

AN ABSTRACT OF THE THESIS OF

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Title: Climate Variability and Plant-Pollinator Networks in the Cascade Range, Oregon

Abstract approved: _____

Julia Jones

Abstract

Worldwide, networks of plants and pollinators are faced with the threat of climate change. The extent of this threat and the degree of adaptability is not yet understood. In Oregon, climate change is predicted to bring hotter and drier summers which may have consequences for pollinators and the resources they rely on. This study examined a system of wild bees (solitary bees, *Bombus* spp., and feral *Apis mellifera*) and floral resources in montane meadows of the western Cascade Range, where tree encroachment has reduced meadow area by more than half since 1950. The analysis tested how climate variation was related to frequency of flowering, plant-pollinator interactions, plant phenology, and interaction timing over multiple weekly sampling periods in summers of nine years (2011 to 2018, 2021) in ten sub-plots in each of twelve montane meadows ranging from 0.25 to 4.4 ha at 1,308 to 1,536 m elevation in the H.J. Andrews Experimental Forest, western Cascade Range, Oregon. Study sites included mesic (n = 5), wet (n = 2), and xeric (n = 5) meadows in three meadow complexes separated by up to 10 km. Climate and weather were characterized using cumulative degree days and antecedent precipitation from meteorological stations in the Andrews Forest. Network structure was characterized using the bipartite function in R and results were interpreted to assess how climate

variability is related to plant-pollinator network structure. Beta diversity (Sørensen index) was calculated using the betapart function in R and resulting values of turnover and species replacement were related to climate variables to assess how climate may influence network rearrangement via rewiring (defined as adaptations leading to the formation of new mutualistic relationships) and turnover (defined as extirpation or exclusion following the inability of species to adapt).

The most frequently occurring flowering species in the network were *Eriophyllum lanatum*, *Gilia capitata*, and *Orthocarpus imbricatus*. The most frequent pollinators were *Apis mellifera*, *Bombus mixtus*, and *Bombus bifarius*. The most frequent interactions were between *Apis mellifera* and *Gilia capitata* (20% of total), *Apis mellifera* and *Eriophyllum lanatum*, *Bombus mixtus* and *Delphinium nuttallianum*, and *Bombus bifarius* and *Orthocarpus imbricatus*. Species composition and interactions for both bees and flowers varied greatly within and between years in all twelve meadows. Floral abundance and the length of the flowering period were inversely related to heat (cumulative degree days) in mesic meadows but less so in wet meadows and not at all in xeric meadows. Bee abundance was not related to heat (cumulative degree days), and neither flower abundance nor bee abundance was related to moisture.

The network was characterized by high levels of redundancy and significant rewiring (Sørensen's pairwise dissimilarity > 0.5 between all years) in plant-pollinator interactions over time. Most bee species were generalists (meaning they visited multiple flower species), but the network included specialist bee species including *Dufourea calochorti* and *Dufourea trochantera*. Turnover (species replacement) of flowers was positively related to turnover of plant-pollinator interactions. Turnover of flowers was positively related to differences in air temperature between years, but turnover of plant-pollinator interactions was not related to this

measure of climate variability. Although neither bee abundance nor turnover of plant-pollinator interactions was directly related to climate variability, shortened flowering periods during hotter and drier summers associated with climate change may reduce bee abundance and enhance turnover in floral composition, potentially speeding turnover in bees, particularly in specialists, which may not be able to adapt via rewiring.

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Climate Variability and Plant-Pollinator Networks in the Cascade Range, Oregon

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Melinda Vickers, Author

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Dr. Julia Jones contributed to the conceptual development and edits to multiple sections.

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Climate Variability and Plant-Pollinator Networks in the Cascade Range, Oregon

1. INTRODUCTION

1.1. Motivation

In Oregon, climate change is expected to lead to warming temperatures with accentuated warming and drying in summer months (Mote et al., 2010). In the Cascade Range, warming temperatures are leading to earlier spring snowmelt and more spring precipitation in the form of rain instead of snow (Nolin, 2012). Montane environments are home to some of the most fragile ecosystems in the world and thus are expected to experience significant biodiversity loss and habitat contraction with changing climate (Inouye, 2020; Nogués-Bravo et al., 2007).

Meadows are particularly sensitive to variation in temperature and moisture (Debinski et al., 2000). In the western Cascade Range of Oregon, meadows have contracted significantly over the past two hundred years due to a variety of factors including climate change, fire suppression, and the loss of controlled burning by indigenous peoples (Highland, 2011; Miller & Halpern, 1998; Takaoka & Swanson, 2008).

Climate change is leading to substantial biodiversity loss in systems of plants and pollinators (Kudo & Ida, 2013; Mathiasson & Rehan, 2019). Among other factors, warming and fluctuating temperatures pose a serious threat to ectotherms, including bees (Paaijmans et al., 2013). Due to a lack of long-term studies focused on plant-pollinator networks, the extent of this loss and its potential implications are not yet understood, and more research is needed focused on specific climate variables in a variety of locations (Vasiliev & Greenwood, 2021).

Mutualistic interactions may be especially affected by climate change because they rely on spatial and temporal alignment in species life history stages or phenology (Burkle et al., 2013). In plant-pollinator networks, phenological timing is partly regulated by climate and thus

these systems may be highly impacted by climate change (Bartomeus et al., 2011). The concept of temperature-driven phenology is well studied (e.g., Primack et al., 2004; Sevenello et al., 2020). However, the consequences of changing phenology in plant-pollinator relationships are not well documented due to limited data, both in terms of geographic scope and a shortage of long-term studies (Caradonna et al., 2017).

1.2. What is known and gaps in knowledge

1.2.1 Flowering phenology

Worldwide, climate change is shifting flowering times, typically towards earlier flowering (Miller-Rushing et al., 2008). In addition to earlier flowering, different species of plants and pollinators respond at different rates to changing conditions (Theobald et al., 2017). Some species might not shift their phenology at all, while others might shift earlier, lengthen, or shorten their flowering times. Shifts in phenology can cause changes in community structure in ways that are not fully understood (Forrest et al., 2010; Theobald et al., 2017). Changes in flowering and co-flowering timing can alter the period of available resources for pollinators and create new competitive interactions among flower species for pollination services.

In previous research, flower phenology response to climate warming varied by meadow type (xeric, mesic, bog; or dry, moderate, wet) (Debinski et al., 2000, 2010). Flowers in mesic meadows were most impacted by climate change while those in xeric meadows were least affected, likely due to built-in drought resistance (Debinski et al. 2010).

1.2.2. Bees and floral resources

Bees may be directly affected by climate change effects on temperature or moisture, or they may be affected indirectly via changing access to floral resources and changing floral phenology (Ogilvie et al., 2017). Extreme years might play a disproportionate role in shaping these communities (Forrest & James, 2011). Both top-down and bottom-up forces may reshape plant-pollinator communities (Forrest et al., 2010). Such forces could include increased opportunities for parasitism, better climate conditions for non-native species than native species, and others (Ogilvie et al., 2017).

In the Oregon Cascades, climate change is expected to lead to longer summers (Mote et al., 2010). If longer summers lead to longer flowering periods, this could extend the period of bee activity and pollen foraging and flowering (Stemkovski et al., 2020). Based on long-term observations in the Rocky Mountains, researchers have hypothesized that in the event of longer summers, bees could produce two generations within one flowering season, and the second generation of bees would likely be maladapted to winter conditions (Stemkovski et al., 2020). Alternatively, longer summers might shorten flowering periods via heat or drought stress. How these late season, low flower periods may affect bees is not yet understood (Kudo, 2016).

The consequences of climate change will not be uniform across all species of pollinators. Pollinators are either generalists, meaning that they have a wide range and can pollinate a variety of different flowers, or specialists, meaning that they have a small range and are adapted specifically for pollinating certain flowers (Osborne et al., 2008). Specialist pollinators are more effective than generalist pollinators, but because they rely on specific floral resources, they may be less able to adapt to phenological shifts than generalists (Larsson, 2005; Ogilvie & Forrest, 2017).

Furthermore, bees are either social (meaning they live in large colonies with divided labor) or solitary, and this distinction may affect their ability to adapt (Crone, 2013). Unlike solitary bees who only reproduce once per year, social bees can produce multiple cohorts of worker bees within one summer and thus can change their colony size to take full advantage of changes in floral resources (Chole et al., 2019).

1.2.3. Competition and non-native bees

The presence of the non-native European honeybee (*Apis mellifera*) may also influence how ecosystems adapt to climate change. For instance, weather-related declines in floral resources led to *Apis mellifera* outcompeting local *Bombus* spp., leading to a decrease in populations of local bumblebees (Thomson 2016). Furthermore, *Apis mellifera* are less effective pollinators than their native counterparts, and thus the presence of *Apis* within an ecosystem could reduce overall network productivity and the viability of flowering plants (Valido et al., 2019). However, the impacts of introduced honeybees are not uniform across landscapes (Thomson, 2004). More heterogenous landscapes appear to mitigate competition between honeybees and bumblebees (Herbertsson et al., 2016). Competition also varies based on physiological traits. Honeybees compete more with shorter tongued bees than with longer tongued bees, who can shift to deeper floral resources in communities with introduced *Apis* (Walther-Hellwig et al., 2006).

1.2.4. Phenological mismatch

Within a network of plants and pollinators, the phenology of flowers is more likely than that of pollinators to shift earlier in response to warming temperatures, as demonstrated in a

long-term study of plants and pollinators in Rocky Mountain meadows (Forrest & James, 2011). Hence, a warming climate could result in early season flowering with few to no pollinators. There is insufficient research on this subject to determine whether this occurring and, if it is occurring, what the potential consequences might be (Inouye & Wielgolaski, 2013).

Earlier flowering phenology could also lead to partial phenological mismatch or even phenological decoupling. Phenological mismatch occurs when the life history stages necessary for two species to accomplish a mutualistic interaction do not coincide (Visser & Gienapp, 2019). In extreme cases of mismatch, phenological decoupling may occur when the timing of phenological stages of two species in a mutualistic relationship shift so drastically that the mutualistic interaction does not occur (Forrest and James, 2011).

In their observations of plant-pollinator phenology, Forrest and James (2011) concluded that partial mismatches are unlikely to threaten the persistence of populations. However, phenological mismatch does not have to be extreme to be problematic (Kudo & Ida, 2013). Flowers emerging before their pollinators may lead to decreased seed production and changing population dynamics (Memmott et al., 2007). Thus, both phenological mismatch and phenological decoupling are worthy of study.

1.2.5. Network structure

Studying plant-pollinator interactions as a network has become increasingly common in pollinator ecology (Inouye, 2020; Knight et al., 2018). In a network approach, each species within a given ecosystem is a node. Plant-pollinator networks are “bipartite”, meaning that species are connected based on which pollinator interacts with which plant (Ings et al., 2009). Using a network model allows ecologists to study interactions as a community and thus to draw

more contextually relevant conclusions about ecological and evolutionary processes (Vázquez et al., 2009).

Ecological networks tend to be nested, consisting of a core group of generalist species that all interact with each other and a larger group of specialists that only interact with generalists (Vázquez et al., 2009). Networks are highly susceptible to the extirpation of species in the core group and more robust to the extirpation of species with fewer links (Vázquez et al., 2009). Building a network model for an individual ecosystem involves surveying the flowers present in the system and observing which pollinators pollinate which flowers. A greater sampling effort has the potential to reveal more species and more links in the network, and nestedness is less sensitive to sampling bias (tendency to oversample common species) than number of species or links within a network (Nielsen & Bascompte, 2007).

In a study of plant-pollinator diversity and network structure using an aggregation of global data, Doré et al. (2021) found that richness and network structure respond differently to anthropogenic stressors and that a focus on species richness did not fully account for changes in network structure. For instance, networks tend to shift towards generalist species under stress (Burkle et al., 2013). Species richness and network structure respond to different variables with varying consequences, and thus pollinator communities should be studied on a network scale in order to account for all changes occurring within the system (Doré et al., 2021).

Most studies of plant-pollinator networks to date have been largely descriptive, rather than focusing on the drivers of network structure (Knight et al., 2018). Network structure is driven by multiple factors including the spatio-temporal distribution of species, species abundance, and species richness, which in turn are controlled by multiple biotic and abiotic

factors, including climate (Vázquez et al., 2009). Understanding these drivers is essential for answering questions about how global change will affect plant-pollinator interactions.

1.2.6. Rewiring and turnover

In a network of plants and pollinators, changes in species composition (including varying abundances), whether due to phenology, geography, or other mechanisms of exclusion, can lead to adaptation, loss of interactions, or loss of species (Forrest and James, 2011). Adaptation is also referred to as “rewiring.” Rewiring is defined as the appearance and disappearance of mutualistic interactions over time, and it occurs when changes in species co-occurrence create new mutualistic relationships between plants and pollinators that allow them to persist (Caradonna et al., 2017). Changes in species composition and changes in phenology of species can cause rewiring. Networks are adapted to some degree of variation; hence rewiring happens on a somewhat regular basis (Caradonna et al., 2017). If variation increases, more instances of rewiring are likely to occur.

If species are unable to adapt to change, this may result in turnover, which occurs when species are completely excluded from the network, leading to their extirpation (Forrest and James, 2011). Turnover may also lead to rewiring: mutualistic interactions may appear or disappear over time based on the loss or gain of species (Caradonna et al., 2017; Kudo and Ida, 2013). Within a system, rewiring and turnover can occur separately or concurrently (Caradonna et al., 2017).

Several aspects of study design affect the detection of rewiring and turnover. A longer study period that encompasses varied climatic conditions may reveal more instances of rewiring and turnover (Inouye and Wielgolaski, 2013). A longer observation period within each year also

captures more life history stages of flowering plants and their pollinators and more potential instances of partial or total mismatch (Inouye, 2020). Studies that include community-scale observations and analyses are more likely to reveal network changes than those that focus on a single species or mutualistic relationship (Caradonna et al., 2017). Surveys that include the timing of both flowering and pollination can reveal how the timing of interactions is related to floral resource availability (Inouye and Wielgolaski, 2013).

Although plant-pollinator networks may be vulnerable to changes based on delicate phenological relationships, they may also be robust due to a high degree of redundancy in interactions (Burkle et al., 2013). Nevertheless, long-term stress on an ecosystem may lead to turnover that could reduce redundancy in a network (Devoto et al., 2012). Less redundancy could lead to negative consequences such as declines in quality and quantity of pollination services (Fang & Huang, 2012). If enough species are lost, loss of redundancy could make the network more susceptible to phenological mismatch (Devoto et al., 2012).

1.2.7. Previous research

This study focuses on long-term dataset of plant-pollinator interactions taken from 2011-2018 and again in 2021 in the H.J. Andrews Experimental Forest, western Cascade Range, Oregon. Previous research in these meadows focused on plant pollinator interactions and meadow contraction (Dailey, 2007; Helderop, 2015; Highland, 2011; Rice, 2009; Jones et al., 2018; Pfeiffer, 2012; Jones, 2016). These studies found that western Cascade meadows are contracting significantly and are at risk of continued tree invasion. Jones et al. (2018) found that while larger meadows were home to greater species diversity, smaller meadows contributed greatly to landscape-scale diversity. Flowering plants varied greatly both between pairs of nearby meadows

and over time, while pollinators did not vary greatly over space but did vary greatly over time; the mechanisms for this variation are not well understood (Helderop, 2015).

1.3. Research questions

In this study, we used nine years of data on the abundance and phenology of flowers and bee visitors to examine the role of heat and moisture in shaping plant-pollinator networks. Our investigation took place in montane meadows of the western Cascade Range. We used cumulative degree days beginning in mid-March as a proxy for heat accumulation and cumulative antecedent precipitation as a proxy for meadow moisture.

First, we established an ecosystem baseline by asking, (1) How do the abundance, phenology, and interactions within and between bees and flowers vary over time? Then, using this information, we asked (2) To what extent does climate variability (measured through heat and moisture) drive variation in this system? We investigated this by species, by meadow, and for the system as a whole. Finally, we investigated the system using a network model asking (3) How does climate variability shape network structure and to what extent does it drive network rearrangement (via rewiring and turnover)?

2. STUDY SITE

This study took place in montane meadows in the H. J. Andrews Experimental Forest (hereafter Andrews Forest), approximately 60 miles east of Eugene near the town of Blue River, Oregon. A total of 12 meadows in the Andrews Forest was sampled from 2011 to 2018. The study meadows are located between Lookout Mountain and Carpenter Mountain in the western Cascades and range in elevation from 1,308 to 1,536 m (Figure 2.1). The climate of the region is

characterized by wet winters and warm, dry summers. Most precipitation falls between November and March (Takaoka & Swanson, 2008). All the study meadows are snow-covered from October through June, but the snow persists longer on north than on south facing slopes; mean annual snow water equivalent exceeds 0.4 m (Jones et al., 2018).

Meadows are classified as xeric, saturated (or bog), and mesic based on soil depth and soil moisture (Miller and Halpern 1998, Pfeiffer, 2012). The twelve study meadows include mesic (n = 5), wet (n = 2), and xeric (n = 5) meadows in three meadow complexes separated by up to 10 km (Figure 2.1). Meadow size ranges from 0.25-4.4 ha.

The study meadows are dominated by herbaceous species which include both the flowering herbs surveyed in this study as well as grasses and forbs. Bracken fern (*Pteridium aquilinum*) is widespread in some meadows. The meadows are surrounded by a mixed conifer forest dominated by Pacific silver fir (*Abies amabilis*), western hemlock (*Tsuga heterophylla*), western red cedar (*Thuja plicata*), Douglas fir (*Pseudotsuga menzeisii*), grand fir (*Abies grandis*), and mountain hemlock (*Tsuga mertensiana*) (Rice, 2009; Highland, 2011; Jones, 2016). The landscape is primarily composed of mature (150-year-old) and old-growth (500-year-old) forests, but around 25% of the landscape includes forest plantations created in the last century (Jones, 2016).

The origin of these montane meadows is debated, but archeological evidence indicates that indigenous peoples were present and may have used these areas for summer encampments, hunting, and food gathering since the early Holocene (past 10,000 years) (Highland, 2011). Historical fire reconstruction in the study area has revealed the role of wildfire as a major disturbance agent affecting forests over the last millennium (Teensma, 1987), but the role of fire in these meadows is unknown. No fires of 0.1 ha or larger have occurred in or near these

meadows since before 1978 (Takaoka and Swanson, 2008). Prior to colonization, indigenous peoples of the region may have maintained and managed these meadows through intentional burning (Turner et al., 2011). Following colonization up until the mid-twentieth century, these meadows were used as summer pastures for sheep grazing (Highland, 2011).

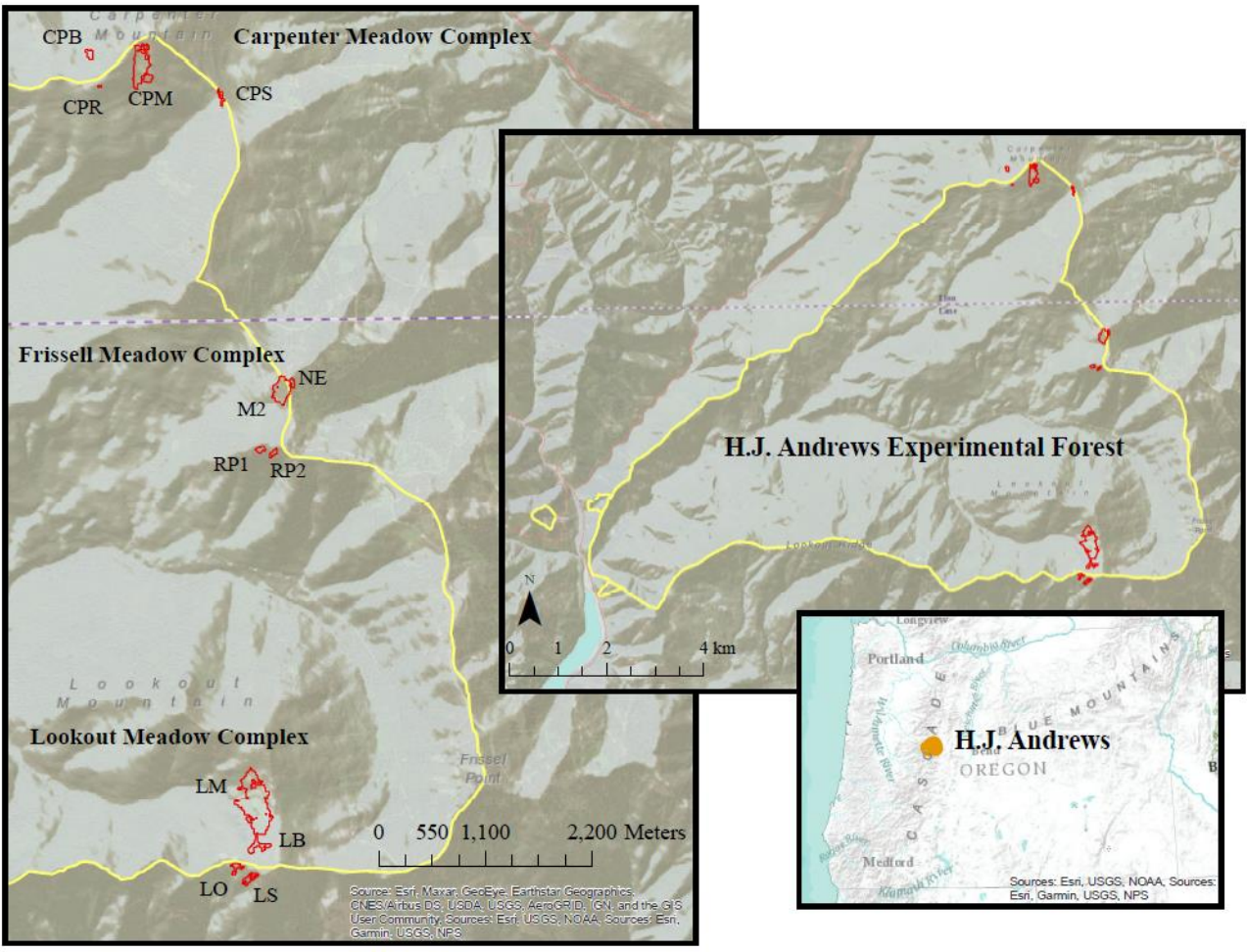


Figure 2.1. Locations of twelve study meadows (two-letter codes) in three meadow complexes in the Andrews Forest and the location of the Andrews Forest in Oregon.

3. METHODS

3.1. Field data collection

The data for this study were collected over a 9-year period from 2011-2018 (Jones, 2022) and in 2021 by the author. Data for 2011 to 2018 included all pollinator visits to flowers, but data collected in 2021 included bees only. Each meadow contains ten, 3 by 3-meter plots marked with metal flagging. Sites have detailed GPS coordinates and plot locations have been maintained since the beginning of the study period. The plots are distributed systematically throughout the meadows (see Pfeiffer, 2012 for more details on the initial sampling design).

In each of the study years, the frequency of flowering plants and pollinator visits to flowers were observed on multiple dates, referred to as “watches” in each plot in the meadows. In each watch, counts were made of all flowers in anthesis (when flowers are opened and sexually functional, i.e. producing pollen (Luo et al., 2010)) in each plot, and all flowers were identified to species using a dichotomous key (*Flora of the Pacific Northwest*, Hitchcock et al., 2018). Flower surveys were conducted via stem counts, rather than using a botanical definition of “flower,” which would count flowering asters as 100 or more flowers. Instead, flower abundance was based on the number of stems (following methods outlined in Sanders et al., 2015). Each stem originating in the soil with one or more individual flower or inflorescence was counted in each plot on each watch. The numbers of flowers per stem on ten stems was counted in each plot, and the average number of flowers per stem was recorded for each plot. The total flower frequency in each plot for each watch was the product of the number of stems and the average flowers per stem. Flowers that were budding, in the process of blooming, or past pollen production were not counted.

Following stem counts, 15- minute pollinator watches were conducted in each plot. Because bees do not forage in inclement weather (Güler & Dikmen, 2017), pollinator watches were conducted on sunny days with no rain, limited cloud cover, and low wind. Watches took place in the sunniest parts of the day (when the sun was overhead i.e., not early morning or late evening) and on days that were either sunny or partly cloudy. In summer 2021, there was no rain during the sampling period, and most watches took place in full sun, but some were conducted on days that were partly cloudy. During each watch, the weather and the presence of shade was noted.

During each minute of the 15-minute watch period, all visits of all bees to all flowers within the plot were counted. In our study, a bee was any species within the superfamily Apoidea. For each visit, the species of bee (or only genus if the species could not be identified), the species of flower(s) visited by the bee, and the number of flowers visited within one minute by each bee were recorded. Only visits that involved active pollination were recorded; active pollination was defined as pollinator contact with the reproductive parts of the flower. Bees that landed on the leaf or petal of the flower but did not visit the reproductive parts of the flower were not counted. Likewise, bees that did not visit any flowers were not counted. This was repeated for every plot with flowers in anthesis and was repeated for each plot one time per watch.

Watches began in early summer as soon as meadows were accessible given snow limitations on road access and snow cover in meadows. In most years, a field crew collected data over a period of 5 weeks. In 2021, watches were performed every other week over a period of 6 weeks and only 10 of the 12 meadows were visited (Lookout Outcrop and Lookout Steep were omitted). Most years did not capture the start date of flowering but did capture the majority of the flowering period.

3.2. Data sources

The dataset used in this analysis were obtained from the plant pollinator dataset (SA026) collected in montane meadows of the H.J. Andrews Experimental Forest from 2011-2018 (<https://doi.org/10.6073/pasta/758d696dde9c48ea65d0be45ea796415>) (Jones, 2022). Data collection originated in 2011 with Vera Pfeiffer and has continued with multiple investigators over the subsequent years with oversight by Julia Jones. Our study uses this dataset combined with original data collected by Melinda Vickers and Logan Kary in the summer of 2021.

3.3. Data analysis

3.3.1 Flowers

3.3.1.1 Abundance

Flower abundance was determined for all species in all meadows in all years, and by meadow, by year, and by species. Because the number of sampling periods differed by year (ranging from 3 to 7), annual flower abundance was calculated on a per watch basis, i.e., total abundance in all watches divided by the number of watches, for each year. Relative abundance of flowers was calculated by ranking total flower abundance. Percent abundance was calculated as the percentage of observed flowers out of total flower abundance. Relative and percent abundance were calculated for all watches in all years.

Six flower species were selected for detailed analysis based on their relative importance to *Bombus* spp. and *Apis mellifera*. These species (and reasons) were: *Gilia capitata* (most frequently visited by *Apis*), *Delphinium nuttallianum* (one of top five species visited by *Bombus*, a key species especially in early season), *Eriophyllum lanatum* (one of the top ten species visited by *Bombus* and second most visited by *Apis*), and *Orthocarpus imbricatus*, *Hypericum*

perforatum, *Cirsium callepsis*, and *Sedum oreganum* (within the top five species visited by *Bombus*). We calculated the annual abundance (as defined above) for each of these flower species. In the remainder of the text, these flower species are referred to by their genus name.

3.3.1.2. Phenology

Flower phenology was determined from the cumulative abundance of flowers for each day of each year, expressed both as counts and as percent of the total number of flowers in that year. Cumulative and percent abundance were calculated for all flower species and the four most visited flower species (*Gilia*, *Eriophyllum*, *Delphinium*, *Orthocarpus*) for all meadows, and for each meadow separately.

Four values were extracted from each cumulative percent abundance curve: start date, peak date, end date, and duration. Start date was defined as the first day when a flower of a given species was observed. Peak date was the day on which the most flowers were counted in a single watch. End date was defined as the day on which more than 95% of flowers were observed. Duration is the end date minus the start date. These four values were determined for each species, year, and meadow.

3.3.2. Bees

3.3.2.1. Abundance

The frequency of bee visits to flowers was determined for all years and all meadows, and by year, by meadow, and by bee species. Annual visit frequency was determined on a per-watch basis, i.e., total frequency in all watches divided by the number of watches, for each year.

Species included *Apis*, *Bombus* (total and by *Bombus* species), and solitary bee species (total and by species or lowest level of identification).

3.3.2.2. Phenology

Bee phenology was determined from the cumulative abundance of interactions for each day of each year, expressed both as counts and as percent of the total number of interactions in that year. Cumulative and percent abundance were calculated for for all bee species, for each of the three main guilds (*Apis mellifera*, *Bombus* spp., and solitary bees), for each of the four common *Bombus* spp. (*B. melanopygus*, *B. vosnesenskii*, *B. mixtus*, and *B. bifarius*), and for each of the three common solitary bee genera (*Osmia* spp., *Dialictus* spp., and *Dufourea* spp.), for all meadows and years, and for each meadow and year. Start date, peak date, end date, and duration for bee visits were calculated using the same method applied to flower abundances.

3.3.2.3. Competition

Competition between bee species was evaluated based on the annual frequency of visits of three bee functional groups (*Apis*, *Bombus*, and solitary bees). Ordinary least squares regressions were fitted to relate frequencies of visits for pairs of functional bee groups (n=12 meadows). Data were annual frequencies of visits and percentages of visits. Two models were fitted: (1) *Bombus* vs. *Apis*, and (2) social bees (*Bombus* plus *Apis*) vs. solitary bees and then were repeated by year. Slope values for each year from the regressions of solitary bees vs. *Bombus* and solitary bees vs. *Apis* were compared using a t-test (in R; Wickham, 2016).

3.3.3. Flowers & bees

3.3.3.1. Abundance

Ordinary least squares regressions were fitted to relate frequency of bee visits (dependent variable) to abundance of flowers (independent variable). Models were fitted for all years and by year (n = 9 years) (n = 12 meadows), for (1) all species of bees and flowers, (2) *Apis* visits vs. abundance of *Gilia capitata* flowers, (3) *Bombus* visits vs. abundance of the flowers of the five most frequently visited flowering species.

3.3.3.2. Phenology

Cumulative bee visits were compared to cumulative flower abundances for all years and by year and meadow, for all bees, all flowers, and for several commonly occurring bee-flower single-species pairs: (1) *Apis mellifera* visits to *Gilia capitata* and *Eriophyllum lanatum* vs. abundances of these flowers, (2) *Bombus* spp. visits to *Delphinium nuttallianum*, *Eriophyllum lanatum*, and *Orthocarpus imbricatus* vs. abundances of these flowers. Ordinary least squares regressions were fitted to peak dates and end dates for all bees vs. all flowers and all single-species pairs (n = 9 years, n = 12 meadows).

3.3.3.3. Preference

Bee preferences for flower species was quantified by ranking each flower species according to the number of visits by all bee species, by each of the three functional groups (*Apis*, *Bombus* spp., all solitary bees), and by the four common *Bombus* species. Preferences were determined for 2011 (coolest and wettest year), 2015, and 2021 (hottest and driest years).

Each flower species also was ranked by abundance, and by the number of visits by *Bombus* spp. and *Apis*, for all years. Scatterplots were created and Spearman's rank correlations were calculated to test how ranked flower abundance was related to (1) ranked flower preference based on visits by *Bombus* and (2) ranked flower preference based on visits by *Apis*. Scatterplots were examined to identify flower species which were preferred, avoided, or visited based on their ranked abundance. Relative preferences of *Apis* and *Bombus* for flower species visited by both bee genera were determined by dividing the rank of visits (by *Apis* and by *Bombus*) by the rank of flower species abundance and comparing these ratios in a scatterplot.

3.3.4. Climate

Data on daily precipitation and mean daily temperature were obtained from the CENMET weather station, located at 1020 m elevation in the Andrews Forest, and within a few kilometers of all meadows. An antecedent precipitation index was calculated based on

$$AP_t = AP_{t-1} + P_t^k \quad [1]$$

where AP_t = antecedent precipitation index on day t , P_t = precipitation on day t , and k = a decay constant set at 0.9. Cumulative antecedent precipitation (CAP) was calculated as

$$CAP_t = CAP_{t-1} + AP_t \quad [2]$$

Cumulative degree days were calculated as a sum of all temperatures above 10 °C as:

$$CDD_t = CDD_{t-1} + (T_t - 10) \quad [3]$$

Where CDD_t = cumulative degree days on day t and T_t = mean daily temperature on day t . Air temperature data were obtained from CENMET AIRCEN01 air temperature sensor at 450 cm (4.5 m) above the ground. The antecedent precipitation index, cumulative antecedent

precipitation, and cumulative degree days were for each year for all days from March 15 to September 15. The relationship between cumulative antecedent precipitation on July 15 and cumulative degree days on July 15 was evaluated using ordinary least squares regression. The model was fitted for $n = 9$ years.

3.3.5. *Climate & flowers*

3.3.5.1. Abundance

The relationship of flower abundance to climate was tested using second order polynomial regression, with total flower abundance on July 15 (dependent variable) and cumulative antecedent precipitation (CAP) or cumulative degree days (CDD) on July 15 (independent variables). July 15 was chosen because flower abundance and bee visits tended to peak near this date in most years; second order polynomial regression was chosen because the flower abundance tended to peak at intermediate values of CAP and CDD. Models were fitted for flower abundance of all species ($n = 9$ years, $n = 12$ meadows), and for *Delphinium nuttallianum*, *Eriophyllum lanatum*, *Gilia capitata*, and *Orthocarpus imbricatus* because they were most frequently visited by *Apis* and *Bombus* spp. Meadows were grouped into three categories based on soil moisture: xeric (CPR, CPS, NE, LO, LS), mesic (LM, M2, RP1, RP2, CPM), and wet (CPB, LB), and second order polynomial regressions were fitted for each meadow category.

3.3.5.2. Phenology

The relationship of flower phenology to climate was tested using ordinary least squares regressions fitted for start date, peak date, and end date (dependent variables) vs. CDD and CAP (independent variables). Models using start date were related to early season CDD and CAP on June 15. Models using peak date, were related to mid-season CDD and CAP on July 1. Models using end date were related to CDD and CAP on July 15. Models were fitted for all flower species, and for *Delphinium nuttallianum*, *Eriophyllum lanatum*, *Gilia capitata*, and *Orthocarpus imbricatus* (n = 9 years).

Because the start date for flowering often preceded the first date of sampling, duration was estimated using an ordinary least squares regression fitted to the stem count on the first day of observation (dependent variable) vs. the CDD on that day (independent variable) for all years (n=9). The X-intercept of this equation was presumed to be the temperature threshold for flowers to begin blooming, and the start date used to estimate duration was defined as the date on which the CDD exceeded this threshold. The duration of flowering was related to CDD and CAP using second-order polynomial regression because the duration of flowering was predicted to peak during moderate years.

3.3.6. Climate & bees

3.3.6.1. Abundance

The relationship of bee visits to climate was tested using second order polynomial regression (CDD) or linear regression (CAP), with total bee visits on July 15 (dependent variable) and cumulative antecedent precipitation (CAP) or cumulative degree days (CDD) on

July 15 (independent variables). Models were fitted for all bee visits, visits by *Apis*, and visits by *Bombus* spp. (n = 9 years).

3.3.6.2. Phenology

The relationship of bee phenology to climate was tested using ordinary least squares regressions fitted for start date, peak date, end date, and duration (dependent variables) vs. CDD and CAP (independent variables). Bee visitation peak date and end date were determined using the same methodology used for flowers (Section 3.3.5.2). However, the start date for bee visits often preceded the first date of sampling. To estimate the true start date, an ordinary least squares regression was fitted to the number of bee visits observed on the first day of observation (dependent variable) vs. the CDD on that day (independent variable) for all years (n=9). The X-intercept of this equation was presumed to be the temperature threshold for bees to begin visiting flowers, and the start date for bee activity in each year was defined as the date on which the CDD exceeded this threshold. Models were fitted as described above for flower phenology. Models were fitted for all bee visits, visits by *Apis*, and visits by *Bombus* spp. (n = 9 years).

3.3.7. Network analysis

3.3.7.1. Specialization and redundancy

Specialization, generalization, and principal interactions within the plant-pollinator network were evaluated using the bipartite function in R. A matrix was constructed of plant-pollinator interactions that were observed 10 or more times throughout the study period for each year for the first and last watch of each year.

Redundancy was evaluated using the network package in R and the bipartite package in R to plot all interactions with plants for all years, weighted by the number of interactions (Carter Butts et al., 2021; Dormann et al., 2009). A visualization of the network was constructed using the `ggnet` function in `ggplot2` in R, showing the connections among all flower species and their pollinators.

The degree (the number of flower species visited by each bee species, and vice-versa) was extracted from the bipartite tables for each bee species in each year. The degrees for bee visits (i.e., the number of flower species visited by each bee species) were used to construct a degree distribution for each year. Steeply sloping degree distributions indicate a network structure more dominated by a few bee species visiting multiple flower species, whereas less steeply sloping degree distributions indicate the opposite. A long tail on the degree distribution indicates rare bee species that visit few flowers. The five most connected (highest degree) species of both plants and bees were identified for each year, and the number of years in which each bee or flower species was in the top five most connected species was determined. The average degree for flower species and bee species were determined for all years.

3.3.7.2. Rewiring and turnover

Tables created from the bipartite function in R (Section 3.3.7.1) were used to create a matrix to quantify rewiring. Each flower species and plant-bee interaction was given a value of 1 for years in which it was observed and a value of 0 for each year in which it was not observed. These numbers were used to construct frequency distributions of the numbers of years in which each flower species and interaction was observed and how consistent the network remained

overall. These matrices were created for all years for all meadows and for each meadow separately.

Temporal dissimilarity was determined from the 0/1 matrices using beta diversity (Sørensen dissimilarity index) for all pairs of years (2011-2018, 2021), for all meadows pooled and for each meadow. The Sørensen dissimilarity index is one of the most common indices for comparing species composition in two locations (Chao et al., 2005). Here, we used it to compare the dissimilarity both of flower species and of species interactions (as a measure of rewiring). Sørensen dissimilarity is split into measures of turnover and nestedness (a measure of whether species in one site or year are a subset of species in a different site or year) (Jones et al., 2018). Sørensen values are measured as a fraction of total species change from one site to another (in this case over time) where 0 represents no species replacement and 1 represents a total species replacement (Jones et al., 2018). Sørensen dissimilarity was determined using the `betapart` package in R (Baselga, et al., 2022; Baselga & Orme, 2012).

To determine the role that heat and precipitation play in rewiring and turnover, pairwise values (i.e., the Sorenson dissimilarity in year i vs. year j) were compared with pairwise comparisons of cumulative degree days and cumulative antecedent precipitation in year i vs. year j , for all pairs of years (2011-2018, 2021). The relationships between species turnover for both flower species and interactions (dependent variables) and change in temperature ($CDD_{i,j}$) or change in moisture ($CAP_{i,j}$) (independent variables) were assessed for all meadows, and for each meadow separately, using ordinary least squares regression. A simple linear regression was performed to compare species interaction dissimilarity and floral dissimilarity between years for all interactions and by meadow ($n = 12$).

4. RESULTS

4.1. Flowers

4.1.1. Abundance

Total flower abundance varied greatly between years (Figure 4.1.1). Flower abundance in 2011 was more than one standard deviation above average, whereas flower abundance in 2015 and 2021 was more than one standard deviation below average. Flower counts also varied between years within each meadow (Figure A1).

Eriophyllum lanatum was the most abundant flower, accounting for ~15% of total flowers observed, followed by *Gilia capitata* which accounted for ~13% of observed flowers (Figure A2, Table 4.1.1). All other flower species accounted for less than 10% and most were less than 1% of total flowers. Approximately 200 species of flowers were observed during the study period (Figure 4.1.3).

Patterns of abundance of commonly occurring flower species varied among years (Figure 4.1.2). Either *Gilia* or *Eriophyllum* were the most observed flower species in every year. Total flower abundance was least in 2015, 2018, and 2021. *Gilia* abundance was least in 2015 and 2021, but *Eriophyllum* and *Delphinium* abundance were close to average in 2021.

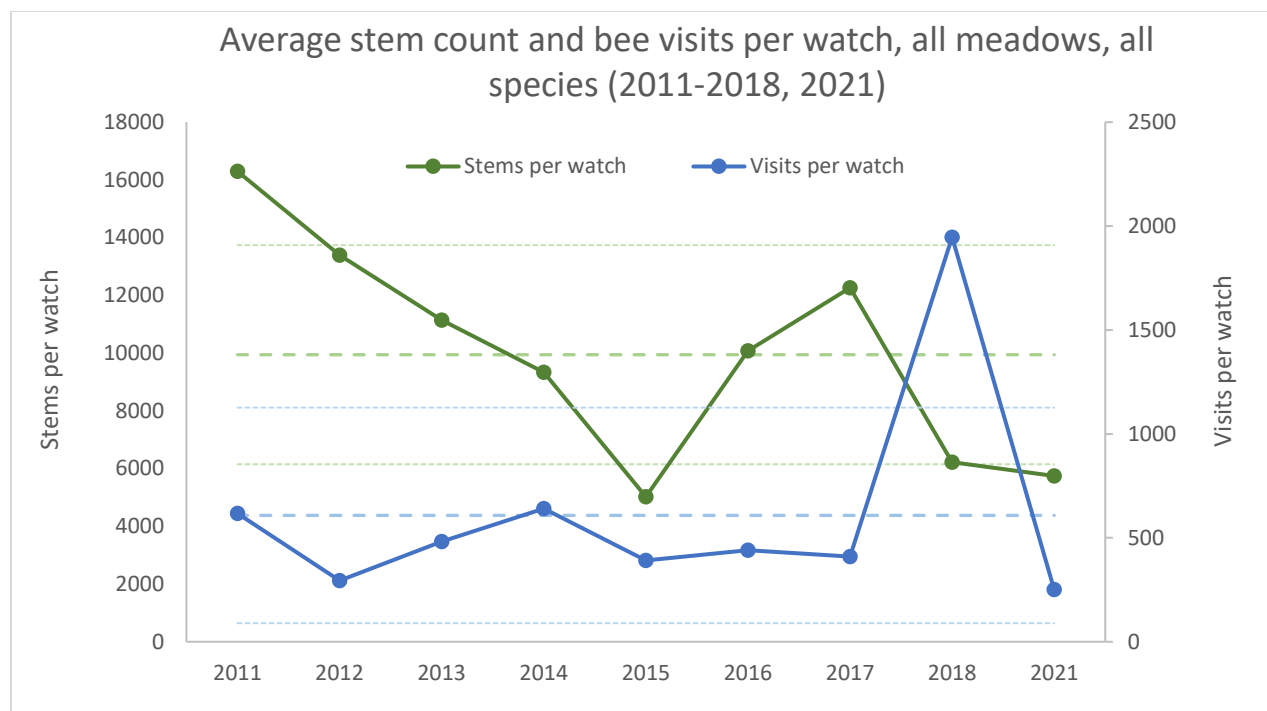


Figure 4.1.1. Each point represents the average stem count or number of bees per sampling period. These numbers were obtained by taking the total abundance divided by the number of “watches” or sampling efforts each year. The green dashed line represents the average of 9943 stems/watch (with a standard deviation of 3795, represented by the green dotted lines). For bees, the orange line represents the total average (608 with a standard deviation of 518, represented by the blue dotted lines).

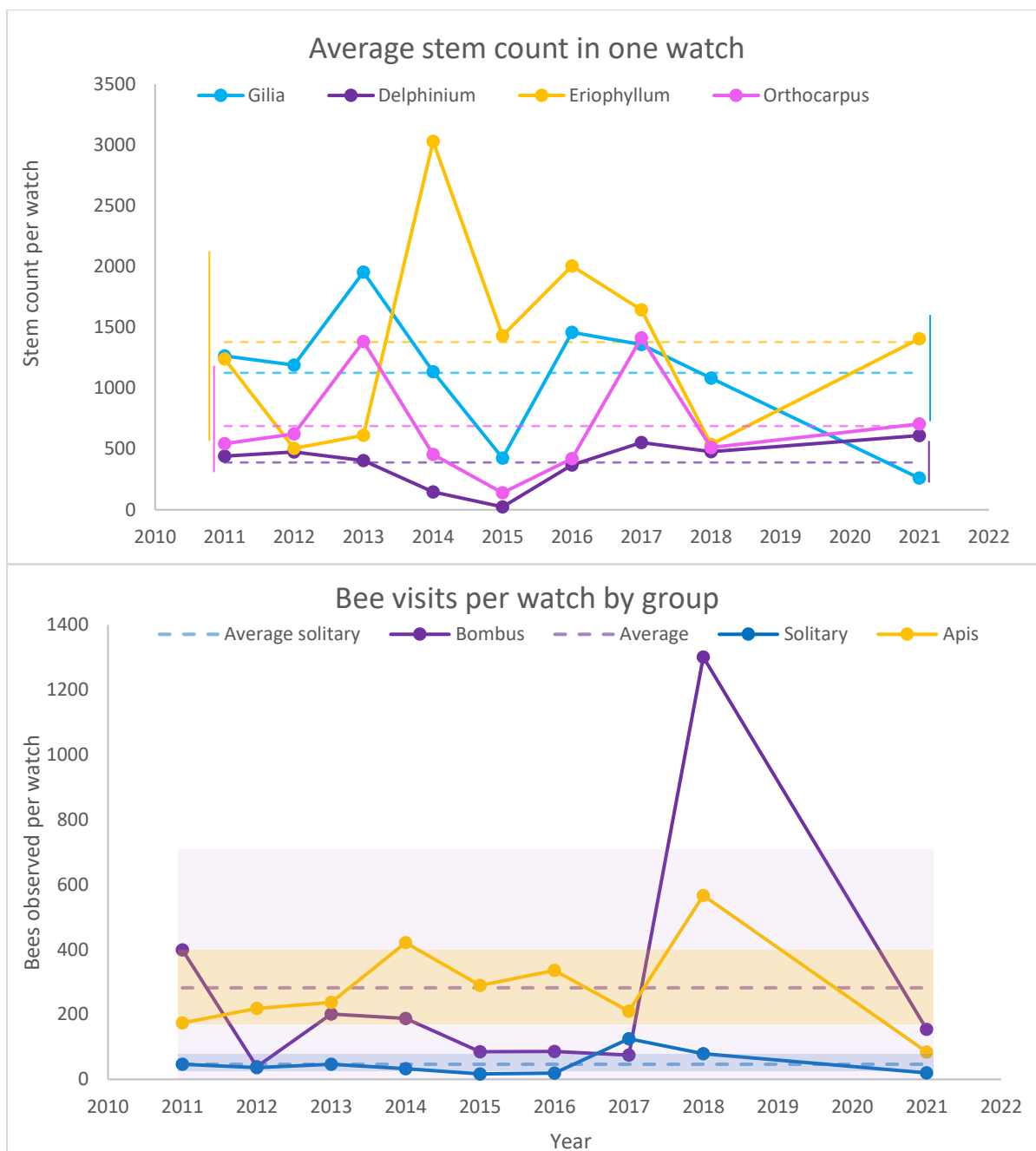


Figure 4.1.2. These graphs focus on the abundance of major species over the study period. Each point represents one year. (top) Average stem count per watch for four flower species of highest importance to *Apis* and *Bombus*. 2011 to 2018 and 2021, in all meadows. (bottom) Average number of visits of bees per watch by group (*Apis mellifera*, *Bombus* spp., solitary) 2011 to 2018 and 2021, in all meadows. Horizontal dashed lines represent the average stem count (top) and bee visits (bottom) per watch for all years by flower species (top) and bee group (bottom). Purple dotted line (bottom) is the average for both *Apis* and for *Bombus* while the standard deviation of each group is represented by their corresponding colors in vertical lines (top) and boxes (bottom).

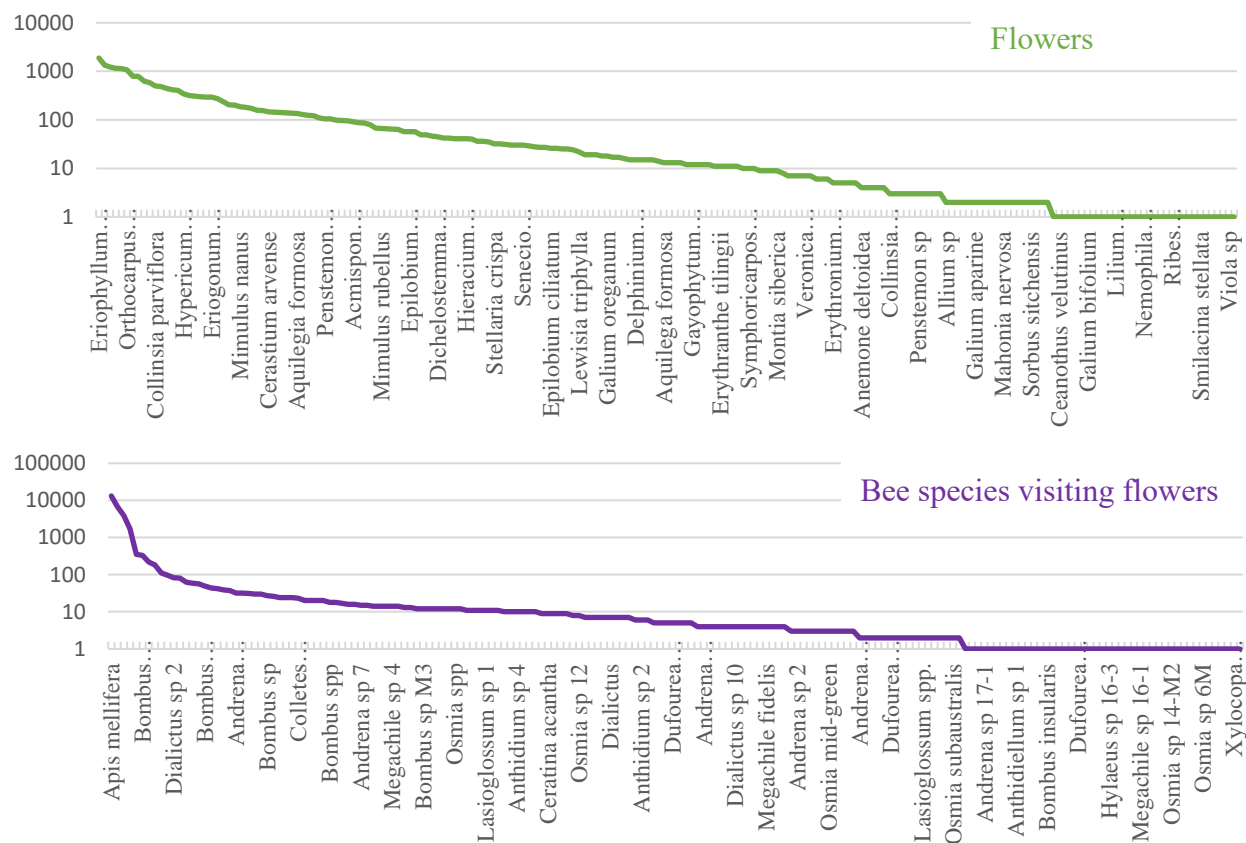


Figure 4.1.3. Frequency abundance of flower and bees visiting flowers, all years. Over the entire study period, 203 species of flowers were observed, and 182 species of bees were observed visiting flowers.

Table 4.1.1. The top 20 most observed species of flowers, the family the species belongs to, whether the species is an annual or a perennial, the percentage of observations that each species accounts for, and the absolute abundance of each species.

| Rank | Family | Species | Annual /Perennial | Percent of total | Total Count of Stalks |
|-------------|----------------|--------------------------------|------------------------------|-----------------------------|----------------------------------|
| 1 | Asteraceae | <i>Eriophyllum lanatum</i> | Annual | 15.51 | 61710 |
| 2 | Polemoniaceae | <i>Gilia capitata</i> | Annual | 13.92 | 55356 |
| 3 | Orobanchaceae | <i>Orthocarpus imbricatus</i> | Annual | 8.26 | 32872 |
| 4 | Polemoniaceae | <i>Phlox gracilis</i> | Annual | 6.32 | 25138 |
| 5 | Ranunculaceae | <i>Delphinium nuttallianum</i> | Perennial | 4.38 | 17415 |
| 6 | Phrymaceae | <i>Mimulus nanus</i> | Annual | 3.42 | 13617 |
| 7 | Polygonaceae | <i>Rumex acetosella</i> | Perennial | 3.38 | 13463 |
| 8 | Phrymaceae | <i>Mimulus guttatus</i> | Annual | 3.08 | 12260 |
| 9 | Plantaginaceae | <i>Collinsia parviflora</i> | Annual | 2.79 | 11091 |
| 10 | Asteraceae | <i>Erigeron foliosus</i> | Perennial | 2.58 | 10256 |
| 11 | Polemoniaceae | <i>Navarretia divaricata</i> | Annual | 2.48 | 9854 |
| 12 | Orobanchaceae | <i>Castilleja hispida</i> | Perennial | 2.22 | 8819 |
| 13 | Phrymaceae | <i>Mimulus tilingii</i> | Perennial | 1.93 | 7687 |
| 14 | Asteraceae | <i>Achillea millefolium</i> | Perennial | 1.83 | 7272 |
| 15 | Apiaceae | <i>Ligusticum grayi</i> | Perennial | 1.81 | 7205 |
| 16 | Fabaceae | <i>Lupinus laxiflorus</i> | Perennial | 1.81 | 7187 |
| 17 | Polygonaceae | <i>Eriogonum umbellatum</i> | Perennial | 1.78 | 7085 |
| 18 | Hypericaceae | <i>Hypericum perforatum</i> | Perennial | 1.15 | 4564 |
| 19 | Polygonaceae | <i>Eriogonum compositum</i> | Perennial | 1.04 | 4126 |
| 20 | Asteraceae | <i>Senecio triangularis</i> | Perennial | 0.98 | 3902 |

4.1.2. Phenology

The start date of flowering varied within a period of about two weeks (Figure 4.1.3). Flower start date was earliest (around June 19) in 2018 and 2017 and latest in 2011 (July 11). Flowering end date was earliest in 2015 and 2021 (around July 11) and latest in 2011 (early September). Both start and end dates of flowering were earlier in 2013 than other years.

The timing of peak flowering varied greatly among years in all mesic meadows (LM, CPM, RP1, RP2, and M2) and in one xeric meadow (CPR) (Figure A4). The timing of peak flowering varied little among years in xeric or wet meadows (LB, CPB, NE, and CPS) (Figure A4). Peak flowering was much earlier than average in 2015 and 2021 (except for *Eriophyllum* in 2021) and flowering occurred much later than average in 2011. Overall, the most visited flowers tended to bloom later in earlier years, but this pattern was not consistent (Figure A3).

The most frequently occurring plant species had a consistent order of flowering: *Delphinium*, *Gilia*, *Eriophyllum*, *Orthocarpus*, *Hypericum* (Figure 4.1.4). This order was maintained in almost all study years (Figure A5). The main source of variation between years was in the timing of *Eriophyllum*. In some years, *Eriophyllum* bloomed at the same time or closer to *Gilia* and other years it bloomed later with *Orthocarpus*.

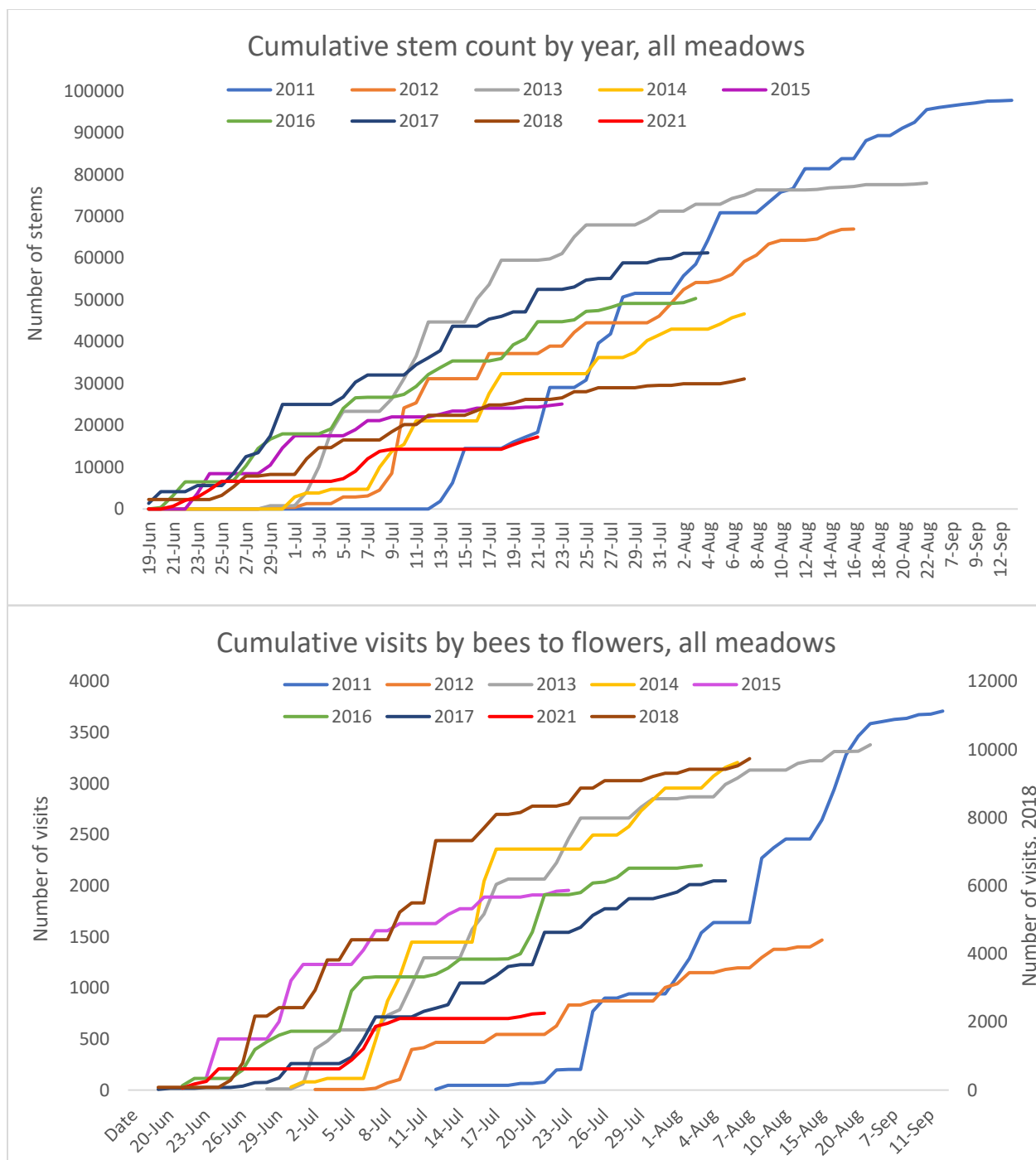


Figure 4.1.3. Accumulated total flower count (top) and bee visits to flowers (bottom) by day of year, showing the variation among years in start date, peak date, and end date. Note separate right-hand axis in bottom graph reflecting the much higher number of bees observed in 2018.

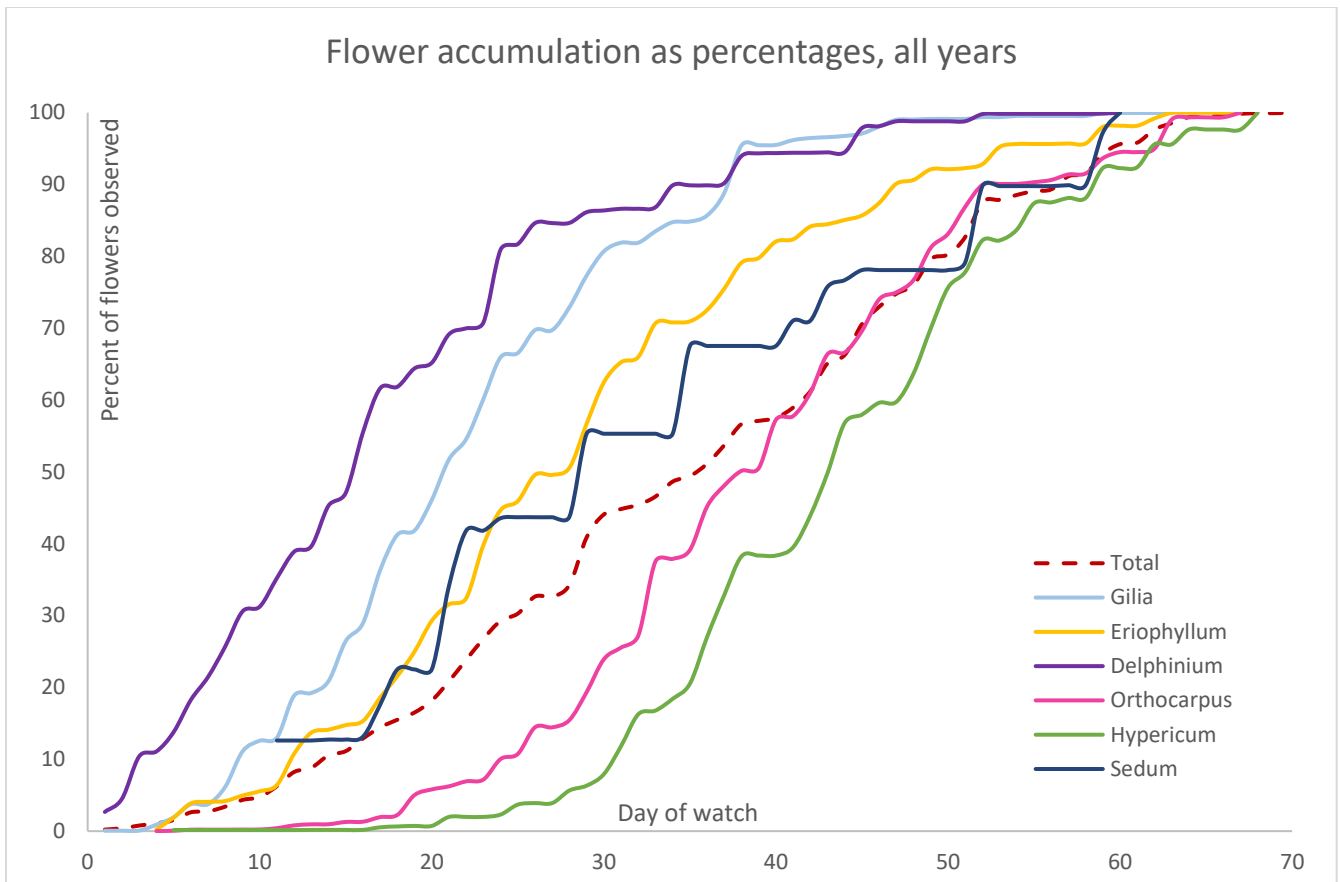


Figure 4.1.4. Accumulated counts of five frequently visited flower species by day of year as a percent of total flowers, averaged for all years. The dashed line represents the percent accumulation of all flower species for all years. Day 0 is June 19 and day 70 is September 13.

4.2. Bees

4.2.1. Abundance

Approximately 250 to 650 bee visits to flowers were observed per watch in all years except 2018, when 1947 bees were observed per watch (Figure 4.1.1). Bee visits were also high in 2011 and 2014 and lowest in 2012 and 2021. In all other years bee visits per watch varied between 400 and 500.

In most years, more *Apis* than *Bombus* visits were observed, and substantially fewer solitary bee visits were observed than either group of social bees (Figure 4.1.2). More *Bombus* than *Apis* visits per watch were observed in 2011, 2018, and 2021. An average of 1301 *Bombus* per watch were observed in 2018, or more than six times the average for other years. In general, *Bombus mixtus* was the most frequently observed flower visitors among *Bombus* spp., accounting for more than 50% of observations. The most frequently observed solitary bee visitors were *Osmia* spp. (almost 30% of visits by solitary bees) and *Dialictus* spp. (approximately 17% of visits by solitary bees) (Table B1). More than 160 distinct species of solitary bees were observed over the entire study period.

4.2.2. Phenology

The start date of bee visits varied by approximately one month among years (Figure 4.1.3). Bee visit start date was earliest (around June 19) in 2021 and 2016 and latest in 2011 (July 11). Bee visit end date was earliest in 2021 (around July 11) and latest in 2011 (early September). Some of this variation is attributable to a late start of observations relative to bee activity. However, in most years, bee activity appeared to lag cumulative flower abundance (compare in Figure 4.1.3). After a slow start, the rate of bee observations increased before

peaking and leveling out later in the season. Late season bee visitation phenology differed most among years. Bee visits slowed significantly in mid-July in 2015 and 2021, whereas in most years bee visits slowed in August or did not slow within the study period.

Overall, *Apis* and *Bombus* visitation began and ended around the same time, but their patterns of accumulation followed a different rate (Figure B1). *Bombus* visits accumulated linearly on average throughout each season in the study period, whereas cumulative *Apis* visits followed more of a logistic pattern. Solitary bee visits had the slowest start in each year but then followed a similar pattern as *Bombus* for the rest of the summer.

The timing of flower visits by the four commonly occurring *Bombus* species was consistent among years (Figure B2). *Bombus melanopygus* was observed first, and *Bombus bifarius* was observed latest in the season. Both *Bombus mixtus* and *Bombus vosnesenskii* were observed around the same time, in between the other two species.

The timing of flower visits by the most commonly occurring genera of solitary bees was also consistent among years (Figure B3). *Dufourea* spp. were mainly observed early in the summer, and *Dialictus* spp. were observed throughout the summer, mainly in midsummer. *Osmia* spp. were observed throughout the summer with two main peaks in early summer and in late summer.

4.2.3. Competition

Flower visits by *Bombus* and *Apis* were inversely related across the meadows (Figure 4.2.1). Some meadows were dominated by *Bombus* while those in other meadows were dominated by *Apis*, and these patterns persisted throughout the study period (Figure 4.2.2). Flower visits by *Bombus* exceeded those by *Apis* in all the meadows in the Carpenter meadow

complex, whereas flower visits by *Apis* exceeded those by *Bombus* in the meadows in the Frissel meadow complex. *Bombus* and *Apis* visited similar numbers of flowers in meadows in the Lookout complex (except Lookout Steep) (Figure 4.2.1). Absolute numbers of flower visits by *Apis* were not related to flower visits by *Bombus* ($R^2 = 0.07$, Figure 4.2.1), and absolute numbers of flower visits by solitary bees were not related to flower visits by social bees (Figure 4.2.3).

Flower visits by solitary bees were not related to visits by *Bombus* spp. on a per-meadow basis (slope = -0.075, $R^2 = 0.10$, Figure B4), except for 2015, when there was a slight, not significant positive relationship (slope = 0.047, $R^2 = 0.18$). Flower visits by solitary bees were slightly but not significantly negatively related to visits by *Apis* (slope = -0.038, $R^2 = 0.09$, Figure B5). In 2015 and 2021 the slope of the relationship was slightly positive and in all other years the relationship was slightly negative, all with a low correlation. Flower visits by solitary bees were slightly but not significantly negatively related to visits by social bees (*Apis* plus *Bombus*, slope = -0.07, $R^2 = 0.14$, Figure 4.2.3), except for 2015 and 2021 where there was a slight positive relationship. There was no evidence that *Bombus* and solitary bee abundance had a more negative relationship than *Apis* and solitary bee abundance ($p = 0.28$, one-sided t-test).

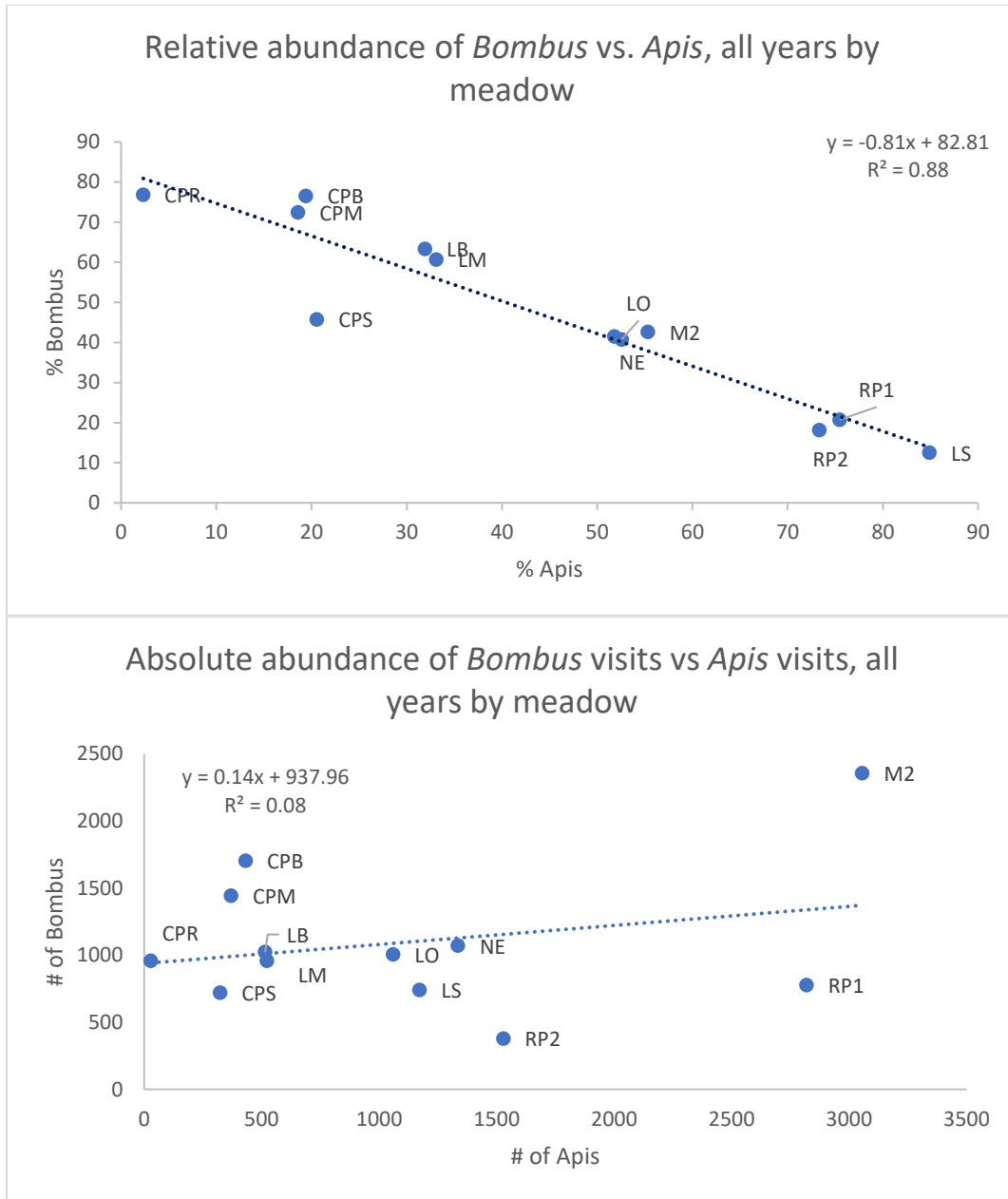


Figure 4.2.1. Relative (top) and absolute (bottom) abundance of *Apis* compared to *Bombus* for all years by meadow. The relative abundance is the percentage of bees out of all bees by meadow.

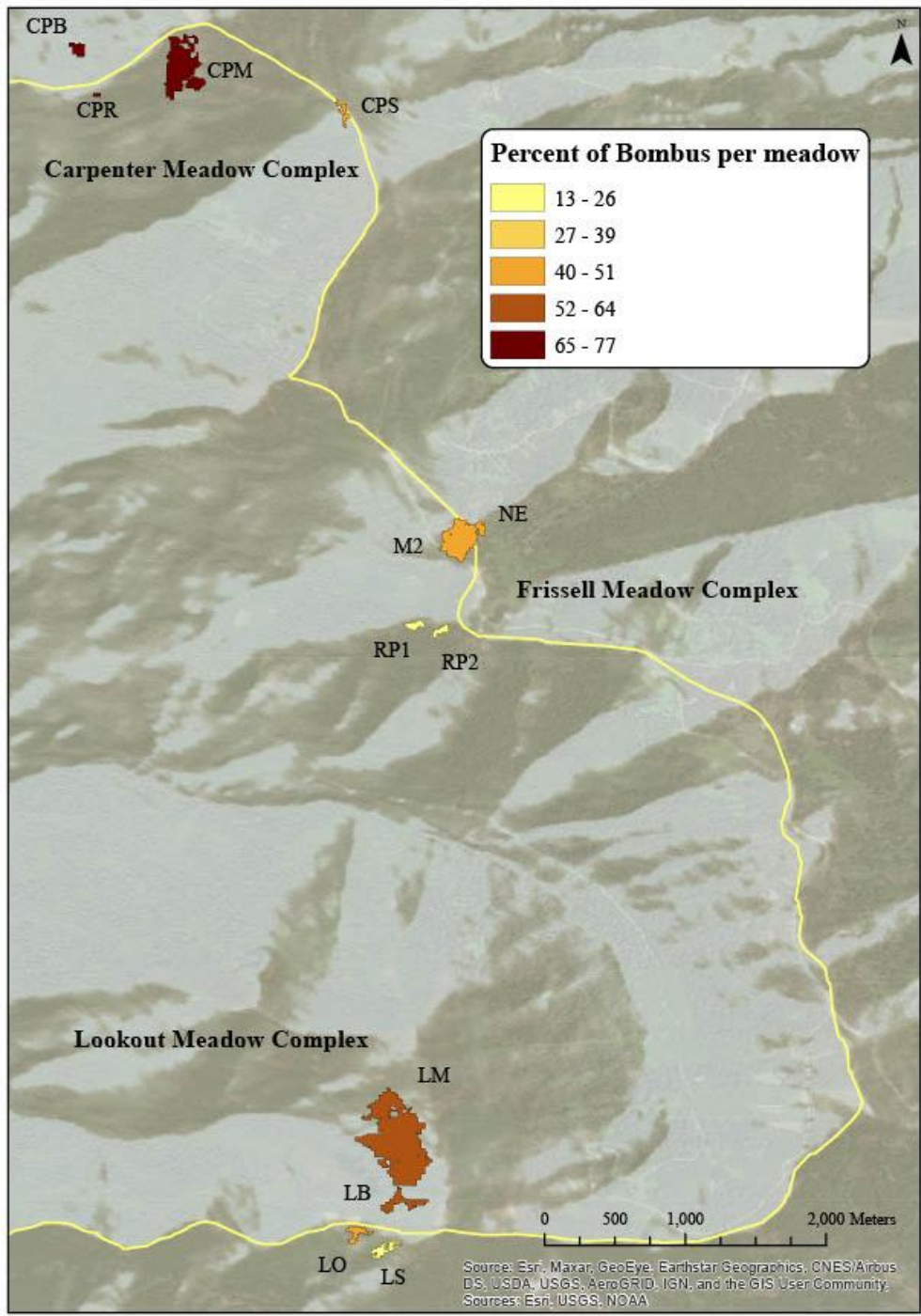


Figure 4.2.2. Percent of *Bombus* per meadow. Darker red areas have a higher percentage of *Bombus* (as in the Carpenter meadows on top) and a lower percent of *Apis* while yellow and light orange have the reverse.

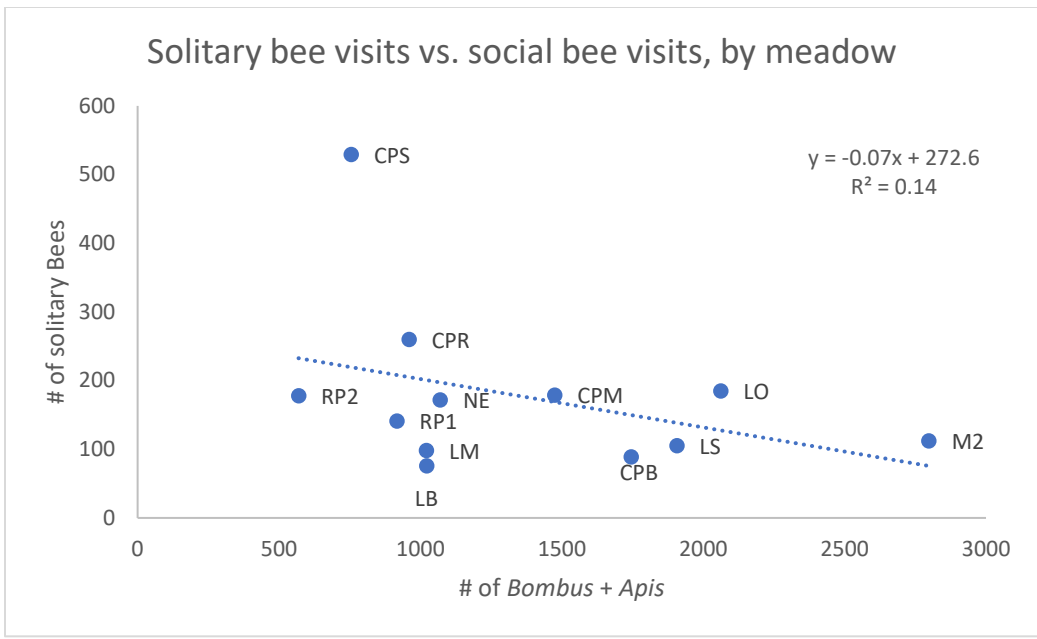


Figure 4.2.3. Absolute abundance of *Bombus* plus *Apis* vs. absolute abundance of solitary bees by meadow for all years.

4.3. Flowers & bees

4.3.1. Abundance

The number of bee visits was positively related to the number of flowers per meadow for all years pooled ($R^2 = 0.59$, $n = 12$ meadows, Figure C1) and for each year (Figure C5). M2 consistently had the most bee visits and the most flowers, while Carpenter Saddle and Carpenter Ridge consistently had the fewest, and Lookout Main had fewer bee visits given its number of flowers than other meadows. In most years, the slope of the regression (0.03 or less) indicated 3 or fewer bee visits per 100 flowers in each watch, except in 2015, when the slope (0.07) indicated 7 bee visits per 100 flowers. In 2018, the slope of 0.28 indicated 28 bee visits per 100 flowers in each watch. For the nine years in the study, the number of bee visits per 100 flowers was unrelated to the total number of bee visits or the number of flowers (Figure C5).

The number of *Apis* visits per meadow was positively related to the number of flowers per meadow in all years pooled, largely due to high *Apis* visits and flower numbers in RP1 and M2 (Figure C3). In most years, the slope of the regression (0.01 or less) indicated <1 *Apis* visit per 100 flowers, except in 2018, when the slope (0.11) indicated 11 *Apis* visits per 100 flowers (Figure C4). The number of *Bombus* visits per meadow was not related to the number of flowers per meadow in all years, although *Bombus* visits and flower numbers were high in M2 (Figure C3).

The percentage of total bee visits made by *Bombus* in a meadow (relative abundance) was positively related to the percentage of total flowers that were of the five most frequently visited species by *Bombus*, for all years pooled (slope = 1.2, $R^2 = 0.35$, Figure 4.3.1), and for most but not all years. The relative abundance of *Apis* visits in a meadow also was related to the relative abundance of *Gilia* (slope = 1.5, $R^2 = 0.82$, Figure 4.3.1). This relationship remained consistent

in all years. *Apis* visits occurred, but were not frequent, in meadows lacking *Gilia*. The number of *Apis* visits to *Gilia* was not significantly related to the number of *Gilia* the following year ($R^2 = 0.12$, Figure C6). For the nine years in the study, the number of *Apis* visits per 100 flowers (regression slope) was unrelated to the total number of *Apis* visits, although both numbers were high in 2018 (Figure C4).

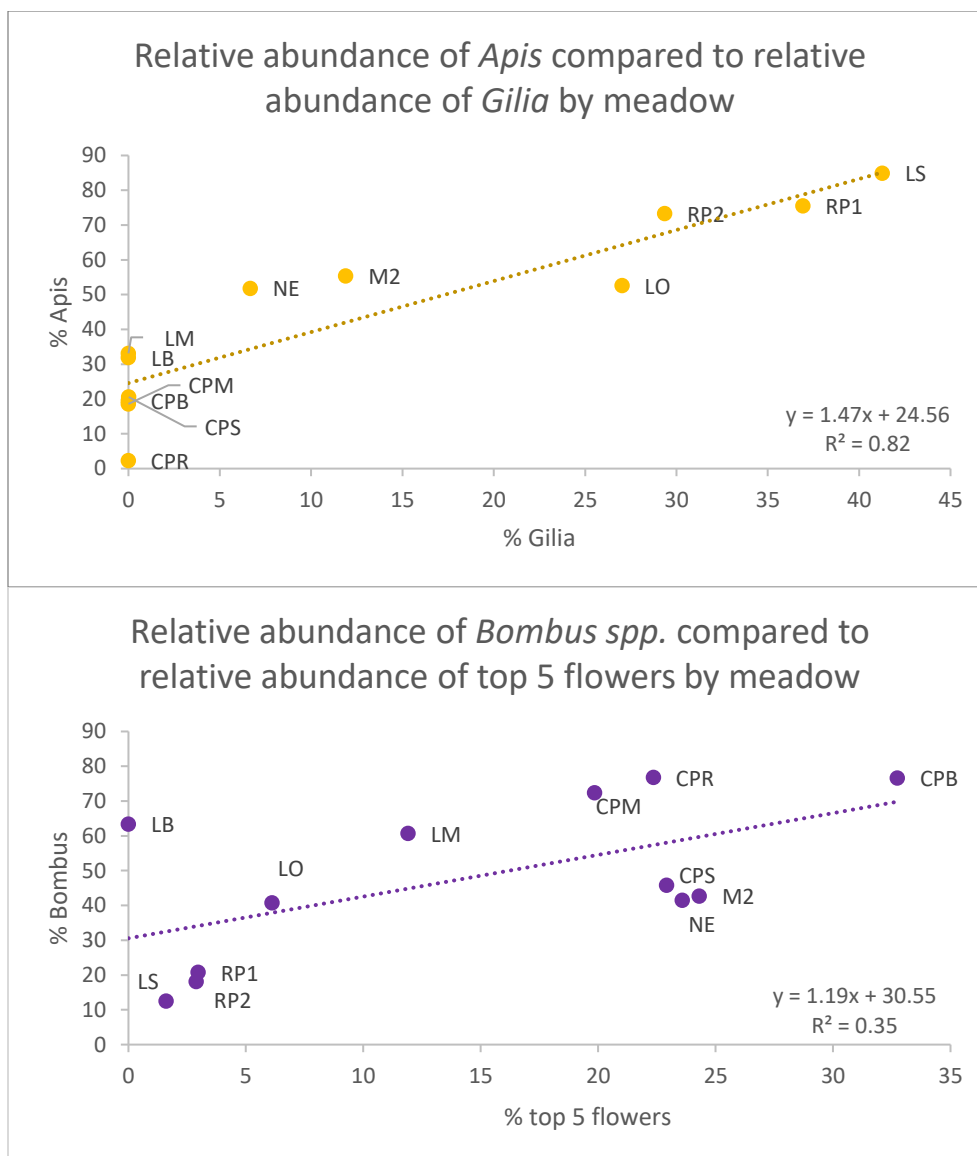


Figure 4.3.1. Relative abundance for all study years of *Apis* as a function of the relative abundance of *Gilia capitata* (top) and relative abundance of *Bombus* (bottom) as a function of the relative abundance of the five flowers most frequently visited by *Bombus*: *Orthocarpus imbricatus*, *Hypericum perforatum*, *Cirsium callopsis*, *Sedum oreganum*, and *Delphinium nuttallianum*. These comparisons are for all years and separated by meadow.

4.3.2. Phenology

The rates of bee visit accumulation matched the rate of flower accumulation (Figure C7). In years that captured the whole flowering period (as in 2012), there was a slow start, followed by an acceleration and a slow decline later in the summer (a logistic curve).

In most years, visits by *Apis* to *Gilia* (Figure C7) peaked in early July. In 2011 they peaked much later, in 2015 the few observations were in June, and in 2021 there were very few observed interactions between *Apis* and *Gilia*. In most years, visits by *Apis* to *Eriophyllum* (Figure C7) peaked in mid-July. In 2015 there were significantly more visits before the beginning of July and all the visits in 2011 were in August.

In every year but 2011, the visits by *Bombus* to *Delphinium* (Figure C7) had begun to plateau by or before early July. In 2011, most of the visits were observed in late July. The visits by *Bombus* to *Eriophyllum* (Figure C7) followed a similar pattern. In addition, the visits by *Bombus* to *Eriophyllum* peaked and declined earlier in 2015 and 2021 than in other years by approximately two weeks. The visits by *Bombus* to *Orthocarpus* (Figure C7) did not vary in timing as much as the other visits discussed here.

The peak date for visits by all species of bees was related to the peak date of flowering for all species of flowers ($R^2 = 0.49$, Figure 4.3.2). The end date for visits by all species of bees was related to the end date of flowering for all species of flowers ($R^2 = 0.92$, Figure 4.3.3). The slope of both relationships was close to 1, meaning that the date of flowering phenology was approximately the same as the corresponding date for bee phenology. Relationships of visits of individual bee species and their most frequently visited flowers were less strong for peak dates (Figure 4.3.2) but strong for end dates (Figure 4.3.3). In 2015 and 2021 the peak date for both *Apis* and *Bombus* coincided with the peak date for *Eriophyllum* (Figure 4.3.2).

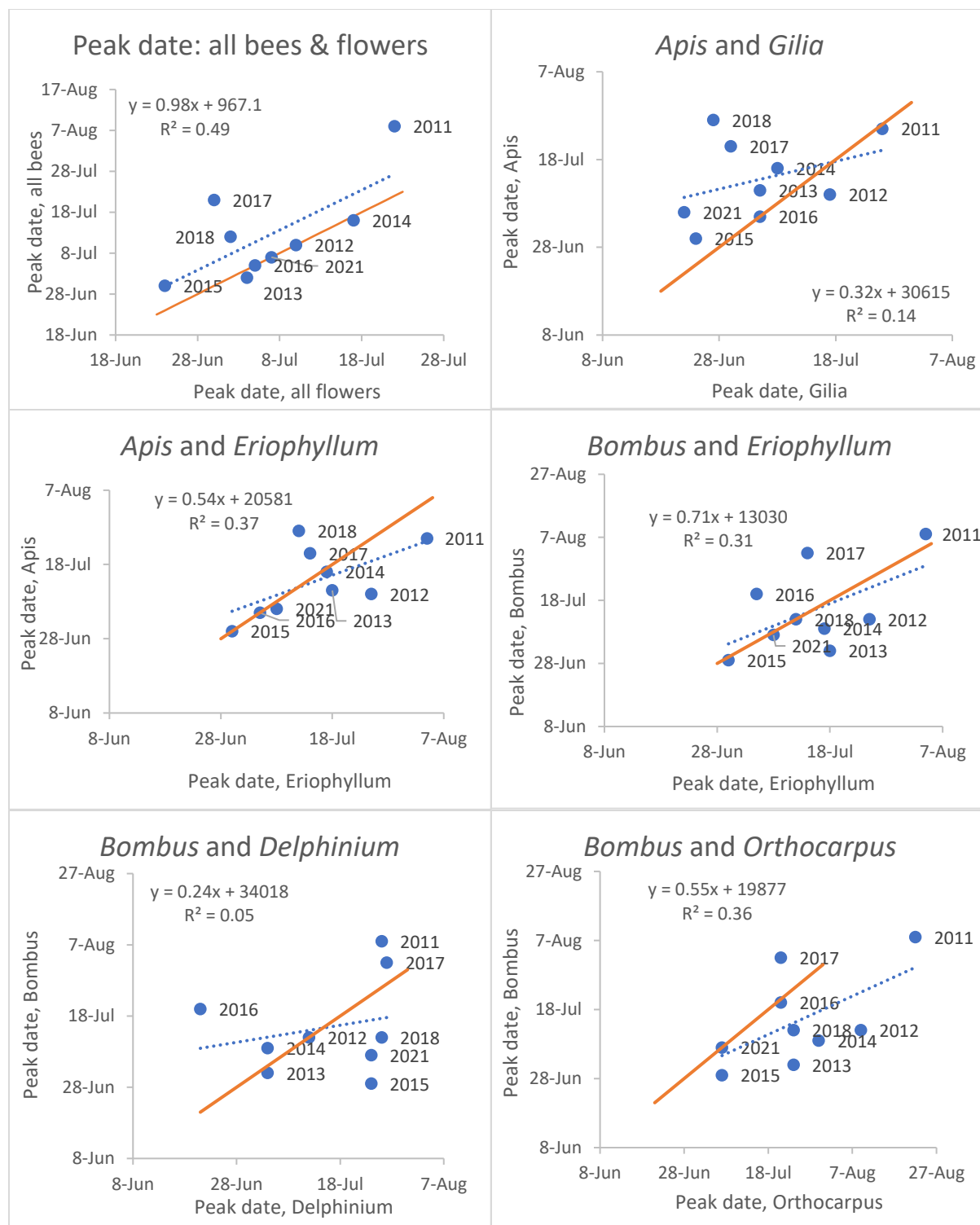


Figure 4.3.2. Peak date for flowers compared to the peak date for all species of bees for all flowers (top left) and for specific flower species and bees that visit these flowers (remaining graphs). The orange line represents a perfect relationship indicating that peak flowering and peak bee visits occurred on the same day.

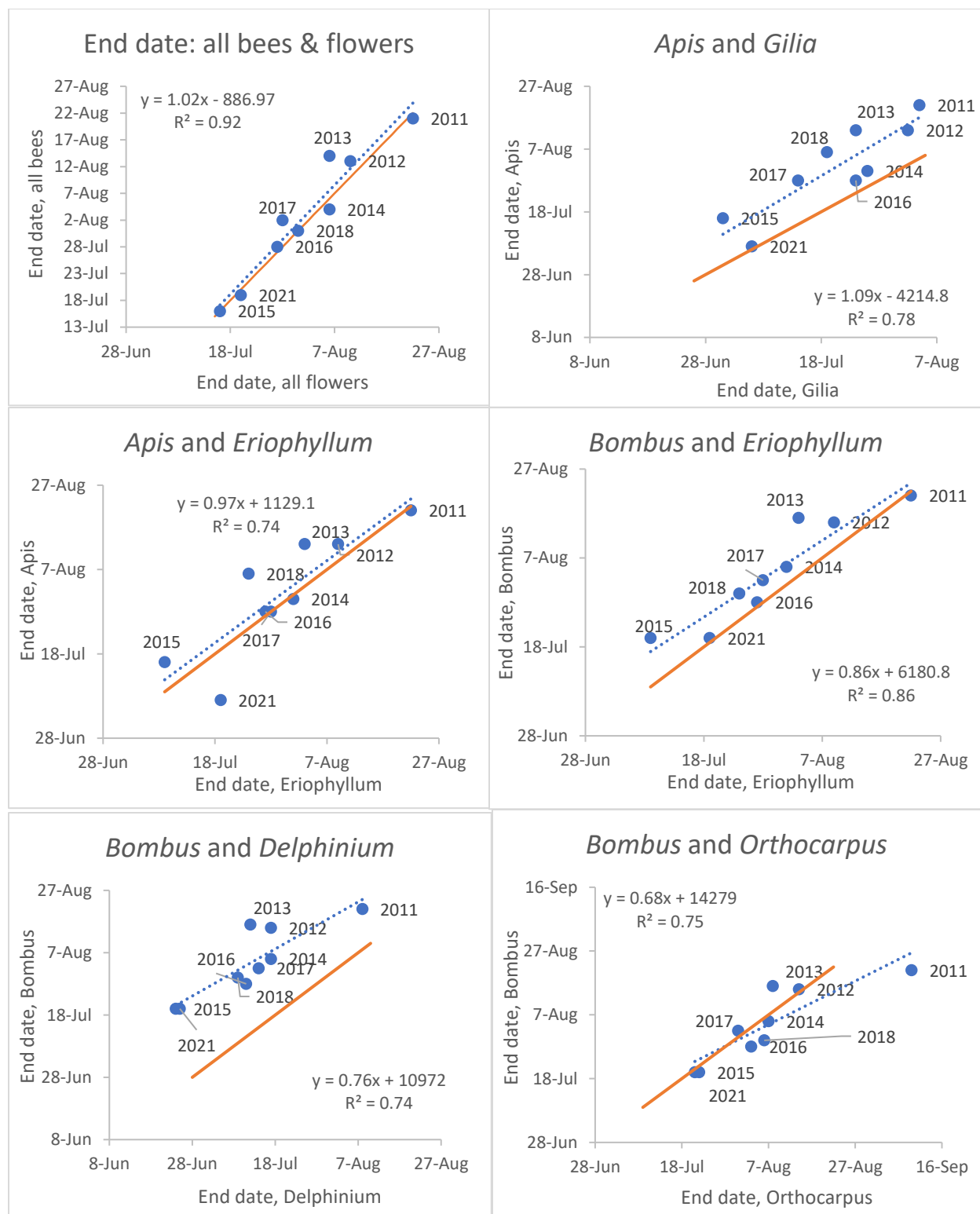


Figure 4.3.3. End date for flowers compared to the end date for all species of bees for all flowers (top left) and for specific flower species and bees that visit these flowers (remaining graphs). The orange line represents a perfect relationship indicating that peak flowering and peak bee visits occurred on the same day.

4.3.3. Preference

Apis visits were highest to *Gilia capitata* (almost half of all visits) and *Eriophyllum lanatum*, and it also frequently visited *Erigeron foliosus*, *Ligusticum grayi*, *Boykinia major*, *Angelica arguta*, and *Eriogonum compositum* (Figure C8). *Bombus* visits were less concentrated on a couple of species than *Apis*. *Bombus* visits were highest to *Orthocarpus imbricatus*, *Hypericum perforatum*, *Cirsium callepsis*, *Sedum oregonum*, and *Delphinium nuttallianum*; these five flower species accounted for approximately 50% of all *Bombus* visits (Figure C8). Solitary bees only showed preference for *Sedum oregonum*.

Visit frequency also varied among *Bombus* species (Figure C9). *Bombus bifarius* visited *Orthocarpus imbricatus* most frequently; *Bombus melanopygus* visited *Dodecatheon jeffreyi* most frequently; and *Bombus vosnesenskii* visited *Hypericum perforatum* most frequently. *Bombus mixtus* visited *Delphinium nuttallianum* most frequently but it also frequently visited *Cirsium*, *Sedum*, *Orthocarpus*, *Hypericum*, and other species (Figure C9). The preferences of individual *Bombus* species were not consistent among years.

In 2015 and in 2021, *Eriophyllum* was the top flower visited by *Apis* while in 2011, *Gilia capitata* was more frequently visited than average (Figure C10). The preferences of *Bombus* were not as consistent as those of *Apis* (Figure C10).

The rank of *Apis* visitation was positively related to the rank of flower abundance (Spearman's rank correlation $\rho = 0.407$). The rank of *Bombus* visitation was positively related to the rank of flower abundance (Spearman's rank correlation $\rho = 0.567$).

Apis visited some flower species more frequently than expected based on flower abundance (Figure C11). Out of the top 20 most visited flowers, 14 were visited on or near the rate predicted by their abundance. Of the 20 flower species most visited by *Apis*, *Apis* visited

only 6 species more often than expected based on their abundance. Most notably, *Angelica arguta* was ranked 72 based on overall abundance but was the 6th most visited flower by *Apis*.

Bombus also visited some flower species more frequently than expected based on flower abundance but, like *Apis*, *Bombus* mainly visited flowers based on abundance (Figure C12). Most notably, *Cirsium callepsis* was the 4th ranked flower species visited by *Bombus* but the 41st in terms of flower abundance. Of the 20 flower species most visited by *Bombus*, *Bombus* visited only 4 species more often than expected based on their abundance. For both *Bombus* and *Apis*, more flower species were avoided than preferred.

In Figure 4.3.4, Most flowers had a ratio of two or less for both *Bombus* and *Apis* with some notable exceptions (Figure 4.3.4).

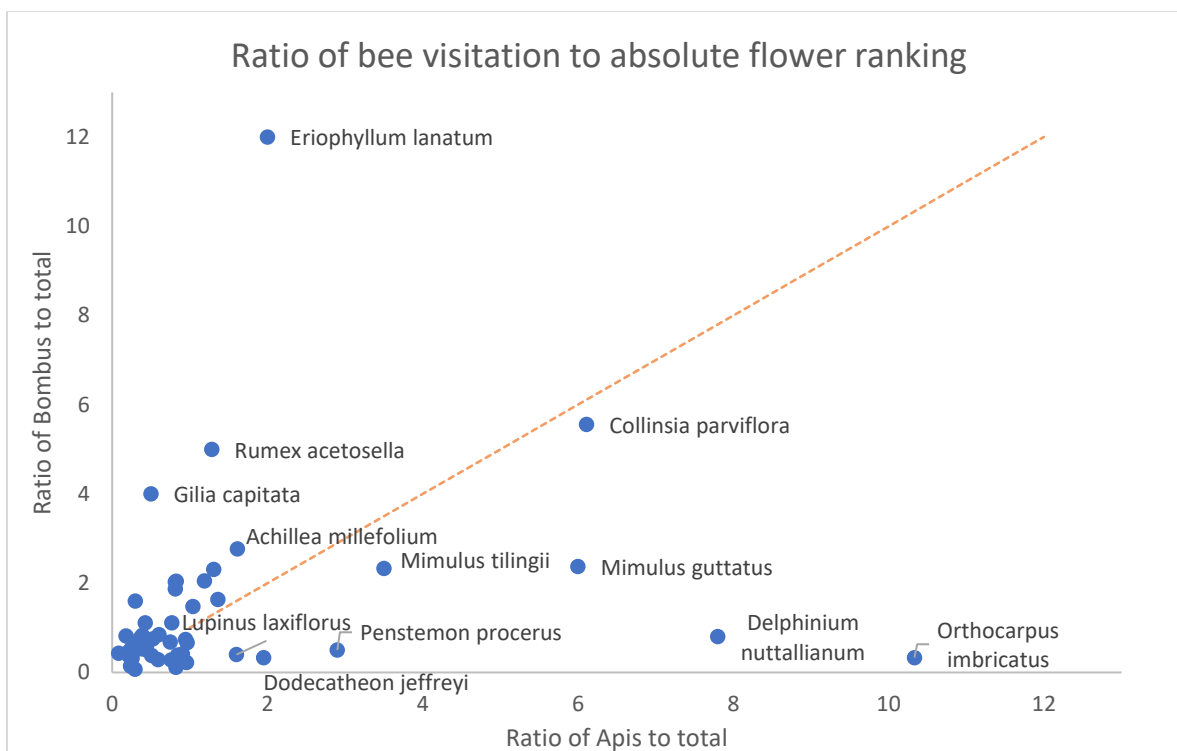


Figure 4.3.4. Relative preferences for flower species, *Apis* vs. *Bombus* for all flower species that are visited by both *Apis* and *Bombus*. Numbers on the X and Y axis are ratios of the rank of visits to a flower species by that bee group vs. the rank of the abundance of that flower species; high numbers indicate that this flower species is visited by that bee group more often than expected based on flower abundance (refer to Figures C8 to C12). Flower species with ratios near 1 for both species 1 indicate that both bee groups visited flowers of that species as frequently as expected based on the rank abundance of that flower. Points in the lower right corner indicate relative avoidance of this flower species by *Apis* compared to *Bombus*, whereas points in the upper left corner indicate relative avoidance of this flower species by *Bombus* compared to *Apis*. Note that only species included in this figure. The orange line represents species where the ratio is the same for both *Apis* and *Bombus*.

4.4. Climate

Precipitation varied considerably among years in the study (Figure D1); precipitation was least in 2015 and 2021 and greatest in 2011, 2012, and 2014. Total cumulative degree days (CDD) ranged from 500 °C in 2011 to almost 900 °C in 2021 (Figure D2). The temporal pattern of temperature also varied among years: in most years, temperature accumulation surpassed 100 °C by early June except for in 2011 and 2012.

CAP and CDD varied among years (Figure 4.4.1). The years 2015 and 2021 were much hotter and much drier, whereas 2011 and 2012 were both cooler and wetter than other years. 2017 was hotter than most other years, but the antecedent precipitation was higher than in other hot years.

Within the study period, years that had higher cumulative degree days also had lower cumulative antecedent precipitation (Figure D3, $R^2 = 0.63$, simple linear regression).

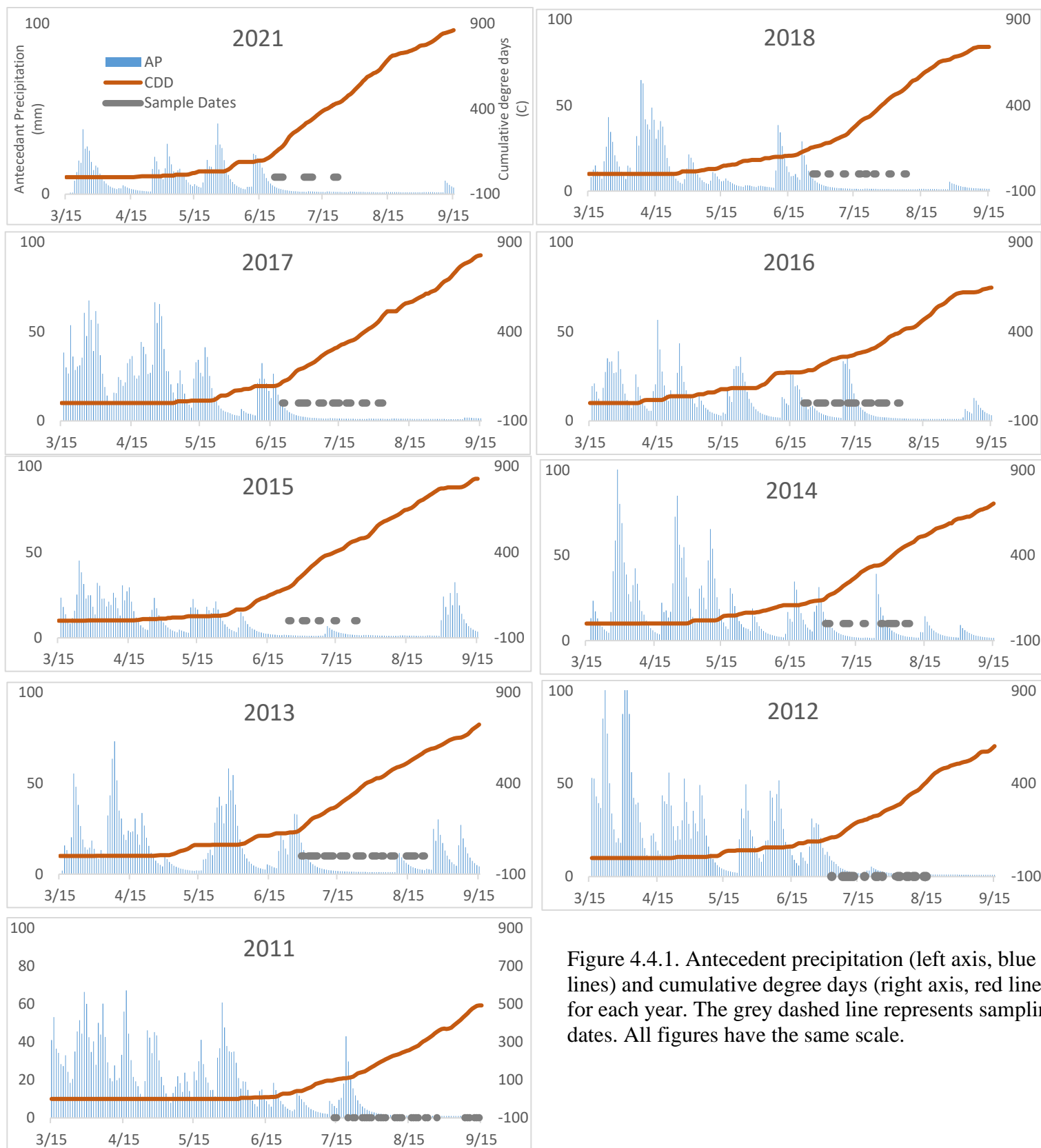


Figure 4.4.1. Antecedent precipitation (left axis, blue lines) and cumulative degree days (right axis, red line) for each year. The grey dashed line represents sampling dates. All figures have the same scale.

4.5. Climate & flowers

4.5.1. Abundance

Flower abundance was highest in years with intermediate CDD and lowest in cool and hot years ($R^2 = 0.40$, polynomial regression, Figure 4.5.1.). Flower abundance was high in years with moderate precipitation ($R^2 = 0.27$, polynomial regression, Figure 4.5.1.).

Of all the flowers, *Gilia* abundance was the most correlated with CDD and CAP (Table E1, $R^2 = 0.46$ for CDD and $R^2 = 0.55$ for CAP, polynomial regression). All flowers except *Eriophyllum* were much less abundant in hot years than in average years (Figure E1). *Eriophyllum* abundance was not correlated with CDD ($R^2 = 0.01$, polynomial regression). All flowers were also less abundant in drier years and most abundant in years with medium levels of precipitation (see Table E1 for more specific equations and R^2 values).

Flower abundance was negatively related to CDD and positively related to CAP in mesic meadows (Figure 4.5.2, $R^2 = 0.36$ for CDD, $R^2 = 0.67$ for CAP, polynomial regression). Flower abundance was not related to CDD or CAP in xeric meadows (Figure 4.5.2).

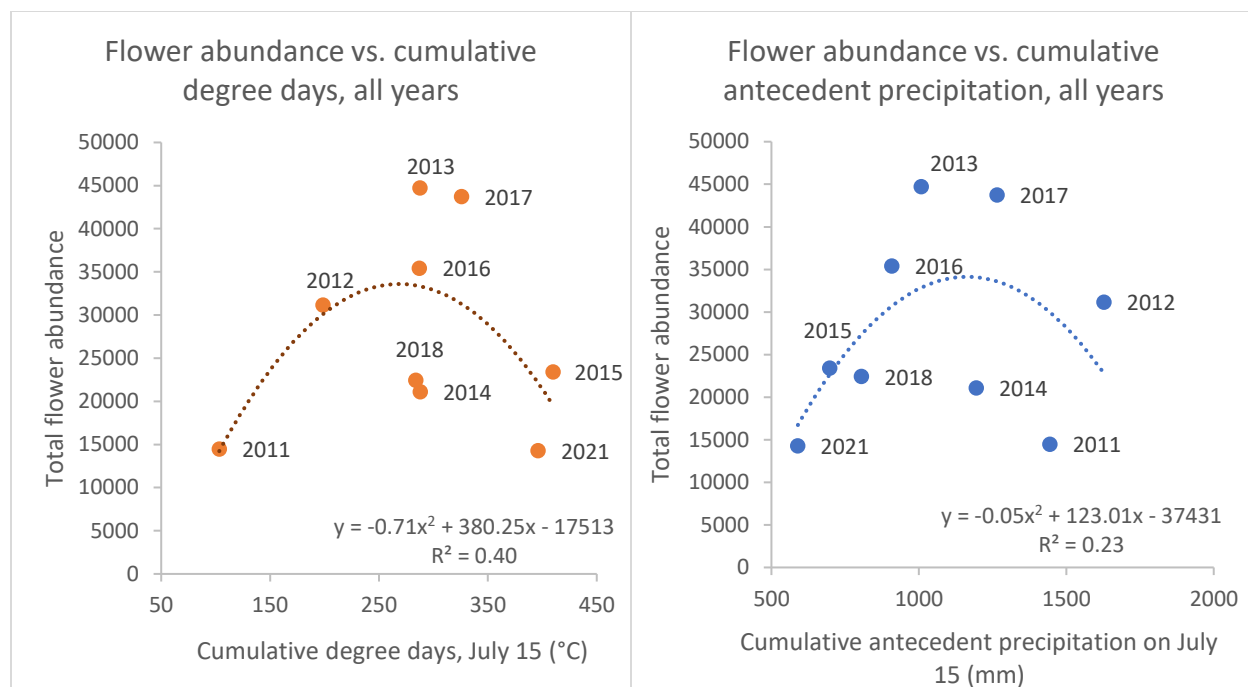


Figure 4.5.1. Total cumulative flower abundance for all years and all species compared to summer cumulative degree days and cumulative antecedent precipitation. Both graphs are fitted with a polynomial regression line to test the hypothesis that flowers are most productive in years with moderate temperatures and precipitation.

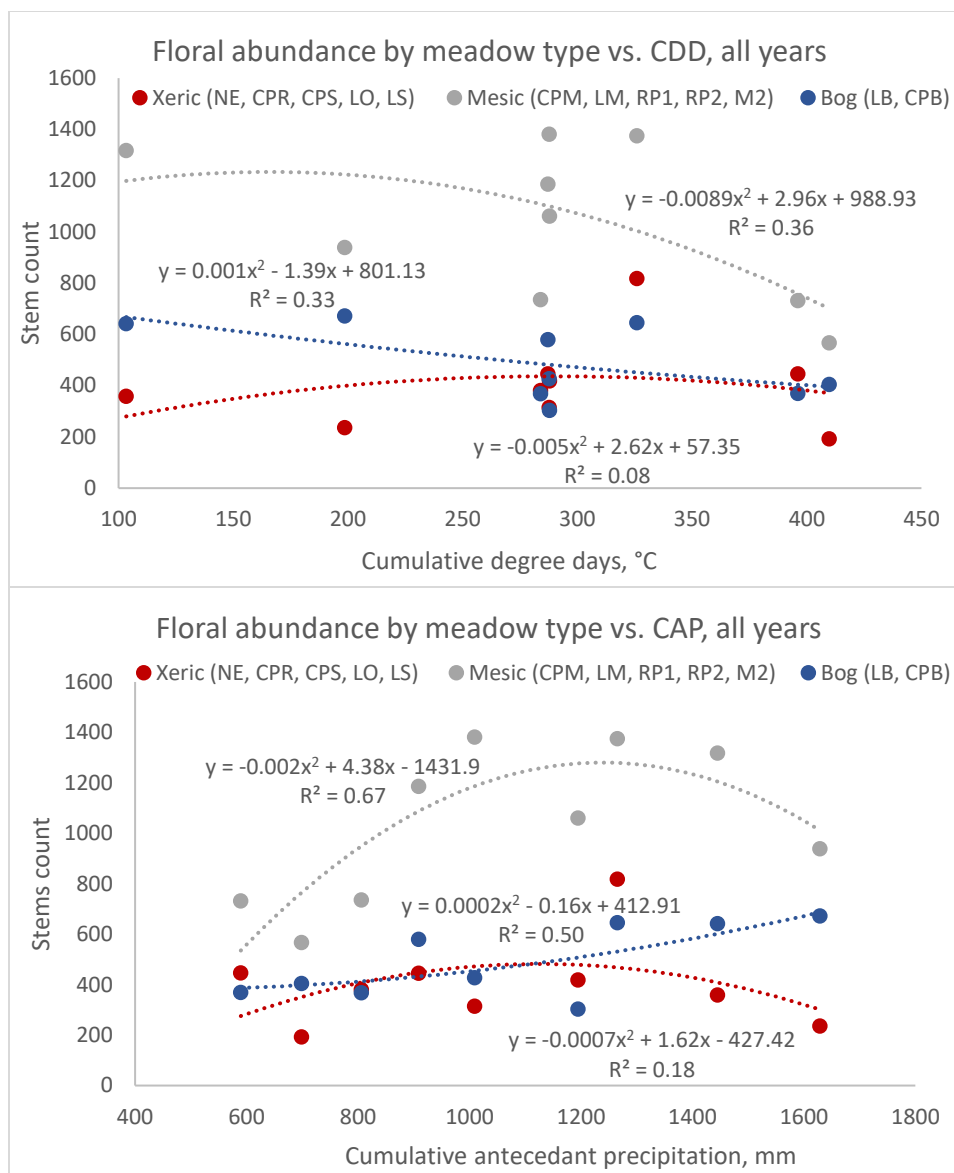


Figure 4.5.2. A comparison of floral abundance by meadow type to (1) cumulative degree days and (2) cumulative antecedent precipitation on July 15 where each point represents one year. Here floral abundance looks at the number of stems per watch and is averaged based on meadow type. The xeric meadows were CPR, CPS, LO, LS, and NE. The mesic meadows were CPM, LM, M2, RP1, and RP2. The wet or bog meadows were CPB and LB.

4.5.2. Phenology

Flowering began, peaked, and ended earlier in hot and dry years. Start date, end date, and peak date of flowering varied by about a month among years (Figure E3). Flowering duration was significantly longer in years with moderate CDD on July 15 ($R^2 = 0.84$) and longer overall in years with moderate CAP on July 15 ($R^2 = 0.26$, Figure 4.5.3). Start date was advanced when CDD was high on June 15 ($R^2 = 0.52$) and delayed when CAP was high on June 15 ($R^2 = 0.35$, Figure E4). Peak date was advanced when CDD was high on July 1 ($R^2 = 0.64$) and delayed when CAP was high on July 1 ($R^2 = 0.33$, Figure E4). End date was considerably advanced when CDD was high ($R^2 = 0.92$) and delayed when CAP was high ($R^2 = 0.65$, Figure 4.5.4).

The start date, peak date, and end date for *Gilia*, *Eriophyllum*, and *Orthocarpus* were related to CDD and CAP (Figure E6-E7). The start date and even peak date for *Delphinium* were likely missed by measurements, but the end date was strongly related to both CDD and CAP. Flowering duration for all four species was more strongly related to CDD than to CAP (Figure E5, Table E2).

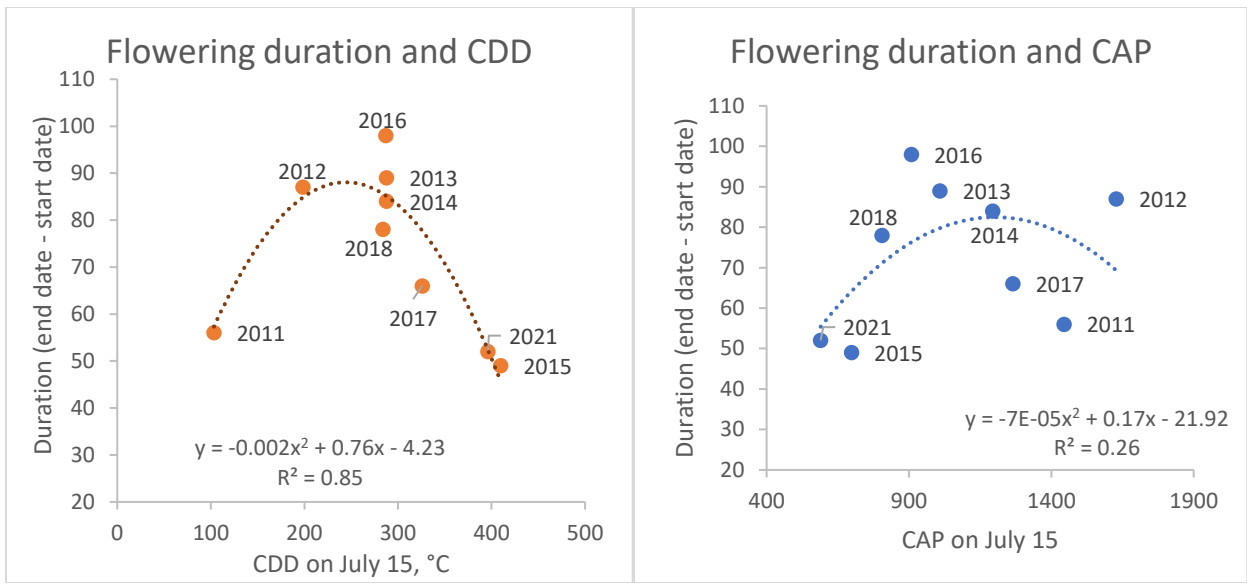


Figure 4.5.3. Flowering duration (estimated using a proxy for start date) compared to CDD and CAP on July 15.

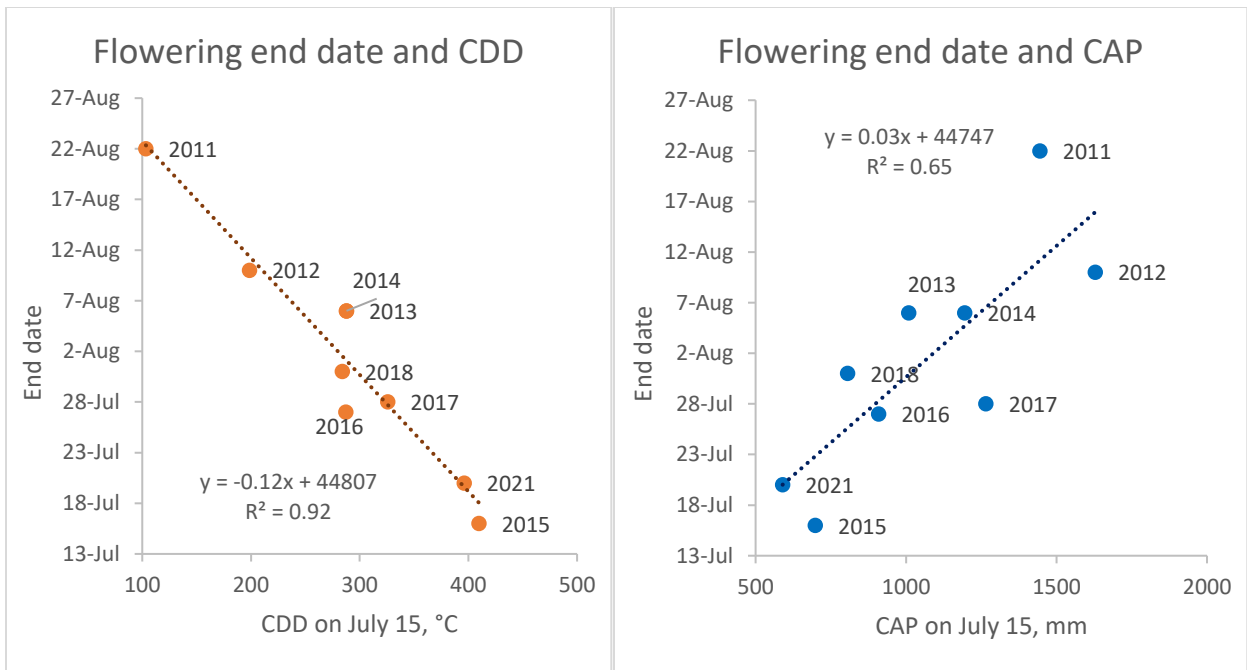


Figure 4.5.2.BH. End date (day where >95% of flowers had been observed) is inversely proportional to CDD and positively related to CAP.

4.6. *Climate & bees*

4.6.1. Abundance

The frequencies of visits to flowers by all bees, *Apis*, and *Bombus* were not related to CDD or CAP (Figure 4.6.1., Figure F1).

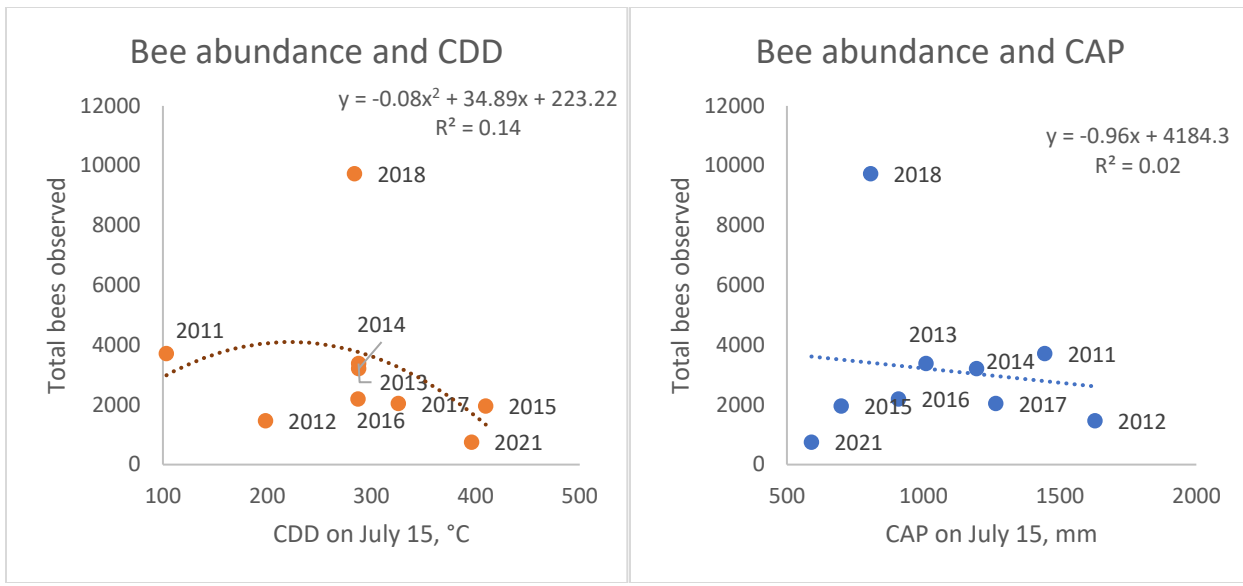


Figure 4.6.1. Bee abundance for all species compared by year for both cumulative degree days and cumulative antecedent precipitation.

4.6.2. Phenology

Bee visits began, peaked, and ended earlier in hot and dry years. Bee visit phenology varied greatly among years (Figure F3). Based on the estimation of CDD (Figure F2, described in 3.3.6.2), bees began visiting flowers when CDD exceeded 96 °C. The duration of bee visitation was greatest in years with moderate temperature and precipitation, and it was least in hot and cool years ($R^2 = 0.66$) and dry and wet years ($R^2 = 0.54$, Figure 4.6.2). Visitation peak date was advanced with high mid-season CDD ($R^2 = 0.55$) and delayed with high CAP ($R^2 = 0.36$, Figure F4). End date had a strong negative relationship with late season CDD ($R^2 = 0.81$) and a positive relationship with late season CAP ($R^2 = 0.67$, Figure F4). These results were similar for *Apis* and *Bombus* analyzed separately.

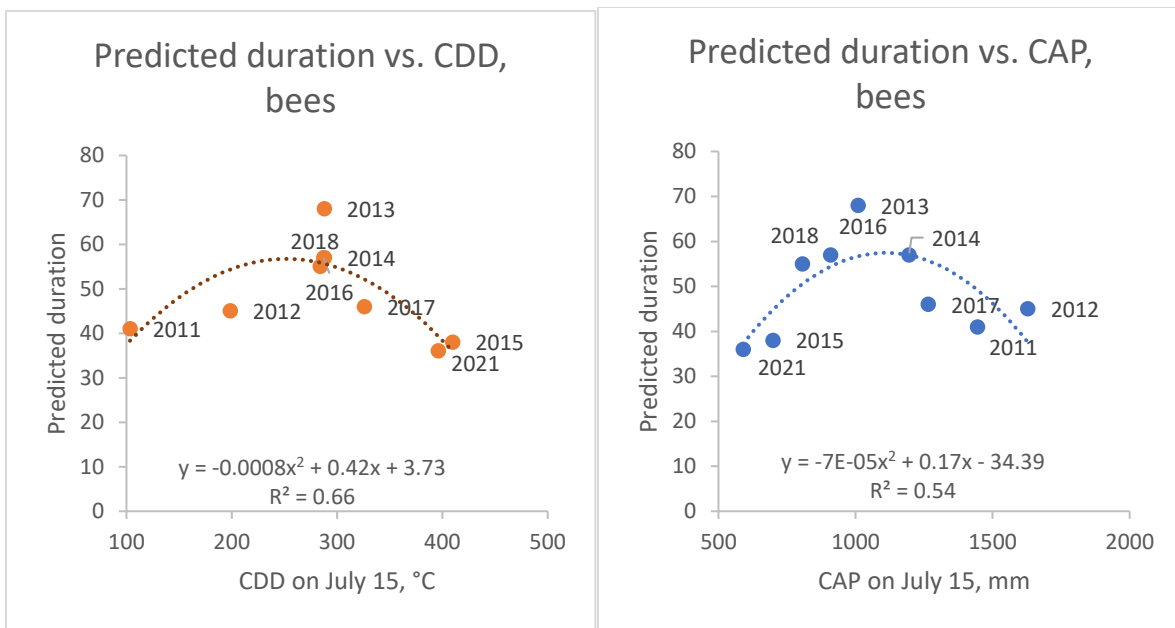


Figure 4.6.2. Based on the start date derived from Figure F2, the duration of bee visits by all bees is compared to CDD and CAP.

4.7. Network

4.7.1. Specialization and redundancy

Plant-pollinator interactions that played a key role in the network over time are illustrated in the interaction matrices (Figures 4.7.1). The darker cells represent more frequent interactions (interactions that were observed ten or more times). Generalists are clustered at the top. From early summer to late summer, there is complete turnover of the flower species frequently visited by bees, and less turnover of bee species (Figure 4.7.2).

There was a high level of redundancy in this network (Figure 4.7.4). All plants and pollinators were connected to the network; there were no interactions that were entirely separate or disconnected from the rest of the network. Most of the interactions (in the center) had a high degree of redundancy, meaning that multiple pollinators visited the same plants (generalists). On the outside ring, there were approximately 20 bee species (approximately 20%) that visited only 1-2 species of flowers (specialists) and more than 20 species of flowers (or approximately 15%) that were visited by only one species of bee. These flowers were likely visited by other pollinators apart from bees and thus redundancy or specialization in the flowers cannot be concluded from this analysis.

The number of degrees varied considerably between years, but the shape of the degree distribution remained consistent over time (Figure 4.7.3). In this network, a few bee generalist species visited many flowers, many bee species visited few species of flowers, and a small number of specialist bee species that visited only one species of flower. The same was true for the number of pollinators that visited each flower, with less of an extreme difference between the most visited and the least visited flowers (Figure G2).

The three most connected bee species remained one of the top 5 most connected bees in all 9 years but otherwise, the most connected species varied between years (Table 4.7.1).

Eriophyllum lanatum was the only species of flower that remained in the top 5 most connected flowers for all 9 study years (Table G1). The other most connected flowers only remained there for a maximum of 5 out of 9 years for *Erigeron foliosus* and *Gilia capitata*, and 3 or less years for every other flower.

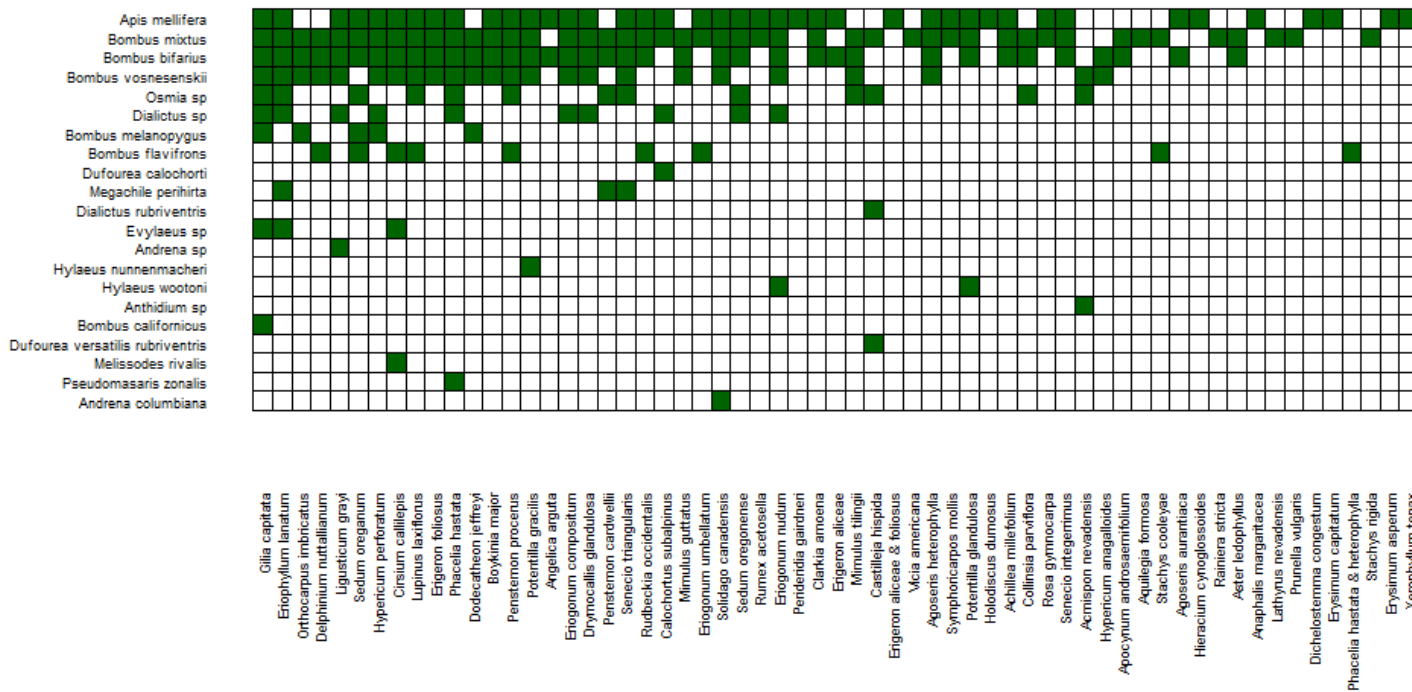


Figure 4.7.1. The principal plant and pollinator interactions for all meadows and all years. Interactions between bee species (rows) and flower species (columns) that were observed at least 10 times within the 9-year study period are shown in dark green.

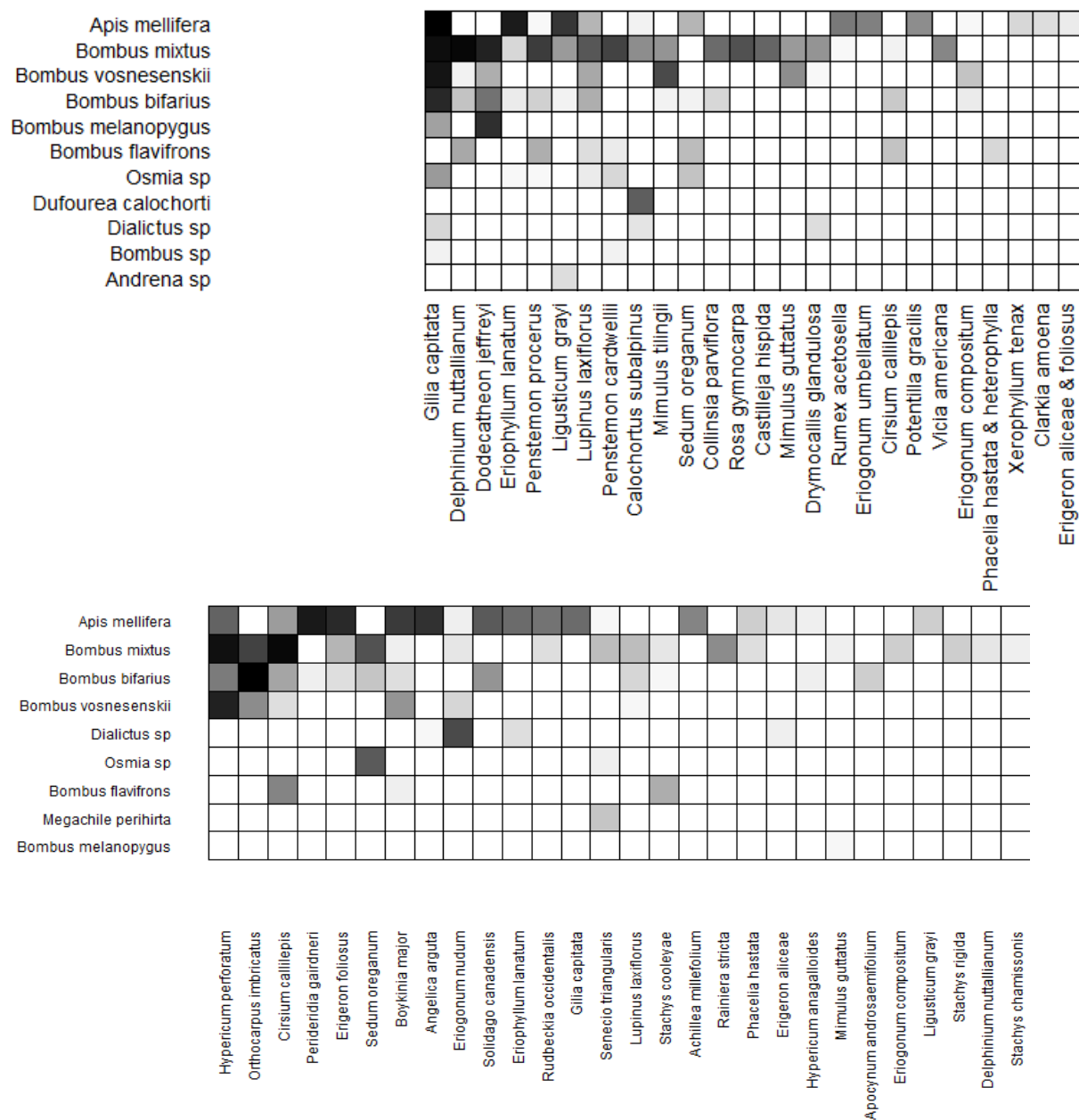


Figure 4.7.2. The principal plant and pollinator interactions for all meadows for the first watch (left, late June) and the last watch (right, early August) in all years. Interactions between the 10 most frequently occurring flower species in each time period (columns) and their bee species (rows) are shown in shades of gray and black: more frequent interactions are given darker colors. Note that flower species differ between the early and late season, but most of the bee species are present in both periods.

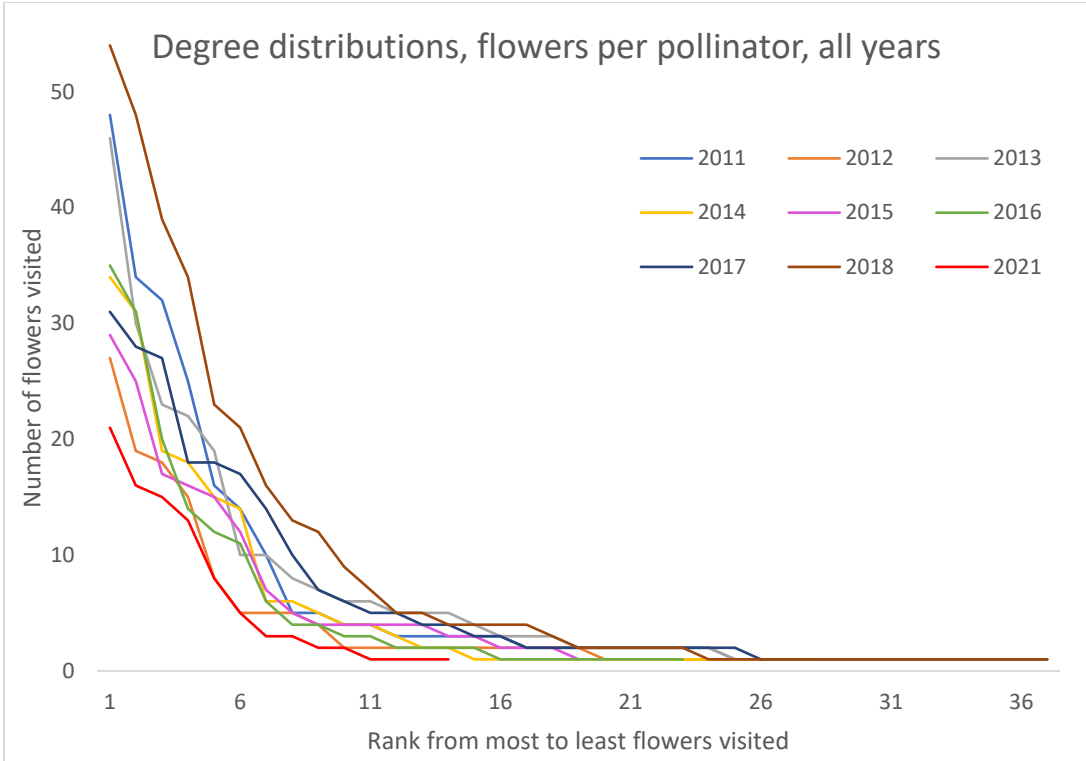


Figure 4.7.3. A distribution of the number of flowers visited by each pollinator. These distributions are ranked by the most to the least and are plotted by year.

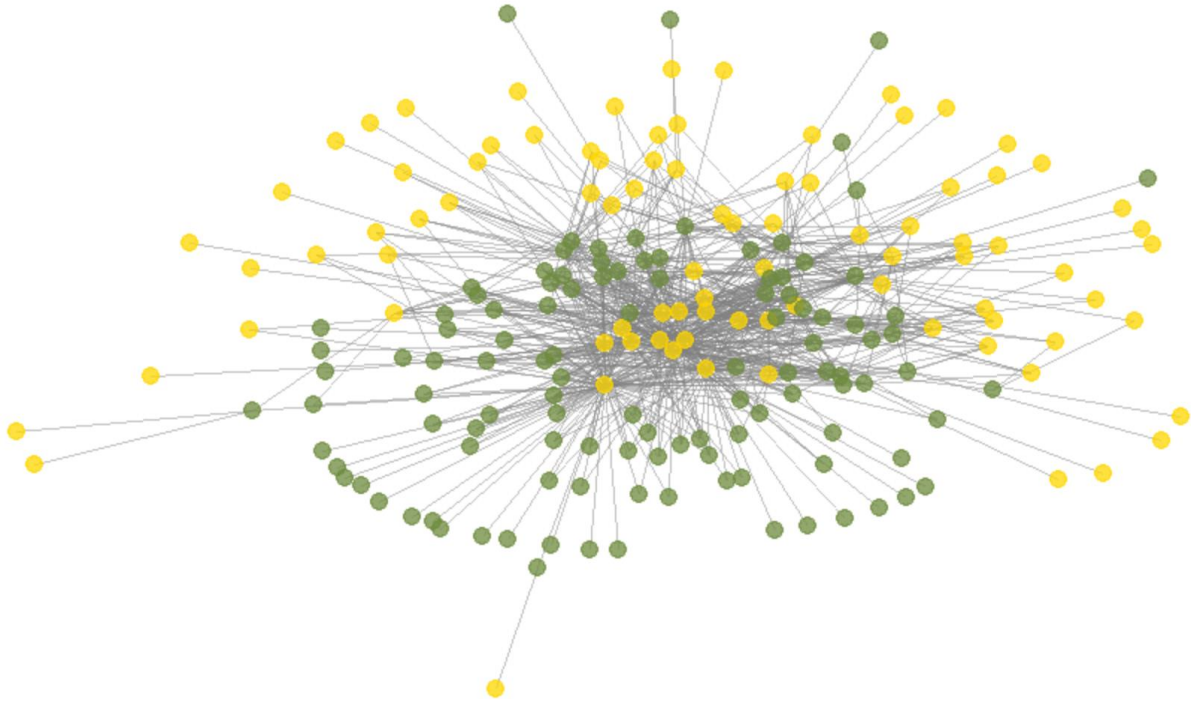


Figure 4.7.4. A visualization of the network: all bees and all flowers over the entire study period. Plants are in green, and bees are in yellow. The lines indicate which bees visited which flowers. Specialist bees are on the outer rim. These bees only have one connection to the network, all via plants visited by generalist bees. Generalist species are in the middle. The levels of connection visible here illustrate a high degree of nestedness and redundancy.

Table 4.7.1. Number of years in which each bee species ranked in the top five bee species based on number of flower species visited in that year, and number of flower species visited by each species of bee per year in the 9-year study.

| Species | Number of years in top 5 (out of 9) | Average number of flower species visited |
|----------------------------|-------------------------------------|--|
| <i>Apis mellifera</i> | 9 | 29.44 |
| <i>Bombus bifarius</i> | 9 | 22.56 |
| <i>Bombus mixtus</i> | 9 | 33.44 |
| <i>Bombus vosnesenskii</i> | 6 | 17.67 |
| <i>Osmia</i> spp. | 4 | 15.22 |
| <i>Bombus flavifrons</i> | 2 | 17 |
| <i>Bombus melanopygus</i> | 2 | 7.67 |
| <i>Dialictus</i> sp. | 2 | 17.33 |
| <i>Andrena</i> spp. | 1 | 3.13 |

*Note: *Bombus flavifrons* and *Dialictus* sp. were only observed in three of the nine study years.

4.7.2. Rewiring and turnover

Over all 9 study years, 243 different interactions were observed. On average, each interaction was present for 2.39 years (Table G2). A total of 54% of interactions were observed in only 1 year, and 71% were observed in only 1-2 years. Only 16.5% of interactions were observed in over half (5 or more) of the years and only 2.5% of all interactions (or 6 total) were observed in all 9 years.

Plant-pollinator interactions were highly dissimilar among years. All pairwise Sørensen values exceeded 0.5, meaning that in every year, more than 50% of the interactions differed from those in any other year (Table G3). The 2021 year was most dissimilar: 6 of 8 comparisons with other years exceeded 0.7. In all pairwise comparisons, only 9 dissimilarity values exceeded 0.7.

Flower dissimilarity was much lower than interaction dissimilarity (Table G4). No pairwise Sørensen values exceeded 0.5, meaning that in every year, more than 50% of the flower species were the same as those in other years. The highest dissimilarity values for flower species (> 0.4) involved comparisons of 2015 and 2021 with other years.

Pairs of years that differed in CAP were slightly more likely to differ in CDD ($R^2 = 0.30$, Figure G3). However, Sørensen pairwise dissimilarity of plant-pollinator interactions was not related to CAP or CDD (Figure 4.7.5).

Pairs of years with different CDD or CAP tended to have higher dissimilarity in flower species, but the relationships were not significant (Figure 4.7.6). Flower turnover was only weakly related to interaction turnover ($R^2 = 0.14$, Figure 4.7.7).

Meadows had different degrees of interaction turnover (Table G6). CPR had the least turnover in interactions (5 Sørensen values less than 0.5). M2 also had some low turnover in interactions (3 Sørensen values less than 0.5).

Interaction turnover was not related to flower turnover in most meadows (Figure G4). However, interaction dissimilarity was weakly related to flower dissimilarity at NE ($R^2 = 0.41$), and CDD difference was weakly related to floral dissimilarity ($R^2 = 0.16$, Figure G4). Interaction dissimilarity and floral dissimilarity were not related to CDD or CAP at most meadows. However, floral dissimilarity was weakly related to CDD and CAP at RP1 (CDD $R^2 = 0.23$, CAP $R^2 = 0.29$).

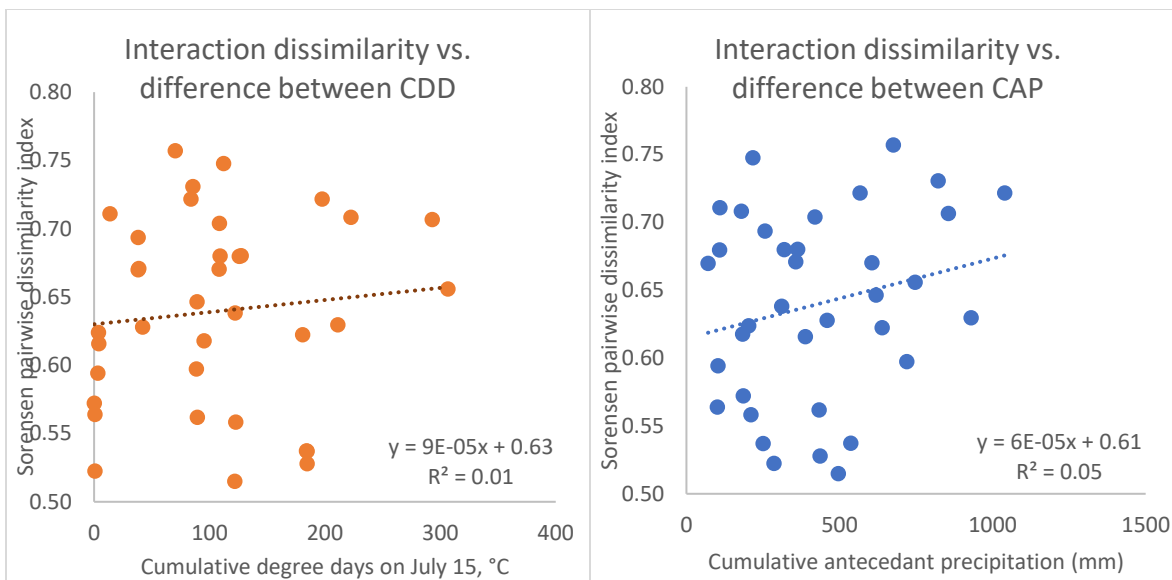


Figure 4.7.5. Interaction dissimilarity using Sørensen pairwise dissimilarity index compared to the dissimilarity between CDD/CAP in the same two years (all positive values).

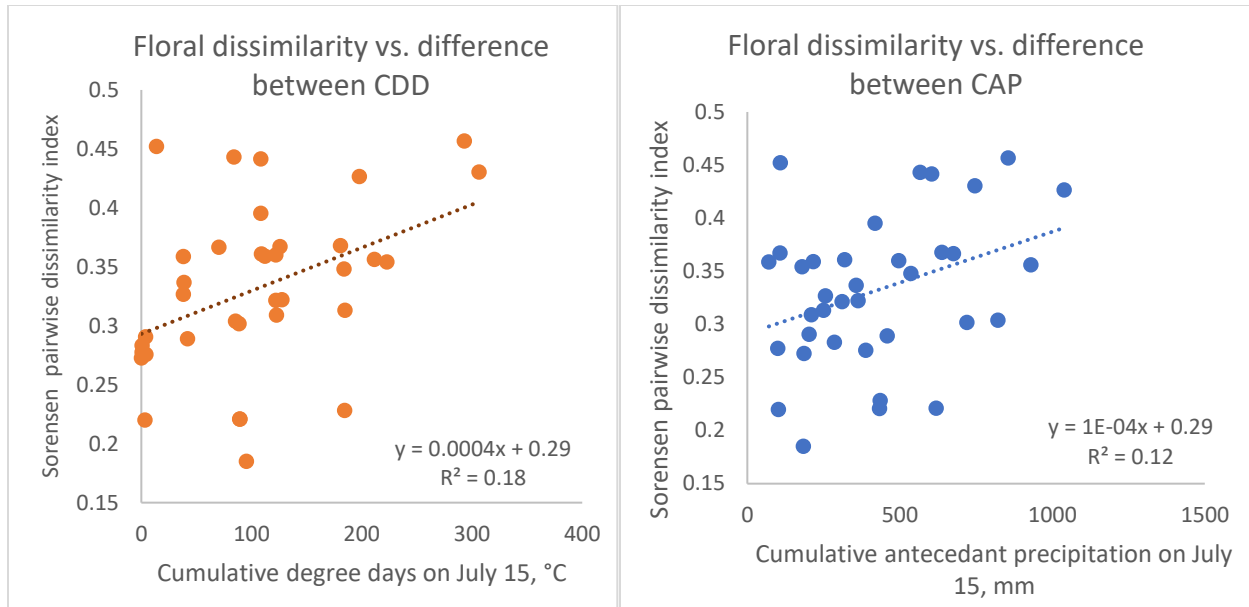


Figure 4.7.6. Interaction dissimilarity using Sørensen pairwise dissimilarity index compared to the dissimilarity between CDD/CAP in the same two years (all positive values).

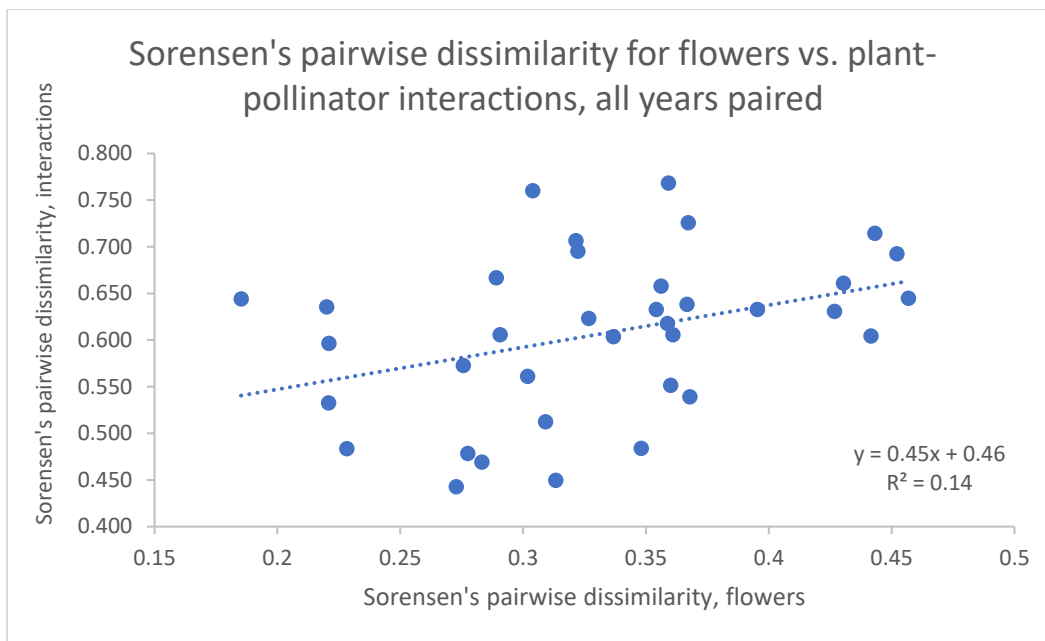


Figure 4.7.7. A comparison of Sørensen pairwise dissimilarity for all pairs of years for flowers and plant-pollinator interactions.

5. DISCUSSION

5.1 Errors, uncertainties, and confirmatory results

5.1.1 Errors and uncertainties

There was some doubt on the correct identification of all flower species in the long-term dataset. Additionally, the names of some species have changed since the beginning of data collection in 2011. For instance, *Zigadenus venenosus* is now *Toxicodendron venenosum*. Some genera have also been changed, namely the *Mimulus* genus is now split into *Erythranthe* and *Diplacus*. In this process, some species have also been subdivided. Because of this, for the purposes of this study, the original names used in the dataset have been kept and not updated because there is not documentation of every flower.

For future data collection, it would be beneficial to keep records of species identification to minimize inconsistency. The flowers identified in 2021 were uploaded to iNaturalist as a form of documentation for future researchers to visit and confirm. iNaturalist or a similar photographic platform would be a useful and quick record for future researchers in case of further species reclassification or questioning of species. For increased accuracy, an herbarium collection could be made. These are important steps because incorrect or inconsistent identification one year might lead to incorrect conclusions on the presence or abundance of flowers.

Furthermore, there is also doubt about the correct identification of bees. Doing a visitation watch has limitations when it comes to species identification, particularly when it comes to solitary bees. Many bees are difficult to correctly identify to species without investigation under the microscope and thus many species in this study are only identified to genus. However, the most common bees observed (*Apis mellifera* and *Bombus* spp.) are relatively easy to identify. *Bombus* spp. are easy to recognize even if the individual species might

be harder to distinguish from field observations. Because of these doubts, we chose to focus more on species in broader groups rather than at the individual species scale.

Nevertheless, despite the limitations of identification, these methods of bee observation are commonly used in other long-term datasets (such as Caradonna et al., 2017; Kudo, 2014) and are valuable. While capturing bees would lead to higher identification accuracy, this method might not have the same level of population accuracy as a study that does not interfere with bee behavior. For the purposes of this study, no interference gives more detailed information about floral resource interactions than a study focused primarily on identification. If future investigators want to improve identification accuracy, a combination of the two strategies would yield the greatest accuracy in both identification and visitation.

Our dataset is also limited in its ability to capture both rewiring and turnover. Rare species and rare interactions could easily be missed in our data collection and thus disappearance of rare species or rare interactions cannot be concluded.

As with any long-term dataset, there is potential for error in consistency. One source of potential error could be in how a stem is counted. Even with clear procedures defined and followed over the years, some flowers have easier inflorescences or stems to count than others and it is possible that some of the variation in floral abundance is due to how stems were counted each year.

Furthermore, cumulative antecedent precipitation was used as a proxy for meadow drying in this analysis but there may be better representations of meadow drying, such as those used in microclimate analyses and future analyses should investigate this further. Cumulative degree days came from a weather station situated between all three meadow complexes but did not fully

capture the true nature of variability between each meadow and the potential variability in temperature between the weather station and the exact temperature and precipitation at each site.

5.1.2. Confirmatory results and ecosystem baseline

In many ways, the results of this research support findings from previous studies. A portion of our analysis was focused on establishing a baseline for the ecosystem examined in this dataset and the results are largely descriptive. These results are not novel (apart from their focus on this specific geographic location) but are necessary for understanding interannual variation and for the analyses discussed in subsequent sections.

Within and between years, we found highly variable interannual flower abundance. Some of the variability in flower abundance might be explained by different sampling periods that may or may not capture the absolute abundance of flowers each year. Along with variable abundance, there was a high level of flowering plant diversity found in these meadows. Helderop (2015) found that the arrangement of species in these meadows varied greatly both geographically and temporally.

We also found a large interannual variation in the number of bees observed per watch, particularly considering 2018 as an outlier with an order of magnitude increase in bee observations. *Apis*, *Bombus*, and solitary bees were not affected in the same way by interannual variation. For example, in 2017 solitary bee abundance was much higher than average but social bee abundance was lower than average. Some of the variation in solitary bee abundance may be due to observation bias (i.e., in plots with lots of bee activity, it might be easy to miss smaller, less conspicuous bees than in meadows with less bee activity).

Apis, *Bombus*, and solitary bees all emerged around the same time and persisted for the same amount of time throughout the summer. Their patterns of visitation were different because of their differing life cycles. At the beginning of the season, *Bombus* queens must first build their colonies before major foraging may occur (Heinrich, 1979). Unlike honeybees, *Bombus* does not rapidly increase foraging to increase honey production, as *Apis* does. Because *Apis* persist through the winter, they can build their colony prior to the onset of flowering and then spend the flowering period storing up as much honey as possible for the winter (Seeley, 1985). In our study, the accumulation of *Apis* visits increased at the faster rate midway through the summer, likely in tandem with peak flowering. Visitation by solitary bees peaked earlier in the summer than either *Bombus* or *Apis*. This may be because solitary bees must build up pollen before they are able to lay their eggs and thus concentrate foraging efforts earlier in the summer (Danforth et al., 2019).

Furthermore, we found four common species of *Bombus* that follow a consistent order over the years. This is consistent with previous research showing that in a given ecosystem, there are a small subset of dominant *Bombus* species that have different phenological niches (Ogilvie et al., 2017). We found the same to be true for the most common solitary bee genera.

In our study, bees visited meadows based on the quantity of flowers found in those meadows. Meadows with more flowers also supported more bees. This supports previous research that bees are found in areas with more abundant assemblages of flowers (such as Elliott & Irwin, 2009). Both *Apis* and *Bombus* visited meadows that have a higher quantity of flowers more often. For *Bombus*, this correlation was strongest in the year with the greatest quantity of *Bombus* (2018).

Furthermore, the meadows in our study remained consistent in flower quantities. If a meadow had a high quantity of bees and flowers or the reverse, it remained that way over time. In a year with significantly more bees (2018), the relationship between number of flowers and the number of visits by bees was much stronger. In years where there were less flowers (2015 and 2021), visits by bees were more connected to flower abundance than in other years.

5.2. *Weather and climate*

5.2.1. Flowers

As in other systems (including alpine meadows in the Rocky Mountains (Inouye, 2008)), the abundance of flowers and bees in this study was driven by weather and most strongly by heat accumulation. Flowers were the most abundant in years with moderate heat and moisture. Years that were hotter and drier than average had a lesser abundance of flowers.

The phenology of flowers in this study also was driven by heat and precipitation. In colder and more moderate years, flowers began blooming, peaked, and finished blooming later. In hot years (especially in 2015 and 2021), flowers bloomed earlier, peaked earlier, and stopped blooming earlier. Not only did phenology shift earlier in the year, but the overall duration of flowering was also shorter in hot years. Heat alone had a strong effect on flowering phenology. A longer-term warming trend could mean earlier and shorter flowering periods.

The phenology and abundance of some species was more tied to accumulated heat and extreme heat events than others. In general, the interannual variation and the degree of connection to these variables differed between species. *Delphinium* and *Orthocarpus* were the most abundant in years with moderate temperature and precipitation. *Eriophyllum* flowering was most abundant with moderate precipitation and was not related to temperature. Based on the

inverse relationship between *Gilia* abundance and heat accumulation, *Gilia* will likely be the most impacted by hotter and drier summers. Therefore, out of the four species investigated, *Eriophyllum* is likely to show the least climate-induced changes in abundance and *Gilia* the most.

The flowering phenology of these four species of flowers were all related or even strongly related to temperature and precipitation. In hotter and drier years, flowers bloomed earlier, peaked earlier, and stopped blooming earlier. Furthermore, in hotter years, *Delphinium*, *Gilia*, *Orthocarpus*, and *Eriophyllum* bloomed for a shorter duration than in cooler years.

5.2.2. Bees

The plants in this study were more sensitive to climate variability than pollinators. There was a stronger connection between temperature and flowering phenology and abundance than to either measure of bee visitation. Total bee abundance was not directly related to variation in heat and moisture. *Apis* and *Bombus* abundance were not correlated with either measure of climate, but *Apis* abundance was slightly heat dependent.

The phenology of bee visitation in our study was partly driven by heat and moisture. Duration of bee visitation by all bees was highest in years with moderate heat and moisture while the peak and end dates were all connected to heat accumulation. Bees stopped visiting flowers earlier in hotter and drier years and visited flowers for a shorter period overall. Part of this visitation pattern is likely due to the indirect effects via the earlier cessation of blooming in hot and dry years. Whether direct or indirect, this has implications for the quantity of pollen and nectar that bees can obtain in a summer season, which in turn has implications for the long-term survival and fitness of bees. However, our data on bee phenology is limited only to observations

of foraging and thus misses other critical phenophases. Therefore, we cannot say conclusively how bees might respond to shorter flowering periods.

5.2.3. Extreme weather

In addition to annual climate variation, this study also adds insight on the role of extreme weather events. In 2021, the heat wave had an immediate impact on the network both in terms of phenology and abundance. Multiple species (including *Gilia capitata*, *Sedum oreganum*, *Ligusticum grayi*, *Angelica arguta*) had visible heat scorching following the heat dome event. The early disappearance of certain flowers (including a post-heat wave disappearance of *Gilia*) led to visible rewiring in common interactions. The long-term effects of this extreme event could lead to turnover. More events like the 2021 heat dome combined with hotter and drier conditions could lead to extirpation of heat-intolerant species. However, the full extent of impacts from the 2021 heat dome will not be understood until the following years. The recovery of both populations of individual species and the network as a whole remains to be seen.

5.2.4. Late season dry periods

In previous research (Stemkovski et al., 2020), phenological responses were observed more frequently and significantly in early season phenomena such as flowers that bloom in early summer and in corresponding phenophases such as bees emerging from hibernation. In this study, we did not have adequate data on early season phenology. This data is also limited to meadow interactions which miss the timing of bee emergence. While we did not have a full sense of early season phenological responses given our study design, we did find that later season phenophases such as the end of flowering had a strong phenological response to climate.

While early season phenological response is likely shifting, hotter and drier conditions also had a noticeable impact on flowering duration and thus merits further investigation.

Much of the previous research on this subject has occurred in systems where flowering is extending with decreased abundance due to extended summers and consistent summer rainfall (Aldridge et al., 2011). However, there are other systems where shortened flowering periods have been noted due to extreme heat (Kudo, 2016). Much of the research on plant-pollinator phenology to date has focused on early season trends. To get a full sense of phenological changes, it is imperative that we also focus on understanding the consequences of late season phenological changes. Kudo (2016) characterized this early end of flowering as a type of phenological mismatch because the life cycles of bees did not keep up with the life cycle of the flowers.

In the Oregon Cascades, late season dry periods may have greater ecological consequences than early flowering. A shortened period of floral resources in a longer summer season puts stress on bee foraging capacity and creates mismatch in bee lifecycles and flowering periods. However, the true consequences of this scenario are not well understood. Using this dataset, we cannot answer this question completely. Likely, bees will forage elsewhere if there are still flowering plants within the forest. Unfortunately, forests do not hold the same abundance of floral resources that meadows do and thus a shorter meadow flowering period could have a negative impact on the long-term survival and fitness of bees. Additionally, a shorter flowering period gives flowers less time to grow and reproduce and could eventually lead to population declines in flowering plants.

5.2.5. Meadows and soil moisture

These findings support previous research (Debinski et al., 2000) that soil moisture content plays a role in the extent to which meadows are impacted by interannual variation. The xeric and wet meadows showed the least amount of interannual variation in floral abundance while the mesic meadows had both the greatest floral abundance and the greatest interannual variation in abundance. In addition, there was substantial interannual phenological variation of flowering time within certain meadows. The wettest and driest meadows had less interannual phenological variation than mesic meadows. In mesic meadows, the timing of flowering (start, peak, end) varied by up to a month while in both wet and dry meadows, flowering varied by less than half that amount.

Furthermore, floral abundance in mesic meadows was strongly correlated with both cumulative degree days and cumulative antecedent precipitation. There was a much weaker relationship in wet meadows and no observable relationship between cumulative degree days or antecedent precipitation and floral abundance in xeric meadows. Therefore, we can assume that the impacts of climate variability are not the same across all meadow types. Wet meadows are more buffered against extreme temperatures or drought because of their high moisture content and species adapted to xeric meadows are already adapted to extreme drought conditions (Debinski et al., 2010). Species common in mesic meadows do not have these built-in adaptations and thus may be more susceptible to climate variation than the other meadow types.

5.3. *Introduced European honeybee*

The role of the introduced European honeybee, *Apis mellifera*, had a substantial impact on the presence and abundance of different species within this network. In 6 out of the 9 study

years, *Apis* was the most abundant bee (even counting all *Bombus* species as one group). Furthermore, in all years, *Apis* was among the top 3 bees in terms of the number of flower species they visited. *Apis* was found in all 12 study meadows (but was consistently absent or close to being absent from the Carpenter Meadow complex). Part of the number of observations was likely due to the sheer size of honeybee colonies. One colony of honeybees may have a population in the tens of thousands (Seeley, 1985), while a colony of bumblebees may have several hundred bees or less (Heinrich, 1979).

The presence of *Apis* in this network is important to note because pollinators help control the reproductive fitness of different plants and play a role in shaping floral neighborhoods (Bruckman & Campbell, 2014). In other systems, *Apis* have been found to decrease network connectivity and impair pollination services because of their decreased pollination quality (Valido et al., 2019).

The origin of feral *Apis* colonies in the Andrews Forest is unknown but may have occurred in the 1960s or 1970s when managed honeybee hives might have been placed in regenerating clearcuts to take advantage of abundant fireweed (Jones et al., 2018). While there is not data from before *Apis* was introduced to the area, it can be inferred based on the abundance of *Apis* that they have played a key role in shaping the network that is seen today.

One potential result of the introduction of *Apis* could be competition with other bees. There is not strong evidence for within-meadow competition of *Bombus* and *Apis*. However, both *Bombus* and *Apis* dominate certain meadow complexes on a spatial scale. This could be due to the location of hives and the relative foraging distance for each meadow, as well as the characteristics of flowers found in each meadow. For instance, Lookout Bog is near other meadows that have an abundance of *Apis* visitors but did not have an abundance of flowers that

Apis preferred to visit. Because the relative proportions of visitation by each group per meadow did not vary much over time, this may suggest that there was some amount of spatial separation of niches between the two groups. Like *Apis*, *Bombus* was found in meadows with the flowers it preferred the most. Also, like *Apis*, *Bombus* tended to be abundant in the same meadows over time.

There is evidence of competition between solitary bees and *Apis*, but also between *Bombus* and solitary bees. In areas where there was a greater abundance of both *Apis* or *Bombus* or both, there were fewer solitary bees, suggesting that solitary bees may be avoiding the same resources used by social bees. This remained true in all years except for 2015 and 2021 where there was no evidence of a negative relationship. In those years, either fewer bees or a decrease in resource availability may have led to less avoidance by solitary bees.

In addition to competition, *Apis* may have played a role in shaping the floral community visible today. *Apis* visitations were closely tied to *Gilia* presence, inferring that they support one another and that the abundance of *Gilia* may be tied to the presence and abundance of *Apis*. *Apis* strongly preferred *Gilia* and were only abundant in meadows that also had *Gilia*. Over the study period, *Gilia* was the second most observed species of flower and made up around 13% of the total stem count. It is unclear whether *Apis* visited *Gilia* because it was one of the most abundant flowers or whether *Gilia* was one of the most abundant flowers because of the preferences of *Apis*. Without records prior to the introduction of *Apis*, it is hard to be sure, though it is likely that both played a role in positive reinforcement.

5.4. Network structure and climate, weather

5.4.1. Generalists and specialists

The network investigated in this study was characterized by many generalist pollinators that comprised most of the interactions and a few other, more specialized pollinators. Some of this count was likely due to observation limitations or bias. Visits of rare or less common bees to flowers may have been missed, potentially indicating more or less specialization than is present. The most common pollinators did not vary substantially over time, but the most connected plants varied considerably both within and between years. This implies that interannual variation had a smaller effect on visitation patterns for key pollinators than it did on the plants visited by these pollinators.

5.4.2. Preference

Many of the bees observed expressed preference for certain flowers, adding another layer of complexity onto how changes in co-flowering may impact network dynamics.

Apis overwhelmingly preferred *Gilia* in every year except for the two hot, dry years where *Gilia* populations were lower. In those years, they shifted towards visiting *Eriophyllum*. If this pattern remains consistent, in more years like 2015 and 2021, *Apis* might shift towards visiting more *Eriophyllum* overall. This may have consequences for other pollinators that also visit *Eriophyllum* and could lead to increased interspecific competition.

Bombus as a group did not express as strong of a preference for an individual flower species as *Apis*, but some individual *Bombus* species had preferred flowers. For the total group of *Bombus* species, there was a small group of flowers that *Bombus* visited preferentially.

Although there was more limited data on solitary species, there are more specialists in solitary bees than social bees (Strickler, 1979). In this dataset, the only specialists found were solitary bees. For example, the solitary species *Dufourea calochorti* was only observed visiting one flower (*Calochortus subalpinus*). A high level of specialization can make species more vulnerable to change, unless the plant is highly adaptable and the pollinator is able to shift temporally and geographically with the plant it specializes in (Jacquemin et al., 2020).

Beyond a preference for species, both *Apis* and *Bombus* visited flowers based on their relative abundance, with a few exceptions. Both avoided certain flowers and went out of their way to visit other flowers, even if these flowers were relatively lower in abundance. Some of these flowers might be beneficial for bees to seek out for increased amounts of nectar while others (such as *Delphinium*) have coevolved directly with *Bombus* (Pyke, 1978). Furthermore, meadow visitation and foraging phenology by bees was tied to certain flowers that they prefer. In the hotter and drier years, visitation was tied to more thermotolerant flowers, including *Eriophyllum*. Flowers that were sought out by each group of bees are worth investigating for indirect effects of interannual variation.

Because the bees observed in this study exhibited preference for certain flowers over another, it is possible that changes in co-flowering patterns will have a negative effect on the flowers that are less preferred. For instance, if summers are shortened or flowers shift their phenologies at differing rates, novel floral synchronization may result in different pollination patterns. If less preferred flowers begin to flower at the same time as preferred flowers, they may receive decreased pollination services.

5.4.3. Network redundancy

On a network scale, the system studied here had a degree of built-in redundancy. All the key plants (the plants most visited by common pollinators) investigated in the network analysis had multiple pollinator visitors, meaning that they would not lose pollination services with the extirpation of an individual pollinator. A small percentage (~15%) of flower species were only visited by one bee species, but these may be pollinated by non-bee visitors. Furthermore, all the species of bees that were observed to be specialists (~20% of bees that were only observed visiting one flower) visited flowers that had other bee visitors. This implies that this network has a high degree of nestedness (as described in Vázquez et al., 2009), meaning there is a core group of generalist species (mainly *Bombus mixtus*, *Apis mellifera*, and *Bombus bifarius*) with a large group of more specialized species that interact mainly with the generalists. Looking only at bees, the degree of nestedness visible in this network implies that it could be robust to potential extirpation. The loss of most species will likely not cause cascading extinction because of the level of nestedness and redundancy.

5.4.4. Rewiring

Rewiring was observed in this study, both as interannual variation and as a response to climate variation. In comparisons of interaction matrices both within and between years, the majority of network links appeared and disappeared over time while other more common interactions persisted throughout all or most of the study. In years that were hotter and drier than average, multiple key interactions changed.

Because *Gilia*, *Delphinium*, *Eriophyllum*, and *Orthocarpus* were important flowers for *Apis* and *Bombus*, variations in their abundance and phenology may have an impact on bees. In hotter and drier years, shorter flowering periods led to shorter visitation periods.

Both the abundance and overall flowering period of *Gilia* were less in hot and dry years. In years with less *Gilia* for a shorter period, *Apis* visited more *Eriophyllum* during the same period where they would normally visit *Gilia*. In the same years, *Bombus* visited *Eriophyllum* earlier and more frequently. In 2018, *Bombus* visited *Eriophyllum* both much more and for a much longer period, likely because of the order of magnitude increase in the overall *Bombus* population. *Eriophyllum* was less prone to interannual variation caused by climate and thus more pollinators may rely on it as resource in years where other plant species are affected.

Some visitation patterns were less prone to rewiring. Visits by *Bombus* to the early-blooming *Delphinium* remained consistent over time. The same was true of visits by *Bombus* to the late-blooming *Orthocarpus*.

In the overall network, significant rewiring occurred between all pairs of years. Rewiring was common but it was not driven by either climate measure. Variation in heat and precipitation between years did not predict rewiring (measured in interaction dissimilarity). However, interaction dissimilarity was highest in 2021 compared to all other years which could mean that either abnormal weather conditions or the heat dome may have contributed to greater rewiring.

There was a much higher dissimilarity between years in terms of plant-pollinator interactions than in terms of floral composition. Some of this discrepancy may be due to sampling error—it is easier to sample plants and easier to miss uncommon interactions between pollinators and plants. However, in years with the highest rates of dissimilarity in floral composition, there was also a higher rate of rewiring. Therefore, one of the drivers of rewiring

could be floral reassembly. That dissimilar floral composition led to greater rates of rewiring may be indicative of network adaptability.

In networks of plants and pollinators, links between species form and dissolve regularly over time, both within and between years (Caradonna et al., 2017). The occurrence of rewiring under extreme climate conditions is evidence of a level of resilience within this network. Even if climate leads to phenological mismatch or the decreased abundance of key species, rewiring may allow the network to persist and adapt via shifts in visitation patterns. In the process, if there are specialists who are unable to shift either temporally or to a different food source, these species may be excluded from the network. However, most bees may be robust to changing floral resources and shifting floral phenology.

5.4.5. Turnover

Rewiring was observed but turnover is harder to detect. It is possible that turnover is occurring, but true proof of turnover is not traceable with our study design. For instance, there are multiple species of *Bombus* (such as *Bombus flavifrons*) that were abundant or present in previous years and not observed in 2021. There are also several species of solitary bees that were observed in the earlier years of observations (2011-2013) but not in later years (including *Ceratina acantha*, *Ceratina nanula*, and *Colletes simulans nevadensis*). In addition to bees, there were also several species of plants that were observed in the first part of the study but not in the latter half (including *Lomatium triternatum* and *Arenaria capillaris*). Whether this is an anomaly, an error, or a true instance of turnover remains to be seen.

On a broader network scale, heat did have a small connection to turnover in floral composition. This implies that more extreme changes in temperature could lead to greater

degrees of turnover in floral composition. While pollinators may be able to adapt via rewiring, the presence of certain plants appeared to be somewhat connected to heat accumulation.

Observable turnover that leads to extirpation might occur over a longer period, perhaps after multiple concurrent extreme climate years. The disappearance of plants is easier to measure than the disappearance of bees based on a greater ease of observation. However, for both plants and bees, it is easy for less common or rare species of plants and bees to be excluded from sampling. Future sampling efforts should keep these in mind and note species that may no longer be observed.

5.4.6. Phenological mismatch

Beyond late season mismatch, phenological mismatch was not conclusively observed in this study but could be occurring. In a system with so much variation and with regular instances of rewiring, phenological mismatch is much harder to detect, particularly when looking at the system on a community scale. In order to detect mismatch, a baseline of interactions must be established over multiple years. Data on these interactions could be used to determine which interactions are consistent over time and worth investigating for possible mismatch. Moreover, phenological mismatch should ideally start with the first flowering and include data on bee phenophases outside of meadow interactions. This is worth further investigation.

5.4.7. Changes in co-flowering

Potential changes in phenology with hotter and drier conditions could lead to changes in co-flowering patterns. In this study, flower species were impacted differently by interannual variation. The overall trend was that flowers bloomed earlier in years that were hotter and drier

than average. However, different species were affected to different degrees by climate variation. Because of this, community composition might be disrupted by extreme climate years. Throughout the season, different arrangements of flowers co-occur with different pollinators. Since flowers were impacted at different rates by climate variability, it is likely that novel communities of flowers (novel because their flowering has never overlapped before) may form. Changes in co-flowering patterns have community-level consequences in terms of nectar quality and availability and may lead to network-level rearrangement (Theobald et al., 2017).

5.5. Predictions for climate change

If montane meadows of the western Cascade Range continue to experience hot and dry summers (as predicted with climate change), there will be consequences for networks of plants and pollinators. Flowering plants in these meadows that are not heat-tolerant are likely to be severely impacted by hot and dry summers and by extreme weather events and may be extirpated. Heat tolerant plants include plants that had the most shortened flowering period in 2015 and 2021 and that showed the most effects following the heat dome event. Notably, *Gilia* did not display heat tolerance in the study period and thus will likely be severely impacted or extirpated if hot and dry conditions persist.

Other, more thermotolerant plants may experience stress via changes in co-flowering patterns and the combined stress of other factors. Plants in mesic meadows are most likely to experience extreme climate-induced stress while plants in xeric and wet meadows are likely to be more buffered against change.

Bees are likely to be less impacted than flowers. Based on observed instances of rewiring and some degree of built-in redundancy, many bees are likely to adapt to climate-induced

changes. *Apis mellifera*, a generalist that has adapted to live in many different climate conditions and visits a wide range of flower species, will likely continue to persist at current population numbers unless there is a significant decline in floral resources.

Species of *Bombus* are also generalists and will likely continue to persist, with some potential exceptions. Many species of *Bombus* are adapted to cold conditions and are not used to heat or long periods of summer and will have to adapt or suffer population declines (Rasmont & Iserbyt, 2012). For example, both *Bombus bifarius* and *Bombus mixtus* are commonly found in high altitude environments and thus have a high tolerance for extreme cold but not extreme heat (Wilson et al., 2010). *Bombus bifarius* reaches a critical thermal limit (where they are at risk of death) around 40 °C and does not function at full capacity above approximately 30 °C (Oyen et al., 2016). During the heat dome event in 2021, temperatures reached close to 40 °C in the Andrews Forest, meaning that some mortality in *Bombus bifarius* may have occurred. On the other hand, *Bombus vosnesenskii* and *Bombus melanopygus* are found in a wide range of climatic conditions and thus have a greater thermotolerance than other species of *Bombus* (McFrederick & LeBuhn, 2006). With more extreme heat events or hotter temperatures overall, we may see a shift towards more thermotolerant species of *Bombus*.

Certain solitary bees are likely the most threatened by continued years of climate anomalies due to their tendency towards specialization. Specialist bees that are not able to adapt their visitation patterns may be extirpated if the flower they visit is not heat tolerant or if their phenophases do not shift in tandem with their preferred floral resource.

Other factors not included in this study will also play a role in influencing network dynamics and long-term survival of species. As discussed earlier, continued meadow encroachment in the area is leading to habitat loss and loss of meadow connectivity (Jones et al.,

2018). Parasitism, disease, invasive species, and shifting species ranges will all play a role in shaping this network in the coming years. Climate variables not investigated in this study will also influence the ecosystem. Changing snowpack and snow persistence combined with potential post-snowmelt frost may contribute to increased mortality or phenological shifts in plants and pollinators (Inouye, 2008). Additionally, as most bees only spend a portion of their lifecycle within a meadow, forest conditions will also be critical for bee adaptation and survival (Mola et al., 2021).

The system investigated in this study has a unique set of climate and geographic conditions. In other areas, summer rainfall allows flowering to persist if the summer lasts longer. Here, longer, hotter, and drier summers may have greater consequences. Furthermore, in other areas, species have been observed moving up in elevation with warming conditions. The meadows investigated in this study are already at the highest points in the western Cascade Range and a geographic shift with changing climate is not possible. However, species that are currently found at lower elevations may move up in elevation and may become a new source of competition in these meadows.

Based on this investigation, it seems likely that the network will persist if hot and dry conditions continue. Within the network, certain species may not be able to adapt to changing conditions and changing network dynamics and thus may be extirpated. The largest climatic threat to bees in this system may be shorter flowering periods in longer summers that lead to a late season period of sparse floral resources. Overall, however, with the persistence of hot and dry summers, pollination services will continue, and the network will likely persist, though with different assemblages of species.

5.6. Future research and implications for management

5.6.1. Future research

There are limited long-term datasets studying plant-pollinator interactions and thus it is imperative that data collection continues for this one. A longer study period will give a greater sense of climate variability and will allow for the continued monitoring of how this system varies and changes over time. Continued monitoring will also be important to understand the long-term effects of the 2021 heat dome event as many of the aftereffects may not have been visible in 2021.

Along with continued monitoring, future research could try to reconstruct historic data of plant assemblages and phenology using herbarium specimens or other datasets from the area. If bee specimens or observations are available, the same could be done for bees. Flowering phenology observed in the 20th century may have been quite different from what has been observed in our dataset and merits further investigation. In addition, if there are records available from before the introduction of *Apis*, this data could be used to understand the impact that *Apis* has had on the network.

More research is possible using the current dataset. In this study, we performed a simple network analysis looking only at the bees. An expanded network analysis that incorporates all pollinators would be beneficial. Beyond further network analysis, research should be done incorporating both geographic and temporal shifts in plant-pollinator arrangements. Future research using this dataset could also investigate whether species arrangements within *Bombus* spp. have shifted over time or if *Bombus* spp. species assemblages are related to heat or moisture.

Furthermore, only studying the foraging patterns of bees misses a significant portion of their life cycles. Many bees spend the majority of the year in other areas, especially forested

habitats (Mola et al., 2021). Understanding the relative role that non-meadow habitats play in the survival of bees is important to conservation efforts. Future research in meadows of the Andrews Forest should make an effort to study bees beyond the meadows and in other life stages.

Finally, as these meadows are shrinking and are threatened by climate change, further research should be aimed at understanding how to promote the long-term survival of these ecosystems. Researchers should seek to understand how restoration and conservation can play a role in protecting these meadows. Additionally, because of the role that indigenous peoples likely played in maintaining landscapes of the Cascade Range, researchers should work on learning and applying traditional ecological knowledge to the long-term survival of these places.

5.6.2. Implications for management

Montane meadows in the Oregon Cascades are facing threats from multiple angles. On one side, tree encroachment is considerably decreasing meadow area in the western Cascade Range (Takaoka and Swanson, 2008). This encroachment is leading to a decline of meadow species (Celis et al., 2017). Our results show that while the effects of climate change will be variable, they will add stress to an already threatened ecosystem. Because of these combined stressors, land managers should make an effort to support meadows in the western Cascade Range.

Tree removal, either with or without fire, has been successful in reversing or slowing conifer encroachment in meadows of the western Cascade Range (Halpern & Antos, 2021). Intentional tree removal should be implemented by land managers in the region to preserve meadow habitat. Because of the role that indigenous people likely played in the existence and management of these meadows (Turner et al., 2011), future management plans should also

include input and knowledge from local tribes. The effects of climate change will be harder to mitigate than those of tree invasion and thus a focus on bolstering overall ecosystem health may be the best strategy for assisting in maintaining network redundancy. In other systems, restoration has been proven to reestablish the robustness of plant-pollinator networks (Gao et al., 2021). With a more robust network, turnover is less likely and thus the system may be more adaptable (Vázquez et al., 2009).

While certain rare, specialist bees may be at the highest risk of extirpation, it may not be the most beneficial to make these species the only focus of conservation (see Doré et al., 2021). Conservation efforts should approach plant-pollinator systems as a network. Some species play a larger role in maintaining the network and thus deserve equal focus as rare specialists. A population decline in one of these species may have a greater impact on the overall network than the extirpation of a rare specialist.

In these meadows, *Bombus mixtus* and *Bombus bifarius* are common pollinators that play a major role in the network. However, both species have limited, mostly alpine ranges and thus may be facing a greater threat with climate change than other network generalists. Conservation efforts should prioritize these bees in addition to rare and potentially endangered specialist species because of the role they play in maintaining network connectivity and the quantity of pollination services that they provide.

Furthermore, while a conclusive answer is beyond the scope of this study, it is possible that *Apis mellifera* has a negative influence on this community, as other studies have found (Schweiger et al., 2010). Given this, conservation efforts should prioritize habitat and food sources preferred by native bees over those used by *Apis mellifera*.

Finally, because response to variability was different among meadow types, meadow conservation and restoration efforts should prioritize mesic meadows because they are the most affected by increased heat and decreased moisture.

6. CONCLUSION

The plant-pollinator networks sampled over nine years in twelve montane meadows of the western Cascade Range, Oregon USA are characterized by a high level of variation for both bee visitors and flowers, both within and between years. In hot years (high cumulative degree days), floral abundance and flowering durations were lower. These impacts were moderated in wet meadows and not observed in xeric meadows. Bee abundance was not related to heat and neither bee nor floral abundance was related to moisture (cumulative antecedent precipitation).

The network had a high level of redundancy and significant rewiring in interactions between pollinators and plants. Turnover of flowers was related to differences in heat, but turnover of plant-pollinator interactions was not related to climate variability. Bee abundance was not related to climate variability by any direct measure but may be indirectly impacted by hotter and drier summers associated with climate change via reduced flowering periods and a late season period of low floral resources. In these conditions, bees may have to contend with shorter flowering periods and increased floral turnover, potentially decreasing bee abundance and increasing turnover in bees, particularly in species that are not able to adapt via rewiring.

7. LITERATURE CITED

- Aldridge, G., Inouye, D. W., Forrest, J. R. K., Barr, W. A., & Miller-Rushing, A. J. (2011). Emergence of a mid-season period of low floral resources in a montane meadow ecosystem associated with climate change. *Journal of Ecology*, *99*(4), 905–913. <https://doi.org/10.1111/J.1365-2745.2011.01826.X>
- Bartomeus, I., Ascher, J. S., Wagner, D., Danforth, B. N., Colla, S., Kornbluth, S., & Winfree, R. (2011). Climate-associated phenological advances in bee pollinators and bee-pollinated plants. *Proceedings of the National Academy of Sciences of the United States of America*, *108*(51), 20645–20649. <https://doi.org/10.1073/pnas.1115559108>
- Baselga, A., Orme, D., Villeger, S., De Bortoli, J., Leprieur, F., Logez, M., & Henriques-Silva, R. (2022). Betapart: Partitioning Beta Diversity into Turnover and Nestedness Components. *R Package Version 1.5.6*. <https://doi.org/https://CRAN.R-project.org/package=betapart>
- Baselga, A., & Orme, C. D. L. (2012). betapart: an R package for the study of beta diversity. *Methods in Ecology and Evolution*, *3*(5), 808–812. <https://doi.org/10.1111/J.2041-210X.2012.00224.X>
- Bruckman, D., & Campbell, D. R. (2014). Floral neighborhood influences pollinator assemblages and effective pollination in a native plant. *Oecologia*, *176*(2), 465–476. <https://doi.org/10.1007/S00442-014-3023-6>
- Bryan N. Danforth, Robert L. Minckley, John L. Neff, F. F. (2019). *The Solitary Bees: Biology, Evolution, Conservation*. Princeton University Press. <https://books.google.com/books?hl=en&lr=&id=4ceXDwAAQBAJ&oi=fnd&pg=PP9&dq=solitary+bee+life+cycle&ots=KMgAy5SYsS&sig=z4jQS3aA0VIYdEo9ODTD24Gb8YM#v=onepage&q=solitary+bee+life+cycle&f=false>
- Burkle, L. A., Marlin, J. C., & Knight, T. M. (2013). Plant-pollinator interactions over 120 years: Loss of species, co-occurrence, and function. *Science*, *340*(6127), 1611–1615. <https://doi.org/10.1126/science.1232728>
- Caradonna, P. J., Petry, W. K., Brennan, R. M., Cunningham, J. L., Bronstein, J. L., Waser, N. M., & Sanders, N. J. (2017). Interaction rewiring and the rapid turnover of plant-pollinator networks. *Ecology Letters*, *20*(3). <https://doi.org/10.1111/ele.12740>
- Carter Butts aut, A. T., Hunter ctb, D., Handcock ctb, M., Bender-deMoll ctb, S., Horner ctb, J., & Wang ctb, L. (2021). *Package “network” Title Classes for Relational Data*. <http://statnet.org/>
- Celis Charles Halpern F Andrew Jones, J. B. (2017). Intraspecific trait variation and the differential decline of meadow species during conifer encroachment. *Plant Ecology*, *218*, 565–578. <https://doi.org/10.1007/s11258-017-0712-3>
- Chao, A., Chazdon, R. L., & Shen, T. J. (2005). A new statistical approach for assessing similarity of species composition with incidence and abundance data. *Ecology Letters*, *8*(2),

- 148–159. <https://doi.org/10.1111/J.1461-0248.2004.00707.X>
- Chole, H., Woodard, S. H., & Bloch, G. (2019). Body size variation in bees: regulation, mechanisms, and relationship to social organization. *Current Opinion in Insect Science*, 35, 77–87. <https://doi.org/10.1016/J.COIS.2019.07.006>
- Crone, E. E. (2013). Responses of Social and Solitary Bees to Pulsed Floral Resources. *The American Naturalist*, 182(4), 465–473. <https://doi.org/10.1086/671999>
- Dailey, M. (2007). *Meadow classification in the Willamette National Forest and conifer encroachment patterns in the Chucksney-Grasshopper meadow complex, Western Cascade Range, Oregon* [Oregon State University]. https://ir.library.oregonstate.edu/concern/graduate_thesis_or_dissertations/gt54kq39p?local_e=en
- Debinski, D. M., Jakubauskas, M., Kindscher, K., & Jakubauskas, M. E. (2000). Montane Meadows as Indicators of Environmental Change. *Environmental Monitoring and Assessment*, 3(2). <https://doi.org/10.1023/A:1006432030089>
- Debinski, D. M., Wickham, H., Kindscher, K., Caruthers, J. C., & Germino, M. (2010). Montane meadow change during drought varies with background hydrologic regime and plant functional group. *Ecology*, 91(6), 1672–1681. <https://doi.org/10.1890/09-0567.1>
- Devoto, M., Bailey, S., Craze, P., & Memmott, J. (2012). Understanding and planning ecological restoration of plant–pollinator networks. *Ecology Letters*, 15(4), 319–328. <https://doi.org/10.1111/J.1461-0248.2012.01740.X>
- Doré, M., Fontaine, C., & Thébault, E. (2021). Relative effects of anthropogenic pressures, climate, and sampling design on the structure of pollination networks at the global scale. *Global Change Biology*, 27(6), 1266–1280. <https://doi.org/10.1111/GCB.15474>
- Dormann, C.F., Fruend, J., Bluethgen, N. & G. B. (2009). Indices, graphs and null models: analyzing bipartite ecological networks. *The Open Ecology Journal*, 2, 7–24. <https://orcid.org/0000-0002-7079-3478>
- Elliott, S. E., & Irwin, R. E. (2009). Effects of flowering plant density on pollinator visitation, pollen receipt, and seed production in *Delphinium barbeyi* (Ranunculaceae). *American Journal of Botany*, 96(5), 912–919. <https://doi.org/10.3732/AJB.0800260>
- Fang, Q., & Huang, S. Q. (2012). Relative Stability of Core Groups in Pollination Networks in a Biodiversity Hotspot over Four Years. *PLOS ONE*, 7(3), e32663. <https://doi.org/10.1371/JOURNAL.PONE.0032663>
- Forrest, J., Inouye, D. W., & Thomson, J. D. (2010). Flowering phenology in subalpine meadows: Does climate variation influence community co-flowering patterns? *Ecology*, 91(2), 431–440.
- Forrest, J. R. K., & James, D. T. (2011). An examination of synchrony between insect emergence

- and flowering in Rocky Mountain meadows. *Ecological Monographs*, 81(3), 469–491.
<https://doi.org/10.1890/10-1885.1>
- Gao, E., Wang, Y., Bi, C., Kaiser-Bunbury, C. N., & Zhao, Z. (2021). Restoration of Degraded Alpine Meadows Improves Pollination Network Robustness and Function in the Tibetan Plateau. *Frontiers in Ecology and Evolution*, 9, 194.
<https://doi.org/10.3389/FEVO.2021.632961/BIBTEX>
- Güler, Y., & Dikmen, F. (2017). Potential Bee Pollinators of Sweet Cherry in Inclement Weather Conditions | Journal of the Entomological Research Society. *Journal of the Entomological Research Society*, 19(1), 9–19.
<https://www.entomol.org/journal/index.php/JERS/article/view/505>
- Halpern, C. B., & Antos, J. A. (2021). Rates, patterns, and drivers of tree reinvasion 15 years after large-scale meadow-restoration treatments. *Restoration Ecology*, 29(5).
<https://doi.org/10.1111/rec.13377>
- Heinrich, B. (1979). *Bumblebee economics*. Harvard University Press.
<https://doi.org/10.1038/280850a0>
- Helderop, E. (2015). *Diversity, Generalization, and Specialization in Plant-Pollinator Networks of Montane Meadows, Western Cascades, Oregon* [Oregon State University].
https://ir.library.oregonstate.edu/concern/graduate_thesis_or_dissertations/hx11xh98r?local_e=en
- Herbertsson, L., Lindström, S. A. M., Rundlöf, M., Bommarco, R., & Smith, H. G. (2016). Competition between managed honeybees and wild bumblebees depends on landscape context. *Basic and Applied Ecology*, 17(7), 609–616.
<https://doi.org/10.1016/J.BAAE.2016.05.001>
- Highland, S. A. (2011). The Historic and Contemporary Ecology of Western Cascade Meadows: Archeology, Vegetation, and Macromoth Ecology. In *Geography*. Oregon State University.
- Hitchcock, C. L. (Charles L., Cronquist, A., Giblin, D., Legler, B., Zika, P. F., & Olmstead, R. G. (2018). *Flora of the Pacific Northwest : an illustrated manual* (2nd ed.).
<https://uwapress.uw.edu/book/9780295742885/flora-of-the-pacific-northwest>
- Ings, T. C., Montoya, J. M., Bascompte, J., Blüthgen, N., Brown, L., Dormann, C. F., Edwards, F., Figueroa, D., Jacob, U., Jones, J. I., Lauridsen, R. B., Ledger, M. E., Lewis, H. M., Olesen, J. M., Van Veen, F. J. F., Warren, P. H., & Woodward, G. (2009). Review: Ecological networks – beyond food webs. *Journal of Animal Ecology*, 78(1), 253–269.
<https://doi.org/10.1111/J.1365-2656.2008.01460.X>
- Inouye, D. W. (2008). EFFECTS OF CLIMATE CHANGE ON PHENOLOGY, FROST DAMAGE, AND FLORAL ABUNDANCE OF MONTANE WILDFLOWERS. *Ecology*, 89(2), 353–362. www.rmbl.org
- Inouye, D. W. (2020). Effects of climate change on alpine plants and their pollinators. *Annals of*

- the New York Academy of Sciences*, 1469(1), 26–37. <https://doi.org/10.1111/NYAS.14104>
- Inouye, D. W., & Wielgolaski, F. E. (2013). Phenology at High Altitudes. *Phenology: An Integrative Environmental Science*, 249–272. https://doi.org/10.1007/978-94-007-6925-0_14
- Jacquemin, F., Violle, C., Munoz, F., Mahy, G., Rasmont, P., Roberts, S. P. M., Vray, S., & Dufrière, M. (2020). Loss of pollinator specialization revealed by historical opportunistic data: Insights from network-based analysis. *PLOS ONE*, 15(7), e0235890. <https://doi.org/10.1371/JOURNAL.PONE.0235890>
- Janine Rice. (2009). *Forest-meadow dynamics in the central western Oregon Cascades : topographic, biotic, and environmental change effects* [Oregon State University]. https://ir.library.oregonstate.edu/concern/graduate_thesis_or_dissertations/f7623f931?locale=en
- Jones, J. A., Hutchinson, R., Moldenke, A., Pfeiffer, V., Helderop, E., Thomas, E., Griffin, J., & Reinholtz, A. (2018). Landscape patterns and diversity of meadow plants and flower-visitors in a mountain landscape. *Landscape Ecology*, 34(5), 997–1014. <https://doi.org/10.1007/s10980-018-0740-y>
- Jones, K. (2016). *Spatio-Temporal Patterns of Tree Establishment in the M1 Meadow of the H.J. Andrews Experimental Forest* [Oregon State University]. https://ir.library.oregonstate.edu/concern/graduate_thesis_or_dissertations/0p0969927?locale=en
- Knight, T. M., Ashman, T. L., Bennett, J. M., Burns, J. H., Passonneau, S., & Steets, J. A. (2018). Reflections on, and visions for, the changing field of pollination ecology. *Ecology Letters*, 21(8), 1282–1295. <https://doi.org/10.1111/ELE.13094>
- Kudo, G. (2014). Vulnerability of phenological synchrony between plants and pollinators in an alpine ecosystem. *Ecological Research*, 29(4), 571–581. <https://doi.org/10.1007/S11284-013-1108-Z/FIGURES/5>
- Kudo, G. (2016). Landscape Structure of Flowering Phenology in Alpine Ecosystems: Significance of Plant–Pollinator Interactions and Evolutionary Aspects. In *Structure and Function of Mountain Ecosystems in Japan* (pp. 41–62). Springer, Tokyo. https://doi.org/10.1007/978-4-431-55954-2_3
- Kudo, G., & Ida, T. Y. (2013). Early onset of spring increases the phenological mismatch between plants and pollinators. *Ecology*, 94(10), 2311–2320. <https://doi.org/10.1890/12-2003.1>
- Larsson, M. (2005). Higher pollinator effectiveness by specialist than generalist flower-visitors of unspecialized *Knautia arvensis* (Dipsacaceae). *Oecologia*, 146(3), 394–403. <https://doi.org/10.1007/s00442-005-0217-y>
- Luo, S. X., Chaw, S. M., Zhang, D., & Renner, S. S. (2010). Flower heating following anthesis

- and the evolution of gall midge pollination in Schisandraceae. *American Journal of Botany*, 97(7), 1220–1228. <https://doi.org/10.3732/AJB.1000077>
- Mathiasson, M. E., & Rehan, S. M. (2019). Status changes in the wild bees of north-eastern North America over 125 years revealed through museum specimens. *Insect Conservation and Diversity*, 12(4), 278–288. <https://doi.org/10.1111/ICAD.12347>
- McFrederick, Q. S., & LeBuhn, G. (2006). Are urban parks refuges for bumble bees *Bombus* spp. (Hymenoptera: Apidae)? *Biological Conservation*, 129(3), 372–382. <https://doi.org/10.1016/J.BIOCON.2005.11.004>
- Memmott, J., Craze, P. G., Waser, N. M., & Price, M. V. (2007). Global warming and the disruption of plant–pollinator interactions. *Ecology Letters*, 10(8), 710–717. <https://doi.org/10.1111/J.1461-0248.2007.01061.X>
- Miller-Rushing, A. J., Inouye, D. W., & Primack, R. B. (2008). How well do first flowering dates measure plant responses to climate change? The effects of population size and sampling frequency. *Journal of Ecology*, 96(6), 1289–1296. <https://doi.org/10.1111/j.1365-2745.2008.01436.x>
- Miller, E. A., & Halpern, C. B. (1998). Effects of environment and grazing disturbance on tree establishment in meadows of the central Cascade Range, Oregon, USA. *Journal of Vegetation Science*, 9(2), 265–282. <https://doi.org/10.2307/3237126>
- Mola, J. M., Hemberger, J., Kochanski, J., Richardson, L. L., & Pearse, I. S. (2021). The Importance of Forests in Bumble Bee Biology and Conservation. *BioScience*, 71(12), 1234–1248. <https://doi.org/10.1093/BIOSCI/BIAB121>
- Mote, P. W., Salathé, E. P., Mote, P. W., & Salathé, E. P. (2010). Future climate in the Pacific Northwest. *Climatic Change* 2010 102:1, 102(1), 29–50. <https://doi.org/10.1007/S10584-010-9848-Z>
- Nielsen, A., & Bascompte, J. (2007). Ecological networks, nestedness and sampling effort. *Journal of Ecology*, 95, 1134–1141. <https://doi.org/10.1111/j.1365-2745.2007.01271.x>
- Nogués-Bravo, D., Araújo, M. B., Errea, M. P., & Martínez-Rica, J. P. (2007). Exposure of global mountain systems to climate warming during the 21st Century. *Global Environmental Change*, 17(3–4), 420–428. <https://doi.org/10.1016/j.gloenvcha.2006.11.007>
- Nolin, A. W. (2012). Perspectives on climate change, mountain hydrology, and water resources in the Oregon Cascades, USA. *Mountain Research and Development*, 32(SUPPL. 1). <https://doi.org/10.1659/MRD-JOURNAL-D-11-00038.S1>
- Ogilvie, J. E., & Forrest, J. R. (2017). Interactions between bee foraging and floral resource phenology shape bee populations and communities. *Current Opinion in Insect Science*, 21, 75–82. <https://doi.org/10.1016/J.COIS.2017.05.015>
- Ogilvie, J. E., Griffin, S. R., Gezon, Z. J., Inouye, B. D., Underwood, N., Inouye, D. W., &

- Irwin, R. E. (2017). Interannual bumble bee abundance is driven by indirect climate effects on floral resource phenology. *Ecology Letters*, 20(12), 1507–1515. <https://doi.org/10.1111/ELE.12854>
- Osborne, J. L., Martin, A. P., Carreck, N. L., Swain, J. L., Knight, M. E., Goulson, D., Hale, R. J., & Sanderson, R. A. (2008). Bumblebee flight distances in relation to the forage landscape. *Journal of Animal Ecology*, 77(2), 406–415. <https://doi.org/10.1111/J.1365-2656.2007.01333.X>
- Oyen, K. J., Giri, S., & Dillon, M. E. (2016). Altitudinal variation in bumble bee (*Bombus*) critical thermal limits. *Journal of Thermal Biology*, 59, 52–57. <https://doi.org/10.1016/J.JTHERBIO.2016.04.015>
- Paaijmans, K. P., Heinig, R. L., Seliga, R. A., Blanford, J. I., Blanford, S., Murdock, C. C., & Thomas, M. B. (2013). Temperature variation makes ectotherms more sensitive to climate change. *Global Change Biology*, 19(8), 2373–2380. <https://doi.org/10.1111/GCB.12240>
- Pfeiffer, V. (2012). *Influence of spatial and temporal factors on plants, pollinators and plant-pollinator interactions in montane meadows of the western Cascades Range* [Oregon State University]. https://ir.library.oregonstate.edu/concern/graduate_thesis_or_dissertations/9c67wq420?locale=en
- Primack, D., Imbres, C., Primack, R. B., Miller-Rushing, A. J., & Del Tredici, P. (2004). Herbarium specimens demonstrate earlier flowering times in response to warming in Boston. *American Journal of Botany*, 91(8), 1260–1264. <https://doi.org/10.3732/AJB.91.8.1260>
- Pyke, G. H. (1978). Optimal foraging in bumblebees and coevolution with their plants. *Oecologia* 1978 36:3, 36(3), 281–293. <https://doi.org/10.1007/BF00348054>
- Rasmont, P., & Iserbyt, S. (2012). The Bumblebees Scarcity Syndrome: Are heat waves leading to local extinctions of bumblebees (Hymenoptera: Apidae: *Bombus*)? *Ann. Soc. Entomol. France*, 48(4), 275–280. <https://doi.org/10.1080/00379271.2012.10697776>
- Sanders, A., Childs, M., Traub, E., & Jones, J. (2015). *An Analysis of Long-term Data Consistency and a Proposal to Standardize Flower Survey Methods for the EISI Pollinator Project*.
- Schweiger, O., Biesmeijer, J. C., Bommarco, R., Hickler, T., Hulme, P. E., Klotz, S., Kühn, I., Moora, M., Nielsen, A., Ohlemüller, R., Petanidou, T., Potts, S. G., Pyšek, P., Stout, J. C., Sykes, M. T., Tscheulin, T., Vilà, M., Walther, G. R., Westphal, C., ... Settele, J. (2010). Multiple stressors on biotic interactions: How climate change and alien species interact to affect pollination. In *Biological Reviews* (Vol. 85, Issue 4, pp. 777–795). John Wiley & Sons, Ltd. <https://doi.org/10.1111/j.1469-185X.2010.00125.x>
- Seeley, T. D. (1985). Honeybee Ecology. *Honeybee Ecology*. <https://doi.org/10.1515/9781400857876>

- Sevenello, M., Sargent, R. D., & Forrest, J. R. K. (2020). Spring wildflower phenology and pollinator activity respond similarly to climatic variation in an eastern hardwood forest. *Oecologia*, *193*(2), 475–488. <https://doi.org/10.1007/s00442-020-04670-4>
- Stemkovski, M., Pearse, W. D., Griffin, S. R., Pardee, G. L., Gibbs, J., Griswold, T., Neff, J. L., Oram, R., Rightmyer, M. G., Sheffield, C. S., Wright, K., Inouye, B. D., Inouye, D. W., & Irwin, R. E. (2020). Bee phenology is predicted by climatic variation and functional traits. *Ecology Letters*, *23*(11), 1589–1598. <https://doi.org/10.1111/ELE.13583>
- Strickler, K. (1979). Specialization and Foraging Efficiency of Solitary Bees. *Ecology*, *60*(5), 998–1009. <https://doi.org/10.2307/1936868>
- Takaoka, S., & Swanson, F. (2008). Change in extent of meadows and shrub fields in the central Western Cascade Range, Oregon. *Professional Geographer*, *60*(4), 527–540. <https://doi.org/10.1080/00330120802212099>
- Teensma, P. (University of O. (1987). *Fire history and fire regimes of the central western Cascades of Oregon*. <https://andrewsforest.oregonstate.edu/publications/716>
- Theobald, E. J., Breckheimer, I., & Hillerislambers, J. (2017). Climate drives phenological reassembly of a mountain wildflower meadow community. In *Source: Ecology* (Vol. 98, Issue 11).
- Thomson, D. (2004). COMPETITIVE INTERACTIONS BETWEEN THE INVASIVE EUROPEAN HONEY BEE AND NATIVE BUMBLE BEES. *Ecology*, *85*(2), 458–470. <https://doi.org/10.1890/02-0626>
- Thomson, D. M. (2016). Local bumble bee decline linked to recovery of honey bees, drought effects on floral resources. *Ecology Letters*, *19*(10), 1247–1255. <https://doi.org/10.1111/ELE.12659>
- Turner, N. J., Deur, D., & Mellott, C. R. (2011). “Up On the Mountain”: Ethnobotanical Importance of Montane Sites In Pacific Coastal North America. *Journal of Ethnobiology*, *31*(1), 4–43. <https://doi.org/10.2993/0278-0771-31.1.4>
- Valido, A., Rodríguez-Rodríguez, M. C., & Jordano, P. (2019). Honeybees disrupt the structure and functionality of plant-pollinator networks. *Scientific Reports*, *9*(1), 1–11. <https://doi.org/10.1038/s41598-019-41271-5>
- Vasiliev, D., & Greenwood, S. (2021). The role of climate change in pollinator decline across the Northern Hemisphere is underestimated. *Science of The Total Environment*, *775*, 145788. <https://doi.org/10.1016/J.SCITOTENV.2021.145788>
- Vázquez, D. P., Bluthgen, N., Cagnolo, L., & Chacoff, N. P. (2009). Uniting pattern and process in plant–animal mutualistic networks: a review. *Annals of Botany*, *103*(9), 1445. <https://doi.org/10.1093/AOB/MCP057>
- Visser, M. E., & Gienapp, P. (2019). Evolutionary and demographic consequences of

phenological mismatches. *Nature Ecology & Evolution*, 3(6), 879.
<https://doi.org/10.1038/S41559-019-0880-8>

Walther-Hellwig, K., Fokul, G., Frankl, R., Büchler, R., Ekschmitt, K., & Wolters, V. (2006). Increased density of honeybee colonies affects foraging bumblebees. *Apidologie*, 37(5), 517–532. <https://doi.org/10.1051/APIDO:2006035>

Wickham, H. (2016). ggplot2 Elegant Graphics for Data Analysis. *Use R! Series*, 211.
<http://had.co.nz/ggplot2/book>

Wilson, J. S., Wilson, L. E., Loftis, L. D., & Griswold, T. (2010). The Montane Bee Fauna of North Central Washington, USA, with Floral Associations. *Western North American Naturalist*, 70(2), 198–207. <https://doi.org/10.3398/064.070.0206>

Table of Contents (Appendix)

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A. Flowers

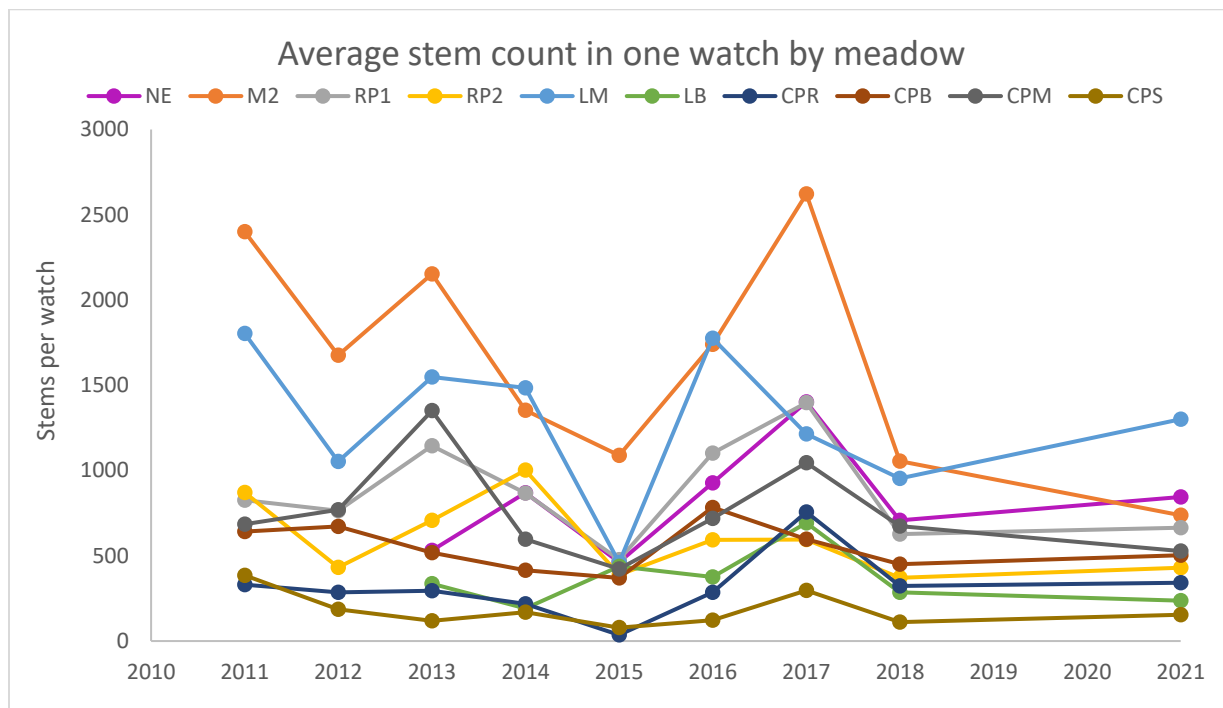


Figure A1. Average sum of stem count per sampling period for all species for each study year, separated by meadow. The variation of absolute abundance is greater in some meadows than in others. Notably, M2 and LM have a large variation in number flowers, and to a lesser extent CPM and RP1. Meanwhile, CPS, CPR, and LB have the lowest abundance in flowers and the least variation in overall abundance.

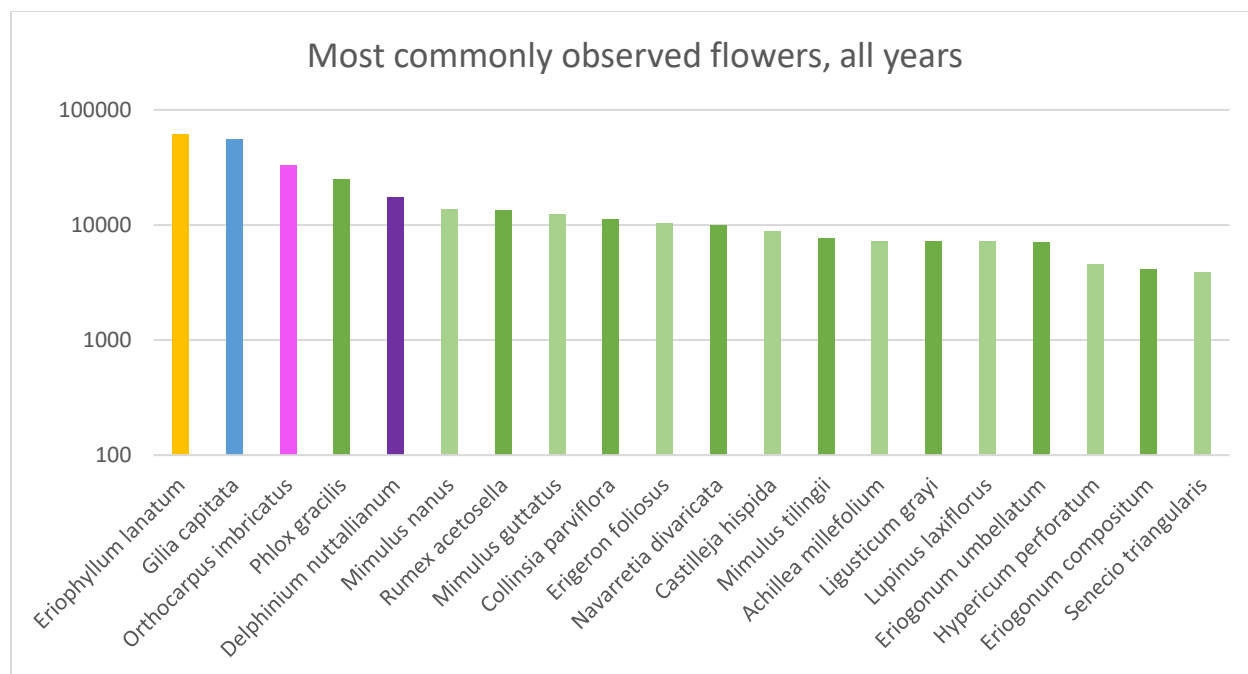


Figure A2. Illustration of the 20 most commonly observed flowers for all meadows, all years combined on a logarithmic scale. These flowers make up 80.7% of the total flower stems counted. Flowers that are emphasized in further analyses are colored according to the color scheme used in subsequent analyses and all other flowers are green.

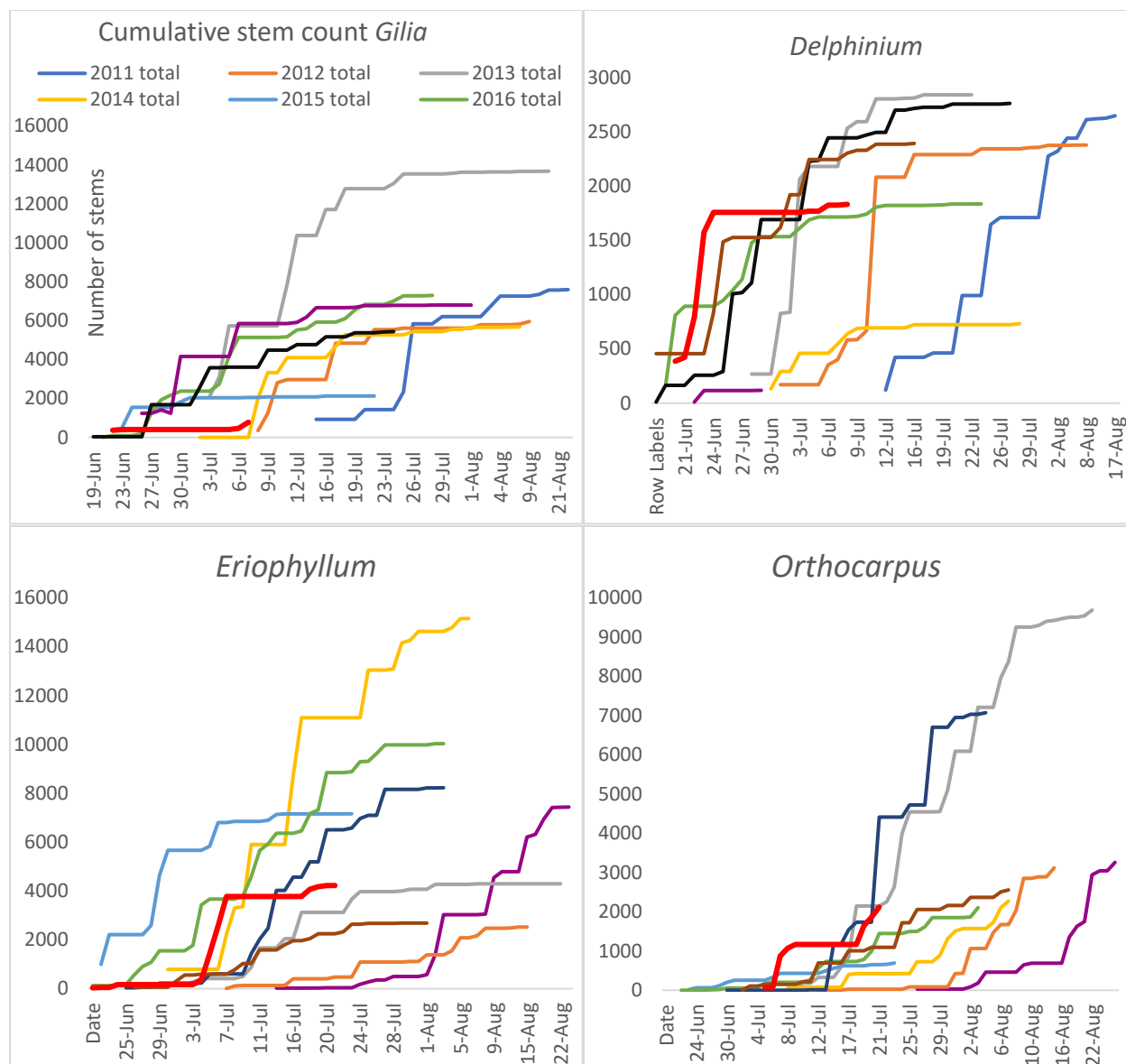


Figure A3. The flowering patterns of *Delphinium* and *Gilia* both varied over a period of approximately 20 days or so (*Delphinium* may be more because the sampling in 2015 appeared to miss most of the flowering). *Eriophyllum* varied a lot between years with a range of more than a month in flower accumulation curves. *Orthocarpus* followed a trend of blooming earlier overall over time with a range around one month long. 2011 and 2021 were notable outliers.

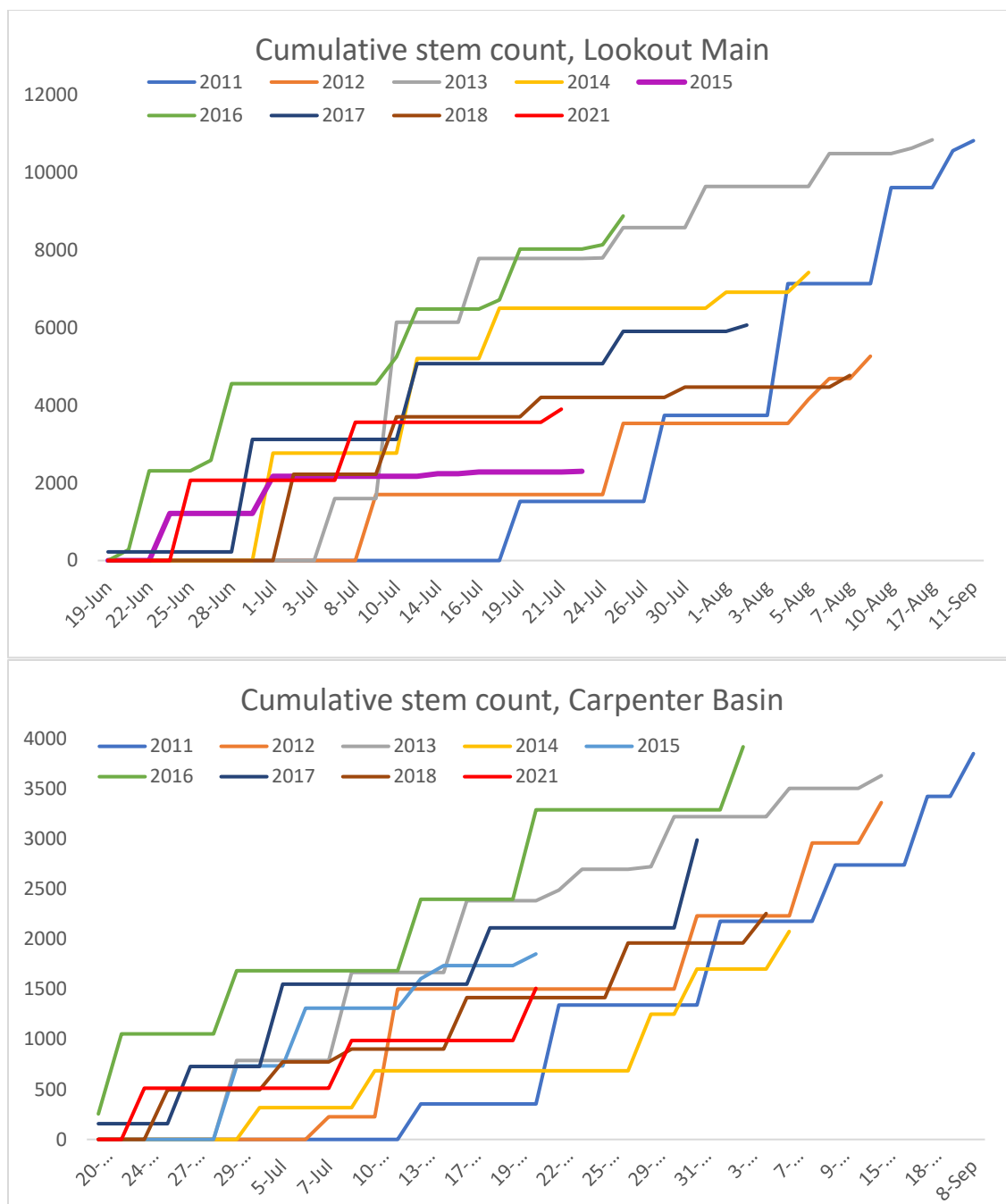


Figure A4. This graph is a representation of the meadows with (top) greater variation in phenology between summers and (bottom) have less of a variation in phenology between summers. (top) Flower accumulation for all species of flowers in Lookout Main. Each line represents a different year and the total accumulated flower count at a given date throughout the study periods. (bottom) Flower accumulation for all species of flowers in Carpenter Basin. It varies between years, but the overall pattern is similar, and the overall range of variation is smaller than in Lookout Main.

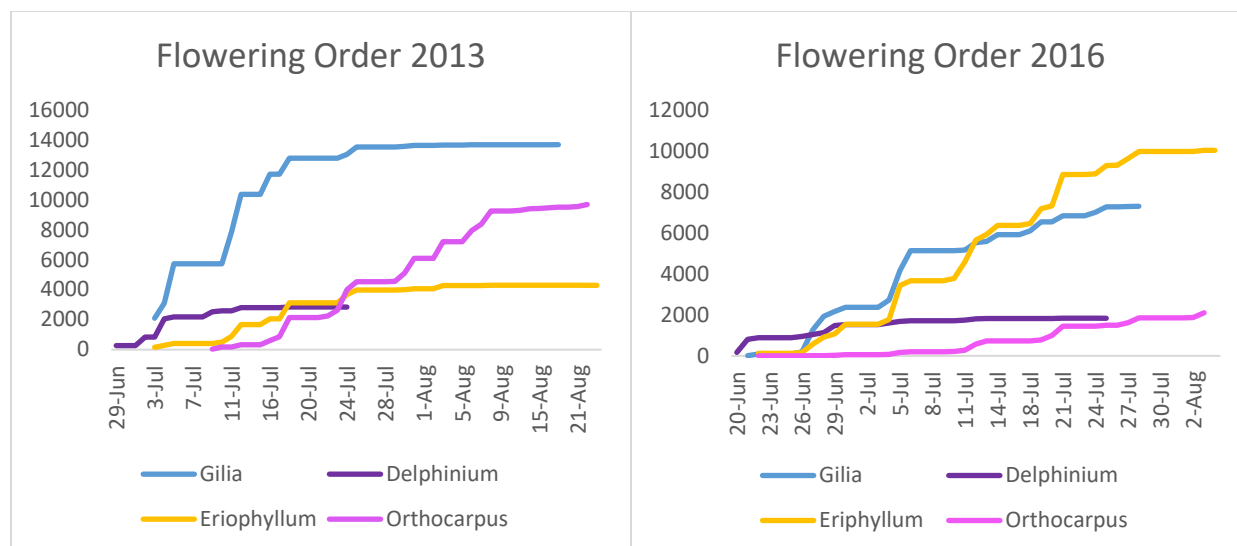


Figure A5. Two atypical years for flowering order. Each graph displays the cumulative flowers by date for four key flowers. In 2013 *Eriophyllum* flowered later than average while in 2016, *Eriophyllum* flowered earlier than average. The other three species flowered at a similar time both years.

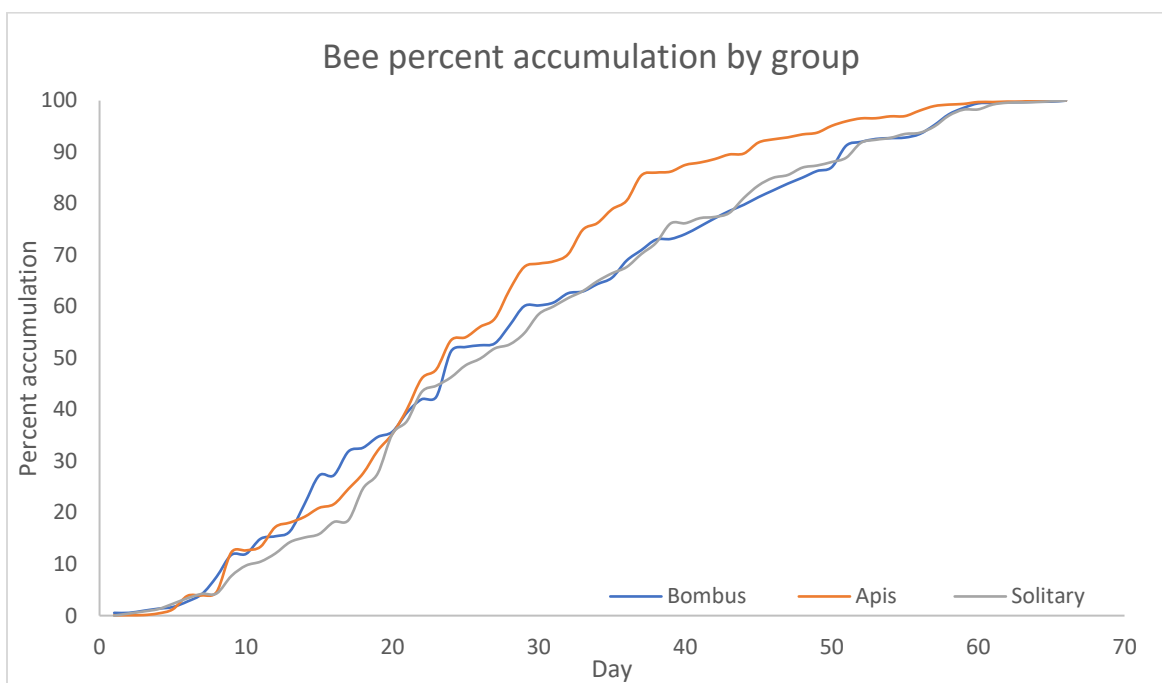
B. Bees

Figure B1. Percent accumulation of *Apis mellifera*, *Bombus spp.*, and solitary bees, all years all meadows. This is plotted over time where day 1 is in June and day 70 is in early September.

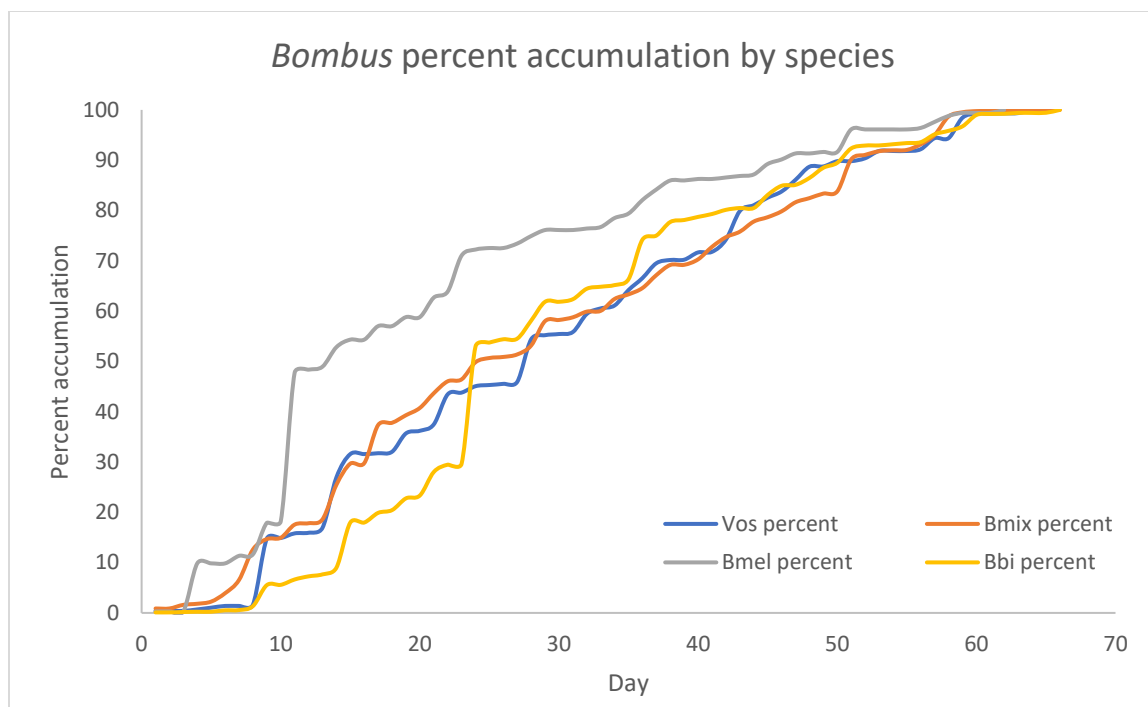


Figure B2. Percent accumulation (as in Figure B1) separated by the four most observed species of *Bombus* (*B. vosnesenskii*, *B. mixtus*, *B. melanopygus*, *B. bifarius*).

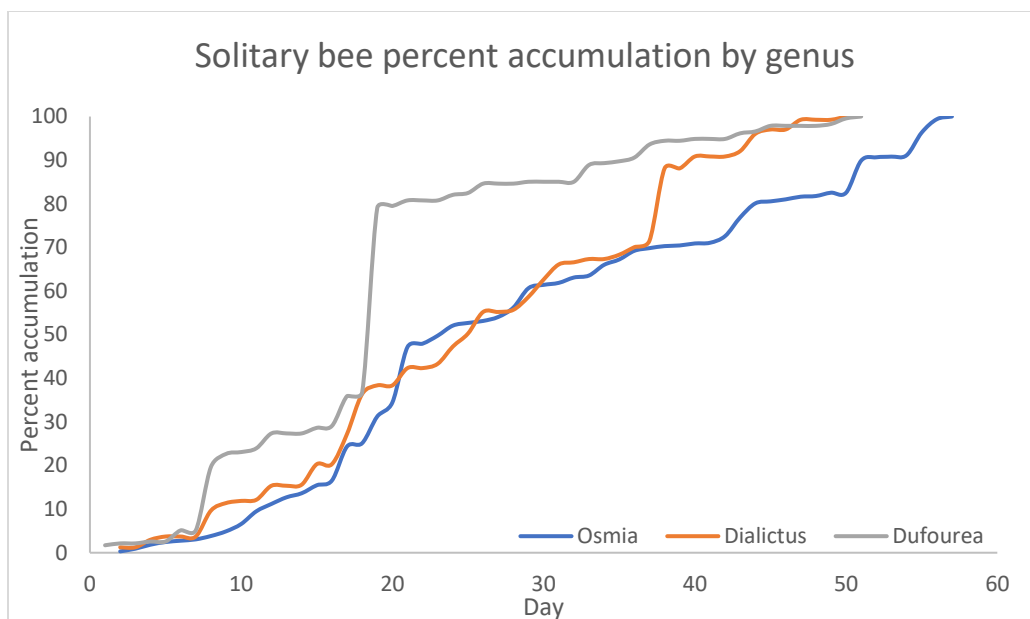


Figure B3. Percent accumulation (as in Figure B1) separated by the three most observed genera of solitary bees (*Osmia* spp., *Dialictus* spp., and *Dufourea* spp.). Day 1 is in mid-June and day 60 is in late August.

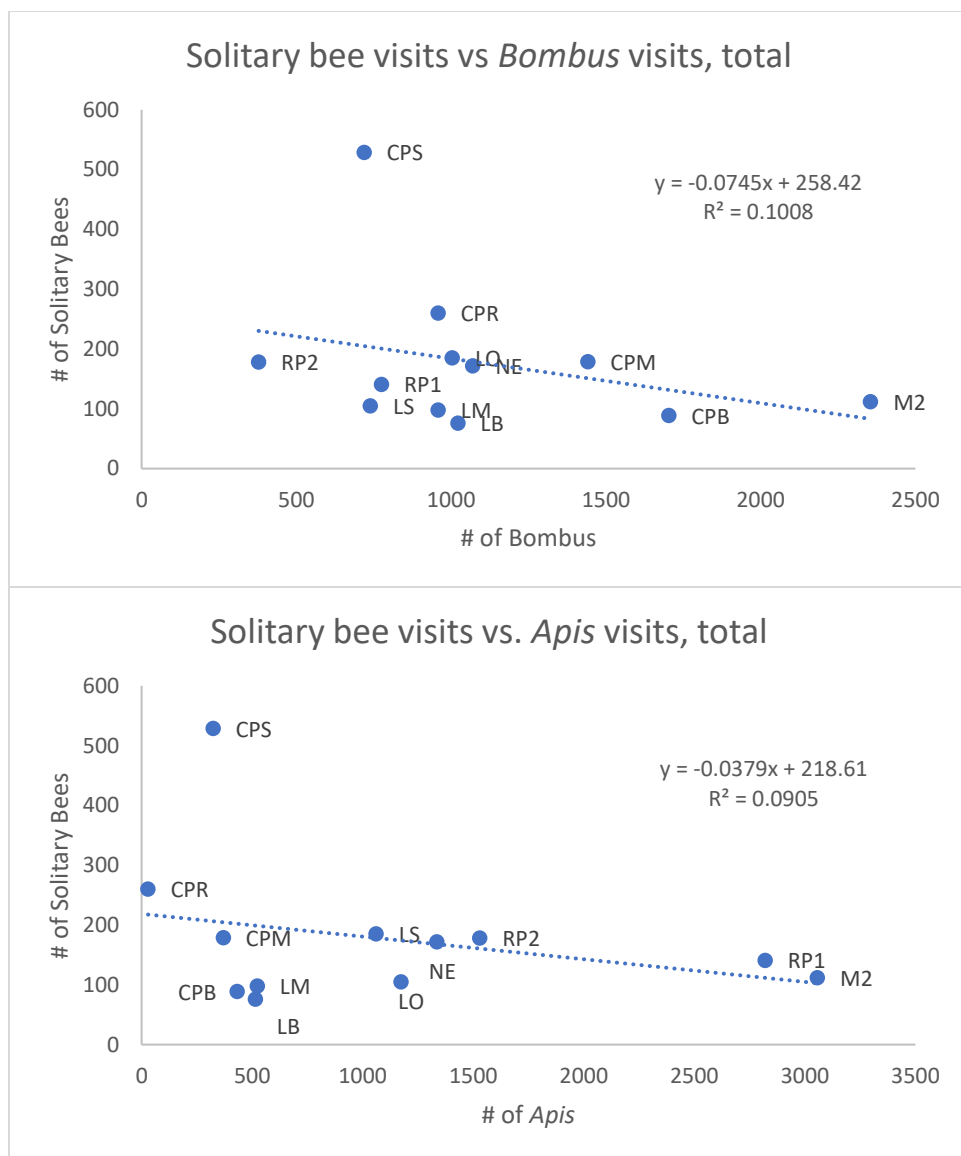


Figure B4. Absolute abundance of (top) *Bombus* and (bottom) *Apis* vs. absolute abundance of solitary bees by meadow.

Table B1. The top 20 species (or genus) of solitary bees observed by percent observed.

| Species | Count | Percent of total visits |
|---|-------|-------------------------|
| <i>Osmia</i> spp | 639 | 29.52 |
| <i>Dialictus</i> spp | 362 | 16.72 |
| <i>Dufourea calochorti</i> | 182 | 8.41 |
| <i>Evyllaesus</i> sp | 105 | 4.85 |
| <i>Hylaeus wootoni</i> | 96 | 4.43 |
| <i>Megachile perihirta</i> | 81 | 3.74 |
| <i>Andrena</i> spp | 71 | 3.28 |
| <i>Dialictus rubriventris</i> | 42 | 1.94 |
| <i>Hylaeus nunnenmacheri</i> | 37 | 1.71 |
| <i>Anthidium</i> spp | 35 | 1.62 |
| <i>Andrena columbiana</i> | 32 | 1.48 |
| <i>Melissodes rivalis</i> | 30 | 1.39 |
| <i>Dufourea versatilis rubriventris</i> | 26 | 1.20 |
| <i>Megachile</i> spp | 25 | 1.15 |
| <i>Colletes simulans nevadensis</i> | 23 | 1.06 |
| <i>Andrena pertristis carliniformis</i> | 20 | 0.92 |
| <i>Melissodes</i> spp | 16 | 0.74 |
| <i>Megachile brevis</i> | 15 | 0.69 |
| <i>Halictus farinosus</i> | 14 | 0.65 |
| <i>Hoplitis fulgida</i> | 14 | 0.65 |

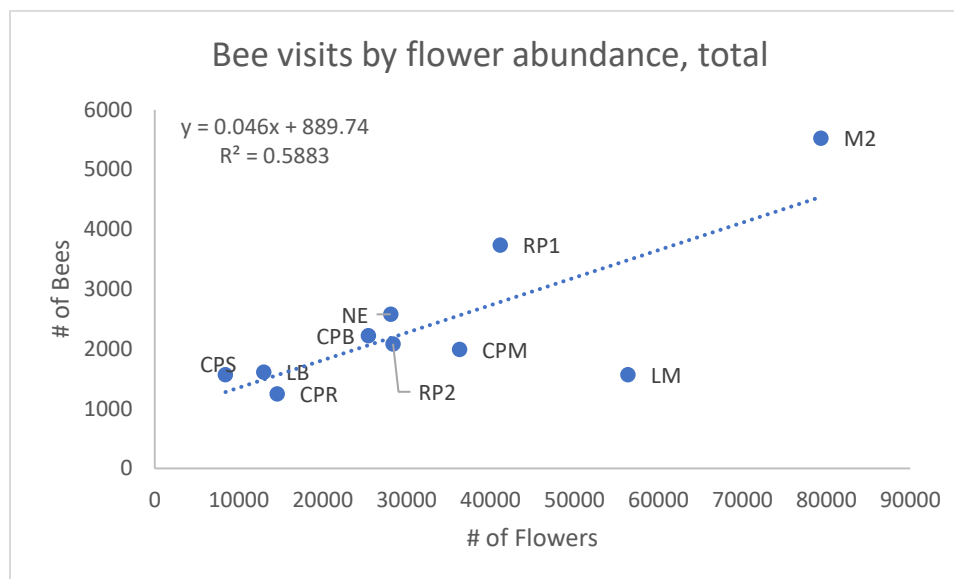
C. Flowers & bees

Figure C1. Total number of flowers per meadow vs. total bees observed per meadow, all years.

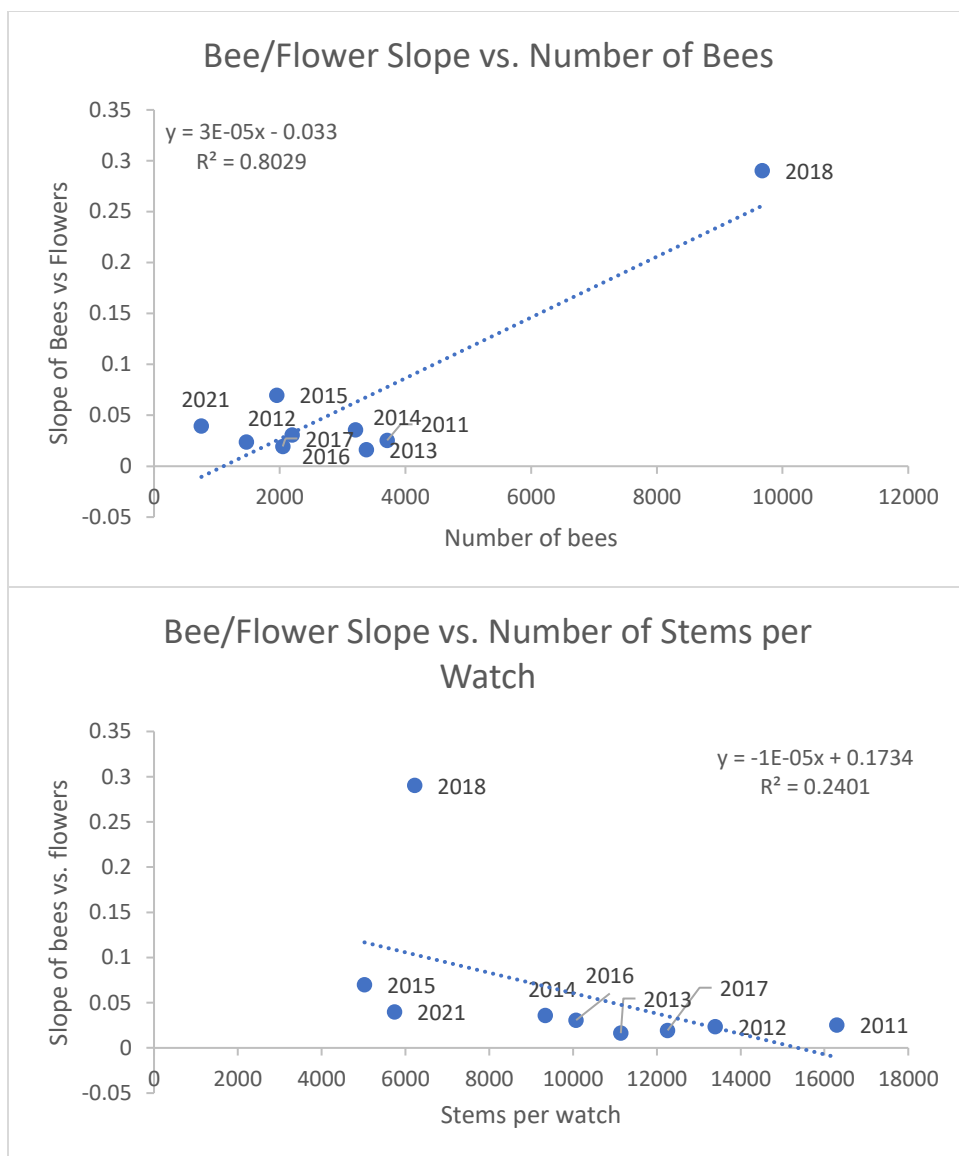


Figure C2. (top) The number of flowers and (bottom) number of bees observed in a year vs. the slope found in part 1 looking at the number of bees vs. flowers by meadow for each year. Note that 2018 is a notable outlier and that there is no relationship without 2018.

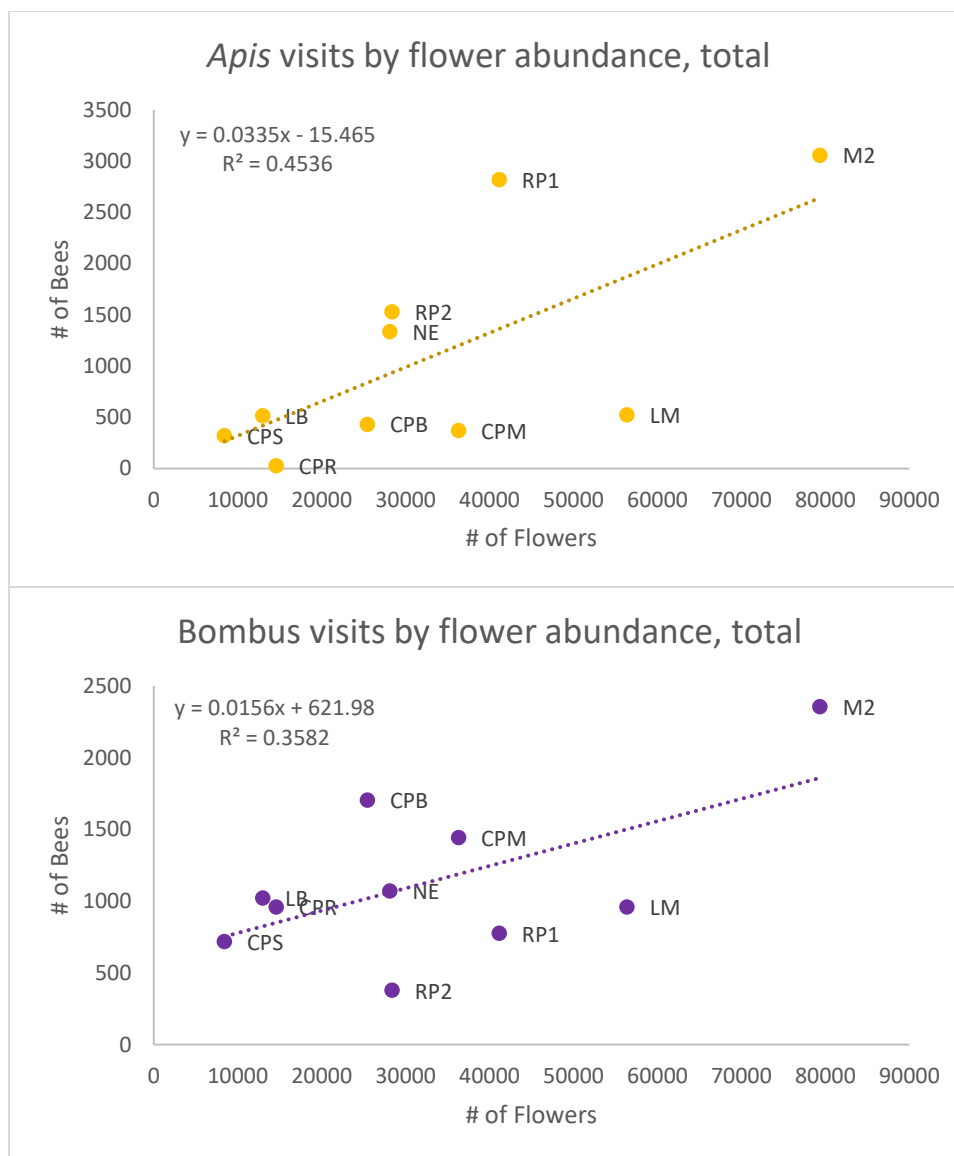


Figure C3. Total number of flowers per meadow vs. total (top) *Apis* and (bottom) *Bombus* observed per meadow, all years.

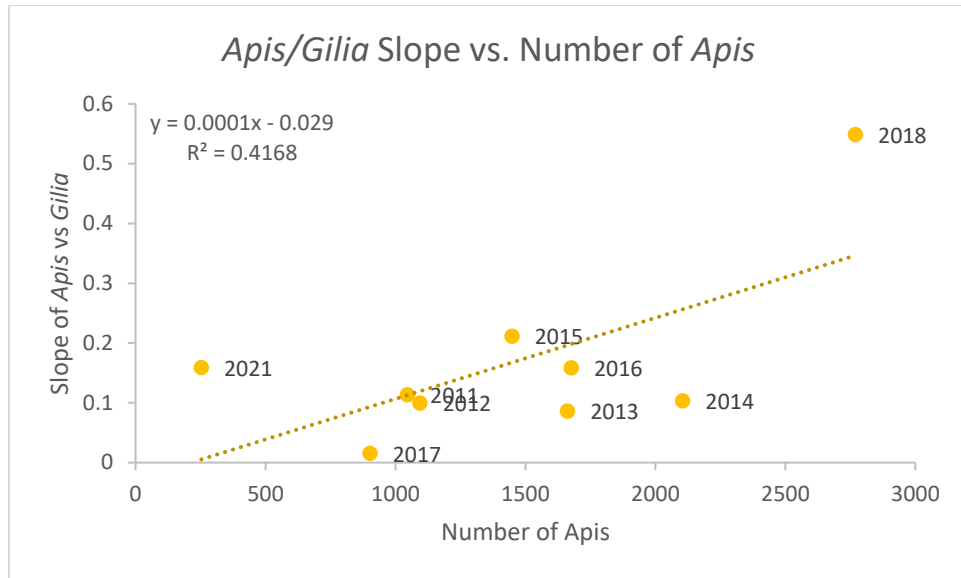


Figure C4. The number of *Apis* compared to the slope of *Apis* vs. *Gilia* by year.

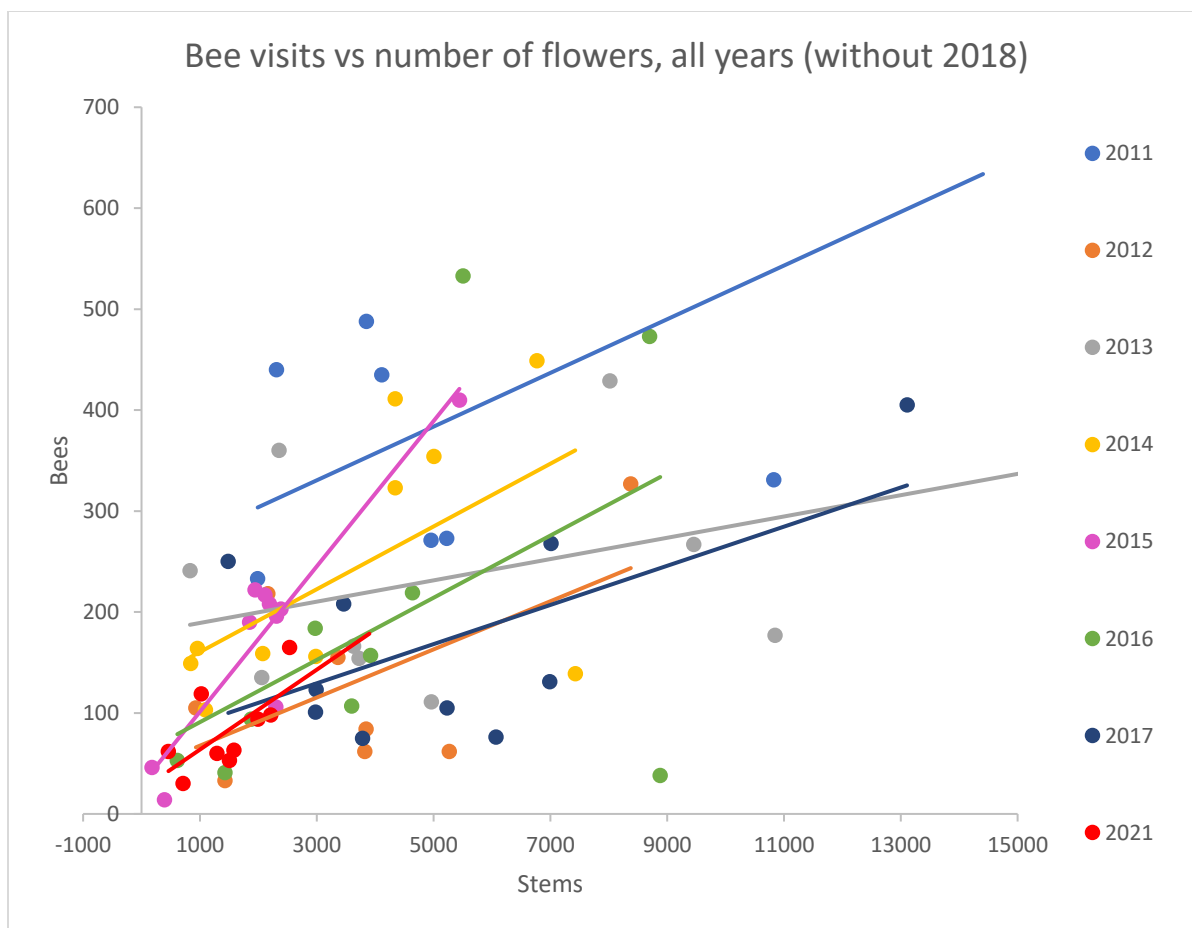


Figure C5. Total number of flowers per meadow vs. total bee visits observed per meadow by year. In this figure, 2018 was excluded because there were so many more bees than other years. The slopes (m) for each year were as follows: $m_{11} = 0.027$, $m_{12} = 0.024$, $m_{13} = 0.011$, $m_{14} = 0.031$, $m_{15} = 0.072$, $m_{16} = 0.031$, $m_{17} = 0.019$, $m_{18} = 0.281$, $m_{21} = 0.040$

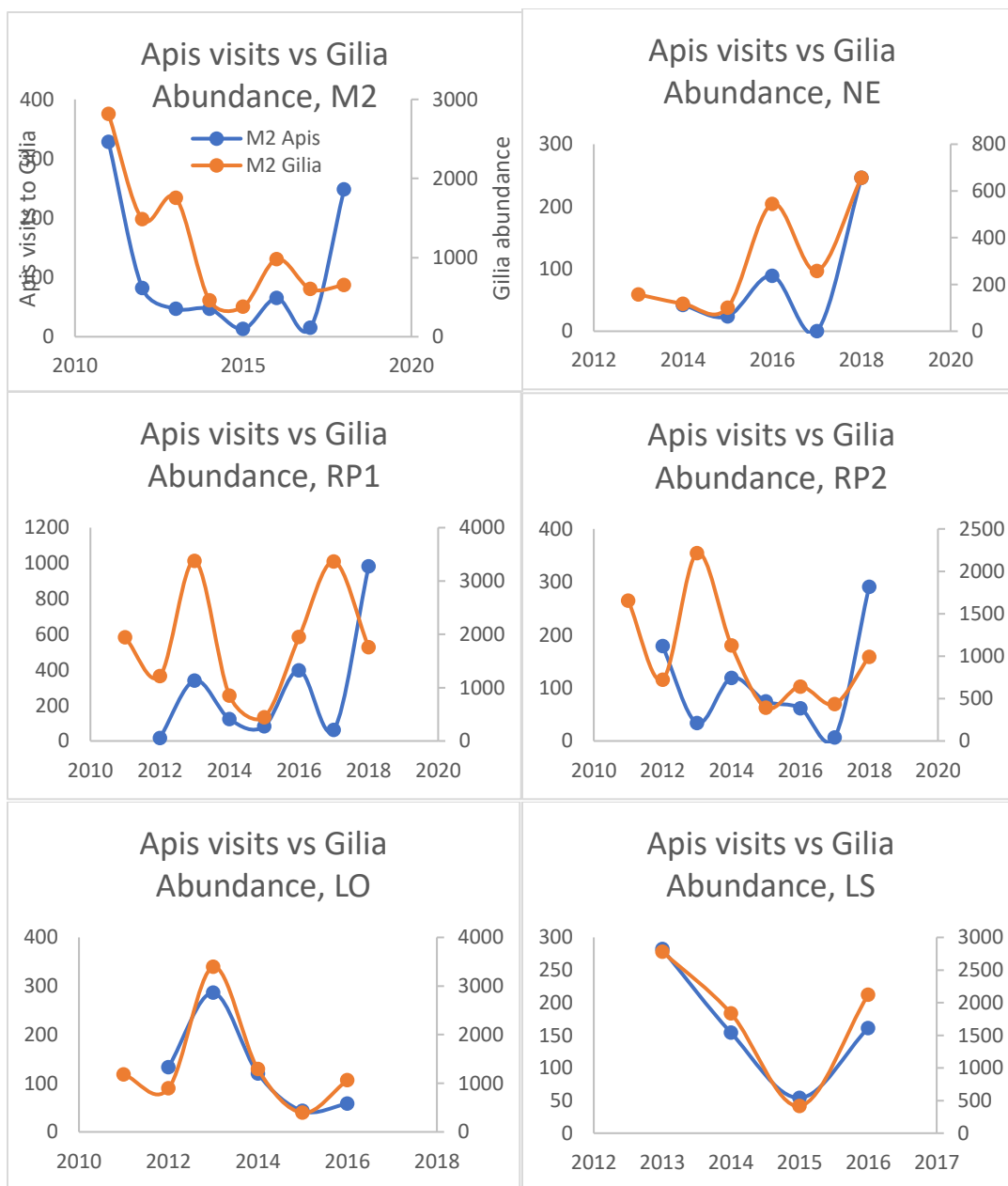


Figure C6. These graphs are time series of the number of *Gilia* over time and the number of *Apis* visits JUST to *Gilia* over time. They are meant to represent trends in *Apis* and *Gilia* visits over time to see if they are immediately correlated or if there is a lag (a lag would indicate that the number of *Apis* visits the prior year might influence the number of *Apis* visits the following year).

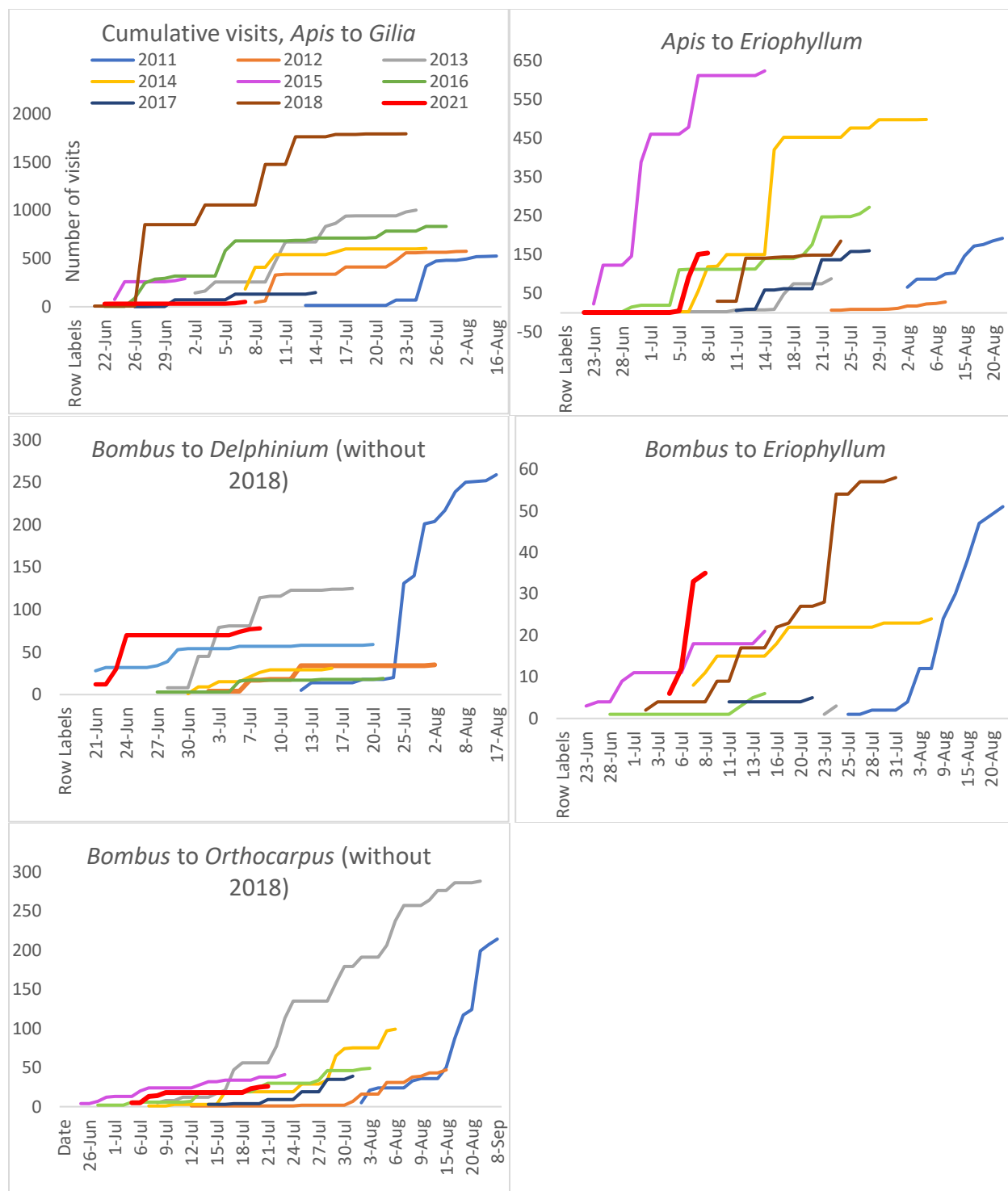


Figure C7. The cumulative visits of all (1) *Apis* to all *Gilia capitata* and (2) *Eriophyllum lanatum*, (3) *Bombus* to *Delphinium* (Note that 2018 was removed because of the order of magnitude increase in *Bombus* that year. There were also zero observations of *Bombus* visiting *Delphinium* in 2015.), (4) *Eriophyllum*, and (5) *Orthocarpus* (2018 removed) in all meadows by year.

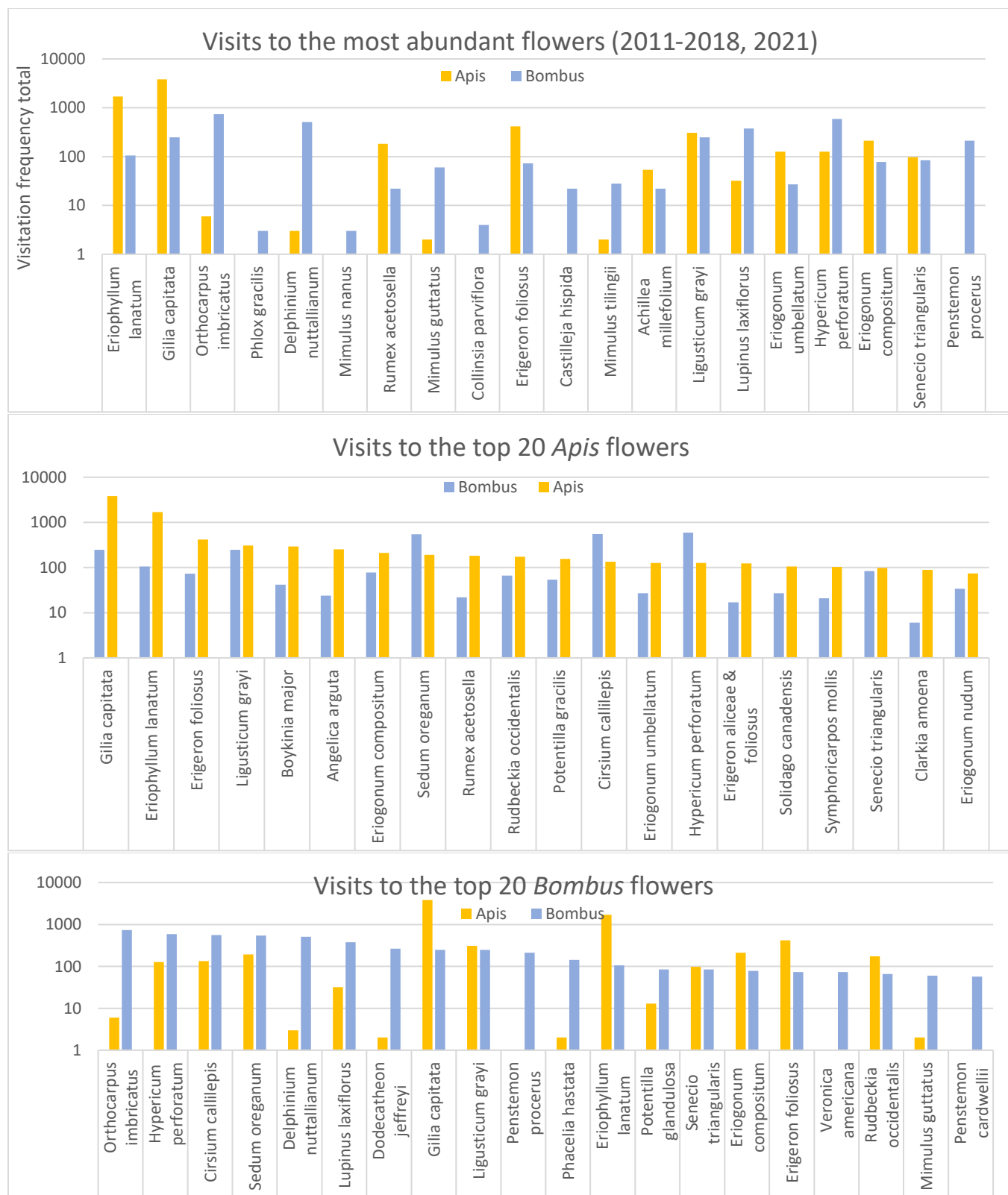


Figure C8. Flower visitation by bees by most abundant flowers, most preferred by *Bombus*, *Apis*. Then numbers underneath the flowers signify their absolute rank for overall abundance.

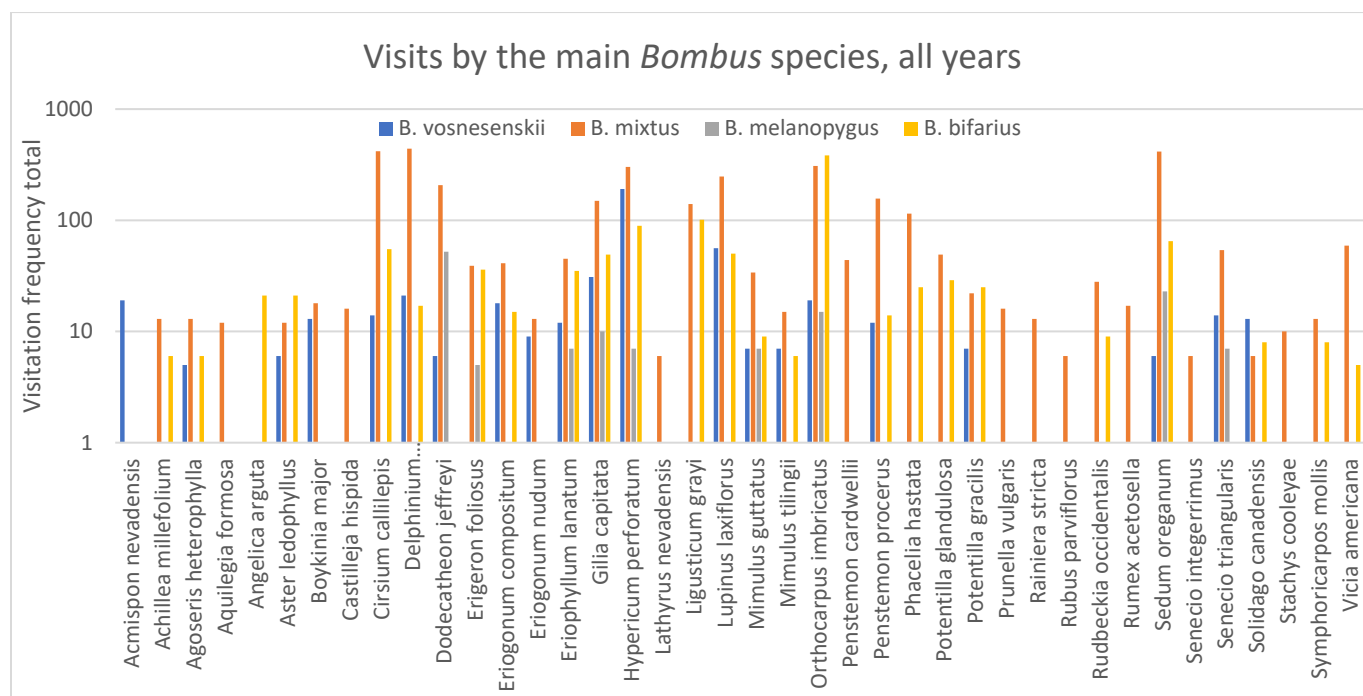


Figure C9. Most visited flowers by each species of *Bombus*, all years. This figure includes all flowers with 5 or more total visits by any species of *Bombus* for the total study period.

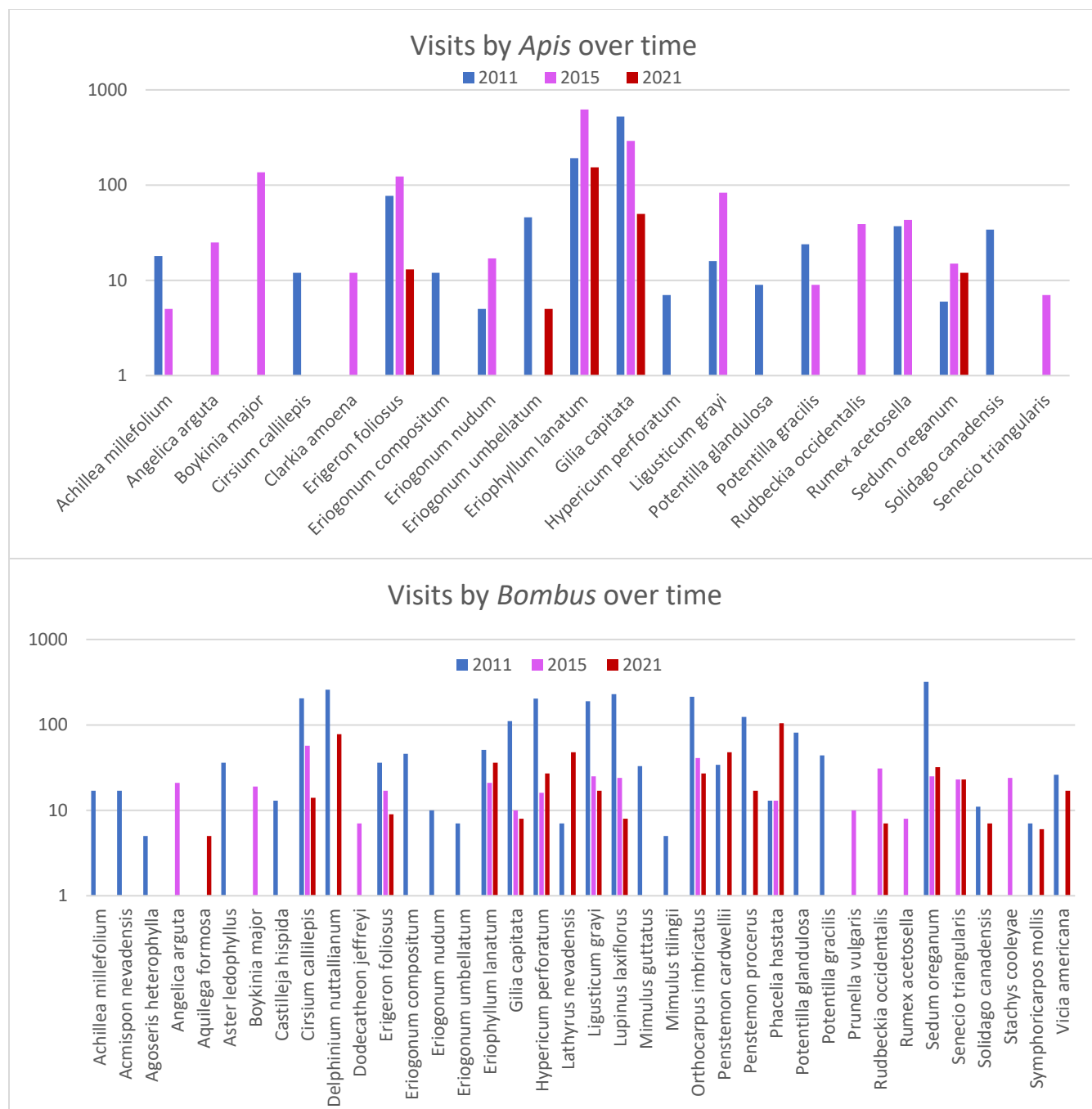


Figure C10. Most visited flowers by (top) *Apis* and (bottom) *Bombus* for 3 climate anomaly years. This figure includes all flowers that have 5 or more observed visits in a given year.

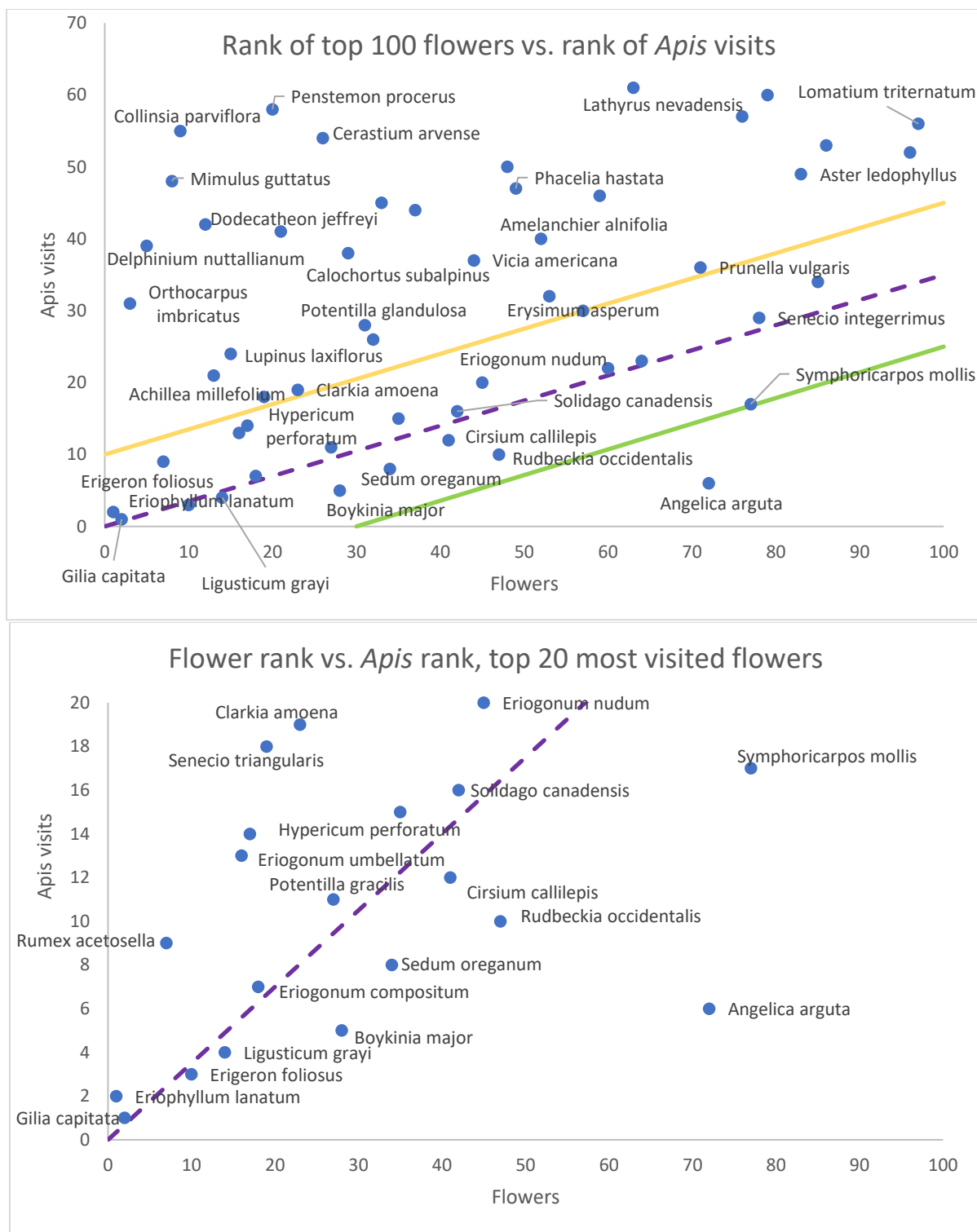


Figure C11. (top) Rank of flowers vs. rank of visit by *Apis* for all flowers in all years. Flowers close to the dotted line represent flowers that *Apis* visit at or close to their level of abundance. Flowers above the yellow line represent flowers that *Apis* avoids while flowers below the green line represent flowers that *Apis* visits preferentially. (bottom) Top 20 flowers by visitation.

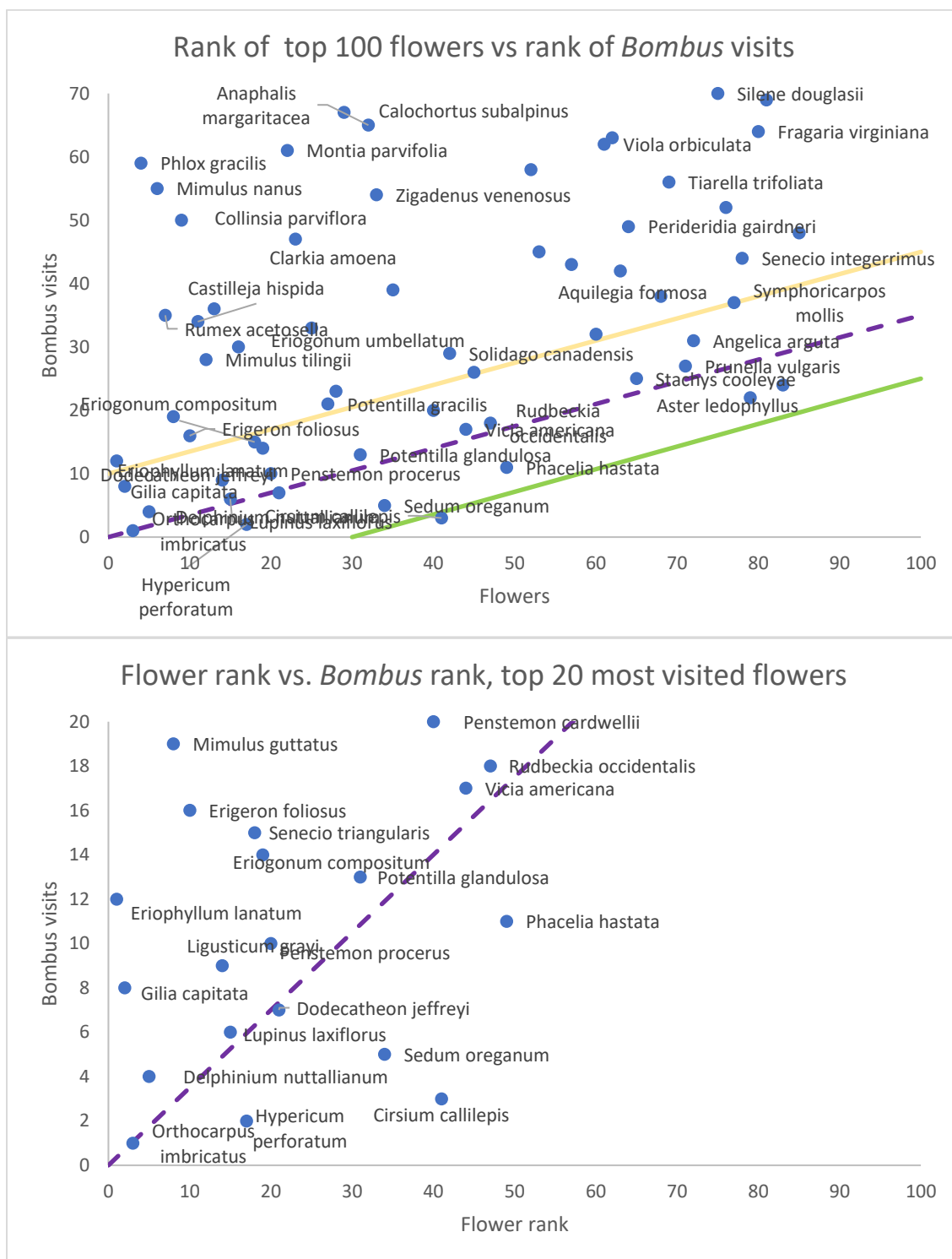


Figure C12. (top) Rank of flowers vs. rank of visits by *Bombus* for flowers, all years. Flowers near the dotted line represent flowers that *Bombus* visit at or close to the abundance. Flowers above the yellow line represent flowers that *Bombus* avoids while flowers below the green line represent flowers that *Bombus* visits preferentially. (bottom) Top 20 flowers by visitation.

D. Climate

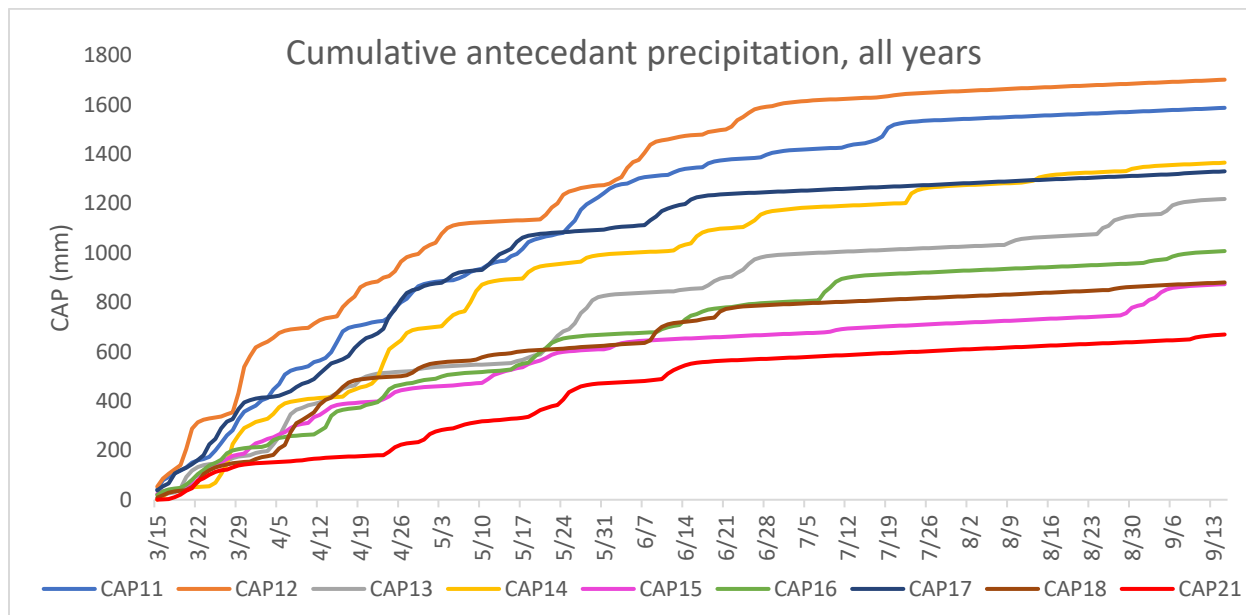


Figure D1. Cumulative antecedent precipitation for all years. Each color represents one year. This figure shows overall precipitation trends by year.

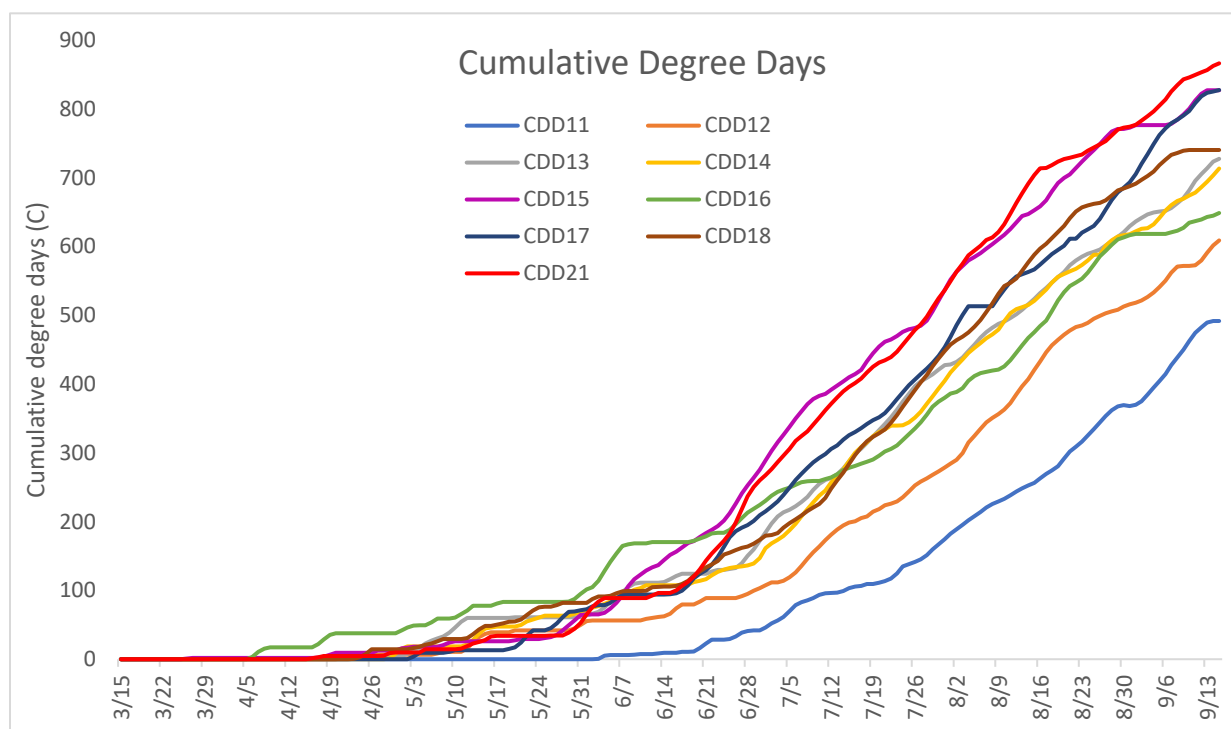


Figure D2. Cumulative degree days in degrees C by year. Each line represents one year.

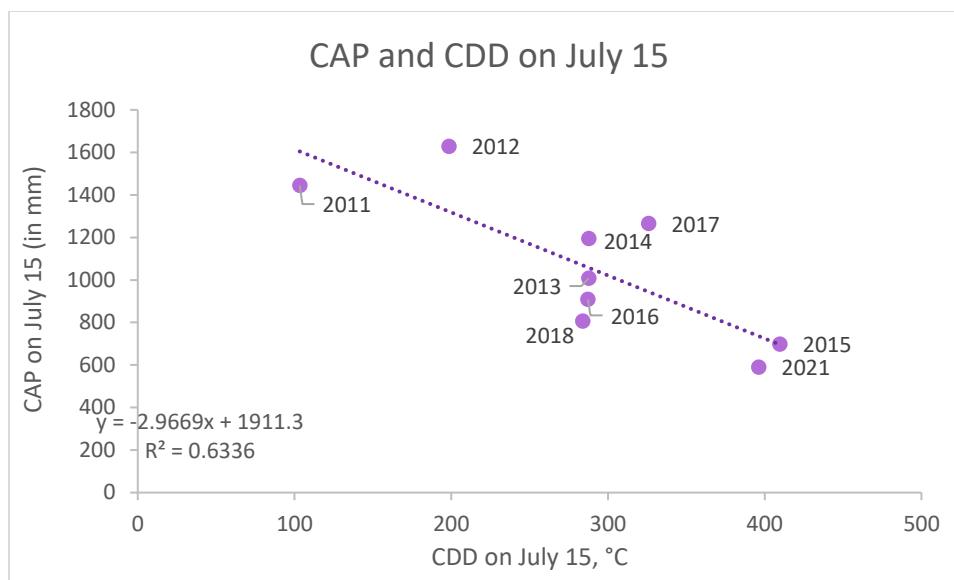


Figure D3. Summers in the study period that were hotter also tended to be drier. (Cumulative antecedent precipitation on July 15 compared to cumulative degree days)

E. Climate & flowers

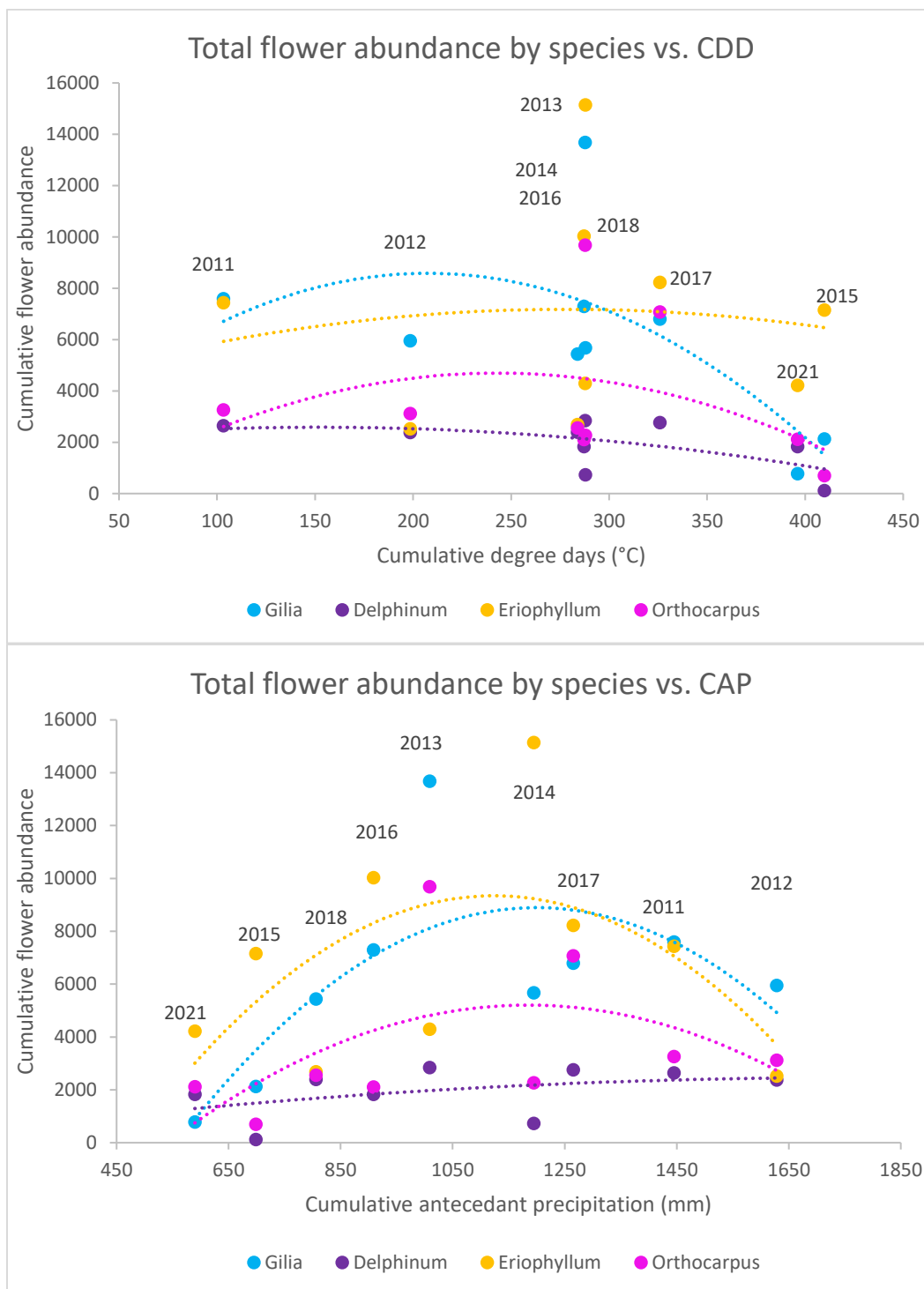
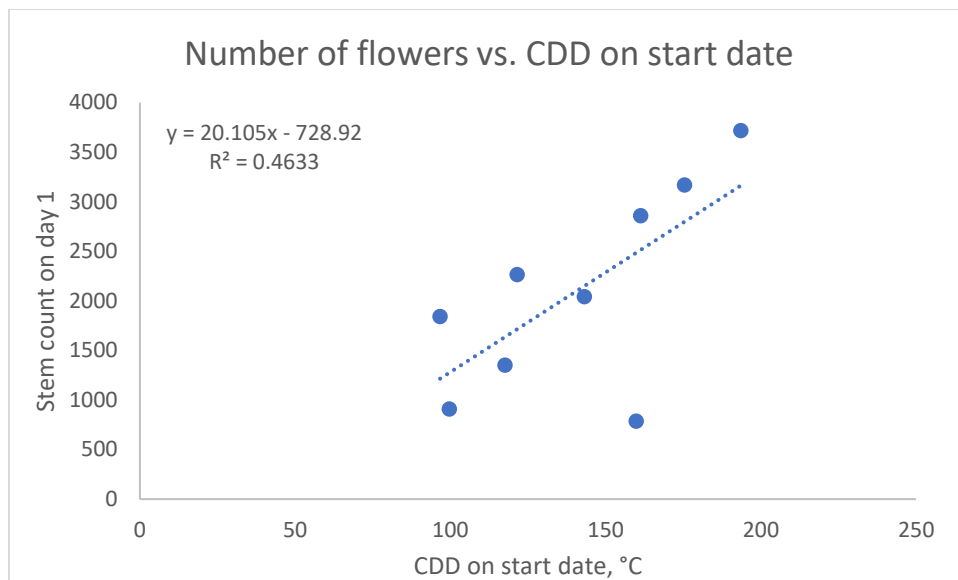


Figure E1. Cumulative flower abundance by species compared to cumulative degree days (top) and cumulative antecedent precipitation (bottom). All species are fitted with a polynomial regression line to test the hypothesis that flowers are most productive in years with moderate temperatures.



E2. Figure used to estimate the CDD threshold for when bees typically begin visiting flowers.

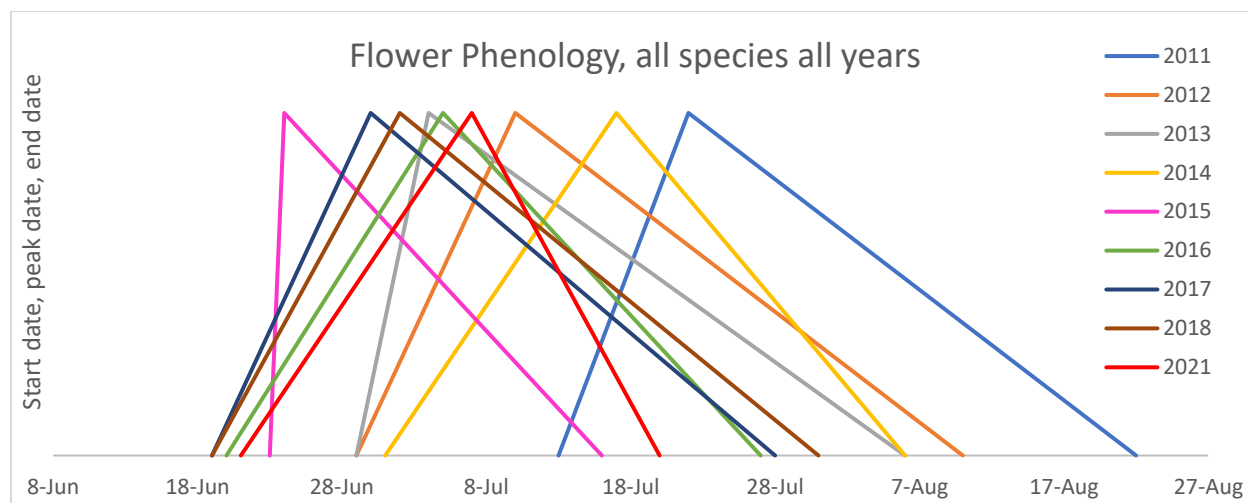


Figure E3. A visual representation of the start date, peak date, and end date for all flowers, separated by year.

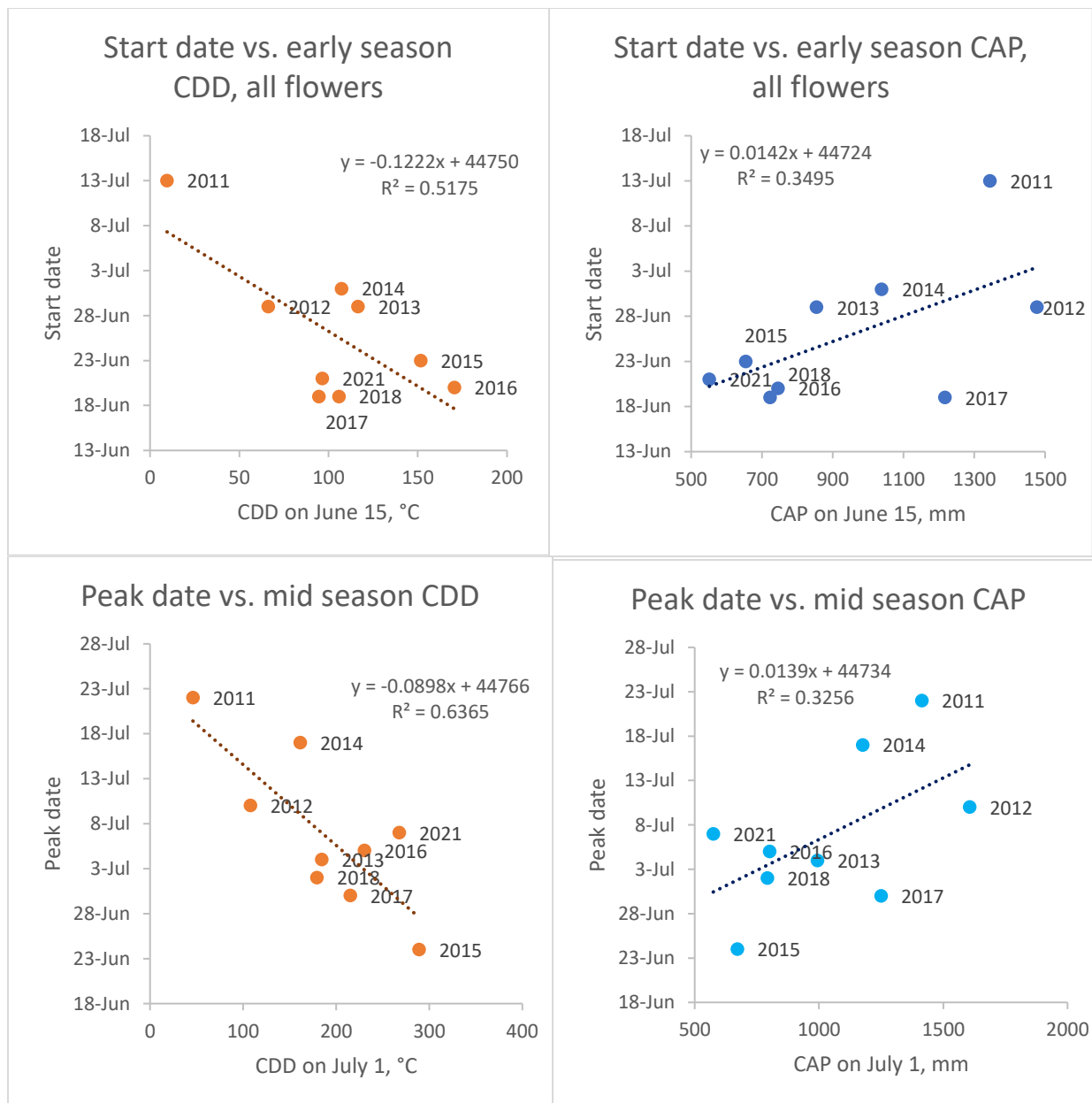


Figure E4. (top) Start date (date of first flowers observed) is inversely proportional to CDD on June 15 and positively related to CAP on June 15. (bottom) Peak date (date where the most flowers were observed in a day) is inversely proportional to CDD on July 1 and positively related to CAP on July 1.

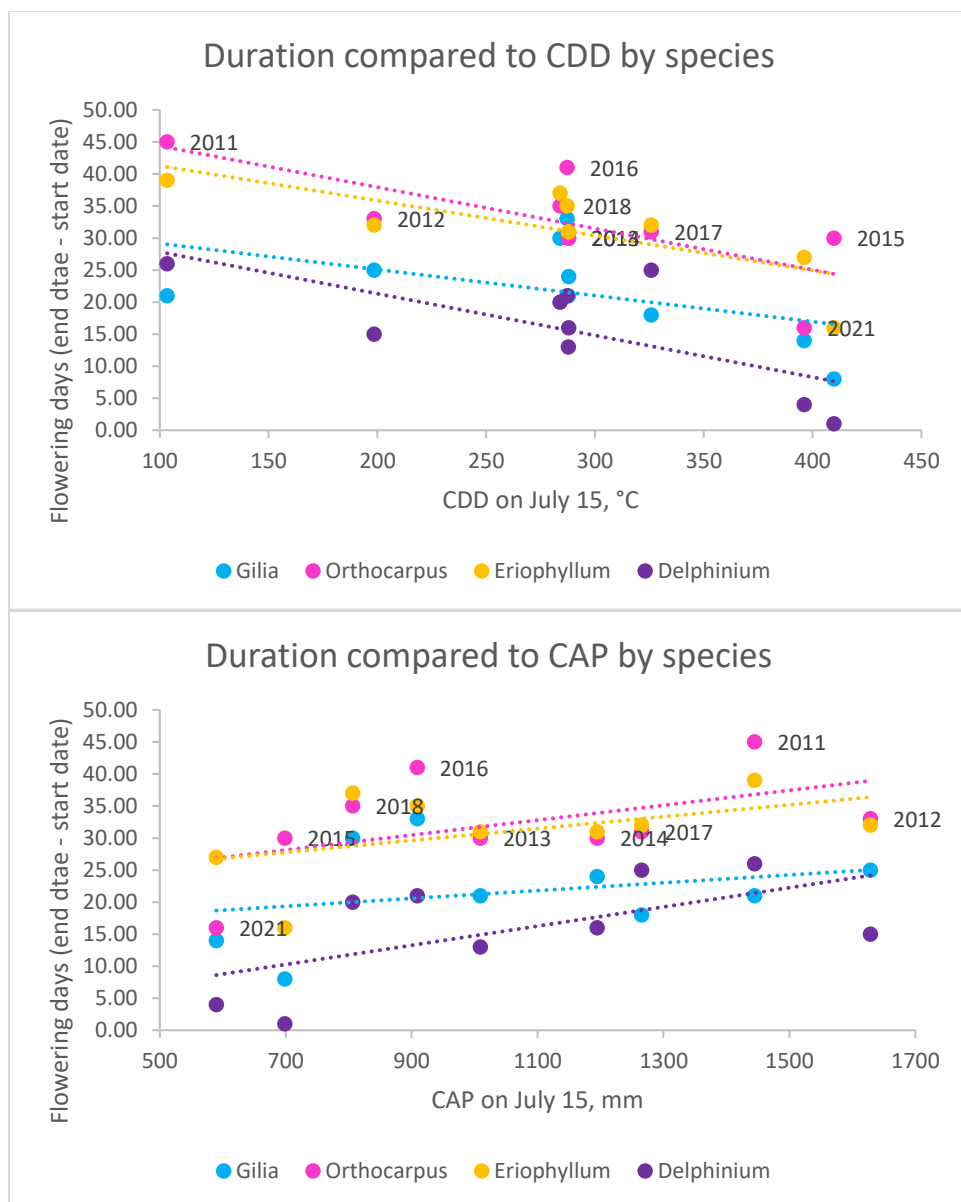


Figure E5. Flowering duration for all four species (the start date subtracted from the end date) was inversely proportional to CDD on July 15 and positively related to CAP on July 15.

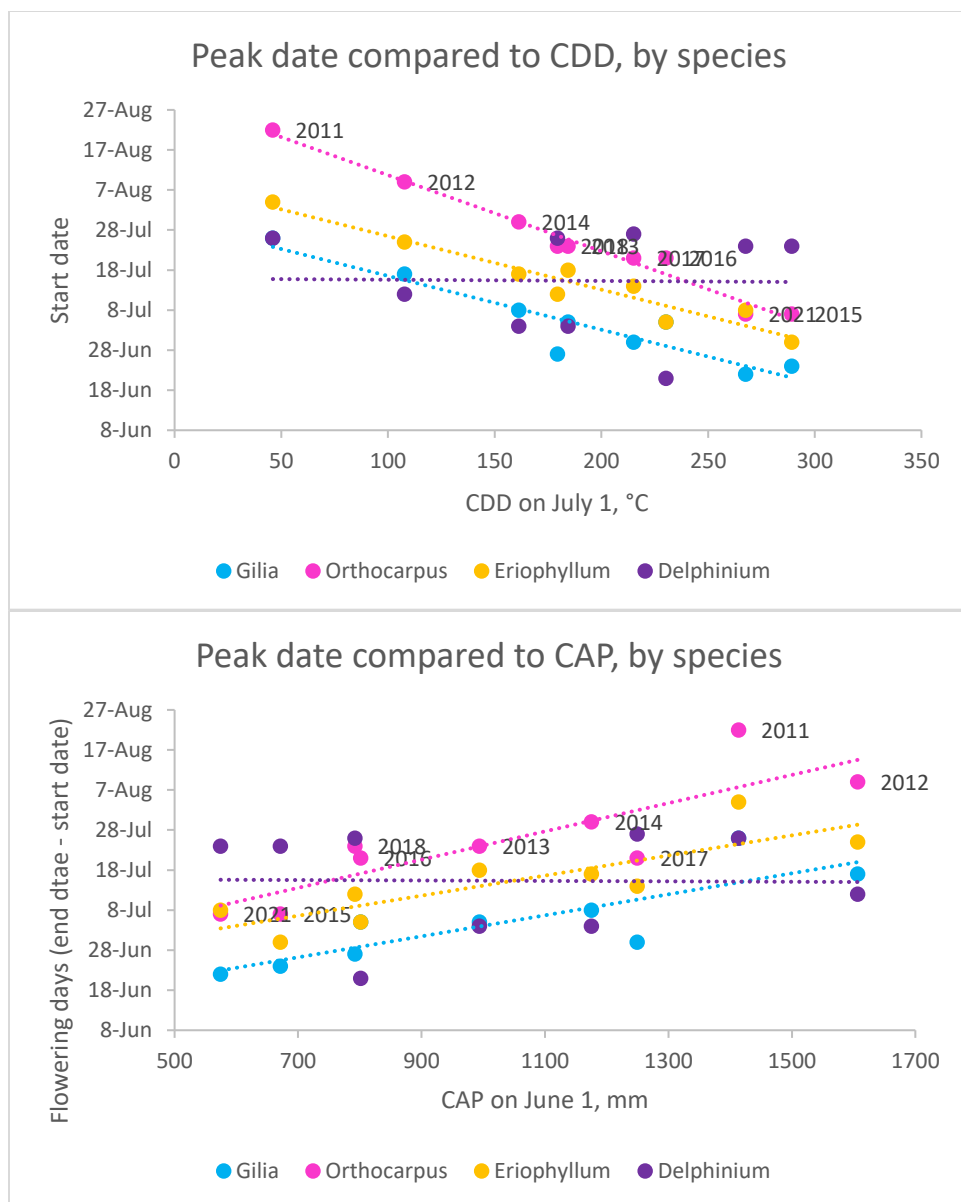


Figure E6. Peak date (date where the most flowers were observed in a day) was inversely proportional to CDD on July 1 and positively related to CAP on July 1 for all species except *Delphinium*. With *Delphinium*, there was no relationship.

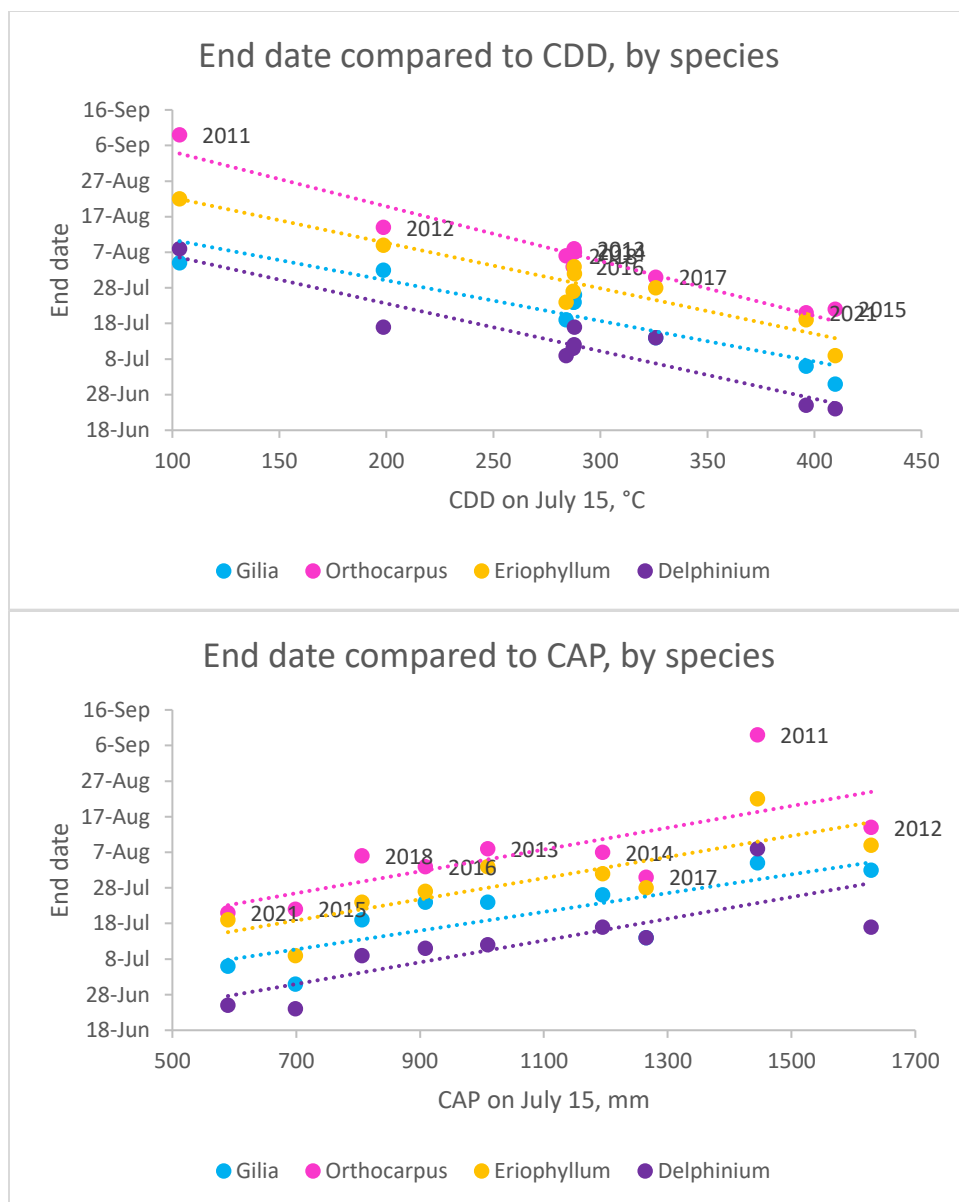


Figure E7. End date (day where >95% of flowers had been observed) was inversely proportional to CDD and positively related to CAP for all species.

Table E1. Resulting equations and R^2 values for the relationship between CAP and species (in blue, Figure E1.) and CDD and species (in red, Figure E1.).

| Flower species | Equation | R^2 |
|--------------------------------|-------------------------------------|--------|
| <i>Delphinium nuttallianum</i> | $y = -0.0008x^2 + 2.9391x - 151.25$ | 0.1787 |
| | $y = -0.0244x^2 + 7.3844x + 2024.8$ | 0.3469 |
| <i>Eriophyllum lanatum</i> | $y = -0.0222x^2 + 49.84x - 18673$ | 0.3358 |
| | $y = -0.041x^2 + 22.776x + 4012.7$ | 0.0118 |
| <i>Gilia capitata</i> | $y = -0.0216x^2 + 51.698x - 22103$ | 0.5455 |
| | $y = -0.1727x^2 + 71.615x + 1156.8$ | 0.4593 |
| <i>Orthocarpus imbricatus</i> | $y = -0.0126x^2 + 29.793x - 12447$ | 0.2785 |
| | $y = -0.1071x^2 + 52.033x - 1623.9$ | 0.1632 |

Table E2. Equations and R^2 values from a simple linear regression for duration, start date, peak date, and end date for each species compared to CDD and CAP (Figures E5-7).

| Measure | <i>Gilia</i> | <i>Delphinium</i> | <i>Eriophyllum</i> | <i>Orthocarpus</i> |
|----------------------|---|---|---|---|
| Duration CDD | $y = -0.0407x + 33.225$ $R^2 = 0.2447$ | $y = -0.0651x + 34.342$ $R^2 = 0.4955$ | $y = -0.0544x + 46.719$ $R^2 = 0.5786$ | $y = -0.0645x + 50.817$ $R^2 = 0.5515$ |
| Duration CAP | $y = 0.0061x + 15.071$ $R^2 = 0.0767$ | $y = 0.015x - 0.2169$ $R^2 = 0.3639$ | $y = 0.0093x + 21.275$ $R^2 = 0.2333$ | $y = 0.0116x + 19.997$ $R^2 = 0.2494$ |
| Start date CDD | $y = -4.1809x + 187157$ $R^2 = 0.5933$ | $y = -4.2294x + 189318$ $R^2 = 0.5431$ | $y = -3.9373x + 176258$ $R^2 = 0.5461$ | $y = -4.1321x + 185001$ $R^2 = 0.8491$ |
| Start date CAP | $y = 30.998x - 1E+06$ $R^2 = 0.6563$ | $y = 26.289x - 1E+06$ $R^2 = 0.4223$ | $y = 30.153x - 1E+06$ $R^2 = 0.6445$ | $y = 20.292x - 907053$ $R^2 = 0.4121$ |
| Peak date CDD | $y = -6.4156x + 287264$ $R^2 = 0.8614$ | $y = -0.1009x + 4701.8$ $R^2 = 0.0003$ | $y = -6.9201x + 309909$ $R^2 = 0.9239$ | $y = -5.1474x + 230623$ $R^2 = 0.9778$ |
| Peak date CAP | $y = 26.807x - 1E+06$ $R^2 = 0.7027$ | $y = -0.3929x + 18617$ $R^2 = 0.0002$ | $y = 27.834x - 1E+06$ $R^2 = 0.6984$ | $y = 20.445x - 914223$ $R^2 = 0.7207$ |
| End date CDD | $y = -7.566x + 338960$ $R^2 = 0.8624$ | $y = -6.6683x + 298720$ $R^2 = 0.8923$ | $y = -7.1085x + 318546$ $R^2 = 0.9074$ | $y = -6.1608x + 276167$ $R^2 = 0.947$ |
| End date CAP | $y = 24.289x - 1E+06$ $R^2 = 0.6397$ | $y = 21.149x - 945445$ $R^2 = 0.646$ | $y = 22.999x - 1E+06$ $R^2 = 0.6836$ | $y = 17.065x - 763119$ $R^2 = 0.523$ |

F. Climate & bees

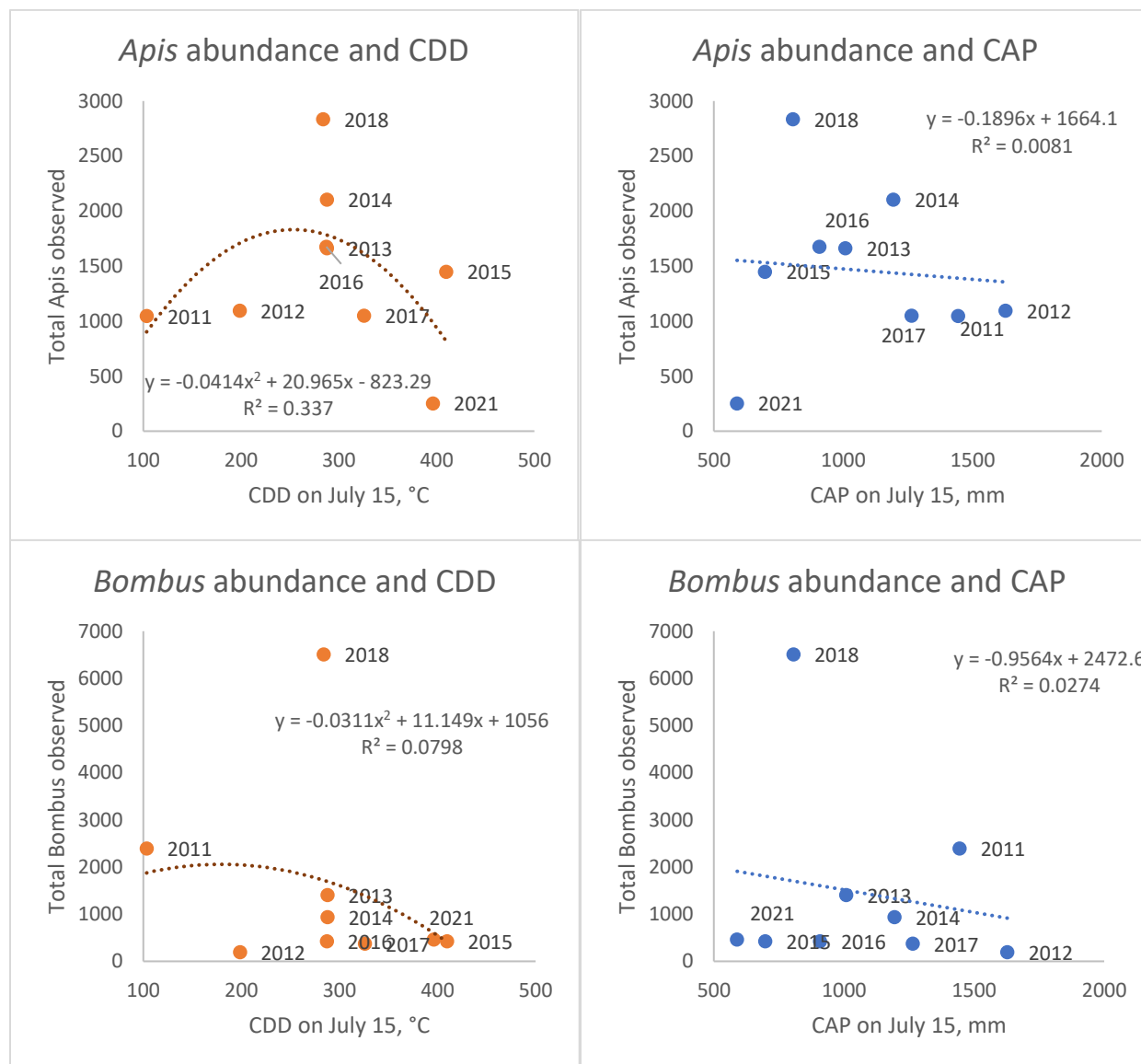


Figure F1. (top) *Apis* and (bottom) *Bombus* abundance compared by year for both cumulative degree days and cumulative antecedent precipitation.

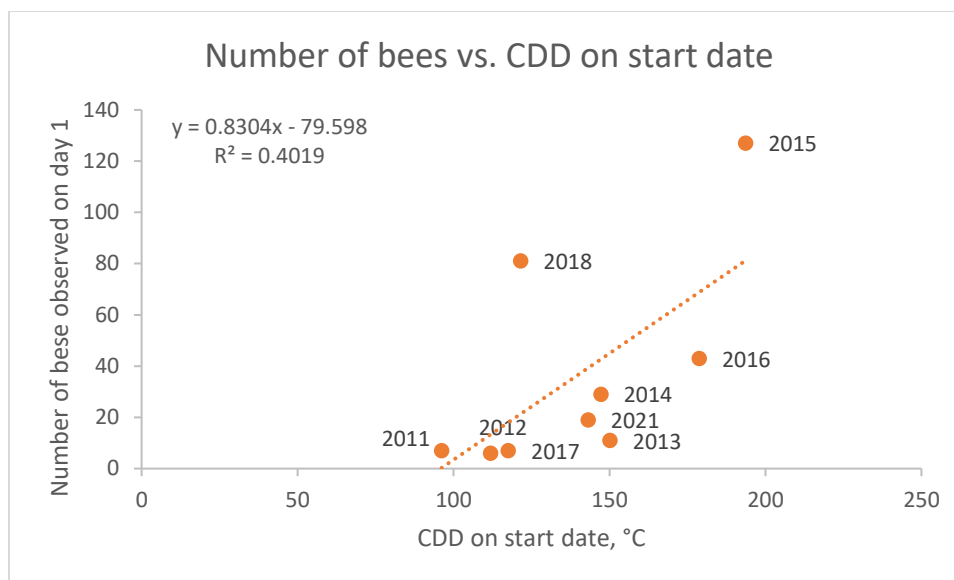


Figure F2. Figure used to estimate the CDD threshold for when bees typically begin visiting flowers.

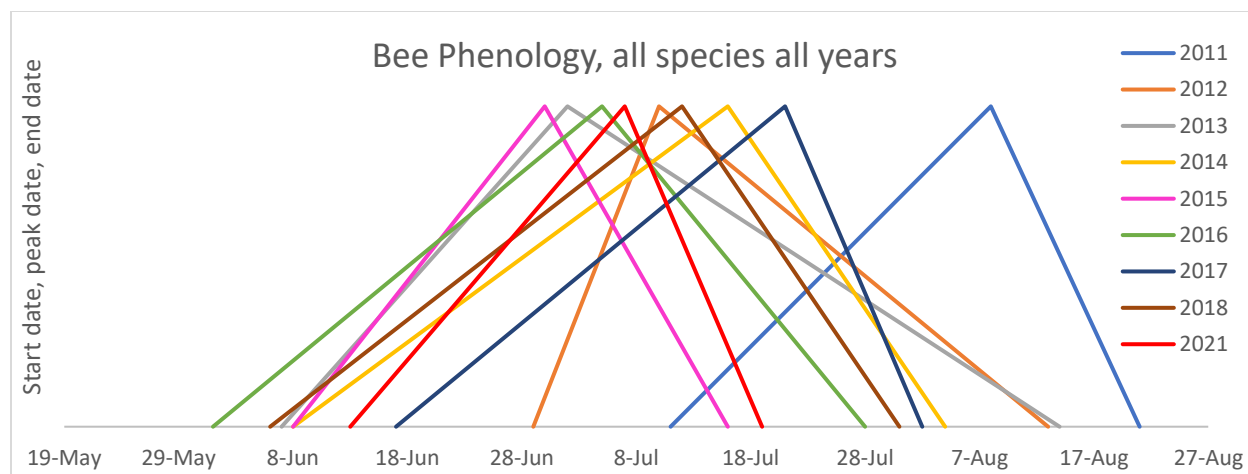


Figure F3. A visualization of bee floral visitation phenology by year.

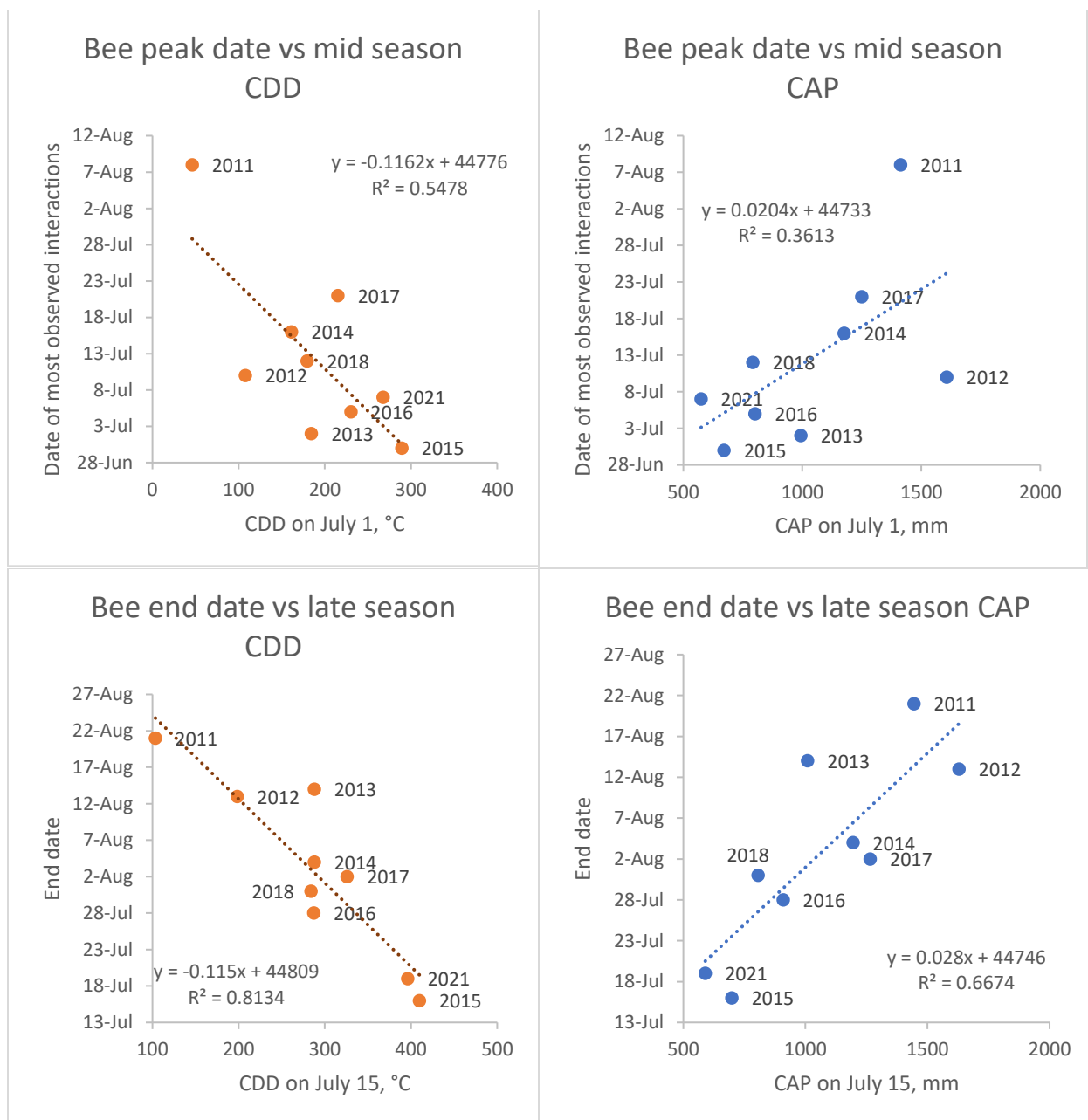


Figure F4. (top) Peak date was inversely proportional to higher mid-season CDD and was later with higher CAP. (bottom) End date had a strong negative relationship with late season CDD and a positive relationship with late season CAP.

G. Network

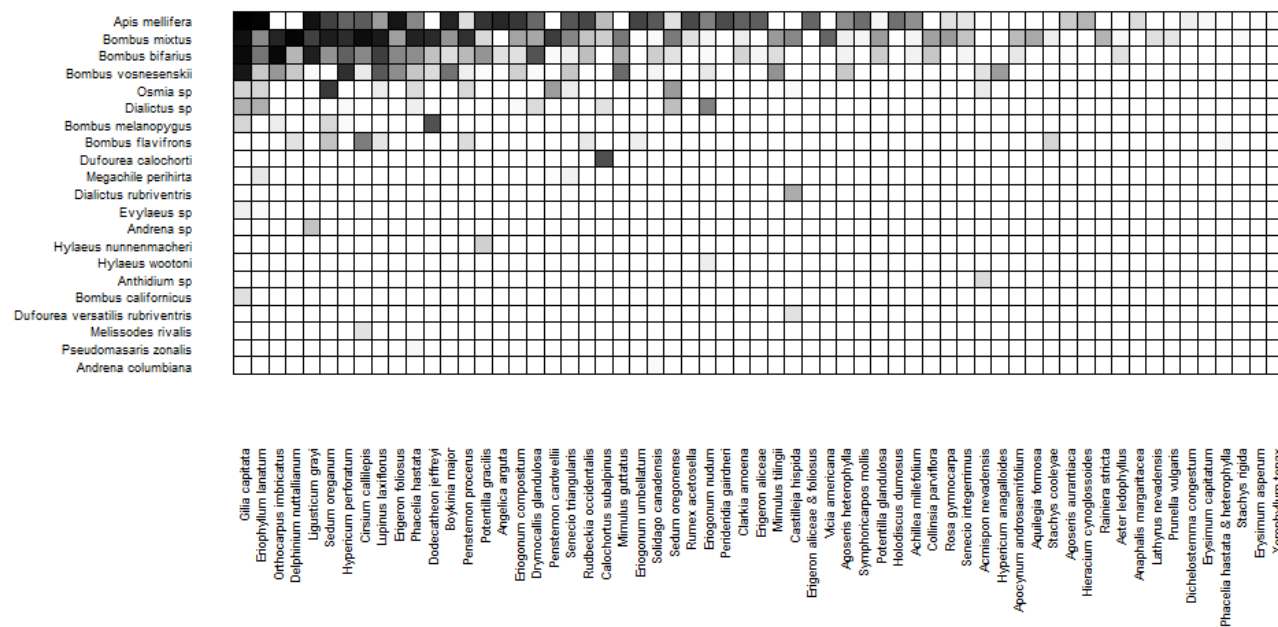


Figure G1. A visual matrix of all the top plant and pollinator interactions for all meadows and all years. This visualization only includes interactions that happened 10 times or more throughout the 9-year study period. It is graded based on the number of times the interaction occurred: the darker the box, the more frequently the interaction was observed.

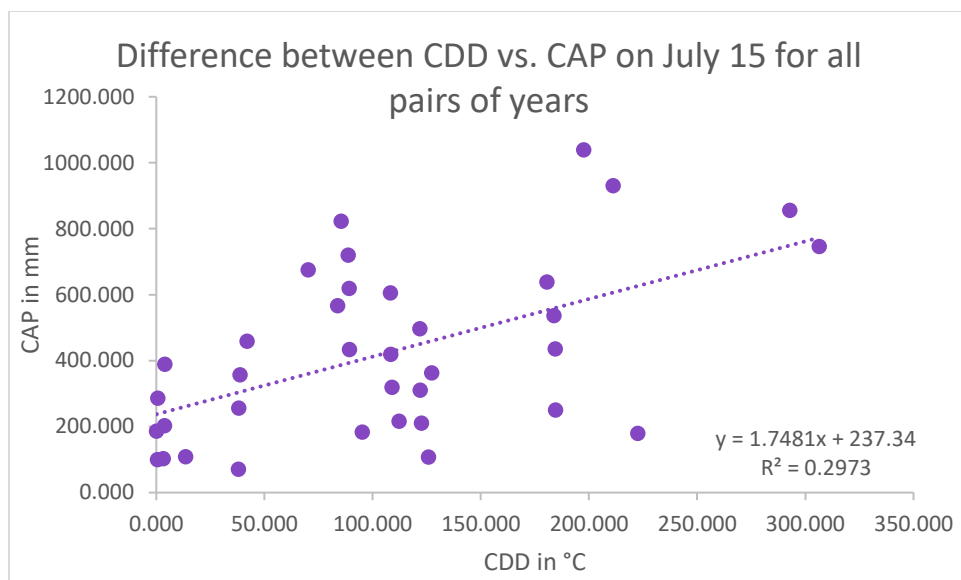


Figure G3. The difference in cumulative antecedent precipitation compared to the difference in cumulative degree days for all pairs of years (non-negative values).

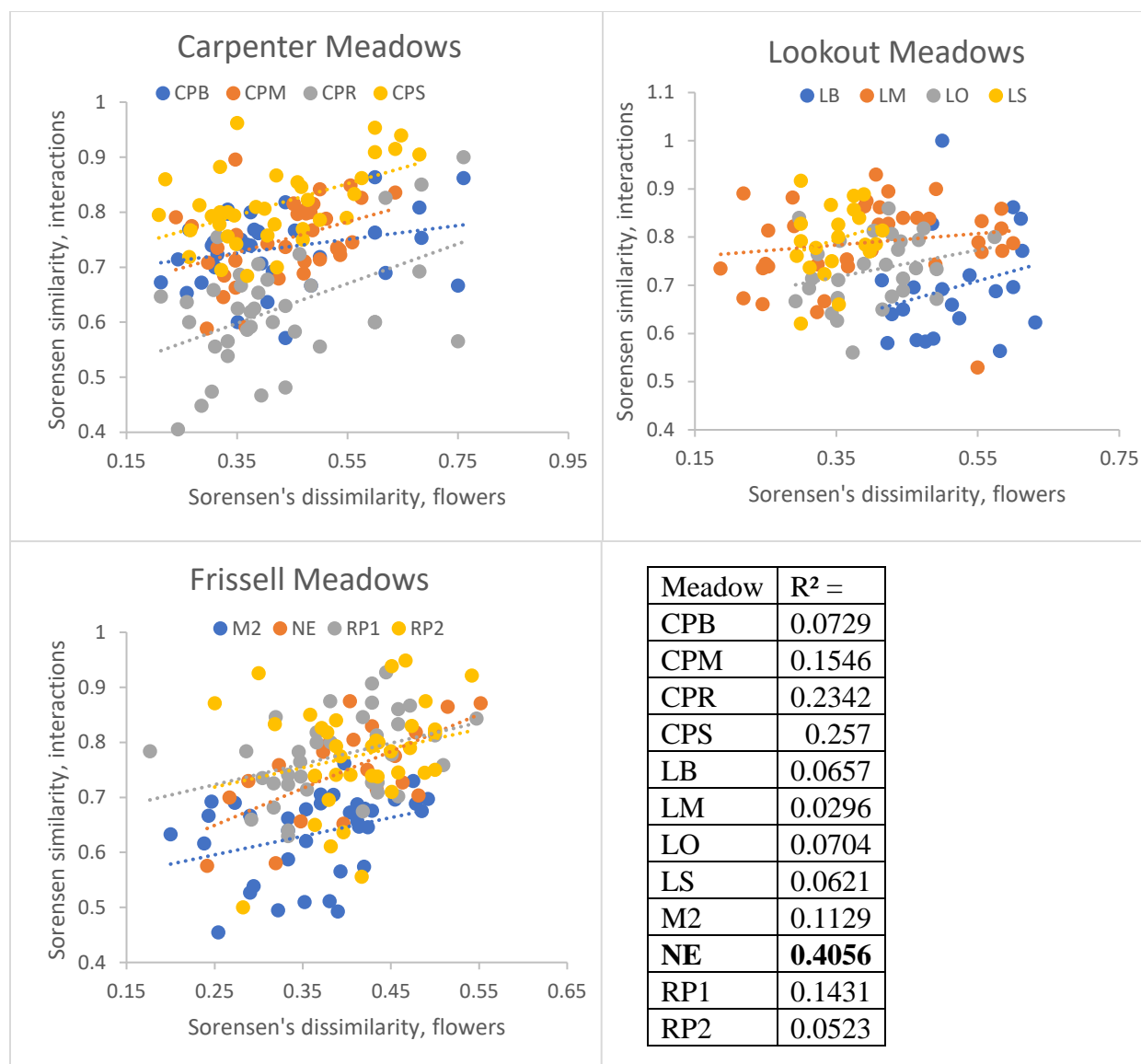


Figure G4. A comparison of Sorensen's pairwise dissimilarity for all pairs of years for flowers and plant-pollinator interactions, split by meadows (each graph displays one of the three meadow complexes).

Table G1. This table looks at the number of bees that visits each species of flower in a year. For each year, the top 5 flowers were ranked based on which flowers were visited by the largest diversity of bee species. This table shows all the flowers that ended up in the top 5 and how many years each flower was ranked in the top 5. The third column shows the average number of bee species that each flower was visited by total (not just the years the flower was in the top 5).

| Plant | Years in top 5 (/9) | Average bee species per plant |
|-----------------------------------|---------------------|-------------------------------|
| <i>Eriophyllum lanatum</i> | 9 | 10.67 |
| <i>Erigeron foliosus</i> | 5 | 8 |
| <i>Gilia capitata</i> | 5 | 8.22 |
| <i>Cirsium callilepis</i> | 3 | 6.22 |
| <i>Sedum oreganum</i> | 3 | 7.22 |
| <i>Achillea millefolium</i> | 2 | 3.78 |
| <i>Boykinia major</i> | 2 | 3.67 |
| <i>Delphinium nuttallianum</i> | 2 | 4.88 |
| <i>Ligusticum grayi</i> | 2 | 6.38 |
| <i>Lupinus laxiflorus</i> | 2 | 5.44 |
| <i>Phacelia hastata</i> | 2 | 5.11 |
| <i>Agoseris heterophylla</i> | 1 | |
| <i>Calochortus subalpinus</i> | 1 | |
| <i>Drymocallis glandulosa</i> | 1 | |
| <i>Erigeron aliciae</i> | 1 | |
| <i>Hypericum perforatum</i> | 1 | |
| <i>Orthocarpus imbricatus</i> | 1 | |
| <i>Penstemon procerus</i> | 1 | |
| <i>Potentilla glandulosa</i> | 1 | |

Table G2. Most persistent plant-pollinator interactions. This table lists the most common interactions (interactions observed 7+ years) and, if it was not observed all 9 years, the years that the interaction was not observed. 2015 and 2021 were highlighted because of the number of times they appear in the “Years not observed” column.

| Years observed | Pollinator | Plant | Years not observed |
|----------------|------------------------|--------------------------------|--------------------|
| 9 | <i>Apis mellifera</i> | <i>Erigeron foliosus</i> | NA |
| 9 | <i>Apis mellifera</i> | <i>Eriophyllum lanatum</i> | NA |
| 9 | <i>Apis mellifera</i> | <i>Gilia capitata</i> | NA |
| 9 | <i>Bombus bifarius</i> | <i>Orthocarpus imbricatus</i> | NA |
| 9 | <i>Bombus mixtus</i> | <i>Cirsium callepsis</i> | NA |
| 9 | <i>Osmia sp.</i> | <i>Sedum oreganum</i> | NA |
| 8 | <i>Apis mellifera</i> | <i>Potentilla gracilis</i> | 2021 |
| 8 | <i>Bombus mixtus</i> | <i>Delphinium nuttallianum</i> | 2015 |
| 8 | <i>Bombus mixtus</i> | <i>Orthocarpus imbricatus</i> | 2015 |
| 7 | <i>Apis mellifera</i> | <i>Boykinia major</i> | 2012, 2021 |
| 7 | <i>Apis mellifera</i> | <i>Eriogonum compositum</i> | 2015, 2021 |
| 7 | <i>Apis mellifera</i> | <i>Eriogonum umbellatum</i> | 2015, 2018 |
| 7 | <i>Apis mellifera</i> | <i>Ligusticum grayi</i> | 2013, 2021 |
| 7 | <i>Apis mellifera</i> | <i>Sedum oreganum</i> | 2016, 2018 |
| 7 | <i>Bombus bifarius</i> | <i>Gilia capitata</i> | 2017, 2021 |
| 7 | <i>Bombus mixtus</i> | <i>Phacelia hastata</i> | 2012, 2015 |
| 7 | <i>Bombus mixtus</i> | <i>Sedum oreganum</i> | 2012, 2015 |
| 7 | <i>Bombus mixtus</i> | <i>Vicia americana</i> | 2015, 2017 |

Table G3. This table shows the final Sørensen pairwise dissimilarity values for plant-pollinator interactions for all years.

| Dissimilarity | 2011 | 2012 | 2013 | 2014 | 2015 | 2016 | 2017 | 2018 | 2021 |
|---------------|-------|-------|-------|-------|-------|-------|-------|-------|------|
| 2011 | | | | | | | | | |
| 2012 | 0.618 | | | | | | | | |
| 2013 | 0.528 | 0.646 | | | | | | | |
| 2014 | 0.537 | 0.562 | 0.572 | | | | | | |
| 2015 | 0.656 | 0.630 | 0.638 | 0.515 | | | | | |
| 2016 | 0.537 | 0.597 | 0.564 | 0.522 | 0.558 | | | | |
| 2017 | 0.708 | 0.680 | 0.694 | 0.670 | 0.722 | 0.671 | | | |
| 2018 | 0.622 | 0.731 | 0.624 | 0.616 | 0.680 | 0.594 | 0.628 | | |
| 2021 | 0.707 | 0.722 | 0.704 | 0.670 | 0.711 | 0.680 | 0.757 | 0.748 | |

Table G4. This table shows the final Sørensen pairwise dissimilarity values for floral composition for all years.

| Flower dissimilarity | 2011 | 2012 | 2013 | 2014 | 2015 | 2016 | 2017 | 2018 | 2021 |
|----------------------|----------|----------|----------|----------|----------|----------|----------|----------|------|
| 2011 | | | | | | | | | |
| 2012 | 0.185185 | | | | | | | | |
| 2013 | 0.228261 | 0.22093 | | | | | | | |
| 2014 | 0.313253 | 0.220779 | 0.272727 | | | | | | |
| 2015 | 0.43038 | 0.356164 | 0.321429 | 0.36 | | | | | |
| 2016 | 0.348066 | 0.301775 | 0.277487 | 0.283237 | 0.309091 | | | | |
| 2017 | 0.354167 | 0.322222 | 0.326733 | 0.358696 | 0.443182 | 0.336683 | | | |
| 2018 | 0.367876 | 0.303867 | 0.29064 | 0.275676 | 0.367232 | 0.22 | 0.2891 | | |
| 2021 | 0.45679 | 0.426667 | 0.395349 | 0.441558 | 0.452055 | 0.360947 | 0.366667 | 0.359116 | |

Table G5. This table shows the difference between CDD and CAP between pairs of years (column-row).

| CDD | 2011 | 2012 | 2013 | 2014 | 2015 | 2016 | 2017 | 2018 | 2021 |
|------|---------|---------|---------|---------|---------|---------|---------|---------|------|
| 2011 | | | | | | | | | |
| 2012 | 95.210 | | | | | | | | |
| 2013 | 184.420 | 89.210 | | | | | | | |
| 2014 | 184.550 | 89.340 | 0.130 | | | | | | |
| 2015 | 306.430 | 211.220 | 122.010 | 121.880 | | | | | |
| 2016 | 183.860 | 88.650 | -0.560 | -0.690 | 122.570 | | | | |
| 2017 | 222.560 | 127.350 | 38.140 | 38.010 | -83.870 | 38.700 | | | |
| 2018 | 180.610 | 85.400 | -3.810 | -3.940 | 125.820 | -3.250 | -41.950 | | |
| 2021 | 292.830 | 197.620 | 108.410 | 108.280 | -13.600 | 108.970 | 70.270 | 112.220 | |

| CAP | 2011 | 2012 | 2013 | 2014 | 2015 | 2016 | 2017 | 2018 | 2021 |
|------|----------|----------|----------|----------|----------|----------|----------|----------|------|
| 2011 | | | | | | | | | |
| 2012 | 183.585 | | | | | | | | |
| 2013 | -435.856 | -619.441 | | | | | | | |
| 2014 | -250.063 | -433.648 | 185.793 | | | | | | |
| 2015 | -746.401 | -929.986 | -310.545 | -496.338 | | | | | |
| 2016 | -536.149 | -719.734 | -100.293 | -286.086 | 210.252 | | | | |
| 2017 | -179.532 | -363.117 | 256.324 | 70.531 | 566.869 | 356.617 | | | |
| 2018 | -638.759 | -822.344 | -202.903 | -388.696 | 107.641 | -102.611 | -459.227 | | |
| 2021 | -855.259 | 1038.844 | -419.403 | -605.196 | -108.859 | -319.111 | -675.727 | -216.500 | |

Table G6. This table shows the final Sørensen dissimilarity values for interactions for all years by meadow. The values included are beta diversity, beta similarity (Beta.SIM), and beta nestedness (Beta.SNE).

| Meadow | Beta diversity | Beta.SIM | Beta.SNE |
|--------|----------------|----------|----------|
| CPB | 0.879 | 0.846 | 0.033 |
| CPM | 0.872 | 0.818 | 0.054 |
| CPR | 0.827 | 0.730 | 0.097 |
| CPS | 0.903 | 0.852 | 0.051 |
| LB | 0.812 | 0.707 | 0.105 |
| LM | 0.882 | 0.790 | 0.092 |
| LO | 0.855 | 0.809 | 0.046 |
| LS | 0.875 | 0.815 | 0.060 |
| M2 | 0.824 | 0.760 | 0.064 |
| NE | 0.858 | 0.808 | 0.050 |
| RP1 | 0.889 | 0.859 | 0.030 |
| RP2 | 0.873 | 0.810 | 0.063 |