DO FLOWER PHENOLOGY AND TRAITS VARY ACROSS SPECIES AND PROVENANCES AND IMPACT PLANT-POLLINATOR INTERACTIONS?

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ABSTRACT

DO FLOWER PHENOLOGY AND TRAITS VARY ACROSS SPECIES AND PROVENANCES AND IMPACT PLANT-POLLINATOR INTERACTIONS?

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The response of plant-pollinator interactions to climate change is a growing body of research. Pollinators are key components of most terrestrial systems, and most plants depend on these mutualisms for reproduction. This common garden study aimed to understand how climate provenance is associated with the phenology of flowering and floral traits, and subsequently how the variation in phenology and floral traits is associated with the abundance and richness of pollinator functional groups. Eight populations of ten common forb species were collected across a climate gradient in the southwestern US and planted in a common garden. Populations were measured for phenology and floral traits (abundance, corolla dimensions) and observed for interactions with insect visitors. Regression analyses were conducted to determine whether population trait variation was predicted by provenance climate, with subsequent correlation analyses to determine if pollinator responses (richness, activity) were associated with trait variation. The majority of the ten forb species demonstrated some degree of trait variation that was predicted by climate; however, the direction and degree of response was variable among species. Compared to the high degree of climate-trait associations within the study plant species, there were few significant responses detected within the pollinator community. However, a small subset of phenological and floral traits impacted pollinator functional group richness/abundance; namely, date of peak floral output and peak floral abundance. These traits were variable between

provenances and predicted by climate source, suggesting that climate influence on traits can have a direct implication for some plant-pollinator mutualisms.

Key words: common garden, forb, restoration

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Introduction

Globally, native pollinator communities are a fundamental component of most terrestrial ecosystems, with an estimated 80% of flowering plants relying on pollinators for reproduction (Devoto et al. 2012, Ollerton et al. 2011). Pollinator populations are in decline due to habitat loss, fragmentation of habitat, pesticide use, and climate change, jeopardizing the critical ecosystem services they provide in both natural and agricultural contexts (Cardosa et al. 2020, Menz et al. 2011, Devoto et al. 2012, Tylianakis 2013, Potts et al. 2010, Kluser and Peduzzi 2007). A loss of pollinators threatens the stability of mutualistic networks and the reproductive capabilities of flowering plants (Tylianakis et al. 2008, Albrecht et al. 2008). Climate change is also altering patterns of plant phenology and ranges (Cleland et al. 2007, Forrest 2016), disrupting the historical overlap that permitted interactions between pollinators and plants (Tylianakis et al. 2008, Gilman et al. 2011, Byers 2017, Memmett et al. 2007, Hegland et al. 2009).

While some populations of plants and animals can shift their range as they follow optimal conditions, others cannot (Cardosa et al. 2020, Chen et al. 2011, Lenoir and Svenning 2015). There is evidence that both plants and pollinators have advanced their emergence or reproductive phenology earlier in the year in response to a warming climate (Chen et al. 2011, Forrest 2016, CaraDonna et al. 2014). However, individual species have different and sometimes conflicting trends around this general, multi-species mean (Cleland et al. 2007, Memmott et al. 2007, Van der Putten et al. 2010). Plants tend to respond to earlier snowmelt and higher temperatures associated with climate change, and early-spring species have responded more drastically than fall species (Cleland et al. 2007, CaraDonna et al. 2014, Gillespie et al. 2016). At the same time,

however, greater shifts in temperature are not necessarily associated with greater plant species response in terms of phenology or range shifts (Chen et al 2011).

While phenological patterns of insects are less well understood than plants, studies have shown that insects respond to snow melt and temperature as well as other cues (e.g., photoperiod, winter conditions, soil temperature) (Forrest 2016, Morton and Rafferty 2017, Adedoja et al. 2020) and are thus subject to phenological shifts as warming occurs. If insect phenology shifts at a different rate or direction than plants, floral resources available to pollinator communities could be reduced significantly (Memmott et al 2007) or could result in novel plant-pollinator communities (Morton and Rafferty 2017, Van der Putten et al. 2010, CaraDonna et al. 2014, Memmot et al. 2007).

There are a number of plant traits that are important to pollinators, like phenology, physiology, and floral display (Scaven and Rafferty 2013). Floral display traits (flower abundance and size) vary in wild populations due to climate with temperature and water limitation considered major drivers (Dart et al. 2012, Mason et al. 2017, Flo et al. 2018); drought-prone populations tend to produce fewer, smaller flowers than mesic counterparts (Galen 2005, Lambrecht and Dawson 2007, Brunet and Van Etten 2019, Flo et al. 2018, Lambrecht et al. 2017, Descamps et al. 2018, Descamps et al. 2020). There are trade-offs with such a strategy: fewer flowers limit water lost through floral transpiration but reduce desirability to pollinators (Galen 2005, Burkle et al. 2016), as pollinator visitation is positively associated with larger floral displays (Thompson 2001, Potts et al. 2003, Blaauw and Isaacs 2014, Hegland and Totland 2005). While these general relationships between water availability and temperature exist for floral displays, there is demonstrated variation in species-specific responses (Scaven and Rafferty 2013, Lambrecht et al. 2017, Descamps et al. 2020). How climate drives variation

in floral traits, and how pollinators respond to this variation, is key to understanding how plant-pollinator interactions may shift with climate change.

One way to assess plant responses to climate is through tests of local adaptation, a well-recognized phenomenon where local genotypes outperform foreign genotypes in climates similar to their origin (Joshi et al. 2001, Leimu and Fischer 2008, Baughman et al. 2019). Local adaptation is generally investigated through the use of common garden studies in which populations sourced from a range of climates are grown in a common environment (Leimu and Fischer 2008, Joshi et al. 2001). These types of studies are used to understand how populations respond to climate factors, how climate change may shift plant ranges (Peterson et al. 2018), and how to develop plant materials that will be successful in a restoration environment (Bower et al. 2014, Broadhurst et al. 2008). The primary emphasis of common garden studies has historically been on the plants themselves, with relatively little effort made to understand the response of mutualists associated with those plants, such as the native pollinators that depend on them (Boberg et al. 2014, Burcharova 2017, Gibson et al. 2016, Morton and Rafferty 2017). For example, a recent review of 308 studies on local adaptation showed that less than 1% of those studies measured plant mutualisms as a response variable for plant fitness (Gibson et al. 2016), with only one of those measuring pollinators (e.g., Streisfield and Kohn 2007). Furthermore, a review by Morton and Rafferty (2017) found that in five common garden studies investigating intraspecific variation in plant-pollinator interactions, none examined how climate adaptations in plants affect the pollinator community.

The southwestern U.S. is a diverse and environmentally heterogeneous landscape with large elevational, temperature, and precipitation gradients, resulting in high plant and pollinator diversity (Smith et al. 2015, Wood et al. 2015). Climate change forecasts in this region predict

higher temperatures, more severe droughts, advanced snow melt, and increase in frequency of large-scale fire-related disturbances (Garfin 2013, Guirguis et al 2018, Cayan et al. 2010). These predictions will have direct implications for plant, pollinator, and animal communities. Given the range of environmental variation in the Southwest, it is reasonable to expect that plant species would exhibit a great amount of intraspecific variation and local adaptation (Winkler et al. 2018, Wood et al. 2015, Baughman et al. 2019). In a recent review, Baughman et al (2019) showed that many species of trees, shrubs, and grasses are locally adapted to climate in the Great Basin. However, this analysis included only five forb-focused studies, even though forbs are widespread, abundant in many communities, and pollinators depend on them. The paucity of studies investigating climate adaptation in forbs leaves a large gap in the understanding of climate-mediated plant-pollinator interactions in this region (Simpson and Neff 1987, Smith et al 2015).

This study aims to fill a gap in knowledge about forb species on the Colorado Plateau by measuring the pollinator community response in a common garden setting designed to examine patterns of local adaptation in plants that pollinators depend on. The objective of this study was to understand how these pollinator communities respond to intraspecific variation in plant performance, focusing on a suite of native species commonly used in restoration. We asked the following questions: (i) to what degree do these target plant species demonstrate intraspecific variation in traits important to pollinators (phenology, floral display/traits), and to what extent is that variation driven by adaptation to climate? (ii) how does the native pollinator community respond to these patterns across plant species? We hypothesize that most species will demonstrate some degree of trait variation that is predicted by climate provenance. When this

trait variation impacts traits known to be important for pollinators (e.g., floral display), we hypothesize a response in the diversity and interaction abundance of pollinator groups.

Materials and Methods

Study site and design. A common garden was established in the summer of 2019 in the Sierra Ancha Experimental Forest (SAEF), Tonto National Forest (Figure 1). This garden sits at 1592 m, with mean annual temperature 11.4°C and mean annual precipitation 64.6 cm, with ~36% annual precipitation falling during the monsoon season. Native vegetation (*Senegalia greggii*, *Larrea tridentata*, *Lycium* spp.) was manually removed from the garden site prior to planting, and periodically weeded during the growing season within and adjacent to plots. A fully randomized block design was then implemented, with six ~700 m^2 blocks established across the site. Within each block, 80 1.3 x 1.6 m plots were established (N = 480) with space that allowed researchers to pass between and among plots. The number of plots in each block corresponded to the ten study species, each with representation from eight different source locations (Table 1). No protection was provided against invertebrate herbivores; however, a small subset (18) plots had vertebrate herbivore exclusion cages for a concurrent experiment in the garden.

Seed collection and plant propagation. The study plant species are relatively common forbs/shrubs in the southwestern United States and were chosen due to widespread abundance (Wood et al. 2015, Kilkenny et al. 2015) (Table 1): *Asclepias subverticillata* A. Gray (hereafter *Asclepias*), *Brickellia californica* Torr. & A. Gray (hereafter *Brickellia*), *Dieteria canescens* Pursh (hereafter *Dieteria*), *Ericameria nauseosa* Pall. ex Pursh (hereafter *Ericameria*), *Gaillardia pinnatifida* Torr. (hereafter *Gaillardia*), *Gutierrezia sarothrae* Pursh (hereafter

Gutierrezia), *Heliomeris multiflora* Nuttall (hereafter *Heliomeris*), *Heterotheca villosa* Pursh (hereafter *Heterotheca*), *Linum lewisii* Pursh *(*hereafter *Linum),* and *Senecio flaccidus* Lessing (hereafter *Senecio*).

In the summer and fall of 2018 seeds were collected from these ten forb and shrub species across the southwest United States (AZ, NM, NV, CO, UT, CA). Collections for each species were geographically widespread and across a range of elevations and climatic conditions (Table 1). In December 2018 seeds were planted into peat pellets (120ml, Jiffy Pellets (J36100), Stuewe and Sons) that expanded to 3.8 cm diam x 10 cm depth. For each species, multiple seeds were placed into a single plug to increase chances of germination; plugs were thinned to a single germinant during the first month of emergence. Plants were watered daily until germination, thereafter several times per week until outplanting in May. In April, all seedlings were placed outside to harden and watered every day in preparation for outplanting in May.

In May 2019, each plot was planted with six individuals (N = 2880 plants) in a 2 x 3 grid formation so that each individual was ~30 cm away from its neighbor. After planting, all seedlings were watered daily for 3 weeks to encourage establishment, after which they were watered approximately 3x per week until September. Watering continued longer than intended because the summer of 2019 was an extremely dry year, and the gardens did not receive normal monsoon precipitation; 6.2 cm of monsoon moisture was measured between time of planting and September 1 (data from on-site weather station), which is approx. 67% below average. No watering occurred during the 2020 season.

Data collection: plant and floral traits. Beginning in March 2020, the garden was visited approximately every 2-3 weeks to perform a census on the number of flowers in each plot, for a

total of 12 census points between March and October. At each census time point, the number of open flowers (i.e., with receptive stigmas and/or actively pollen-producing anthers) in each plot was counted. These data were used to estimate reproductive output and phenology of all species, and to inform timing of pollinator observations.

Census data were used to estimate phenology, floral output, and total length of flowering season as components of plant performance (Joshi et al. 2001). Peak flowers for every plot were estimated as the maximum number of flowers counted at any time point, divided by the number of living plants in each plot to obtain an average peak number of flowers per plant. Phenological data were taken for each plot, including date of first bloom (first census with flowers), and day of peak flowers (census day with highest recorded flower number). Total flowering season length was the estimated time a plot had flowering individuals. If a plot was observed to be flowering at only one census point, the total season length was estimated as the number of days in the interval between the midpoint of that census point and the previous one, and the midpoint of that census point and the following one. For example, if a plot was only flowering during the fifth census, the total season length was the number of days in the interval of the midpoints between censuses 4 and 5 and between censuses 5 and 6. This method cannot detect within-season flowering starts and stops, which are possible in this region (Crimmens et al. 2014) but develops a general timeframe in which flowering occurs.

Floral traits were also measured (modified from Thompson 2001). Three fully opened flowers were randomly selected in each plot and measured using digital calipers to 0.1mm. Corolla length was measured from the base of the flower to the edge of the petal. Corolla width was measured by lightly flattening the flower petals to span the entire width. The diameter

(width) of disk flowers was also measured for study species in the Asteraceae family that have distinct disk flowers (Table 4).

Data collection: pollinator observations. Following each floral census, up to three rounds of pollinator observations were performed over the next few days. Only plots that contained open flowers were observed for pollinators. Observations were performed during the day, between 08:00 and 16:00 hours under conditions of moderate wind speed (<3.7m/s) and no precipitation. Plots were randomly ordered and assigned to observers to spread observations for each plot throughout the day; however, *Linum* closed its flowers by noon, so those plots were prioritized for the morning. There was a total of 23 days in which observations took place, and 608 rounds of observations over the season, equaling ~101 hours of observations. While we did not measure pollen transfer by visitors, only individuals that contacted the reproductive structures of a flower were included in calculations and for simplicity will hereafter be referred to as "pollinators," even though some visitors organisms may not have effectively transferred pollen.

For each plot, one round of observations was 10 minutes long, broken up into two parts: "scanning" and "focal individual," following methods from Aslan et al. (2019). The observer counted the number of plants with open flowers and the number of flowers visible from the observation position. During the first "scanning" minute, an observer visually swept the plot for pollinators, noting the functional group and number of visitors present; non-pollinator visitors (e.g., grasshoppers, beetles, true bugs) were also noted. The next 9 minutes were designated as the "focal individual" period, during which the observer tracked and timed a single pollinator for as long as it was within the plot, for a maximum of 120 seconds. If multiple pollinators were present at the beginning of this interval, one was chosen haphazardly. As the visitor moved

around the plot, the number of flowers probed per plant were recorded, along with a description of the pollinator (e.g., the presence and location of pollen), and its general behavior. A flower was considered probed if the visitor contacted the reproductive parts of the flower, thus creating the potential for pollination. Once an individual stopped interacting with the study species flowers, left the plot, or 120 seconds had elapsed, a new focal individual was chosen, timed, and tracked. Observers prioritized focal individuals of different functional groups for each new focal individual, but in cases where only visitors of previously-observed functional groups were present in the plot, those visitors were tracked, such that a single functional group might be tracked multiple times during an observation session. Pollinators were placed into the following functional groups, which are recommended for citizen science observation of pollination (Ullmann et al 2010): bumble bee, carpenter bee, wasp, honeybee, striped sweat bee, green sweat bee, tiny dark bee, hairy belly bee, hairy leg bee, cuckoo bee, butterfly, moth, muscid fly and syrphid fly. When an observer was not able to identify a visitor to one of these functional groups, the pollinator was listed as "other native bee" or "other fly."

Pollinator importance values were calculated for each functional group in relation to each plant species, and each population within a species (Aslan et al. 2019). Importance values represent the average number of flowers probed of the study species/population, per unit time of interaction; these values were then scaled relative to the highest importance value within the plant species level. A network graph was created using bipartite() program in R to visualize the connections and patterns for all garden plant-pollinator interactions (Dormann et al. 2008). To aid in comparisons, specifically between populations of a species, importance values were also calculated for broad taxonomic groups by lumping the above functional groups into the broader categories bees, Diptera (flies), Lepidoptera (butterflies and moths) and wasps.

Climate analysis. Nineteen bioclimatic variables for each provenance were extracted from the WorldClim dataset (Version 2) using 2.5-minute resolution averages for the years 1970-2000 (Fick 2017). In addition to these 19 bioclimatic variables, elevation, latitude, and longitude of source collection sites were documented. To reduce the dimensionality of these variables, a principal component analysis (PCA) was developed using the princomp() function in the base R program (R Core Team 2020) without further standardization of the data. The PCA was conducted using the climatological variables across all provenances of all species in the study (N = 80). The first three axes were then used for subsequent analyses for each species in the study separately. Using the climate variables from all source populations of all species in the study in order to predict individual species patterns allowed us to describe a broader and more robust picture of the climatological variability of the region; assessing patterns for all species using the same "scale" allows us to examine species with overlapping ranges and their responses to general climate of the Southwest.

The first three principal components explained 80.5% of the variance in the bioclimatic variables; the first two principal components (PC1 and PC2) explain 65% of variance, but an accepted standard is 70-90% (Jolliffe 2002), thus PC3 was also included in regression models. Each of the first three axes describes broad climatological trends, as inferred from the loadings of each axis (Table 2). PC1 encompasses several temperature and precipitation variables, where high temperatures, low precipitation, and low elevation correspond to a low PC1 value, while high elevation, cooler temperatures and higher annual precipitation correspond to a high PC1 value. Thus, this axis is an indicator of tendency toward drought. PC2 describes the degree of monsoonal patterns (low PC2) versus a more temperate rain pattern (high PC2) due to the strong

contribution of latitude, isothermality and precipitation variables. PC3 explains an additional 15% of the climate variation, encapsulating the regional degree of winter precipitation and strength of winter where negative values indicate colder winters with more snowfall and positive values indicate a milder winter with less precipitation.

Statistical analyses. All floral trait metrics were tested for normality using Shapiro-Wilks tests and log-transformed where necessary. Generalized mixed-effect models (GLMM) were used for each species separately to analyze the degree to which the PC axes predicted variation in population response. The GLMMs were conducted using lme4 (Bates 2015). Transformed response variables were used in the models when appropriate, but figures show untransformed data. In these models, PC values were included as predictors, with block as a random effect (Table 3). A best-fit model was determined using an ANOVA test between models including all three PC values, and PC1 and PC2; when the p-value was less than 0.05, the full model with PC1, 2, and 3 was used.

Spearman's rank correlations were used to examine relationships between the pollinator community, plant traits, and provenance climate (Table 6). These tests were used to examine whether floral display or phenological timing were correlated with population variation in pollinator functional group richness and the number of individuals counted in "scans" described above. These values were corrected by the total number of scans in each population/species, as there was a strong positive relationship between scans and richness in the observation data (R^2 = 0.8). Correlations between pollinator responses and climate PC axes were also examined.

Results

Date of first bloom. Plant species differed in their flowering phenology from each other, with about 150 days between the first flowering of the earliest (*Linum*) and latest species to flower (*Ericameria*). Four species bloomed in the first 50 days of the study period ("early blooming" species: *Linum, Gaillardia, Heterotheca, Senecio*), three were "mid-blooming" (*Asclepias, Dieteria, Heliomeris*), and three were "late-blooming" (*Brickellia, Ericameria, Gutierrezia*).

Four species did not show significant variation among populations in terms of date of first bloom, nor predictive effects of climate (*Asclepias, Brickellia, Ericameria, Gaillardia*) (Table 3). For five of the remaining species, PC1 was significantly associated with the date of first bloom. For *Dieteria* ($p<0.001$), *Gutierrezia* ($p= 0.004$), and *Heterotheca* ($p= 0.004$), populations from hotter and drier locations bloomed later in the garden, compared to populations from cooler and wetter provenances (Figure 2c, 2f, 2h). *Linum* ($p<0.001$) and *Senecio* (0.0036) showed the opposite pattern, where populations from hotter and drier locations bloomed earlier than their counterparts from cooler wetter locations (Figure 2i, 2j). Date of first bloom was also significantly predicted by PC2 for four species, where provenances from monsoonal regions bloomed earlier in the year (*Gutierrezia*, $p<0.001$; *Heliomeris*, $p<0.001$; *Heterotheca*, $p=0.062$; *Linum*, $p = 0.032$) (Figure 2f, 2g, 2h), except for *Senecio* that showed the opposite pattern ($p = 0.0042$, Figure 2j). Date of flowering was predicted by PC3 for *Heterotheca* ($p=0.032$) and *Senecio* ($p=0.022$), where populations from regions with more precipitation in the winter bloomed later in the year than with a drier winter (Figure 2g, 2j).

Day of Peak. "Day of peak" approximated the day of the growing season that each species produced the peak number of flowers. In general, this response showed similar patterns to that of

date of first bloom, with those species/populations that flowered earlier in the year tending to peak earlier as well. While *Ericameria* displayed significant variation between populations ($p=0.046$), this variation was not predicted by PC1, 2 or 3 (Table 3). PC1 was predictive for *Dieteria* ($p<0.001$) and *Heterotheca* ($p<0.001$) with hotter, drier populations peaking later than cooler, wetter populations (Figure 3c, 3h). *Senecio* maintained the opposite pattern with cooler, wetter populations peaking earlier than hotter and drier populations ($p=0.018$; Figure 3j); this pattern was consistent with date of first bloom. PC2 was a significant predictor of day of peak for five species (Figure 3), with non-monsoonal populations peaking later than non-monsoonal populations for four of those five (*Dieteria*, $p=0.004$; *Gaillardia*, $p=0.05$; *Heliomeris*, $p<0.001$; *Heterotheca*, $p=0.0018$); however, *Senecio* again demonstrated the opposite pattern ($p=0.037$). PC3 was only predictive for *Heterotheca* ($p=0.0025$) with populations from regions with more precipitation in the winter peaking earlier in than provenances from areas with milder winters (Figure 3h). Four species did not significantly vary between populations in their date of peak flowers (*Asclepias, Brickellia Gaillardia, Linum*) (Table 3).

Total flowering season length. Total season length varied between species and ranged from an average of 18-64 days in flower. This final phenological measure did not vary between populations of *Asclepias, Brickellia, Dieteria, Gaillardia* or *Linum* (Table 3). *Heliomeris* displayed significant variation between populations ($p=0.015$), but this variation was not predicted by PC1, 2 or 3 (Table 3). PC1 was a significant predictor of total season length for *Gutierrezia* ($p<0.001$) and marginally for *Ericameria* ($p=0.089$), where populations from hotter, drier areas had a shorter season length than those from cooler, wetter provenances (Figure 4d, 4g). PC2 predicted variation for *Ericameria* ($p=0.007$), *Senecio* ($p=0.059$), and marginally for

Linum (p=0.067) with conflicting patterns. For *Ericameria*, monsoonal provenances had shorter seasons than those from regions with more consistent precipitation (Figure 4d), and the opposite pattern was seen in *Linum* and *Senecio* (Figure 4i, 4j). PC3 significantly predicted variation among populations for *Ericameria* (p=0.007), *Heterotheca* (p=0.059), and *Senecio* (p=0.037) where populations from areas with mild winter conditions had longer season lengths than populations from areas with wetter, colder winters.

Peak flowers. The peak number of flowers varied for five species: *Asclepias, Gutierrezia, Heliomeris*, *Heterotheca*, and *Senecio* (Table 3). The variation in *Asclepias* populations was not significantly predicted by PC1, 2 or 3 (Table 3). *Gutierrezia* patterns of peak floral display was significantly predicted by PC1 values, with hotter, drier populations displaying fewer flowers than cooler, wetter populations ($p<0.001$). PC2 significantly described the patterns of variation in peak flower numbers for *Gutierrezia* ($p<0.001$), *Heliomeris* (p=0.0022), *Heterotheca* (p=0.0289), *Senecio* (p=0.0224). For *Gutierrezia*, *Heterotheca*, and *Senecio*, monsoonal populations had more peak flowers than non-monsoonal populations (Figure 5f, 5h, 5j); *Heliomeris* had the opposite relationship, with monsoonal populations tending toward fewer flowers at their peak compared to non-monsoonal populations (Figure 5g). PC3 was a significant predictor of peak flowers for *Heterotheca* (p=0.0013) and marginally for *Dieteria* (p=0.0643) and *Senecio* (0.0653). Populations of *Heterotheca* and *Senecio* from areas with drier winters had more peak flowers than populations from areas with colder, wetter winter months (Figure 5h, 5j), while *Dieteria* populations demonstrated the opposite pattern, with provenances from colder, wetter winters displaying more peak flowers (Figure 5c).

Floral dimensions. Three floral traits were measured: corolla length, corolla width, and floral disk width (applicable to all Asters with the exception of *Gutierrezia* and *Ericameria*) (Table 4). *Asclepias* and *Brickellia* did not have enough floral measurements for analysis. Corolla length was variable and predicted by climate for most species, except *Dieteria*, *Ericameria* and *Senecio*. PC1 was a significant predictor for *Gaillardia* (p=0.0053), *Heliomeris* (p=0.021) with provenances from hotter drier areas tending to have larger flowers than cooler wetter populations (Figure 6a). PC1 was also significant for *Gutierrezia* (p=0.0067) in the opposite direction, where cooler and wetter populations had longer corollas. PC2 had predictive power for *Heliomeris* (p=0.029) and marginally for *Heterotheca* (p=0.066) with opposite patterns (Figure 6b). *Heliomeris* populations from a non-monsoonal region had longer flowers; *Heterotheca* populations from monsoonal areas had longer flowers. PC3 was a significant predictor of corolla length for *Gaillardia* (p=0.0089), *Heliomeris* (p=0.011), *Senecio* (p=0.04). For *Gaillardia* and *Senecio*, populations from areas with more mild winters tended to have longer corollas than those with cold and wet winters (Figure 6c). *Heliomeris* populations demonstrated the opposite trend and larger flowers were associated with populations from colder areas (Figure 6c).

Corolla width was associated with provenance climate for seven of the eight study species measured for floral dimensions (*Dieteria*, *Ericameria*, *Gaillardia*, *Gutierrezia*, *Heliomeris*, *Heterotheca*, *Senecio*) (Table 3), with *Linum* being the exception. PC1 was predictive of population variance in corolla width for *Dieteria* (p=0.0081) and *Gutierrezia* (p=0.0067) and marginally for *Gaillardia* (p=0.071) and *Heliomeris* (p=0.094). Populations of *Dieteria* and *Gutierrezia* from hotter drier areas tended to have narrower corollas than their colder and wetter counterparts; the opposite pattern was seen for *Gaillardia* and *Heliomeris* (Figure 6a). PC2 predicted corolla width for *Heliomeris* (p=0.03), and *Senecio* (p=0.0178), and

Ericameria (p=0.094) with marginal significance. Monsoonal populations of *Ericameria* and *Senecio* had wider corollas than non-monsoonal populations, while monsoonal populations of *Heliomeris* tended to have narrower corollas (Figure 6b). PC3 was a significant predictor for *Gaillardia* (p=0.069), *Heliomeris* (p=0.01), *Heterotheca* (p=0.07); *Heliomeris* populations from regions with colder, wetter winters had larger flowers than populations from more mild winter conditions (Figure 6c). *Gaillardia* and *Heterotheca* displayed the opposite trend, where larger flowers were associated with populations from mild winter regions (Figure 6c).

Finally, the width of the disk flowers was measured for *Dieteria, Heliomeris, Gaillardia, Heterotheca*, and *Senecio* (Table 4) and all five species had variation in disk width that was associated with at least one PC axis (Table 3). PC1 was significant for *Gaillardia* ($p<0.001$) and populations from hotter and drier areas had larger disks than other provenances. Three species were significantly predicted by PC2. Populations of *Dieteria* (p=0.0094) and *Heterotheca* (p=0.026) from regions with monsoonal precipitation patterns produced larger disk flowers in the garden compared to populations with temperate patterns; *Heliomeris* populations had the opposite trend with larger disk flowers seen in provenances with consistent yearly precipitation (p=0.029). PC3 was only predictive of variation in *Senecio* (p=0.0544), and populations areas with cold wet winters had smaller disks than populations from mild winter conditions.

Pollinator response. Overall, 21 taxa visited the study plant species in the common garden during the summer of 2020, including potential pollinators identified to varying resolution (Table 5). For example, there were known species/genera of visitors (*Apis mellifera* and *Bombus spp*.), recognized functional groups (e.g., hairy belly bee, green sweat bee) (Ullmann et al. 2010), and some uncategorized, general identities (e.g., unknown Diptera, unknown sweat bee). Plant

species differed significantly in visitor functional group richness, but richness was highly correlated to the number of observations (R^2=0.8): based on our protocols, species with more flowering plots were observed more and we detected higher levels of functional group richness. While significance values incorporate surveying effort, it should be noted that there is a strong link between surveying effort and interaction detection (Chacoff et al. 2011), and there is an inherent likelihood that some plant-pollinator interactions were missed. However, we assume that common and important visitors are likely to be detected, and rare interactions missed, making results indicative of generally dominant network characteristics.

Most visitors were in the orders of Hymenoptera and Diptera, with limited visitations from Lepidoptera; since visits were limited to daylight, visitations from night-flying moths were not detected, although daytime moth observations did occur. Bees and wasps were responsible for most of the functional group richness seen in visitors, but flies (Syrphids, other Diptera, Muscid) were by and large the most frequent visitors, and were the most important visitors to all but two plant species, *Brickellia* and *Asclepias* (Table 5; Figure 7, 8). The effect of species was significant in predicting functional group richness per scan (p=0.02), but this effect was largely driven by the reduced richness of *Brickellia* (p=0.022) and *Linum* (p=0.04); all other species were not significantly different in terms of visitor richness. Visitor identity was variable between species, but due to the varying number of observations between species it is difficult to characterize differences as visitor preference or symptoms of sampling discrepancies. However, there are instances of unique plant-visitor interactions between species with high (80+) amounts of observations (*Dieteria*, *Gaillardia*, *Gutierrezia*, *Heterotheca*) implying some degree of insect preference. For example, *Apis mellifera* was only observed interacting with *Gaillardia*, *Gutierrezia* and *Heterotheca*; long horned bees were only observed visiting *Gutierrezia*; moths

were also infrequent visitors and were only observed to interact with *Linum*, *Heliomeris* and *Gutierrezia* (Table 5).

The functional groups in the observation network were lumped into four categories to aid in comparisons: bees, Diptera, Lepidoptera, and wasps. While syrphids are generally recognized as important pollinators, non-syrphids have been shown to be equally important pollen-vectors (Orford et al. 2015), justifying a combining of those groups into Diptera. The taxonomic-level patterns had similar relationships to the fine-scale importance values (Figure 7). Diptera remain the most important pollinator group for the majority of plant species. The importance of bees was much more variable and species-specific; bees were the most important visitor for *Brickellia*, *Dieteria*, and *Senecio*, and had high importance (>0.5) for *Heterotheca* and *Linum* as well. Similarly, wasps were variably important, and most important for *Ericameria*, *Heterotheca* and *Gutierrezia*. Lepidoptera were not important visitors for the majority of plant species but had relatively high importance for *Linum* and *Senecio*.

There were notable patterns for each species in terms of population-level differences in plant-pollinator interactions. Each population of *Asclepias* interacted with 1-5 functional groups – a simple network structure compared to other plant species, which is likely due to limited observations for *Asclepias* because of minimal flowering. Diptera were the most important visitors for three populations while bees largely visited the other two (Figure 9). Both Lepidoptera and wasps interacted with a single population of *Asclepias* (Figure 9). Functional group richness was not significantly correlated with any phenological or floral display trait (Table 6).

Dieteria populations interacted with up to 11 functional groups (mean=5), and richness was not correlated with number of scans ($p= 0.6703$). Diptera, as with *Asclepias*, was an

important visitor but less so than for other species and the garden network in general, and only the most important for two populations (Figure 10). In contrast to other plant species, bees were the most important pollinator taxa across nearly all populations (Figure 10). Wasp visitation was only particularly important for a single population; likewise, Lepidoptera visitation was generally low, with only moderate importance for a single population (Figure 10). Beyond these taxonomic patterns, functional diversity was variable between populations (n= 1-11), yet this variation was not significantly predicted by floral, climatic, or phenological relationships between the populations in Spearman's rank correlation tests (Table 6).

Gaillardia interacted with 16 pollinator functional groups (mean = 8). Syrphids, *Apis mellifera*, and *Steniolia spp.* were observed to interact with all populations, but beyond these trends populations had highly variable degrees of interactions with the four main pollinator taxonomic groups (Figure 11). Diptera dominated for three populations yet were absent in the interactions for the remaining three populations; bees were important for two (>0.5 scaled importance value); wasps were important for three; Lepidoptera were only observed to interact with two of the six populations (Figure 11). There does not appear to be a trend in terms of pollinator interactions and any climatic trends; populations were ordered from lowest to highest provenance elevation, which is strongly predictive of climate, but no overarching qualitative trend can be seen to explain provenance influence on interactions. No quantitative comparison can be made since the scaled importance values are dependent on the amount of spent observing each population, which is variable. Furthermore, total group richness/scan activity were not significantly correlated with any phenological, floral display/trait or climate variable (Table 6).

Gutierrezia on a species-level was visited by nearly all functional groups, yet each population interacted with only a subset of groups. Diptera were the most important visitors for

nearly all populations, and maintained relatively high values for others, except one (Figure 12). Bees interacted with, and were moderately important, for every population. The importance of wasp visitors was also variable: for some populations they were the most important visitor, for others there were no observed interactions (Figure 12). Lepidoptera interactions were only detected for two populations and had relatively low importance (Figure 12)—a result similar to other species.

When considering the effects of provenance on observed variation in pollinator response, mediated through trait variation, there were significant interactions for *Gutierrezia* (Table 6). The degree of functional group richness, corrected with number of scans, was marginally correlated with the average number of flowers in the population (r_s =0.667, p=0.071); this floral metric was strongly predicted by PC2 (p <0.001), indicating that there could be an effect of provenance on the functional diversity of the associated pollinator community. However, functional group richness was not directly correlated with PC2 (p=0.3199). Visitor richness was also marginally correlated with the day of peak flowering of each provenance (r_s =0.662, p = 0.07), with populations that peaked later observed to interact with richer insect communities. Phenological patterns were generally correlated with the number of individuals seen in a scan, corresponding to "activity" level. Populations with later first bloom dates had more individuals per scan (Rs=0.809, p=0.0149), and populations that peaked later also were observed to have more activity, but to a more modest degree (r_s =0.662, p=0.073). Populations that flowered for a shorter period of time had marginally fewer individuals per scan (r_s = -0.642, p=0.08). PC1 was also correlated to number of individuals per scan (r_s = -0.761, p=0.028) where hotter, drier populations had more activity than cooler, wetter populations, despite hotter, drier populations displaying significantly fewer flowers at their peak (p<0.001).

Heliomeris was visited by 14 functional groups, with each population interacting with only a subset (n=1-8) of this richness. The most important group was highly variable between populations: Diptera, bees, and wasps were all the most important visitor for different populations (Figure 13). Despite this, most populations interacted with all four pollinator groups, which was not common for most species; however, Lepidoptera was the most less consistent across populations. Functional richness in populations was positively correlated with the number of peak flowers (r_s =0.785, p=0.0362), and populations with more peak flowers had a higher functional diversity witnessed in observations (Table 6). While peak floral output was significantly predicted by PC2 during regression analyses (Table 3), there was not a direct relationship between PC2 and functional richness (p=0.579) (Table 6).

Heterotheca interacted with a total of 16 functional groups, and each population interacted with between 4-11. While Diptera was the most important group for the entire species, the most important group for each population tended to be bees (Figure 14). Six populations interacted with all four broad taxonomic groups, while the remaining two were notably missing Lepidoptera. The degree of importance for each non-bee taxonomic group was variable; three populations seemed to have more balanced networks, in which non-bee groups had similar importance values to bees, while the remaining five populations had more skewed values, in that non-bees had much lower importance values (Figure 14). While functional richness was not correlated to any floral trait, the number of individuals seen in scans was significantly correlated with the day of peak (r_s =0.714, p=0.0465), in that populations that peaked later in the year were observed to have more activity (Table 6). Populations with fewer peak flowers had more individuals per scan (r_s = -0.904 p=0.002), which was significantly predicted for monsoonal

(PC2) populations during linear regressions (p=0.028). However, no direct relationship between number of individuals per scan and PC2 was detected (p=0.531).

Linum, as noted, did not establish well in the garden, which is reflected in observation results: three of the six populations had less than two plots successfully flower, and had no observed visitors. Despite this, the species interacted with nine insect functional groups with Diptera being the most important group (Figure 15). Each population had interactions dominated by a different functional group (Figure 15). Functional richness and number of scan individuals were both positively correlated with the number of peak flowers (r_s =0.758, p=0.0801; r_s =0.8804, p= 0.0206 respectively), however this floral metric was not predicted by any PC axis (Table 3). No other phenological, floral or climatic metric was significantly correlated with pollinator response (Table 6).

Senecio was generally successful in the garden with 64% of plots flowering, but only nine visitor groups were recorded during observations (Table 5), the same as *Linum* that had half as many flowering plots. Diptera was the most important group for this species as a whole. Each population interacted with between 1-5 functional groups (mean=2.75), and the most important visitor was generally unique (Figure 16). For example, Lepidoptera, Diptera, bees, and wasps were the most important group for different populations (Figure 14). Number of scan individuals was solely correlated with day of peak (r_s =0.6628, p=0.07), with populations that peaked later interacting with more visitors. No other correlations were significant between number of scan individuals or functional group richness and the remaining floral or climatic metric (Table 6), despite this species demonstrating significant trait-climate interactions (Table 3).

Brickellia and *Ericameria* did not establish well in the garden, and most populations did not flower and were thus not observed for pollinators; thus, intraspecific plant-pollinator interactions for these species will not be addressed.

Discussion

We conducted a community-level assessment of climate-driven variation in plant traits and resultant responses in the pollinator community in a common garden. This is a unique step in bridging the gap between studies that investigate ways in which plants respond to climate (e.g., Joshi et al. 2001, Leimu and Fischer 2008, Baughman et al. 2019), and those that examine how pollinator communities respond to plant traits (e.g., Mitchell 1994, Brunet et al. 2015, Ishii et al. 2008, Dart et al. 2012). Drawing links between these two areas is an underrepresented approach in the field of plant-pollinator ecology. The ten study species were analyzed for ways in which climate provenance predicted plant trait variation, specifically in phenological and floral display traits that are important for pollinators. Observations provided insight into the overall pollinator community composition that interacted with species and populations within the garden. Interactions between climate, plant traits, and pollinator responses are particularly important as abiotic conditions are altered by climate change (Cardosa et al. 2020, Menz et al. 2011, Devoto et al. 2012, Tylianakis 2013, Garfin 2013).

Floral display and phenological patterns. Phenology and floral display traits directly influence the reproductive potential of plants, mediated by successful interactions with pollinator mutualists (Tylianakis et al. 2008, Gilman et al. 2011, Byers 2017, Memmett et al. 2017). Climate significantly interacts with these traits, yet often with differing strengths (Cleland et al.

2007, Memmott et al. 2007, Van der Putten et al. 2010, Flo et al. 2018). The results of this study demonstrated varying patterns of floral and phenological traits as a function of climatic origins across the ten study species. Three species exhibited repeated climate-trait associations for all floral and phenological metrics (*Gutierrezia*, *Heterotheca*, *Senecio*), suggesting a potential degree of climate adaptation. The majority of other species showed patterns of trait variation as a function of climate in at least one trait (*Brickellia*, *Dieteria*, *Ericameria*, *Heliomeris*, *Linum*, *Gaillardia*). *Asclepias* was the only species whose floral traits and flowering phenology were invariant across climate sources.

We found that variation in flowering phenology across study species was largely driven by MAT, MAP and monsoonal patterns which are climatic characteristics that influence plant phenology (Baughman et al. 2019, Crimmens et al. 2011). Generally, higher elevation (i.e., cooler, wetter) populations tend to have delayed phenology relative to lower, warmer populations (Crimmens et al. 2011, Freeman et al. 2002, Prendeville et al. 2013, Blionis et al 2001). Surprisingly, the results of this study found the opposite pattern where populations from cooler, wetter source locations tended to flower earlier than those from hotter, drier locations (with the exception of *Senecio*), suggesting a shift in life stage timing by these populations when grown in a lower elevation site under warmer conditions. This response may have been due to the warm, snow-free conditions during the spring at the garden site, since plants often time life events based on snow melt (Walker 1995, CaraDonna et al. 2014, Inouye et al. 2002). The potentially advanced flowering observed in these study species has implications for plant populations at the cooler ends of a species's range; indeed, similar results have been found for many alpine populations with earlier spring snowmelt (Chen et al. 2011, Forrest 2016, CaraDonna et al. 2014, Song et al. 2020).

While “spring” plants are generally seen to advance their phenology more than those who emerge later in the summer (Chen et al. 2011, Thomas 2010, Cleland et al. 2007), we did not observe that pattern here as provenance was important for both ‘early’ and ‘later’ blooming species. There was also no consistent pattern in terms of time of flowering and floral output: we observed that earlier flowering populations produced more flowers for three species (*Heliomeris*, *Heterotheca*, and *Senecio*), and significantly less flowers for two (*Dieteria* and *Gutierrezia*). Some studies indicate negative impacts of advanced phenology, such as early-set bud mortality (Inouye 2008), or detriment from increased rates of pathogen infection (Elzinga et al. 2007). While we did not measure these effects directly, the mixed results of floral output and phenology indicate that flowering early did not necessarily result in reduced reproductive potential in these study species. There is already evidence of advanced phenology with rising spring temperatures in both wild populations (Bertin 2008, Cardosa et al. 2020, Chen et al. 2011, Thomas 2010, Cleland et al. 2007), and common garden experiments (Cooper et al. 2018, Johnson et al. 2010, Johnson et al. 2012, Johnson et al. 2013), and the results of this study suggest phenological shifts in these southwestern forbs could be a likely consequence of climate change, especially along the upper/cooler ends of species distributions.

As with flowering phenology described above, we found that variation in floral display traits were well-predicted by temperature and precipitation patterns for most of the study species (Galen 2005, Lambrecht and Dawson 2007, Brunet and Van Etten 2019). Floral display traits, such as flower abundance and corolla dimensions, are known to vary in response to climate (Dart et al. 2012, Mason et al. 2017, Flo et al. 2018). Variation in floral display traits has been shown consistently in common garden studies, suggesting a genetic component to inflorescent size and abundance (Clausen et al. 1940, Lambrecht and Dawson 2007). Conversely, drought experiments

have demonstrated reduction in floral size and abundance for some species (Burkle and Runyon 2016, Phillips et al. 2018), while warming treatments demonstrate mixed responses: reduced display in some species, increased flower production in others, or no alteration in floral display (Scaven and Rafferty 2013, Lambrecht et al. 2017, Galen 2005, Lambrecht and Dawson 2007, Brunet and Van Etten 2019, Flo et al. 2018, Lambrecht et al. 2017, Basnet et al. 2019). This variation in responses indicate a level of plasticity in reproductive output depending on climatic conditions.

The species in this study demonstrated mixed results in terms of temperature and precipitation provenance effects on flower abundance and corolla dimensions, when grown in a warm and dry site that was particularly dry during the window of growth in 2020. There was equal representation of hotter, drier populations displaying more flowers than cooler populations (e.g., *Brickellia*, *Dieteria*, and *Senecio*), and vice versa (e.g., *Heliomeris* and *Heterotheca*). Similarly, there was no consistent trend for corolla dimensions across species: populations from hotter, drier locations produced significantly longer and/or wider flowers for two species (e.g., *Heliomeris* and *Gaillardia*), and shorter/narrower corollas for others (e.g., *Gutierrezia*, and *Dieteria*). In general, the populations that produced larger flowers also produced more flowers per plant, but because there are so many different floral strategies, it is difficult to generalize what is locally adaptive. For example, it is not safe to assume that more flowers are inherently advantageous given their transpiration effects (Galen 2005, Burkle et al. 2016). Therefore, the mixed outcomes we observed across species further suggest potential species-specific response to warming and drought events.

Pollinator community responses. Pollinator abundance and functional composition varies across elevational gradients (Simpson and Neff 1987, Warren et al. 1988, Brunet 2009, Sundqvist et al. 2013, McCabe and Cobb 2021, Adedoja et al. 2020) and year to year (Flo et al. 2018). In general, however, flies dominate pollinator communities at higher elevations, and bees at lower elevations (Warren et al. 1988, Sundqvist et al. 2013, Richman et al. 2020). We found that at this particular study site, flies (syrphids and other Diptera) were the most important functional group of visitors for seven of the ten study species, with bees the most important for the remaining three species. Even for those three species where bees were most important, flies were consistent visitors and maintained high importance values. At this site with these species, flies were important players in the plant-pollinator interactions we observed.

Native bees were the most important taxonomic group for *Dieteria*, *Brickellia*, and *Senecio*. Others have found regular interactions between *Dieteria* and a variety of native bees and butterflies (Tilley 2014); while we observed interactions between *Dieteria* and native bees in this study, we did not observe interactions between *Dieteria* and Lepidoptera. Bees, Diptera and Lepidoptera were all important visitors of *Senecio*; other studies have noted visitation by a variety of taxonomic groups on *Senecio* as well (e.g., Graumann and Gottsberger 1988). Still others have observed a high visitation rate of bumblebees and butterflies on *Senecio* (Schmitt 1980, Schmitt 1983). While bumblebees were not observed to interact with *Senecio* in this study, and were rare in our garden, Lepidoptera had higher relative importance values for *Senecio*, relative to other plant species visitors. On the other hand, native bees had high relative importance values for both *Heterotheca* and *Linum*. The high importance values of bees and flies for *Linum* is similar to observations by Kearns and Inouye (1994), who also showed that flies

had up to 20x greater visitation and pollen deposition rates on *Linum*, which may have been due to the higher elevation of the sites (>2830m) in that study compared to this one.

Diptera interactions were nearly four times more important for *Gaillardia* compared to bees in this study. This is interesting because others have shown that *Gaillardia* is frequently visited by native bees (Angelella and O'Rourke 2017, McCormick et al. 2019) and consequently many native seed mixes use *Gaillardia spp.* for restoration of native bees (Mallinger et al. 2019, Shadow and Brakie 2013). *Gutierrezia* visitations were similarly dominated by Diptera, followed by native bees which is similar to the results of Solbring (1964) that assessed the pollinator mutualisms of *Gutierrezia*. Interactions of bees, Diptera, and wasps with *Heterotheca* were consistently high and nearly equal in their importance, while Lepidoptera importance was relatively low. Bees and flies are noted as important pollinator groups for *Heterotheca* (Harron-Sweet et al. 2016), but the importance of wasps to *Heterotheca* that we observed in this study has not been documented elsewhere.

Overall, the strength of importance for Diptera relative to the other taxonomic groups that we observed here was high compared to the consensus of the existing literature for the pollinator community associated with these plant species. This emphasizes the importance of flies in the plant-pollinator community found at this study garden. It might also suggest an underrepresentation of Diptera in general pollination schemes found in the plant descriptions of these species (Ssymank et al. 2008, Orford et al. 2015, Ssymank et al. 2001). While syrphid flies are generally recognized and assessed during pollination studies and management plans, non-syrphid flies are often overlooked, even though their pollen deposition rates are equivalent to syrphids (Orford et al. 2015). In this study non-syrphid flies had equally high importance values as syrphid visitors during the observations in the garden. Less is known about the conservation

status and abundance of flies in North American systems (Kearns 2001, Cane and Tepedino 2001), and the importance of Diptera in the study interactions highlights the need for more data on the distribution and threats to this diverse group. While Diptera are effective pollinators, bees generally carry more pollen per insect (Orford et al. 2015, Rader et al. 2011). Considering this efficacy component, and the high diversity of bee species seen in this study, the importance of bees as effective pollinators here should not be minimized, even though Diptera dominated most networks. Measuring pollen deposition in this study network would be an interesting next step in establishing how these visitor groups contribute to successful pollination of these plant species.

Pollinator response to plant performance variation as a function of climate provenance. There is extensive literature demonstrating patterns of local adaptation to climate across a multitude of plant species (e.g., Baughman et al. 2019, Leimu and Fischer 2001, Hereford 2009, Lascoux et al. 2016, Macel et al. 2007). Simultaneously, there is a large body of literature examining how pollinator visitation rates are related to plant traits (e.g., Mitchell 1994, Brunet et al. 2015, Ishii et al. 2008, Dart et al. 2012). Still others have examined how climate factors like drought or warming affect pollinator interactions (e.g., Burkle and Runyon 2016, Scaven and Rafferty 2013, Lambrecht et al. 2017). However, few studies have attempted to understand how pollinators respond to broad climate-driven intraspecific variation in plant traits. Therefore, this study represents a unique assessment of the evidence of local adaptation of native plants to broad climate drivers, and the subsequent associations with the pollinator community.

Floral traits of four of the ten study species (*Gutierrezia*, *Heliomeris*, *Heterotheca* and *Senecio*) varied with climate with subsequent correlations to pollinator responses. *Gutierrezia* populations from hot/dry and monsoonal regions, that flowered and peaked later, had more

visitors and a higher richness of visitor functional groups. Interactions with bees and flies were important for those populations. Oddly, these monsoonal populations that flowered later had fewer peak flowers than the non-monsoonal populations. Considering floral display alone, one would expect that populations with higher peak floral abundance would demonstrate an increase in pollinator diversity/activity (Tylianakis et al. 2008, Gilman et al. 2011, Byers 2017, Memmett et al. 2017), but we did not observe this. This discrepancy could be explained by a potential phenological mismatch between the date of peak flowering we observed across *Gutierrezia* populations and the primary activity window of visitor groups in the garden (Memmett et al. 2007, Hegland et al. 2009).

Heterotheca displayed parallel patterns to *Gutierrezia*, where populations from hot/dry and monsoonal precipitation patterns peaked later in the season and had more pollinator activity per scan than non-monsoonal populations; bees and Dipteran were consistently important across all provenances. This is despite the fact that the cooler, wetter populations of *Heterotheca* displayed more flowers at their peaks, and counterintuitively this peak flower abundance was directly and negatively correlated to pollinator activity (Mitchell 1994, Ohash and Yahara 1998, Brunet et al. 2015, Ishii and Sakai 2002, Dart et al. 2012, Andersson 1996). Other studies have shown that while drought causes reduced floral abundance in *Heterotheca,* that reduction is not directly associated with variation in pollinator visitation rates (Burkle and Runyon 2016). For *Heterotheca*, a potential phenological mismatch could have a greater effect on pollinator activity compared to the abundance of flowers: the cooler populations may have bloomed too early for the pollinator community at this garden site.

In contrast to *Heterotheca* and *Gutierrezia,* visitors to *Heliomeris* had a predictable response where higher peak flower abundance corresponded to greater richness of visitors (Galen

2005, Burkle et al. 2016). These larger floral displays were found in populations from non-monsoonal regions, which also had significantly earlier first and peak blooming. However, only a response to the variation in floral display was detected; so unlike *Heterotheca* and *Gutierrezia*, the variation in phenological timing did not affect visitor activity or richness, and pollinators were interacting with populations in response to floral display size. This suggests the difference in peak floral output between *Heliomeris* populations was not large enough to invoke some degree of mismatch response.

Linum and *Ericameria* populations with more abundant flowers had a significant and positive pollinator response, as has been shown elsewhere (Thompson 2001, Potts et al. 2003, Blaauw and Isaacs 2014, Hegland and Totland 2005). However, there was no significant effect of climate provenance on floral display traits in either of these species. This result could be due to a paucity of observations for several *Ericameria* and *Linum* populations in this study, resulting in a lower ability to detect interactions. At the same time, there may be other factors besides climate driving the variation in peak floral abundance for these species, such as soil type or soil mutualists (Mason et al. 2017, Bower et al. 2014, Macel et al. 2007).

Conclusions. As climate change continues to alter abiotic conditions experienced by plant and pollinator communities of the Southwest (Garfin 2013, Guirguis et al 2018, Cayan et al. 2010), the results of this study suggest that plant species and populations will respond differently to the future hotter and drier conditions. Many populations demonstrated significant variability in phenology and/or floral display in the common garden, while others did not, indicating a species-specific response. While some of this trait variation did elicit pollinator responses, the proportion of changes detected in pollinator abundance/richness was relatively

small compared to the degree of trait variation predicted by provenance climate. This suggests that climate change might not alter the abundance and richness pollinator visitors to an equal degree as alterations to plant traits. However, pollinator communities may also be impacted by climate change themselves which could contribute further to a shift of pollinator and plant overlap (Forrest 2016, Morton and Rafferty 2017, Adedoja et al. 2020).

The results of this study have implications for the restoration potential of these forb species, in terms of supporting abundant and diverse pollinator communities following disturbance and during climate change (Dixon 2009, Menz et al. 2011, Devoto et al. 2012). Increasingly greater efforts are made to incorporate native forb seed collected from ecologically suitable locations, as is evidenced by the national Seeds of Success led by the Bureau of Land Management in collaboration with other federal and non-federal agencies (Barga et al. 2020, Copeland et al. 2018, Elzenga et al. 2019, Wood et al. 2015). However, these efforts have not necessarily had the primary intention of developing healthy pollinator communities, nor incorporating traits that affect pollinators (Wojcik et al. 2018, Dixon 2009), despite the potential for pollinators to enhance the reproductive output of native plants and therefore potentially increase the success of restoration efforts (Tylianakis et al. 2008, Albrecht et al. 2008). For example, while climatic tolerances of plants are foundational to seed zone development, generally phenological patterns are not (Dixon 2009, Bower et al. 2014); yet planting seed that will bloom earlier than is historic for instance, could reduce nectar resources for the local pollinator community that might become active later in the season, impacting pollinator densities and the entire system (Morton and Rafferty 2017, Memmett et al. 2007, Hegland et al. 2009).

As disturbances become more frequent in the southwestern US (Garfin 2013), implementing native forb seed programs that support pollinator communities and incorporate

phenological and floral trait variation will become increasingly important (Dixon 2009). Additionally, understanding of pollinator responses to climate change will also become more important (Tylianakis et al. 2008, Gilman et al. 2011, Byers 2017, Memmett et al. 2007, Hegland et al. 2009). The ways in which climate provenance can influence plant-pollinator communities are complex and can be mediated through the timing and traits of both groups (Tylianakis et al. 2008, Gilman et al. 2011, Byers 2017, Memmett et al. 2007, Hegland et al. 2009). This study demonstrates the importance of climate adaptation in these common forb species of the Southwest and provides a glimpse into how abiotic shifts might impact floral traits and plant-pollinator interactions.

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Figures

Figure 1: Collection location of source populations marked by triangles, colored by species. The SAEF garden location is indicated by a black star. Map gradient corresponds to mean annual temperature (MAT). Modified from Worldclim (Fick 2017) in ArcGIS Pro 2.7.1. (Esri Inc., version 2.72, 2021).

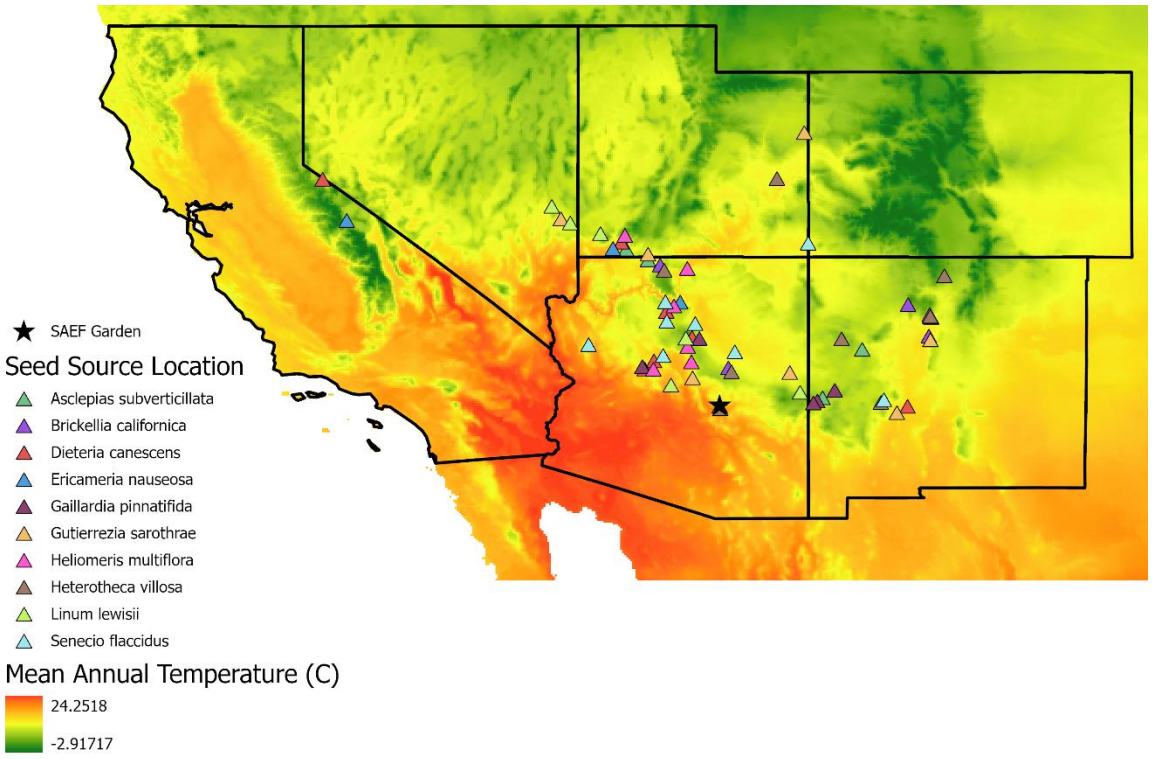


Figure 2*:* Date of first bloom as a function of PC axes in generalized linear mixed models for ten study species. Vertical lines represent the approximate values of each axis for the common garden. Colored asterisks represent significant predictions ($p<0.1$) of the PC for the date of peak flowering. PC3 was included for species where PC3 was included in the best regression model.Note variable x- and y-axes.

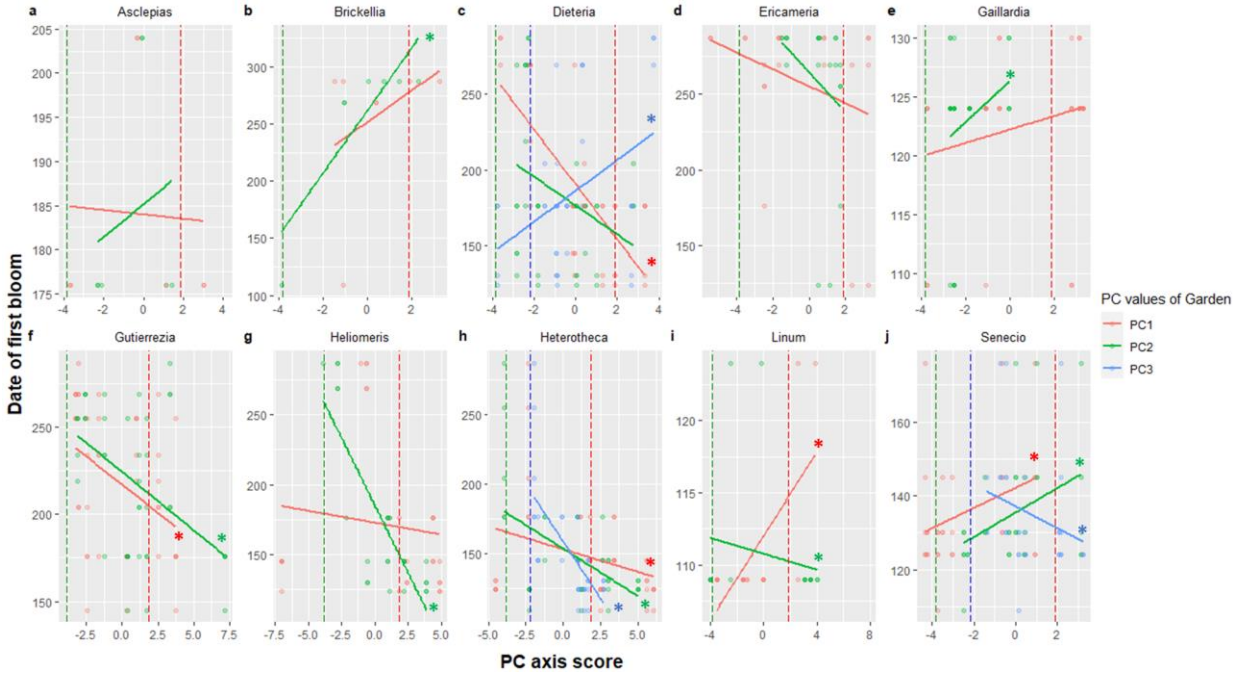


Figure 3: Date of peak flowering as a function of PC axes in generalized linear mixed models for ten study species. Vertical lines represent the approximate values of each axis for the common garden. Colored asterisks represent significant predictions ($p<0.1$) of the PC for the date of peak flowering. PC3 was included for species where PC3 was included in the best regression model. Note different scales of x- and y-axes on different panels.

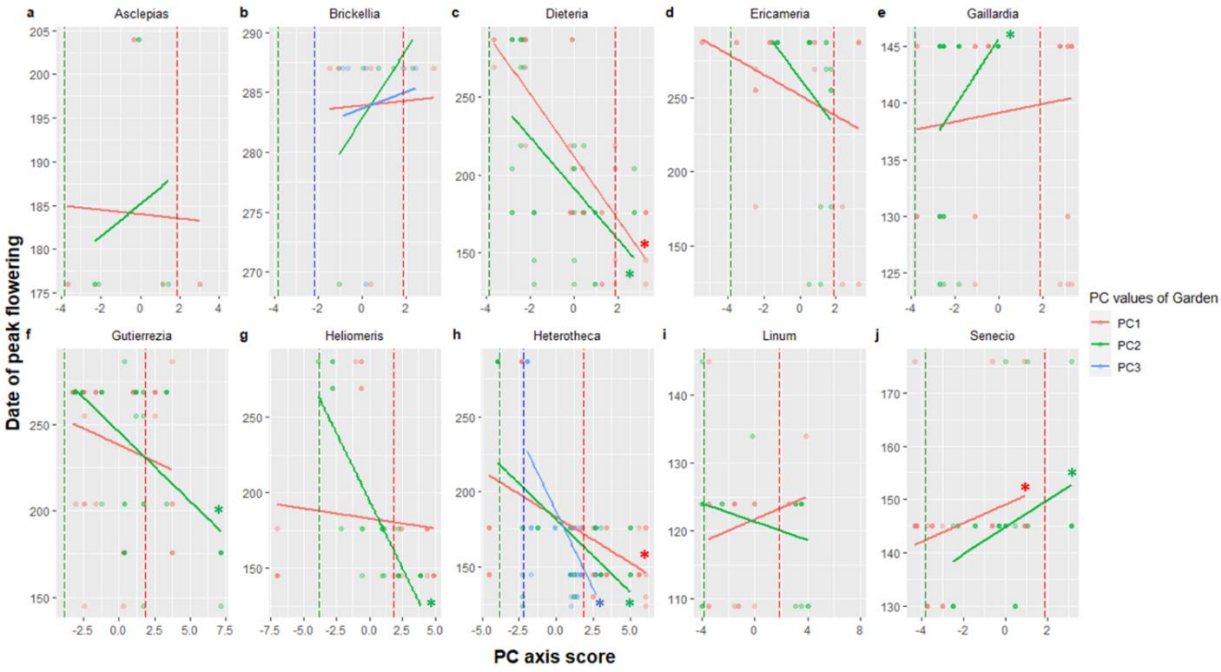


Figure 4: Total length of flowering season as a function of three PC axes for ten study species. Vertical lines represent the approximate values of each axis for the common garden. Colored asterisks represent significant predictions ($p<0.1$) of the PC for total length of flowering season. PC3 was included for species where PC3 was included in the best regression model. Note different scales of x- and y-axes on different panels.

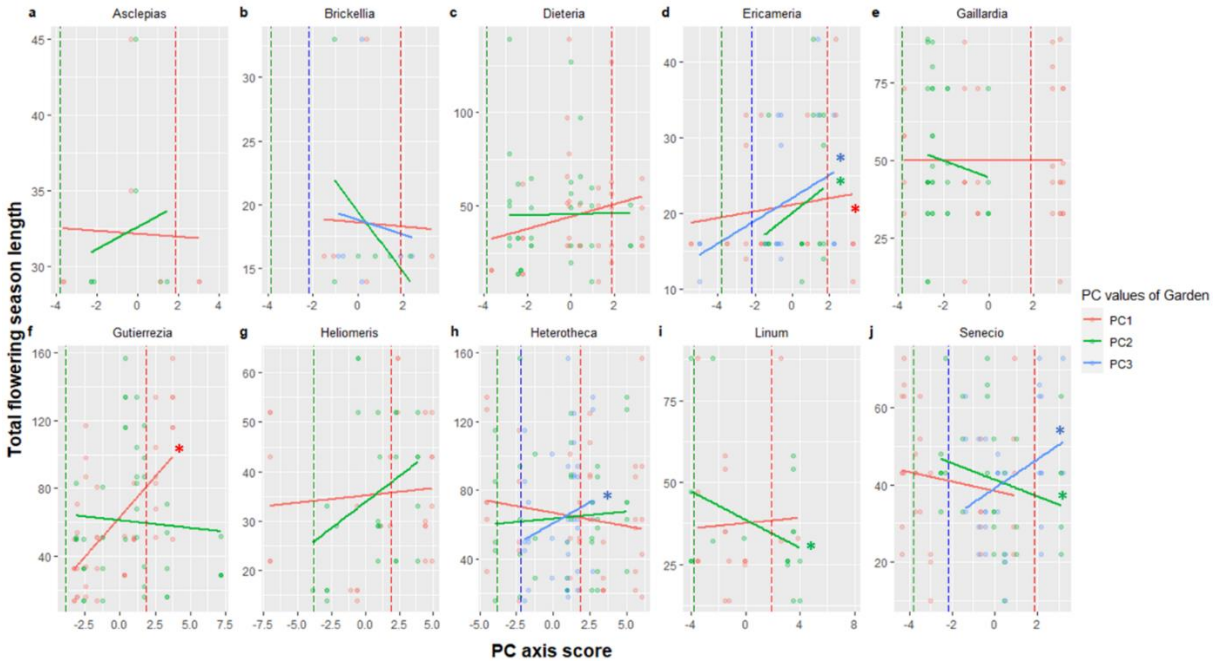


Figure 5: Peak flower numbers as a function of three PC axes for ten study species. Vertical lines represent the approximate values of each axis for the common garden. Colored asterisks represent significant predictions ($p<0.1$) of the PC for peak flowers. PC3 was included for species where PC3 was included in the best regression model. Note different scales of x- and y-axes on different panels.

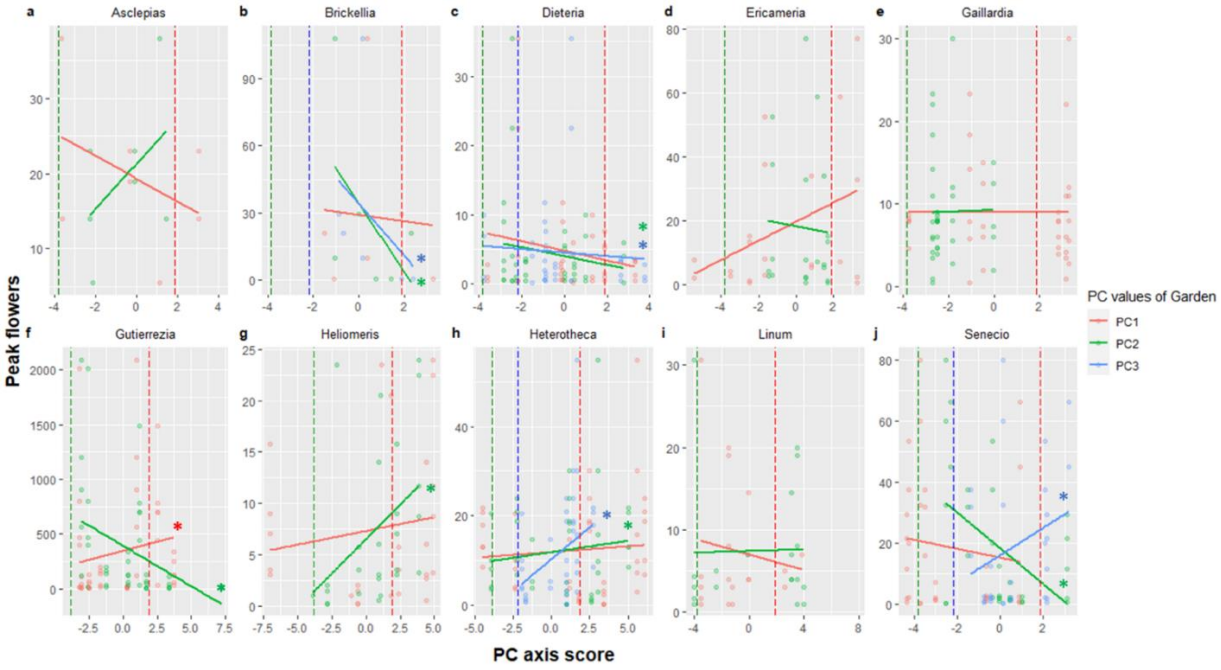


Figure 6: Schematic demonstrating effects of provenance on corolla dimensions (length and width, $p<0.1$); a) Effects of PC1 on corolla dimensions. Red flowers represent negative PC1 values, or areas that are generally hot and dry; blue flowers represent positive PC1 values and provenances that have lower MAT and more precipitation. b) Effects of PC2 on corolla dimensions. Red flowers represent negative PC2 values and provenances from monsoonal regions; blue flowers represent positive PC2 values C) Effects of PC3 on corolla dimensions.

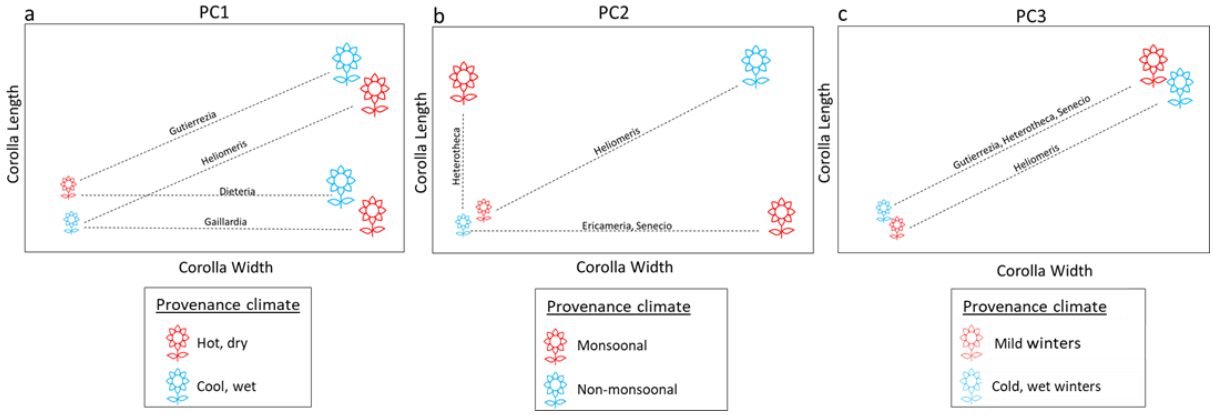


Figure 7: Species scaled importance values of four major taxonomic groups of pollinators: bees, Diptera, Lepidoptera, and wasps. These values represent the average number of flowers probed/minute of interaction, scaled to the most important group for each study species. Numbers inside bars represent the number of functional groups observed within each taxonomic level.

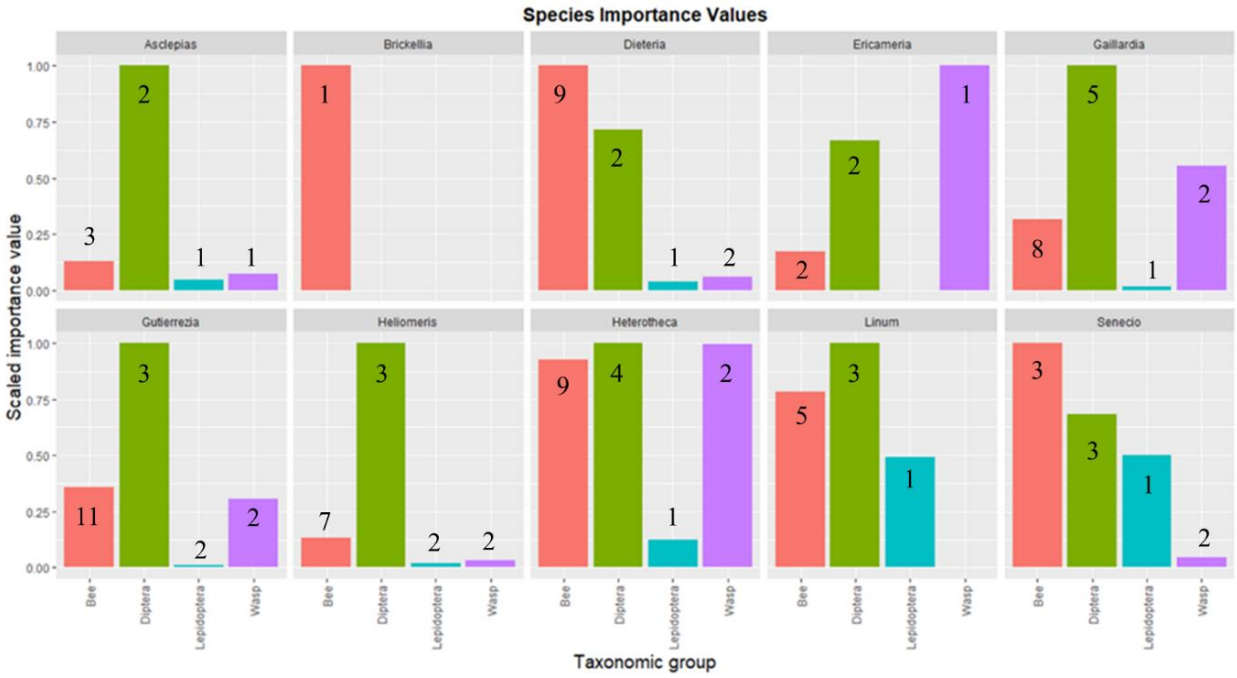


Figure 8: Plant-pollinator network of the gardenfor the 2020 season. Line width represents scaled importance values, which are the relative importance of each visitor functional group to the most important functional group for any given plant species. Importance values represent the average number of flowers probed/minute of interaction.

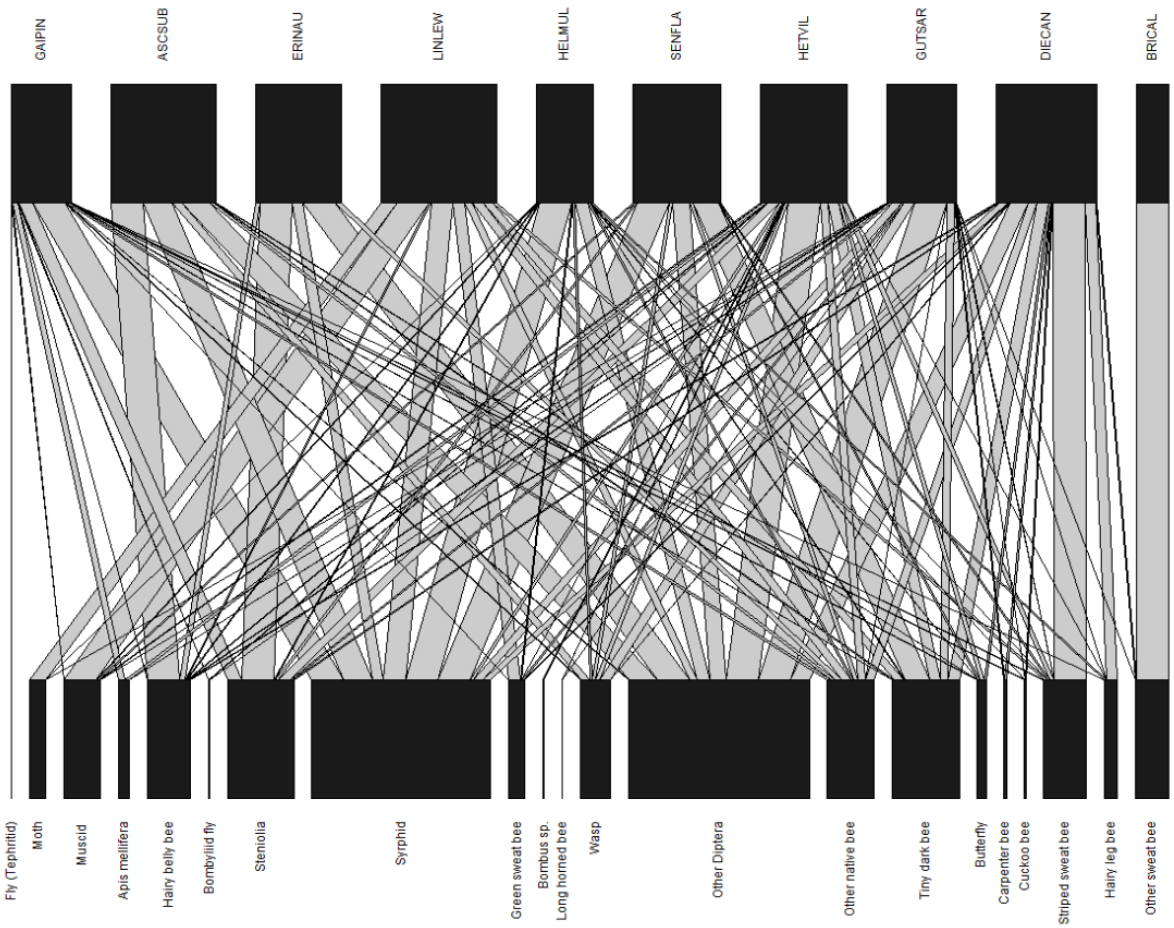


Figure 9: Population scaled importance values for *Asclepias* using four major taxonomic pollinator groups: bees, Diptera, Lepidoptera, and wasps. These values represent the average number of flowers probed/minute of interaction, scaled to the most important group. Numbers inside bars represent the number of functional groups observed within each taxonomic level. Populations are ordered from lowest to highest elevation.

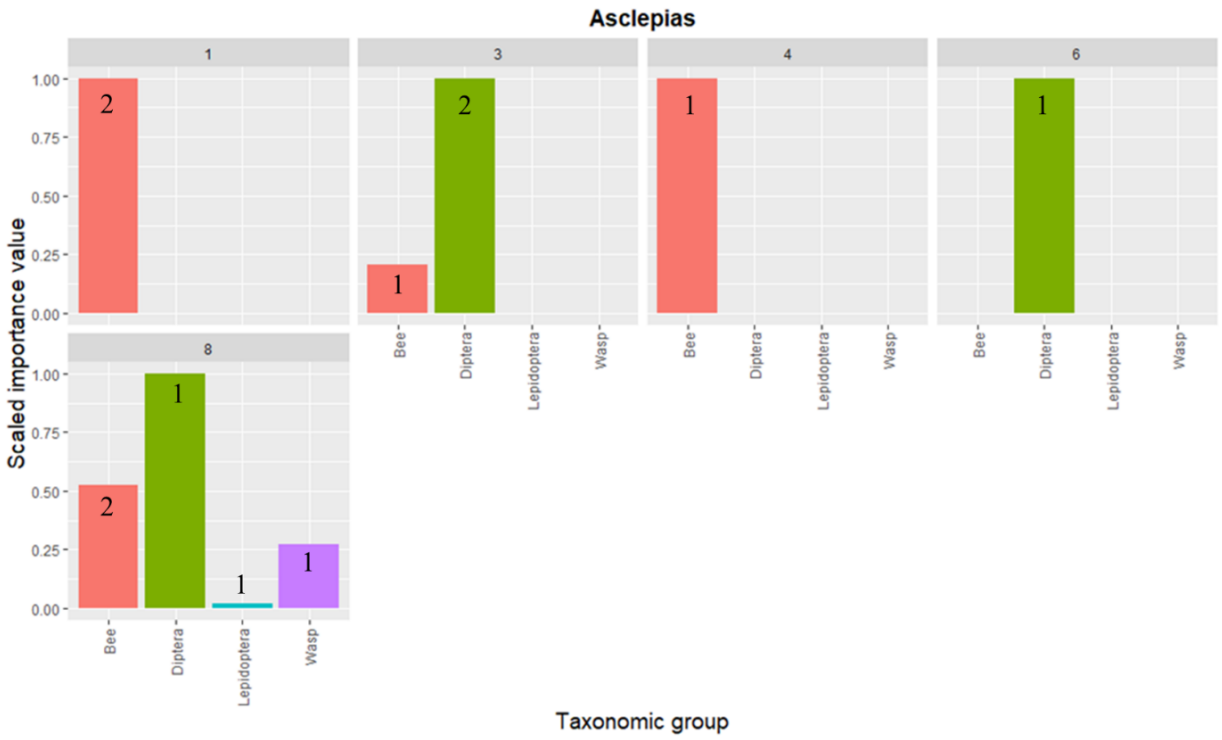


Figure 10: Population scaled importance values for *Dieteria* using four major taxonomic pollinator groups: bees, Diptera, Lepidoptera, and wasps. These values represent the average number of flowers probed/minute of interaction, scaled to the most important group. Numbers inside bars represent the number of functional groups observed within each taxonomic level. Populations are ordered from lowest to highest elevation.

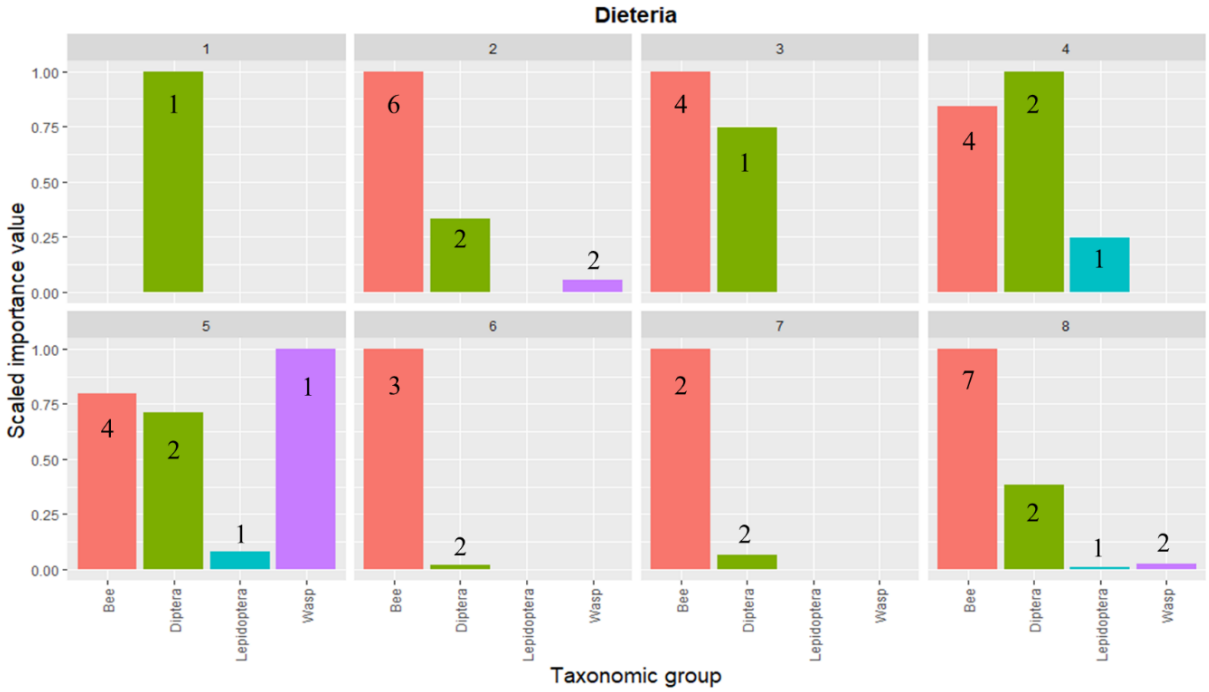


Figure 11: Population scaled importance values for *Gaillardia* using four major taxonomic pollinator groups: bees, Diptera, Lepidoptera, and wasps These values represent the average number of flowers probed/minute of interaction, scaled to the most important group. Numbers inside bars represent the number of functional groups observed within each taxonomic level. . Populations are ordered from lowest to highest elevation.

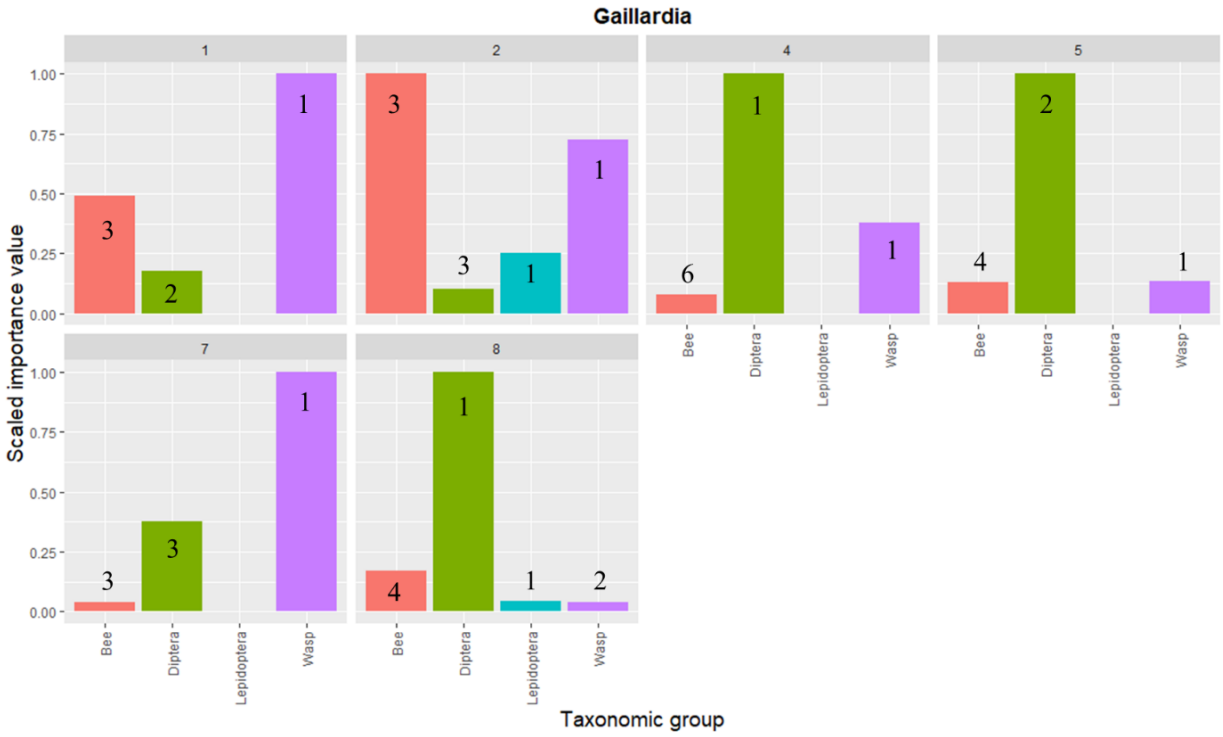


Figure 12: Population scaled importance values for *Gutierrezia* using four major taxonomic pollinator groups: bees, Diptera, Lepidoptera, and wasps. These values represent the average number of flowers probed/minute of interaction, scaled to the most important group. Numbers inside bars represent the number of functional groups observed within each taxonomic level. Populations are ordered from lowest to highest elevation.

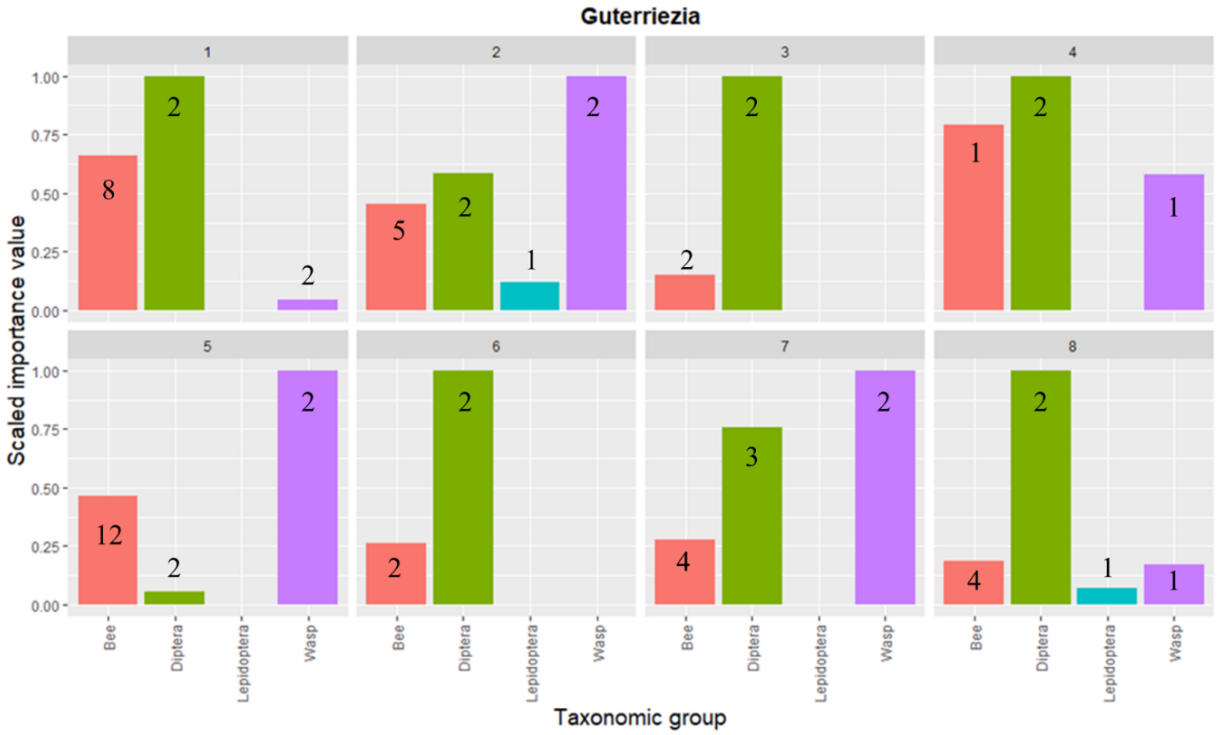


Figure 13: Population scaled importance values for *Heliomeris* using four major taxonomic pollinator groups: bees, Diptera, Lepidoptera, and wasps. These values represent the average number of flowers probed/minute of interaction, scaled to the most important group. Numbers inside bars represent the number of functional groups observed within each taxonomic level. Populations are ordered from lowest to highest elevation.

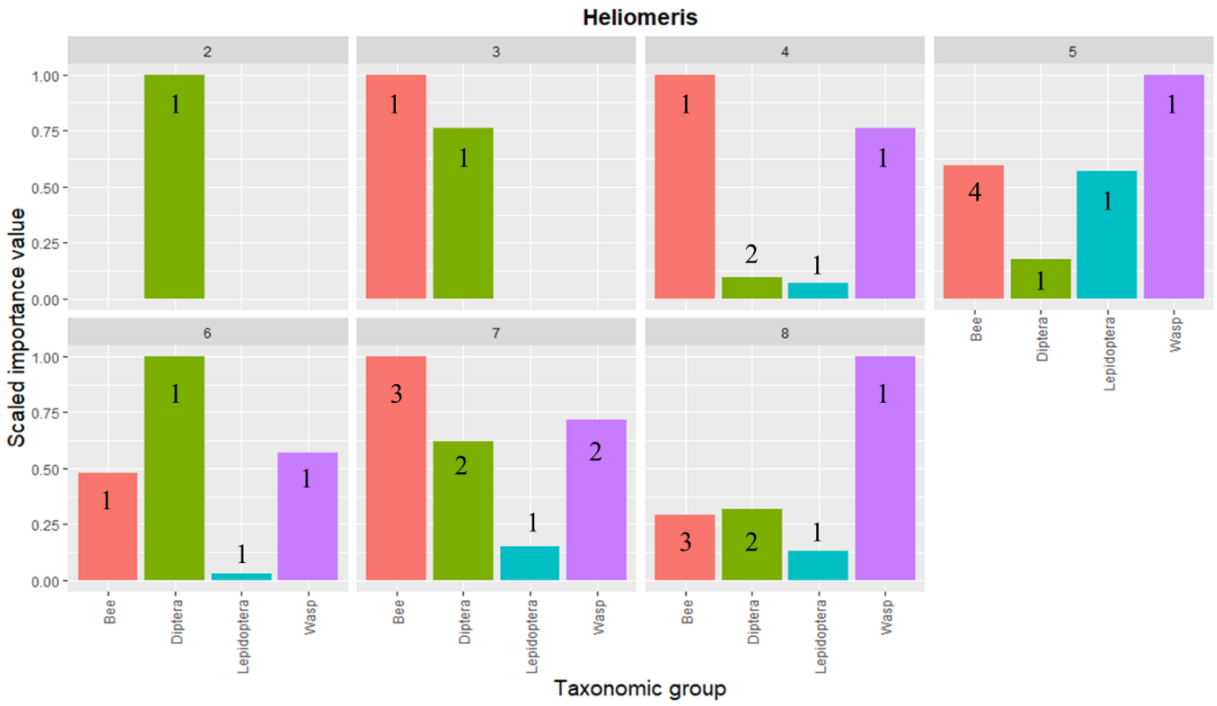


Figure 14: Population scaled importance values for *Heterotheca* using four major taxonomic pollinator groups: bees, Diptera, Lepidoptera, and wasps. These values represent the average number of flowers probed/minute of interaction, scaled to the most important group. Numbers inside bars represent the number of functional groups observed within each taxonomic level. Populations are ordered from lowest to highest elevation.

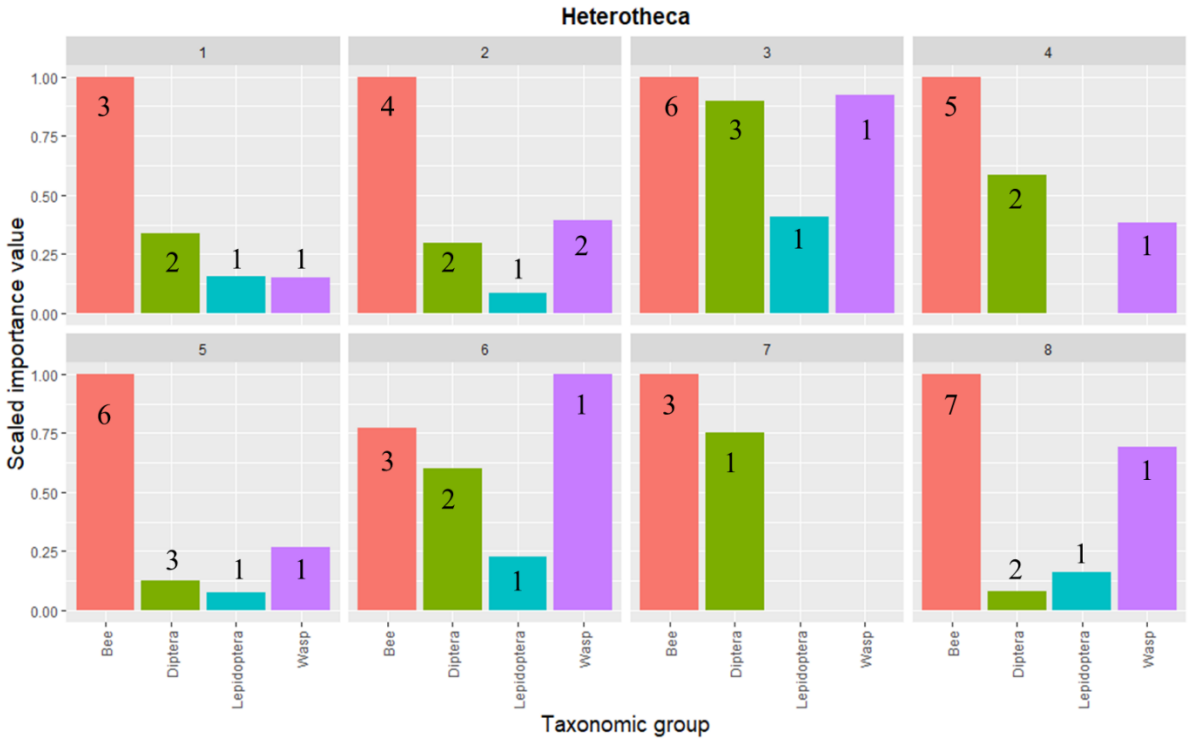


Figure 15: Population scaled importance values for *Linum* using four major taxonomic pollinator groups: bees, Diptera, Lepidoptera, and wasps. These values represent the average number of flowers probed/minute of interaction, scaled to the most important group. Numbers inside bars represent the number of functional groups observed within each taxonomic level. Populations are ordered from lowest to highest elevation.

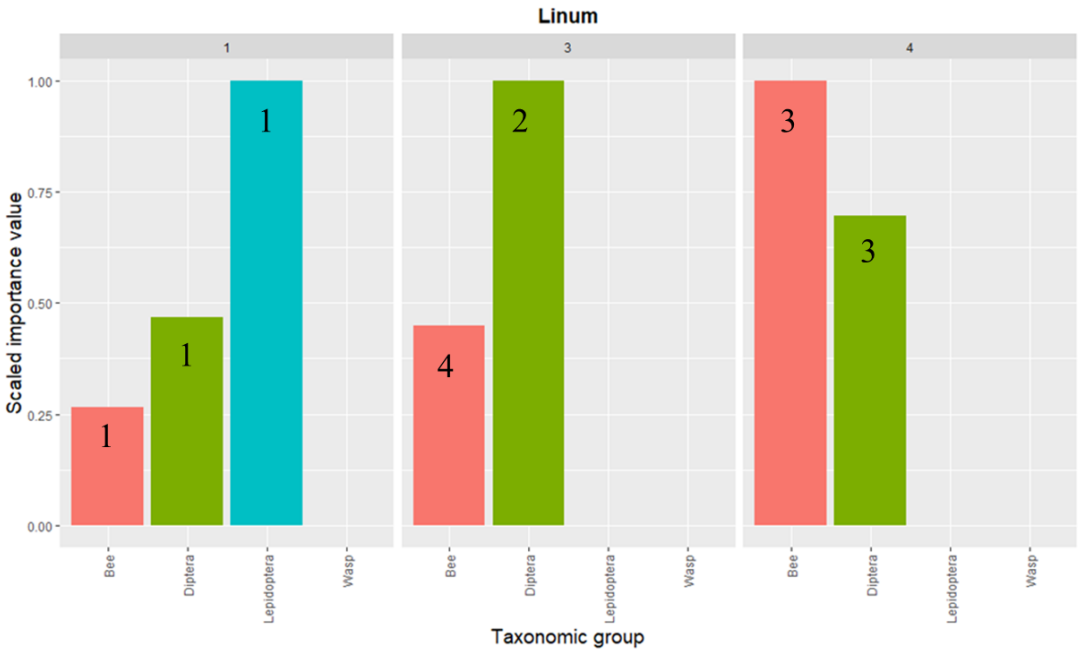
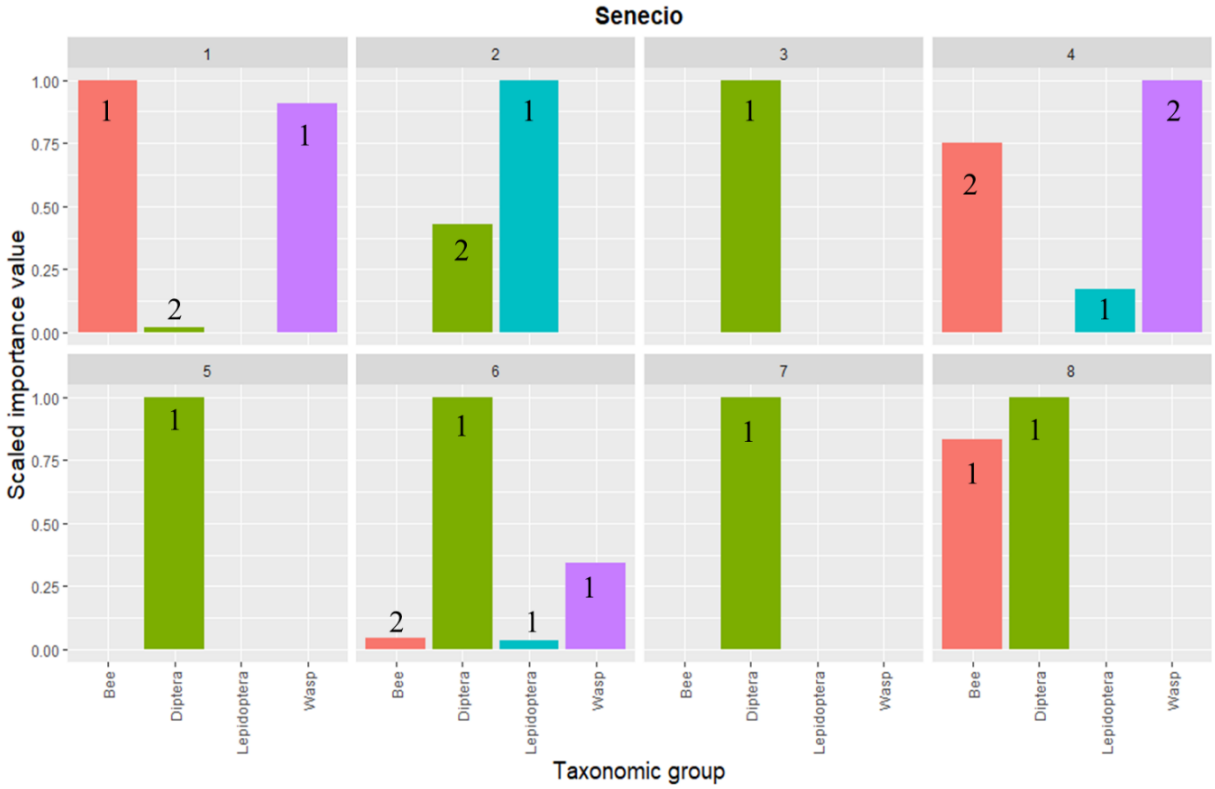


Figure 16: Population scaled importance values for *Senecio* using four major taxonomic pollinator groups: bees, Diptera, Lepidoptera, and wasps. These values represent the average number of flowers probed/minute of interaction, scaled to the most important group. Numbers inside bars represent the number of functional groups observed within each taxonomic level. Populations are ordered from lowest to highest elevation



Tables

Table 1: Species and population seed source descriptions.

	Family	State	Elevation (m)	Latitude	Longitude
Asclepias subverticillata	Asclepiadaceae	UT	1219	37.19014	-113.00063
		AZ	1240	34.86674	-112.20486
		AZ	1432	36.95954	-112.5265
		AZ	1920	34.748509	-111.58511
		UT	1949	37.3052222	-109.92684
		NM	2008	35.02218	-107.8843
		NM	2326	37.11974	-106.92919
		NM	2401	33.97408	-108.74477
Brickellia californica	Asteraceae	NV	1548	39.76918	-117.64541
		AZ	1631	35.12423	-113.9146
		AZ	1910	34.62135	-110.78569
		NM	1975	35.30933	-106.44077
		AZ	1981	36.84668	-112.26205
		AZ	2140	35.278233	-111.5709
		NM	2281	35.98914	-106.89172
Dieteria canescens	Asteraceae	NM	1385	33.78794	-106.9023
		AZ	1463	34.77291	-112.39646
		AZ	1654	34.59477	-112.59676
		AZ	1916	35.84328	-112.1284
		UT	1978	37.33976	-113.10418
		AZ	2140	35.278233	-111.5709
		CA	2312	38.70129	-119.57571
		NM	2386	34.13701	-108.48034
Ericameria nauseosa	Asteraceae	UT	975	37.20298	-113.2868
		AZ	1524	35.1237	-113.81356
		UT	1524	37.0824	-112.526
		AZ	1771	34.51921	-109.45245
		UT	1987	37.06025	-110.82835
		AZ	2084	36.05566	-112.14027
		NM	2089	36.23738	-107.7064
		CA	2368	37.81094	-119.05495
Gaillardia pinnatifida	Asteraceae	AZ	1219	34.88863	-112.19872
		AZ	1524	34.6474	-112.64901

		AZ	1831	35.77102	-112.12977
		AZ	1890	35.255588	-111.41337
		NM	2205	33.90422	-108.85642
		AZ	2212	34.9882	-111.45088
		NM	2216	33.86221	-108.9427
		NM	2386	34.13701	-108.48034
Gutierrezia sarothrae	Asteraceae	NM	1490	33.65226	-107.13302
		UT	1524	37.0824	-112.526
		NV	1578	37.845389	-114.41297
		AZ	1771	34.51921	-109.45245
		AZ	1776	34.4044	-111.56045
		UT	2137	39.71233	-109.14017
		NM	2319	35.73046	-106.41006
		NM	2499	35.22703	-106.40516
Heliomeris multiflora	Asteraceae	AZ	1481	33.79124	-110.97331
		AZ	1585	34.59114	-112.40883
		AZ	1890	34.7498	-111.586
		AZ	2074	35.08484	-111.66523
		AZ	2103	36.77071	-111.67475
		AZ	2278	35.96216	-111.96364
		NM	2455	35.7701	-106.4218
		UT	2743	37.48908	-113.02736
Heterotheca villosa	Asteraceae	AZ	1199	33.7353	-110.95724
		UT	1370	38.71726	-109.73217
		NM	1737	36.82293	-107.6583
		AZ	1973	34.53493	-110.71845
		CO	2170	37.46508	-108.51809
		AZ	2194	36.73139	-112.17505
		AZ	2278	35.96216	-111.96364
		NM	2615	36.61353	-106.10476
Linum lewisii	Linaceae	AZ	1130	34.25077	-112.02775
		NV	1848	38.11611	-114.611
		NV	1979	37.75537	-114.21088
		UT	1981	37.52618	-113.556
		AZ	2246	35.26448	-111.70449
		AZ	2295	34.09194	-109.23133
		CA	2316	38.70129	-119.5757
		NM	2706	35.21687	-106.41743
		AZ	1219	34.88863	-112.19872

Senecio flaccidus	Asteraceae	CO	1478	37.31922	-109.05486
		AZ	1493	34.96811	-110.64557
		AZ	1524	35.1237	-113.81356
		AZ	1650	35.58042	-111.50392
		AZ	1842	35.63189	-112.11888
		AZ	2060	36.04961	-112.14927
		NM	2194	33.9332	-107.41468

Table 2: Explained variance and loadings of the first three principal components extracted from 19 bioclimatic variables (WorldClim, Fick 2017).

	PC1	**PC2**	**PC3**	**Sum**
Explained variance	0.403	0.253	0.151	0.807
Loadings				
Elevation (m)	0.288	0.118		
Latitude		0.379	-0.16	
Longitude	0.105		0.435	
Mean Annual Temperature	-0.29	-0.179		
Mean Diurnal Range		-0.185	0.336	
Isothermality	0.108	-0.332		
Temperature Seasonality	-0.198	0.276	0.191	
Max Temp Warmest Month	-0.318			
Min Temp Coldest Month	-0.238	-0.213	-0.214	
Temperature Annual Range	-0.137	0.194	0.355	
Mean Temp Wettest Quarter		-0.243	0.206	
Mean Temp Driest Quarter	-0.17	-0.174	-0.227	
Mean Temp Warmest Quarter	-0.311			
Mean Temp Coldest Quarter	-0.241	-0.266	-0.102	
Annual Precipitation	0.247	-0.126	-0.239	
Precipitation Wettest Month	0.256	-0.256		
Precipitation Driest Month	0.256	0.152		
Precipitation Seasonality		-0.307	0.213	
Precipitation Wettest Quarter	0.27	-0.228		
Precipitation Driest Quarter	0.241	0.18		
Precipitation Warmest Quarter	0.244	-0.208	0.131	
Precipitation Coldest Quarter	0.121		-0.458	

Table 3: Outputs of all best fit generalized linear mixed effect models conducted on all species for each response metric. All models included the random effect of block, but as evidenced by the variability in the marginal and conditional R^2 values, the block effect was only significant for a subset of models.

Date of first bloom					
	Model	**Variable**	**p-value**	**Marginal R^2**	**Conditional R^2**
Asclepias	PC1 + PC2 + (1|Block)			0.33261	0.332606
		PC1	0.179		
		PC2	0.16		
Brickellia	PC1 + PC2 + (1|Block)			0.68454	0.684537
		PC1	0.468		
		PC2	0.0307		
Dieteria	PC1 + PC2 + PC3 + (1|Block)			0.57912	0.579116
		PC1	< 0.001		
		PC2	0.6689		
		PC3	0.0255		
Ericameria	PC1 + PC2 + (1|Block)			0.14198	0.141975
		PC1	0.278		
		PC2	0.283		
Gaillardia	PC1 + PC2 + (1|Block)			0.13945	0.139453
		PC1	0.119		
		PC2	0.098		
Gutierrezia	PC1 + PC2 + (1|Block)			0.37472	0.3747179
		PC1	0.00403		
		PC2	< 0.001		
Heliomeris	PC1 + PC2 + (1|Block)			0.65504	0.6550417
		PC1	0.802		
		PC2	<0.001		
Heterotheca	PC1 + PC2 + PC3 + (1|Block)			0.57225	0.5722548
		PC1	0.00441		
		PC2	0.06236		
		PC3	0.00148		
Linum	PC1 + PC2 + (1|Block)			0.56953	0.57511
		PC1	<0.001		
		PC2	0.032446		

Senecio	PC1 + PC2 + PC3 + (1|Block)			0.16724	0.8191898
		PC1	0.00365		
		PC2	0.00421		
		PC3	0.02262		
Day of Peak					
	Model	**Variable**	**p-value**	**Marginal R^2**	**Conditional R^2**
Asclepias	PC1 + PC2 + (1|Block)			0.33261	0.332606
		PC1	0.179		
		PC2	0.16		
Brickellia	PC1 + PC2 + PC3 + (1|Block)			0.09407	0.99999
		PC1	0.589		
		PC2	0.613		
		PC3	0.879		
Dieteria	PC1 + PC2 + (1|Block)			0.63734	0.63734
		PC1	< 0.001		
		PC2	0.00451		
Ericameria	PC1 + PC2 + (1|Block)			0.19206	0.1920627
		PC1	0.196		
		PC2	0.201		
Gaillardia	PC1 + PC2 + (1|Block)			0.10073	0.311671
		PC1	0.307		
		PC2	0.0565		
Gutierrezia	PC1 + PC2 + (1|Block)			0.36277	0.3627742
		PC1	0.111		
		PC2	< 0.001		
Heliomeris	PC1 + PC2 + (1|Block)			0.70049	0.7004876
		PC1	0.933		
		PC2	< 0.001		
Heterotheca	PC1 + PC2 + PC3 + (1|Block)			0.74349	0.7552145
		PC1	< 0.001		
		PC2	< 0.001		
		PC3	0.00254		
Linum	PC1 + PC2 + (1|Block)			0.10947	0.10947
		PC1	0.294		
		PC2	0.23		
Senecio	PC1 + PC2 + (1|Block)			0.00922	0.7401569
		PC1	0.0188		

		PC2	0.0374		
Total Season Length					
	Model	**Variable**	**p-value**	**Marginal R^2**	**Conditional R^2**
Asclepias	PC1 + PC2 + (1|Block)			0.24703	0.24703
		PC1	0.25516		
		PC2	0.23269		
Brickellia	PC1 + PC2 + PC3 + (1|Block)			0.06573	0.9998
		PC1	0.6522		
		PC2	0.6739		
		PC3	0.9004		
Dieteria	PC1 + PC2 + (1|Block)			0.05543	0.08885
		PC1	0.15805		
		PC2	0.72131		
Ericameria	PC1 + PC2 + PC3 + (1|Block)			0.36415	0.436027
		PC1	0.1119		
		PC2	0.0898		
		PC3	0.007		
Gaillardia	PC1 + PC2 + (1|Block)			0.01319	0.013188
		PC1	0.962		
		PC2	0.512		
Gutierrezia	PC1 + PC2 + (1|Block)			0.38915	0.4491411
		PC1	< 0.001		
		PC2	0.371		
Heliomeris	PC1 + PC2 + (1|Block)			0.10766	0.1076598
		PC1	0.822		
		PC2	0.106		
Heterotheca	PC1 + PC2 + PC3 + (1|Block)			0.09079	0.3390941
		PC1	0.1434		
		PC2	0.3092		
		PC3	0.0594		
Linum	PC1 + PC2 + (1|Block)			0.12281	0.12281
		PC1	0.613		
		PC2	0.247		
Senecio	PC1 + PC2 + PC3 + (1|Block)			0.2093	0.2093021
		PC1	0.6132		
		PC2	0.0508		

		PC3	0.0372		
Average Peak Flowers					
	Model	**Variable**	**p-value**	**Marginal R^2**	**Conditional R^2**
Asclepias	PC1 + PC2 + (1|Block)			0.19903	0.1990306
		PC1	0.5884		
		PC2	0.5944		
Brickellia	PC1 + PC2 + PC3 + (1|Block)				
		PC1	0.529		
		PC2	0.5213		
		PC3	0.1217		
Dieteria	PC1 + PC2 + PC3 + (1|Block)			0.07111	0.439751
		PC1	0.6138		
		PC2	0.1717		
		PC3	0.0643		
Ericameria	PC1 + PC2 + (1|Block)			0.07797	0.0779663
		PC1	0.228		
		PC2	0.497		
Gaillardia	PC1 + PC2 + (1|Block)			0.00031	0.02983875
		PC1	0.927		
		PC2	0.98		
Gutierrezia	PC1 + PC2 + (1|Block)			0.46266	0.573707
		PC1	< 0.001		
		PC2	< 0.001		
Heliomeris	PC1 + PC2 + (1|Block)			0.32881	0.3418828
		PC1	0.98073		
		PC2	0.00215		
Heterotheca	PC1 + PC2 + PC3 + (1|Block)			0.23189	0.231888
		PC1	0.19521		
		PC2	0.02887		
		PC3	0.00127		
Linum	PC1 + PC2 + (1|Block)			0.01968	0.01968262
		PC1	0.734		
		PC2	0.699		
Senecio	PC1 + PC2 + PC3 + (1|Block)			0.19328	0.4683236
		PC1	0.1919		
		PC2	0.0224		

		PC3	0.0653		
Corolla Length					
	Model	**Variable**	**p-value**	**Marginal R^2**	**Conditional R^2**
Dieteria	PC1 + PC2 + (1|Block)			0.02344	0.31385
		PC1	0.454		
		PC2	0.677		
Ericameria	PC1 + PC2 + (1|Block)			0.23881	0.23881
		PC1	0.992		
		PC2	0.148		
Gaillardia	PC1 + PC2 + PC3 + (1|Block)			0.36402	0.36402
		PC1	0.00537		
		PC2	0.96276		
		PC3	0.00895		
Gutierrezia	PC1 + PC2 + (1|Block)			0.23113	0.23113
		PC1	0.00679		
		PC2	0.22658		
Heliomeris	PC1 + PC2 + PC3 + (1|Block)			0.54764	0.72605
		PC1	0.0219		
		PC2	0.0291		
		PC3	0.0117		
Heterotheca	PC1 + PC2 + PC3 + (1|Block)			0.11397	0.11397
		PC1	0.9438		
		PC2	0.0667		
		PC3	0.1218		
Linum	PC1 + PC2 + (1|Block)			0.613	0.247
		PC1	0.1664		
		PC2	0.3026		
Senecio	PC1 + PC2 + PC3 + (1|Block)			0.28863	0.41622
		PC1	0.11		
		PC2	0.1914		
		PC3	0.046		
Corolla Width					
	Model	**Variable**	**p-value**	**Marginal R^2**	**Conditional R^2**
Dieteria	PC1 + PC2 + PC3 + (1|Block)			0.28363	0.32071

		PC1	0.00814		
		PC2	0.41767		
		PC3	0.1009		
Ericameria	PC1 + PC2 + (1|Block)			0.35267	0.35267
		PC1	0.6118		
		PC2	0.0943		
Gaillardia	PC1 + PC2 + PC3 + (1|Block)			0.1956	0.1956
		PC1	0.0719		
		PC2	0.9533		
		PC3	0.0691		
Gutierrezia	PC1 + PC2 + (1|Block)			0.18961	0.18961
		PC1	0.0205		
		PC2	0.1988		
Heliomeris	PC1 + PC2 + PC3 + (1|Block)			0.5228	0.74243
		PC1	0.0944		
		PC2	0.0305		
		PC3	0.0108		
Heterotheca	PC1 + PC2 + PC3 + (1|Block)			0.5228	0.74243
		PC1	0.5251		
		PC2	0.2887		
		PC3	0.0724		
Linum	PC1 + PC2 + (1|Block)			0.18281	0.18281
		PC1	0.613		
		PC2	0.247		
Senecio	PC1 + PC2 + PC3 + (1|Block)			0.28863	0.41622
		PC1	0.11		
		PC2	0.1914		
		PC3	0.046		
Disk Width					
	Model	**Variable**	**p-value**	**Marginal R^2**	**Conditional R^2**
Dieteria	PC1 + PC2 + (1|Block)			0.23197	0.57239
		PC1	0.2056		
		PC2	0.0094		
Gaillardia	PC1 + PC2 + (1|Block)			0.33975	0.33975
		PC1	< 0.001		
		PC2	0.9453		

Heliomeris	PC1 + PC2 + (1|Block)			0.2811	0.46847
		PC1	0.278		
		PC2	0.029		
Heterotheca	PC1 + PC2 + (1|Block)			0.10066	0.44405
		PC1	0.7223		
		PC2	0.0261		
Senecio	PC1 + PC2 + PC3 + (1|Block)			0.32438	0.32438
		PC1	0.8455		
		PC2	0.6608		
		PC3	0.0544		

Table 4: Corolla measurements of each population (corolla length, corolla width and corolla disk width for a subset of Aster species). Values represent population means ± standard deviation.

Floral dimensions				
	Population	**Corolla length ± SD**	**Corolla Width ± SD**	**Floral disk width ± SD**
Dieteria	1	NA	NA	NA
	2	NA	NA	NA
	3	15.24 ± 1.14	19.36 ± 1.89	6.57 ± 0.98
	4	14.97 ± 2.07	16.93 ± 2.03	4.48 ± 0.98
	5	15.39 ± 2.11	19.71 ± 2.74	5.58 ± 1.88
	6	16.87 ± 3.53	20.67 ± 4.59	5.32 ± 0.66
	7	15.82 ± 0.73	21.63 ± 1.56	6.09 ± 0.3
	8	15.44 ± 1.61	21.44 ± 1.83	6.79 ± 0.68
Ericameria	1	5.84 ± 0	1.67 ± 0	NA
	2	NA	NA	NA
	3	8.02 ± 1.96	1.87 ± 0.18	NA
	4	12.17± 0.94	2.77 ± 0.22	NA
	5	NA	NA	NA
	6	10.02 ± 3.14	2.08 ± 0.86	NA
	7	6.15 ± 1.304	1.41 ± 0.22	NA
	8	NA	NA	NA
Gaillardia	1	21.21 ± 1.38	39.65 ± 7.21	9.62 ± 0.87
	2	16.98 ± 1.42	33.86 ± 3.77	7.9 ± 1.96
	3	29.44 ± 4.83	48.43 ± 2.81	9.01 ± 2.3
	4	16.10 ± 3.18	32.13 ± 6.7	8.26 ± 2.27
	5	18.64 ± 1.09	37.39 ± 2.28	6.76 ± 1.36
	6	28.10 ± 0.66	54.63 ± 3.13	10.26 ± 0.28
	7	18.70 ± 2.73	35.97 ± 4.25	7.17 ± 1.29
	8	19.24 ± 1.01	37.7 ± 3.67	6.72 ± 1.14
Gutierrezia	1	4.97 ± 4.97	4.9 ± 0.56	NA
	2	6.13 ± 6.13	5.8 ± 1.46	NA
	3	4.98 ± 4.98	3.68 ± 0.5	NA
	4	5.59 ± 5.59	4.19 ± 1.22	NA
	5	7.54 ± 7.54	6.51 ± 1.17	NA
	6	7.65 ± 7.65	7.2 ± 2.28	NA
	7	6.51 ± 6.51	5.6 ± 1.04	NA
	8	6.97 ± 6.97	6.52 ± 1.5	NA
Heliomeris	1	NA	NA	NA
	2	NA	NA	NA
	3	NA	NA	NA
	4	13.49 ± 2.68	26.41 ± 3.51	7.32 ± 0.62

	5	15.43 ± 1.19	29.17 ± 4.98	8.15 ± 1.79
	6	15.33 ± 0	31.07 ± 0	9.27 ± 0
	7	12.17 ± 0.82	23.35 ± 1.27	8.17 ± 0.29
	8	16.47 ± 1.67	33.99 ± 4.67	9.47 ± 1.41
Heterotheca	1	16.68 ± 0.07	20.83 ± 1.08	6.83 ± 0.94
	2	15.11 ± 1.33	20.06 ± 2.58	4.84 ± 0.65
	3	16.93 ± 2.9	22.71 ± 4.22	5.53 ± 1.03
	4	12.78 ± 0.64	15.34 ± 1.26	4.38 ± 0.46
	5	18 ± 1.93	23.74 ± 3.09	5.82 ± 1.27
	6	14.19 ± 0.94	17.54 ± 1.73	4.42 ± 0.32
	7	13.52 ± 3.11	16.86 ± 3.85	4.53 ± 0.41
	8	14.46 ± 2.49	20.09 ± 5.45	4.94 ± 0.93
Linum	1	12.27 ± 0	19.77 ± 0	NA
	2	12.8 ± 0	19.67 ± 0	NA
	3	15.47 ± 1.41	24.57 ± 3.39	NA
	4	15.29 ± 2.71	22.21 ± 2.14	NA
	5	14.77 ± 0	26.07 ± 0	NA
	6	13.25 ± 0	23.9 ± 0	NA
	7	NA	NA	NA
	8	NA	NA	NA
Senecio	1	34.7 ± 2.4	7.54 ± 0.54	22.37 ± 0.96
	2	31.6 ± 4.22	5.96 ± 0.38	23.43 ± 5.2
	3	28.57 ± 4.03	6.12 ± 0.93	20.5 ± 1.73
	4	27.12 ± 3.67	6.81 ± 0.8	20.43 ± 4.05
	5	NA	NA	NA
	6	23.49 ± 3.12	6.01 ± 1.31	19.74 ± 2.16
	7	29.23 ± 0	5.8 ± 0	20.4 ± 0
	8	32.55 ± 0.35	7.28 ± 0.02	25.2 ± 1.41

Table 5: Species-level scaled importance values using all 21 pollinator taxa. Green functional groups fall into the bee taxonomic level; pink groups are Diptera; yellow groups are Lepidoptera; orange groups are wasps. Blue gradation in cells relates to the scaled importance for each plant species: darker blues represent more important pollinator interactions.

Functional Group	*Asclepias*	*Brickellia*	*Dieteria*	*Ericameria*	*Gaillardia*	*Gutierrezia*	*Heliomeris*	*Heterotheca*	*Linum*	*Senecio*	Total plant species visited
Apis mellifera	0	0	0	0	0.187663	0.016168	0	0.14162445	0	0	3
Bombus sp.	0	0	0	0	0	0	0	0.05565793	0	0	1
Bombyliid fly	0	0	0	0	0.017733	0	0	0.01308513	0	0	2
Butterfly	0.011321	0	0.067917	0	0.013411	0.011602	0.0158629	0.12291844	0	0.044712078	7
Carpenter bee	0	0	0.046544	0	0	0.033221	0	0	0	0	2
Cuckoo bee	0	0	0.026678	0	0.006287	0.001662	0.0051968	0	0	0	4
Fly (Tephritid)	0	0	0	0	0.000443	0	0	0	0	0	1
Green sweat bee	0	0	0.028661	0	0.004308	0.07408	0.0187293	0.00792186	0.366667	0	6
Hairy belly bee	1	0	0.045057	0.142857	0.00798	0.032833	0.0281019	0.03331237	0.041962	0	8
Hairy leg bee	0	0	0.327929	0	0.005873	0.014393	0.046829	0.01266908	0	0	5
Long horned bee	0	0	0	0	0	0.000563	0	0.00874625	0	0	2
Moth	0	0	0	0	0	7.55E-05	0.0088346	0	0.5	0	3
Muscid	0	0	0	0	0.00544	0.001645	0.0294485	0.04357675	1	0.063017058	6
Other Diptera	0.882587	0	0.58425	1	0.011768	1	0.4008998	1	0.233091	0.511028861	9
Other native bee	0.13586	0	0.273062	0.2	0.104782	0.014591	0.0780999	0.22315721	0.314222	0.113423241	9
Other sweat bee	0	1	0.031125	0	0	0.001645	0	0	0	0	3
Steniolia	0	0	0.053276	1	0.447062	0.082565	0.0395997	0.36565482	0	0.075268605	7
Striped sweat bee	0	0	1	0	0.00656	0.018987	0.0021138	0.13942728	0.127604	0.035287231	7
Syrphid	0.898129	0	0.256257	0.333333	1	0.303383	1	0.08145112	0.693677	1	9
Tiny dark bee	0.047335	0	0.34305	0	0.020315	0.228657	0.0182982	0.33521949	0.312311	0.785380627	9
Wasp	0.282628	0	0.030669	0	0.016492	0.331004	0.0531756	0.11067112	0	0.117624102	7
Total visitor groups	**7**	**1**	**14**	**6**	**16**	**18**	**14**	**16**	**9**	**9**	

Table 6: Spearman's rank correlation statistics between two pollinator responses (functional group richness, number of individuals per scan) and six plant traits. Green coloration indicates plant traits that were significantly predicted by at least one PC axis in linear regression models.

		Date of first bloom		**Date of peak flowering**		**Peak floral output**	
		r_s	**p-value**	**r_s**	**p-value**	**r_s**	**p-value**
Asclepias	Functional richness	-0.725	0.165	-0.725	0.165	0.205	0.740
	Number of individuals/scan	0.707	0.181	0.707	0.181	-0.3	0.623
Dieteria	Functional richness	0.216	0.605	0	1	-0.216	0.605
	Number of individuals/scan	-0.142	0.735	-0.333	0.419	0.166	0.693
Ericameria	Functional richness	0.105	0.894	0.105	0.894	0.948	**0.051****
	Number of individuals/scan	-0.774	0.225	-0.774	0.225	0.258	0.741
Gaillardia	Functional richness	0.714	0.110	0.647	0.164	-0.314	0.541
	Number of individuals/scan	-0.2	0.704	-0.029	0.955	0.314	0.544
Gutierrezia	Functional richness	0.619	0.102	0.662	**0.073***	0.547	0.16
	Number of individuals/scan	0.809	**0.0149****	0.662	**0.073***	0.309	0.455
Heliomeris	Functional richness	-0.107	0.819	-0.214	0.644	0.785	**0.036****
	Number of individuals/scan	0.607	0.148	0.571	0.180	0.214	0.644
Heterotheca	Functional richness	0.406	0.318	0.614	0.105	-0.301	0.468
	Number of individuals/scan	0.598	0.116	0.714	**0.046****	-0.904	**0.002****
Linum	Functional richness	-0.646	0.165	-0.394	0.438	0.758	**0.0801***
	Number of individuals/scan	-0.646	0.165	-0.333	0.517	0.880	**0.02****
Senecio	Functional richness	0	1	0.135	0.749	0.595	0.119
	Number of individuals/scan	0.333	0.419	0.662	**0.073***	0.214	0.610

		Corolla length		Corolla width		Disk width	
		r_s	**p-value**	**r_s**	**p-value**	**r_s**	**p-value**
Asclepias	Functional richness						
	Number of individuals/scan						
Dieteria	Functional richness	-0.371	0.468	-0.028	0.957	0.142	0.787
	Number of individuals/scan	-0.142	0.787	0.2	0.704	0.371	0.468
Ericameria	Functional richness	0.205	0.894	0.105	0.894		
	Number of individuals/scan	-0.774	0.225	-0.774	0.225		
Gaillardia	Functional richness	-0.371	0.468	-0.428	0.396	-0.428	0.396
	Number of individuals/scan	0.2	0.704	0.257	0.622	0.6	0.208
Gutierrezia	Functional richness	-0.333	0.419	-0.142	0.735		
	Number of individuals/scan	-0.5	0.207	-0.428	0.289		
Heliomeris	Functional richness	0.3	0.623	0.4	0.504	-0.1	0.872
	Number of individuals/scan	-0.3	0.623	-0.1	0.872	-0.4	0.504
Heterotheca	Functional richness	-0.192	0.647	-0.156	0.711	-0.204	0.626
	Number of individuals/scan	-0.571	0.139	-0.619	0.101	-0.571	0.139
Linum	Functional richness	0.516	0.294	-0.03	0.954		
	Number of individuals/scan	0.212	0.686	-0.212	0.686		
Senecio	Functional richness	-0.035	0.939	0.357	0.413	0.25	0.588
	Number of individuals/scan	0.107	0.819	-0.357	0.431	0.25	0.588