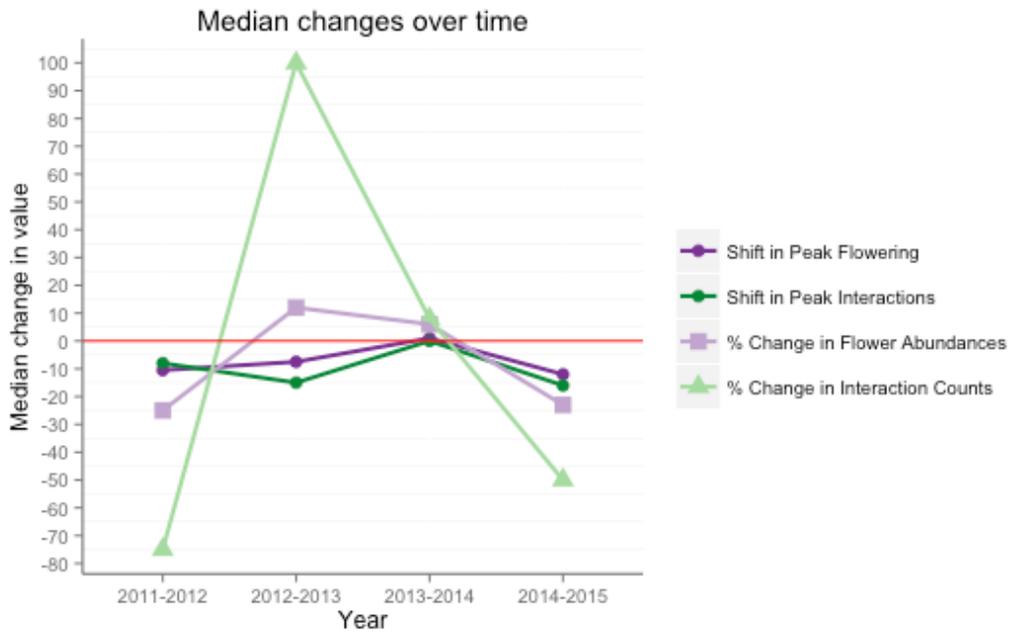


Figure 27. Summary of the changes occurring year-to-year from 2011 to 2015, specifically the shift in median timing of peak flowering, shift in median timing of peak interactions, percent change in flower abundances, and percent change in number of interactions.

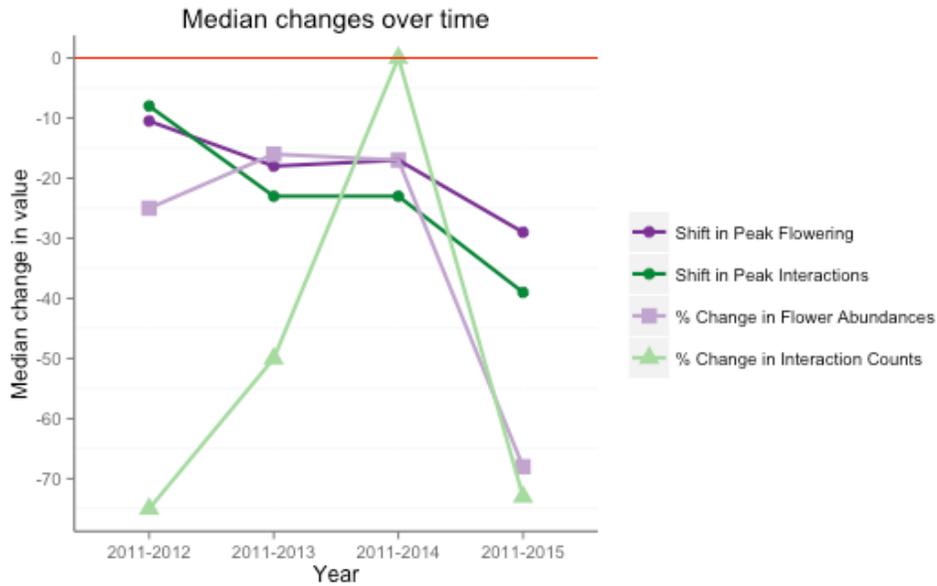


Figure 28. Summary of the changes occurring between 2011 and each year from 2012 to 2015, specifically the shift in median timing of peak flowering, shift in median timing of peak interactions, percent change in flower abundances, and percent change in number of interactions.

IV. Discussion

Discussion of results

Average annual temperatures are gradually increasing over time. In the period from 2011 to 2015, the years that my data span, cumulative degree days (on June 1) increased steadily and drastically. The timing of springtime snowmelt also shifted almost linearly to over two months earlier in spring. Although there are not enough years of data to discuss long-term climate change in the region, the meadows at the study site have definitely experienced local variability in climate.

The results confirm my hypothesis that plants have begun to flower earlier over time. First, peak, and last flowering all shifted by about a month over the five-year period. However, last flowering shifted by the most days while first flowering shifted by the fewest. Peak flowering and particularly last flowering could have changed the most because of plant intolerance of increasingly hot late-summer temperatures. In fact, these three flowering events all closely overlapped in 2014. Such an overlap could occur if the plants cannot flower for as long of a period as they normally do, because of warming temperatures. One study of a 39-year dataset of flowering phenology in the Colorado Rocky Mountains showed that first, peak, and last flowering rarely shift uniformly with each other (Figure 28). Many studies only evaluate the timing of first flowering and fail to address peak or last flowering or changes in abundance, but this overlooks the species that experience shifts in phenology other than in first flowering (Caradonna *et al.*, 2014).

Interestingly, although the timing of snowmelt shifted by over two months, flowering phenology only shifted by about one month. This suggests that there could be an upper limit on the extent to which flowering can shift earlier, or that plants are not exclusively sensitive to the

timing of snowmelt. As mentioned in the introduction, snowmelt could simply be a prerequisite for plants to begin growing, after which the temperatures determine the exact phenology (Forrest & Thomson, 2011).

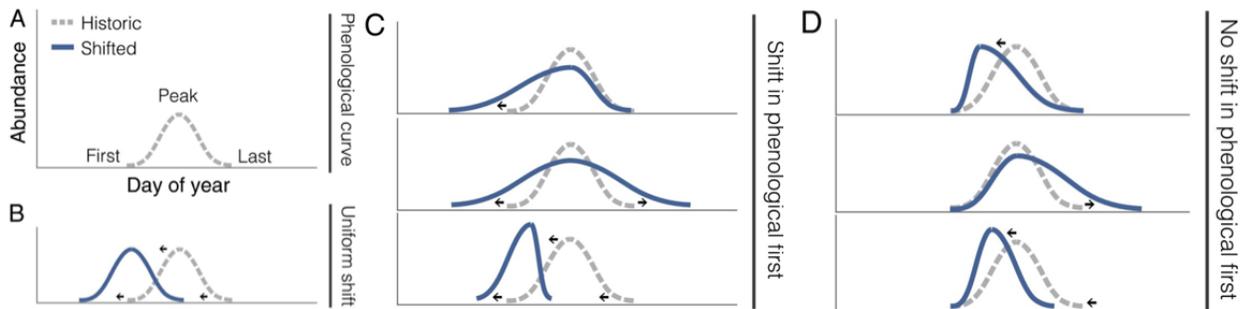


Figure 29. Diagram from CaraDonna et al 2012. "Conceptual representation of shifts in multiple phenological measures for individual species through time. (A) Multiple measures of flowering phenology available for 60 species from a 39-y study of a plant community in the Colorado Rocky Mountains, USA." (B-D) provide examples of the variability in how a phenology curve can shift over time.

The timing at which the number of interactions between plants and pollinators reach their peak also shifted by about a month earlier over the five-year period. In fact, the timing of peak interactions shifted earlier for all the pollinator species with estimates. Because peak flowering shifted earlier by 28 to 36 days (95% confidence interval) and peak interactions shifted similarly by 31 to 37 days, we can conclude that there doesn't seem to be a large system-wide temporal mismatch between the plants and the pollinators. Between 2013 and 2014, there was not a significant shift in timing of peak flowering, and neither was there a significant shift in timing of peak interactions. The pollinators appear to have either adapted to earlier flowering, responded directly to the climate variability, or more likely a combination of the two. Furthermore, looking more closely at the calculated mismatches between plants and pollinators over the five years showed that there was no statistically significant mismatch over the years.

Despite this sustained synchrony between plants and pollinators, the populations still might be suffering. The number of flowers at the peak decreased by 50 to 77 percent (95% confidence interval) per plant species over the five years. However, quantifying the damage of

this decline and knowing at what point a species could go extinct is difficult. Similarly, the number of interactions at the peak decreased by 53 to 76% (95% confidence interval).

Interestingly, counts of flowers and interactions changed in the same direction each year. I would have suspected there to be a lag between a change in the pollinator populations and a change in the plant populations (e.g. the decreased pollinator counts in 2012 would result in fewer plant offspring in 2013), but perhaps both pollinator and plant populations are responding primarily to climate variability at the individual level. Or, perhaps the plants have adapted by self-fertilizing, in the short-term at least, and so can reproduce even with low pollination rates by pollinators.

Changes in abundances are also difficult to interpret because an increase or a decrease might both be a sign of negative sign for the population. For instance, there might be more pollinators out foraging for pollen simply because they are desperate to find sufficient pollen, in which case we might wrongfully conclude that an increase in interactions is a good sign. Similarly, maybe there are more flowers with available pollen because few pollinators are visiting them and taking the pollen.

The phenological shifts and changes in abundances do vary at the species level, which is important for analyzing whether some species will adapt while others will suffer. For example, *Apis mellifera* (honeybee) and *Eriophyllum lanatum* seemed to synchronize in 2012 and again in 2014-2015. For this plant-pollinator pair, the timing of peak interactions shifted earlier sooner than did timing of peak flowering, which suggests that maybe climate change is the primary cause behind shifts in pollinator phenology. The number of interactions over time increased almost exponentially. Perhaps this increase occurred because the honeybees have adapted over time, or more likely, the honeybees needed to compensate for limited availability of flowers and limited pollen availability on each flower by foraging more.

By contrast, *Apis mellifera* and *Gilia capitata* were synchronized from 2011 to 2013, but the number of interactions and the number of flowers decreased over time. Analyzing these two plant-pollinator pairs together, *Apis mellifera* with *E. lanatum* and with *G. capitata*, it seems like *A. mellifera* might be adapting by switching the plant species to which it visits. In other words, *Gilia capitata* generally flowers earlier than *E. lanatum*, so the honeybees are likely interacting more with *E. lanatum* as *G. capitata* shifts out of the activity window of *A. mellifera* and as *E. lanatum* shifts more towards the time interval in which *G. capitata* used to flower. Such adaptations could be key for the robustness of plant-pollinator networks as a whole.

A similar trend occurred in species that flower later in the season. The interactions between *A. mellifera* and *Potentilla gracilis* have decreased over time, while the interactions with *Boykinia major* have increased. *Boykinia major* and *Potentilla gracilis* are both later-flowering species, but *P. gracilis* shifted earlier by a larger amount of days (about 50 days in meadow M2). In 2013 and 2014, the timing of peak flowering of *P. gracilis* was about two weeks earlier than that of *B. major*. So, *A. mellifera* could prefer *B. major* as *P. gracilis* shifts out of its late-summer activity window. These two plants pollinated by *A. mellifera* could be another example of the honeybees pollinating whichever flowers are available during their periods of activity.

The multiple regression models with high R-squared values suggest that timing of peak interactions and timing of peak flowering are indeed very correlated, and that these phenologies relate to warming temperatures. The timings varied by plant species, as expected because of differential temporal periods of flowering. The timing of peak flowering also related to meadow location, probably because the meadows have different aspects and elevations, which affect warming and snowpack. The models did not fit as well for predicting flower abundances or

number of interactions, maybe because these measures are more sensitive to human observation error or because the direction of change in the counts is biologically more challenging to predict.

Limitations of analysis

Primarily, this analysis lacks sufficient years of data to accurately predict species' responses to climate change over the long-term. Moreover, the estimates for first, peak, and last timing naturally had uncertainties because the data points generally occurred about a week apart for a given meadow. However, this research serves as a preliminary analysis of how species respond to climate variability, and I was lucky to have data during a time period with high variability in local climate.

Furthermore, because flowering phenology is indeed shifting earlier over time, the data collection did not capture as many first (or peak) flower abundances in the later years as it did in 2011. As a result, later-flowering species are better described by the data, which could underestimate the changes in phenology because early-flowering species could be more sensitive to warming early springtime temperatures. For many plant species, particularly in more recent years, the peak recorded flower abundance occurred at the first data point for the summer. In that case, I did not include the estimate of a peak without a shoulder. As a consequence, it's possible that many peak events were not estimated for 2015 because of how early they flowered. In fact, the number of plant species for which the peak flowering could not be estimated because of this problem increased from 6 species in 2011 to 22 in 2015. These species that shifted earlier over time to the point that our data collection did not capture the true peaks included multiple meadows with the common flowers *Eriophyllum lanatum*, *Gilia capitata*, *Lupinus laxiflorus*, *Ligusticum grayi*, and *Delphinium sp.* When using the first data point (the maximum value) as an upper bound for the timing of peak flowering, the median timing of peak flowering for these

species that did not have calculated estimates in 2015 (but did in 2011) was day 174. Since the median timing of peak flowering in 2015 for my data analysis was 186, the exclusion of data points without estimates for true peak flowering indeed under-predicts shifts in phenology. When I included these upper bound estimates in my data analysis, the median values were 214, 198, 195, 197, and 180, from 2011 to 2015 chronologically, as opposed to 215, 204.5, 197, 198, and 186 as reported before. These numbers suggest that peak flowering could have shifted earlier by at least 34 days, instead of 29 days.

Another limitation is that interactions between plants and pollinators are more difficult to capture than are simple counts of flowers in the meadow. The observations are constrained by a 15-minute watch of the meadow plots and are more skewed by the observer's degree of vigilance. Pollinators also change behavior based on the day's weather and frequently stop foraging in shade, clouds, early and late time of day, or too high temperatures. Although data were recorded for these variables, I did not address them in my analysis.

Finally, the data preclude full analysis of how climate variability affects the physical health and numbers of the pollinator populations, the quality of pollination itself, and the quantity and quality of available pollen on each flower. Our definition of an "interaction" for data recording limits analysis, too. An interaction is defined as a pollinator pollinating a flower, but interactions then, by definition, can only occur when the flowers are available. Thus, we cannot fully capture the reactions by pollinators. In particular, the estimate for timing of peak interactions may simply be a reflection of the timing of peak flowering because observations of interactions are more frequent when there are flowers in bloom. As a result, my analysis could under-predict mismatches between plants and pollinators. In addition, my insights into pollinator behavior from working in the meadows in the summer of 2015 could not be described in the

data. As the meadows began to dry out in late June, my pen would be poised to jot down an interaction between a plant and a pollinator, but each pollinator would only creep up to a flower before buzzing off again, clearly dissatisfied at the lack of pollen available on the flowers. Multiple pollinators would be buzzing aimlessly around like this, clearly searching for sustenance that was not readily accessible. Since the pollinators never actually landed on the flowers, or landed briefly without pollinating, these behaviors were not recorded in the data. As such, coupling data analysis with physical experience observing the ecological system at work provides a better understanding of overall disruptions and changes.

V. Conclusion

The plants and pollinators in the H.J. Andrews Experimental Forest have indeed responded to climate variability. Contrary to my original hypothesis that the plant-pollinator networks would develop significant asynchronies as a result of differential species responses to warming, the data showed parallel shifts in phenology by plants and pollinators. However, the analysis also could have under-predicted mismatches due to the nature of my estimates for phenology, as discussed earlier. Regardless, the population numbers of both plants and pollinators have declined substantially over the past five years alone and raise concerns about the long-term robustness of the networks.

The threat of climate change to wild pollinators exacerbates the susceptibility of our agricultural industry to a global pollination crisis. Many policymakers demand more precise and detailed attribution of pollinator decline to climate change, but Parmesan *et al.* argue that this is not a productive priority for ecological research. Scientists, including the Intergovernmental Panel on Climate Change, already have “very high confidence” that climate change affects wild

species. A more useful direction is to research effective policy approaches and to implement conservation measures already prescribed by scientists (Parmesan *et al.*, 2013). Few data currently exist for long-term changes in pollinator populations, so we do not know how looming of a threat is a pollination crisis. This data gap reinforces the need for ongoing monitoring of these plant-pollinator networks, such as at this H.J. Andrews Experimental Forest Long-Term Ecological Research site. With rising global food demand, we simply cannot afford to wait until crop yields start dropping before we take action to protect pollinators (Goulson *et al.*, 2015).

Progress on protective policies has been limited. In the United States, the 2014 Farm Bill expanded funding for pollinator research and the bill H.R. 4790 authorized funding for pollinator foraging habitat on millions of acres of highway rights-of-way. H.R. 2692 suspended registration of neonicotinoids and registration of any pesticide with unreasonable adverse effects on pollinators, while H.R. 5447 established expedited approval by the Environmental Protection Agency (EPA) of pesticides that improve pollinator health (Johnson & Corn, 2015). These recent bills are important steps, but on-the-ground changes will be slow. The EPA will not even conduct its review of current neonicotinoid insecticides until 2019 (Stokstad, 2013). However, worsening collapses of commercial pollinator colonies are incentivizing further action. Maryland, which just banned neonicotinoid use by consumers (although not by farmers) starting in 2018, will be the first state to implement major restrictions to prevent pollinator declines (General Assembly of Maryland, 2016). Unfortunately, these small successes, and even the European Union's moratorium on three neonicotinoids, may not amount to much because farmers merely substitute large quantities of other harmful pesticides (Goulson *et al.*, 2015).

Engaging pollinator biodiversity and planting wildflowers near crops comprise a long-term sustainable approach that would effectively maintain pollination services for agriculture.

Currently, only one or two pollinator species precariously prop up our agricultural industry. This single-species management approach arose in the past because increased land cultivation resulted in fewer nearby natural areas and thus in fewer wild bees to provide crop pollination services (Garibaldi *et al.*, 2014). However, the presence of wild bee biodiversity in agricultural landscapes actually provides higher and more stable global crop yields (Garibaldi *et al.*, 2013). Pollinator biodiversity supplies improved quantity and quality of pollination for multiple reasons. For one, different pollinator species visit crops at different times of the day or year and visit different parts of the crop (Goulson *et al.*, 2015). Species also differ in the length of their tongue, so some species can more effectively pollinate flowers with less accessible pollen. The diversity in flower visiting behavior increases the proportion of flowers setting fruit (the stage after successful fertilization) as well as the size of fruit. Most importantly, the differential species responses to climate change and environmental perturbations provide a buffer against any negative impacts (Garibaldi *et al.*, 2014). In a sense, we can hedge our bets and avoid an agricultural pollination crisis by cultivating diverse wild bee populations.

To enrich cropland with wild pollinators, farmers can simply plant wildflowers. Flowering plants in semi-natural habitat, field margins, or hedgerows near the cropland can support wild bee populations and thus increase crop pollination services (Figure 30). These



Figure 30. Images of wildflower strips and hedgerows in agricultural landscapes. Sources: Jennifer Hopwood, Xerces Society (left); Rachael Long, UC Division of Agriculture and Natural Resources (right).

wildflower areas supply nesting sites (e.g. burrowing into soil or plant stems) as well as food for pollinators during the long periods when the crops are not flowering (Goulson *et al.*, 2015).

Using these methods, wild bee populations proliferate. For California almond orchards, one study showed that wild bees only visited almond flowers in orchards with semi-natural habitat nearby (Klein *et al.*, 2012). Similarly, just a few years after planting wildflowers, blueberry farms in Michigan experienced a greater proportion of flowers setting fruit, larger berry weight, and more mature seeds per berry. The benefits to crop yields outweighed the costs of wildflower seeding and maintenance (Blaauw & Isaacs, 2014). As an added bonus, because pollen from different plant species varies significantly in content of protein, amino acids, lipids, starch, vitamins, and minerals, these pollinators are healthier and less susceptible to pathogens and other harms (Goulson *et al.*, 2015). At the Whole Foods grocery store, you can now actually buy “pollinator-friendly” almonds, harvested from orchards with wildflowers growing amongst the almond trees.

Other field practices can also improve pollinator health. For example, integrated pest management strategies such as crop rotation can reduce the need for pesticides, and no-tillage farming and drip irrigation can prevent the destruction of bee ground nests. However, the off-field practices such as wildflower seeding are likely easier to implement because they do not require fundamental changes to the crop management (Garibaldi *et al.*, 2014).

Pollinator health tightly couples with crop yields, so these sustainable approaches are in the best economic interests of farmers. Because the benefits may sometimes take a couple years to surpass the costs, government-sponsored programs can offer compensation to farmers. Government support is reasonable because of the overall societal benefits of pollinator biodiversity and semi-natural habitat, such as reduced soil erosion, improved pest control,

nutrient cycling, and water use efficiency (Girabaldi *et al.*, 2014). To encourage adoption of these simple farming practices, farmers need clear advice about the economic benefits of wild bee biodiversity (Goulson *et al.*, 2014).

More broadly, we need to consider approaches to mitigate climate change to prevent, among other concerns, irreversible damage to the pollinators we so deeply depend on for global agriculture. But for now, just a few small conservation efforts can yield extensive benefits for both pollinators and agriculture.

VI. Acknowledgments

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