The effect of snowpack and temperature on the phenology of montane chaparral species

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Introduction

Extreme weather is a significant consequence of a changing climate. As the surface of the planet continues to rise in temperature, weather patterns are expected to change regionally and locally and have already been observed in many regions across the globe (IPCC 2023). Evolving weather patterns can impact a variety of abiotic and biotic factors, including plant phenology. Plant phenology is an area of particular interest, especially pertaining to transforming weather patterns, because it is heavily affected by the impacts of climate change through precipitation, temperature, moisture, soil content and biogeochemical cycles (Kimball et al. 2010, Wolkovich et al. 2012, Sparks and Menzel 2013). Weather patterns affect phenology in such a high degree that plant phenology is often used as an indicator of a changing climate (Schwartz 1994, Dunne et al. 2003). The major drivers of plant phenology are precipitation (Beatley 1974, Link et al. 1990, Prevéy and Seastedt 2014) and temperature (Hatfield and Prueger 2015, Park 2016). These two elements interact with each other and are both affected by climate change (Cleland et al. 2007, IPCC 2023), so examining one often involves the other because it is difficult to differentiate the sole effect of one of these attributes on phenology (Cleland et al. 2007, Jerome et al. 2021).

Numerous studies have been conducted on the effect of temperature and precipitation, and its variance due to climate change, on plant phenology (Dunne et al. 2003, Thomson 2010, Iler et al. 2013, Carbognani et al. 2016, Chen and Yang 2020, Antala et al. 2022). Plant phenology is vital because of its intricate connection to the reproduction and survival of other organisms, so variations in plant phenology have the potential to reshape ecological processes (Forrest and Miller-Rushing 2010). The general pattern observed in many previous studies showed that as the planet warms, the phenological timing of plants shifts earlier (CaraDonna et al. 2014). Snowpack can be a contributor to this effect, as it is influenced by both precipitation and temperature. Wipf (2010) and Livensperger et al. (2016) found that a faster snowmelt led to earlier blooming times in tundra plants. Conversely, Berend et al. (2020) demonstrated that later snowmelt delayed plant phenophases in alpine snowbanks. Variation in bloom timing can differ by up to a month depending on snowmelt (Thomson 2010). The impact of snowmelt on species that typically bloom at different times has been explored as well. Dunne et al. (2003) found that early snowmelt had a more pronounced effect on the earliest blooming species in subalpine meadows. However, previous studies on plant phenology have not included montane chaparral communities.

Montane chaparral is a shrub-dominated plant community located in mountainous terrain in mid to high elevations (900 meters to 3000 meters) (Risser and Fry n.d.). Oddly, one of the main threats it faces is forest management as increased tree density, reduced shrub understory, land conversion, fire suppression management and longer fire-return intervals have been decreasing chaparral area (Vankat and Major 1978, Taylor 2000). Studying the importance of the flora and fauna in these habitats can add important value for its conservation. The plant community provides contrasting habitat from montane forests that typically dominate the surrounding terrain. Chaparral often occurs as early successional stages after major disturbance, which is vital habitat for many species, including small mammals, birds, reptiles, and insects that may not occur in surrounding habitats (Humple and Burnett 2010). Commonly found plant species in montane chaparral include *Arctostaphylos nevadensis*, *Arctostaphylos patula*, *Ceanothus velutinus*, *Ceanothus cordulatus*, *Quercus vaccinifolia, Purshia tridentata,* and *Prunus emarginata*. The high-elevation environment that montane chaparral occurs in often receives lots of snow during the winter months, which make it a valuable setting to study the effect of snowpack on plant phenology.

To study if the degree of snowfall affects the phenophase of montane chaparral plant species, we explored the relationship between snowpack and the blooming times of several different species of montane plants in the Eastern Sierra Nevada in California. We investigated if a difference exists in the beginning of the flowering period between early-blooming species (*Arctostaphylos patula* and *Purshia tridentata*) and late-blooming species (*Lupinus polyphyllus* and *Heracleum maximum*). We predicted that years with more snowfall and a delayed snowmelt will postpone the flowering period of the early-blooming species and have no effect on the late-blooming species. This is because species that normally bloom relatively much later than the timing of snowmelt should not have their phenophases affected by snow but by other factors instead (Dunne et al. 2003). To determine if air temperature is one of these factors, we compared temperature data with bloom timing as well. We predicted that warmer temperatures would correlate with earlier blooming times across the late-blooming species and have no effect on the early-blooming species.

Methods

2.1 Site description

This study was conducted using data collected from the Valentine Camp at the Valentine Eastern Sierra Reserve (VESR) located on the eastern side of the Sierra Nevada in Mono County, California. The 63-hectare preserve sits 2,400 to 2,600 meters above sea level and receives 500-600 centimeters of precipitation per year on average (Western Region Climate Center 2016), most of which is snow. Snowpack typically peaks in April (VESR n.d. a) but a dense snowpack up to 4 meters high can last until the summer season (SNOFLO 2023). The site is preserved by the University of California Natural Reserve System and is commonly used for research and outdoor youth education programs. The camp hosts a variety of natural habitat including Lodgepole pine forest, montane chaparral, riparian vegetation, wet montane meadow, and Great Basin sagebrush (VESR n.d. b). The region generally has a Mediterranean climate with warm dry summers (4 to 27°C) and cold wet winters (-9 to 7°C) (Howald and Orr 2000). We conducted this study using online data from the years 2012 to 2023.

2.2 Plant species

The focal species used in the present study are *Arctostaphylos patula*, *Purshia tridentata*, *Lupinus polyphyllus var. burkei*, and *Hercleum maximum*. The former two species bloom from April to June and are regarded in the present study as early-blooming species (Calflora 2023). The latter two flower May to July and are classified as late-blooming species.

2.3 Phenology data

Plant phenology data was gathered from the National Phenology Database from the USA National Phenology Network (NPN 2023). The organization collects and organizes phenological data from across the United States through Nature’s Notebook, a national program in which volunteers, researchers, resource managers and educators help contribute to gathering data. Data from the Valentine Camp used in the present study were collected by volunteers through the

California Phenology Project. To gather the desired data for *Arctostaphylos patula*, *Purshia tridentata*, *Lupinus polyphyllus* and *Heracleum maximum* from the National Phenology Database, we first selected the "Individual Phenometrics" dataset and input a date range of January 1, 2012, to July 16, 2023. 2012 was the earliest year in which data for all four target species were collected. The location was set to the state of California and the four focal plant species were filtered. The "Flowers" phenophase was selected and data not in the Valentine Camp were filtered out.

2.4 Data collection

The guidelines that volunteers used to collect phenology data were derived from NPN (Denny et al. 2013). Each species of plant had two or three individuals at the Valentine Camp that were surveyed once every week. Each plant was marked with a flag to ensure that the same individuals were surveyed every week. Volunteers visually classified each individual into an appropriate phenophase based on key indicators described in NPN guidelines and noted the time and date. The analysis in this study only required data in the "Open flowers" category, which required at least one open flower to be present on the plant. We used the day of year (DOY) of the first individual for each species to be recorded in this phenophase in our analysis. This day indicates the beginning of the blooming period for the species for the year.

2.5 Weather data

Snowpack data was gathered online from Mammoth Mountain Ski Area Main Lodge (Mammoth Mountain 2023), which is 11.5 kilometers away from the study site. The total amount of snowfall was summed to yield a yearly total snowfall value for each year between 2012 and

2023. Temperature data was collected online from Weather Underground (2023) with data from the Mammoth Yosemite Airport weather station, located 14.3 kilometers from the study site. Temperature data was gathered only for the precise week of the first bloom for each species in every year from 2012 to 2023.

2.6 Statistical analyses

To compare the first blooming day of the year (DOY) for each plant species with snowfall and temperature, statistical analyses were performed with JMP statistical software v17 (SAS institute inc. 2023). A linear regression analysis was performed comparing annual snowfall and weekly temperature to determine if they were correlated. Linear regression analyses were then conducted with snowpack and temperature separately. The DOY for each plant species across 2012-2023 was compared to determine the effect of annual snowpack and weekly temperature on blooming time. Comparisons of DOY across light and heavy years of snowfall were assessed as well.

Results

We found that annual temperature had no effect on snowfall in the temporal range of 2012 to 2023 (N = 107, R^2 = 0.051, p = 0.0198; Fig. 1). Overall, snowpack did have an effect on the timing of flowering in montane plants while temperature did not. We found that the DOY of *A. patula* (N = 32, R^2 = 0.13, p = 0.0416; Fig. 2), *H. maximum* (N = 11, R^2 = 0.45, p = 0.0249; Fig. 2), and *P. tridentata* (N = 32, R^2 = 0.31, p = 0.0008; Fig. 2) were delayed during years of above average snowfall. Snowpack had a smaller impact on bloom timing in *A. patula* compared to *H. maximum* and *P. tridentata*. No effect of snowfall could be determined for *L. polyphyllus*

($N = 32$, $R^2 = 0.03$, $p = 0.3679$; Fig. 2). Temperature had a small effect on the delay of blooming in *P. tridentata* ($N = 32$, $R^2 = 0.17$, $p = 0.0177$; Fig. 3), but no effect on *A. patula* ($N = 32$, $R^2 = 0.03$, $p = 0.3270$; Fig. 3), *H. maximum* ($N = 11$, $R^2 = 0.02$, $p = 0.7029$; Fig. 3), or *L. polyphyllus* ($N = 32$, $R^2 = 0.00$, $p = 0.9399$; Fig. 3).

The heaviest years of snowfall (2017, 2019, and 2023) averaged 1380 centimeters of snowfall, 497 centimeters more than the mean of the year range, 882 centimeters. These high snowfall years saw the first onset of flowers in *A. patula* about 17 days after the average DOY in that time range. The same years delayed the DOY of *P. tridentata* and *H.* maximum 9 and 19 days later, respectively. The DOY of *L. polyphyllus* arrived 2 days earlier.

The years with the least amount of snowfall (2013, 2015, 2020, and 2022) averaged 374 centimeters less snowfall than the mean of the year range. The DOY of *A. patula*, *H. maximum* and *P. tridentata* were 22, 6, and 10 days earlier, respectively. The DOY of *L. polyphyllus* was 4 days later than its average.

Discussion

Our results show that some species of montane plants had later blooming times during years with greater annual snowfall, indicating that snowpack may influence the phenology of plants. The early-blooming species *A. patula* and *P. tridentata* bloomed later during years of increased snowfall, which matched our predictions that the flowering times of early-bloomers will be delayed with increased snowfall. However, the blooming period of the late-bloomer *H. maximum* was also delayed during years of increased snowfall, which contrasts with our prediction that late bloomers are not affected by snowfall. The delay in blooming was not minimal—all three of these species saw delays in their average DOY by 2-3 weeks. This effect was reversed as well. Years with lower snowpack saw the same three species bloom earlier than average. The effect of snowfall on the phenology of *L. polyphyllus* was indeterminate and could also not be explained by temperature. The only phenophase that temperature may have influenced was *P. tridentata*, even though it is an early bloomer. However, this relation was small. Overall, these results suggest that the phenology of early-blooming montane plants is more likely to be affected by snowpack, but snowpack can also affect the phenology of late-blooming montane species.

An explanation for why early-bloomers flower later when snowpack is greater may be explained by ambient abiotic conditions. Plants may be unwilling to bloom during periods of high snowpack because of resource limitation, non-ideal temperature conditions, poor soil composition or other factors that may affect their fitness (Dunne et al. 2003, Reed et al. 2012, Wheeler et al. 2015, Jerome et al. 2021). These factors are crucial for plants because the timing of blooming can affect the quantity of flowers produced and the time span of the plant's flowering period (Inouye 2008). This can, in turn, affect the reproductive success of the plant by influencing production, dispersal, germination, and establishment of seeds (Cooper et al. 2011). Flowering too soon in a snowy mountain environment can expose the plant to freezing conditions and desiccation, as well as increase the risk of frost damage (Billings and Mooney 1968, Wheeler et al. 2015, Pardee et al. 2019). However, interestingly, in the present study, temperature was generally found to not have an effect or had a small effect on the phenophase of montane chaparral plants. This supports the findings of Wipf (2010), which demonstrated that the sooner a plant develops after snowmelt, the greater its phenological sensitivity was to snowmelt. These results suggest that snowmelt may be the principal phenological indicator that montane plants use to bloom, or plants use snowmelt as an indicator of ambient temperature.

The implications of shifting plant phenological timing include influencing fitness. Flowering with different species of plants around the same time, or co-flowering, can attract pollinators and improve reproductive success (Yang et al. 2013). However, a shift in phenological timing in some plants may cause them to become out of sync with their co-flowerers. It can also cause plants to become out of sync with key pollinators and seed dispersers (Brody 1997, Price and Waser 1998, Memmott et al. 2007, Parmesan 2007, Olesen et al. 2008, Thomson 2010). Invasive plants can exploit shifts in native phenological timing due to reduced interspecific competition by utilizing resources when native species are inactive (Willis et al. 2010, Bradley et al. 2010). For instance, the invasive *Bromus tectorum* was found to bloom earlier due to a warming climate, allowing it to spread more quickly (Howell et al. 2020). This can lead to an expansion in invasive species distribution while competing with native plants, decreasing the chances of successful reproduction in native plants.

Decreased native plant reproduction and distribution can have profound effects on the ecosystem (Peñuelas et al. 2002). Increasing invasive cover and decreasing native cover can alter fire regimes, nutrient composition, and the structure of plant communities (D'Antonio and Vitousek 1992, Dickens and Allen 2014). Habitat and resource availability for animals can become altered as a result. Further study can investigate if decreasing population or production of nectar, fruits or seeds in native plants can affect animals and insects that rely on these sources for food. Larger predators that prey on these smaller animals may become affected as well. Broad-scale ecosystem and community-level studies have also demonstrated the interconnection between plant phenophases, other organisms and the potential repercussions from shifting phenophases (Brody 1997, Parmesan 2007, Ovaskainen et al. 2013). Many ecosystem functions are linked to the composition of vegetation (Carrick and Forsythe 2020). The effect of shifting plant phenophases on biotic, abiotic, and ecological processes should be investigated further to estimate the scale of change that could occur due to varied climate projections.

The implications of the present study demonstrate the potential for substantial repercussions of a changing climate. As climate change continues to progress due to anthropogenic causes, extreme weather conditions and high variability will occur more often in the future (IPCC 2023). A changing climate will affect snow patterns, precipitation levels, and surface temperature, and thus influence the phenology of numerous plant species. A shift in plant phenology, either from changes in precipitation or temperature, can potentially alter landscapes if realized to a large enough spatial and temporal scale by interrupting ecological interactions. Climate models should incorporate these likely effects as they are not only affected by climate but can also contribute to climatic change. For instance, transformations in vegetation can provoke changes in carbon and greenhouse gas cycles, particularly in peatland habitats, which are vital natural carbon sinks (Antala et al. 2022). Additionally, changes in the timing of the vegetative growing season can affect atmospheric carbon (White et al. 1999, Richardson et al. 2009, Peñuelas et al. 2009, Vitasse et al. 2009). The possibility of a positive feedback mechanism from the shifting of plant phenological timing and climate change can be consequential in the future. Widespread effects will likely be more evident as the climate continues to change.

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Tables and Figures

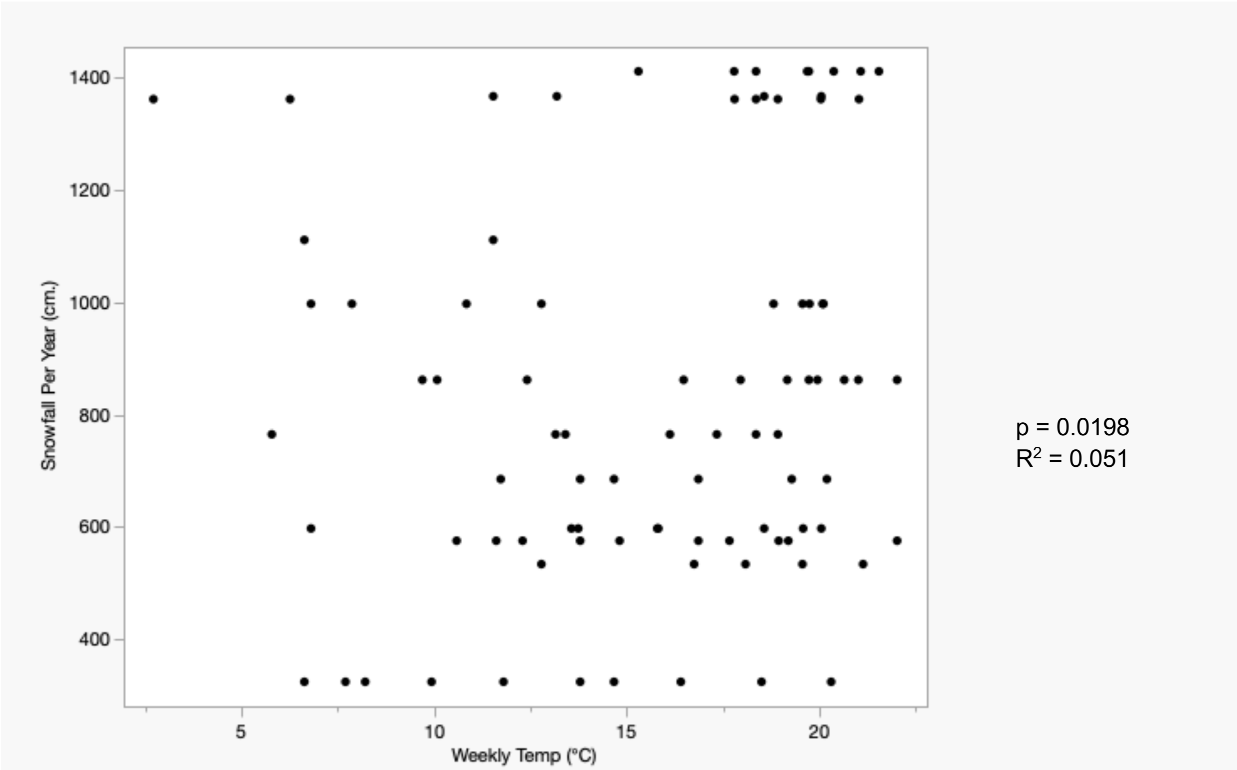

Figure 1. The effect of temperature on snowfall. The Weekly Temperature represents the temperature of the weeks corresponding with the first week flowers are reported in each season for each species. This data was measured at the Mammoth Yosemite Airport weather station. Snowfall is accumulated for an entire year in centimeters at Mammoth Mountain Ski Area Main Lodge. Both data sets are in the temporal range of 2012 to 2023. There is no correlation between temperature and snowfall (p = 0.0198, R^2 = 0.051).

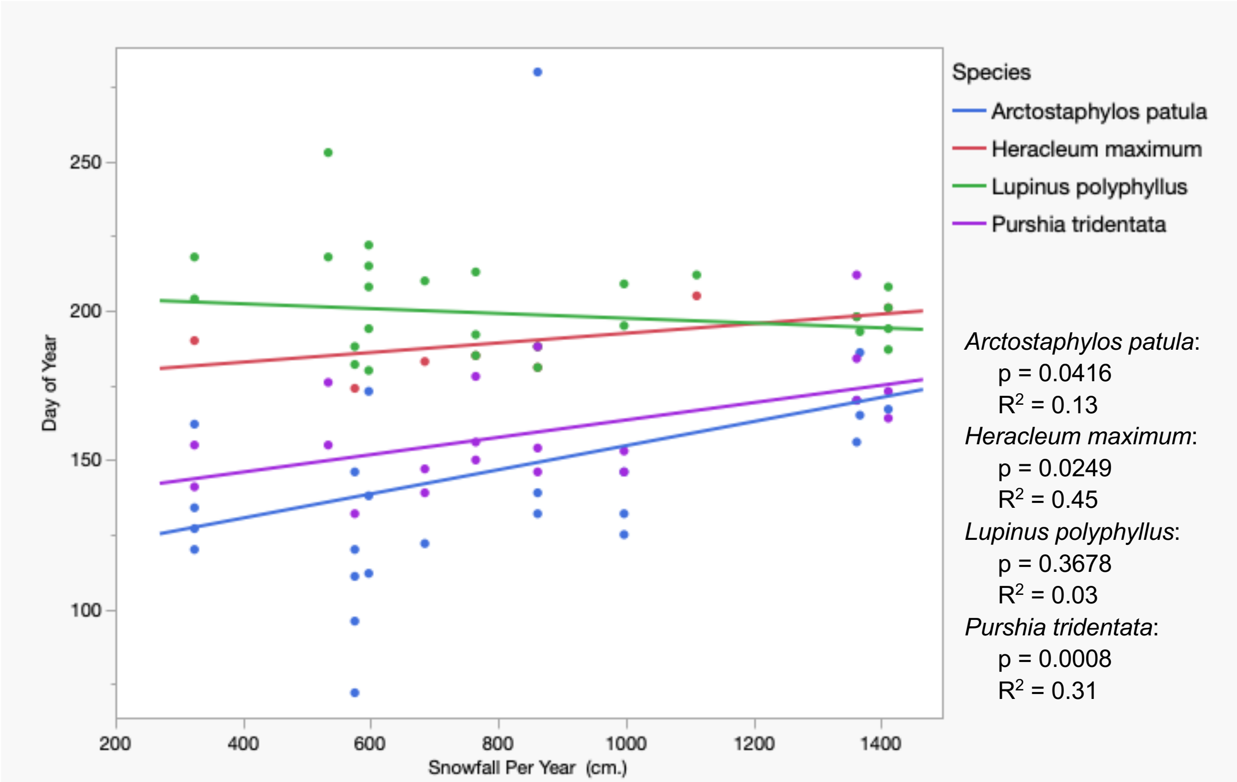

Figure 2. The effect of annual snowfall on the blooming time of plants. Snowfall Per Year is the total amount of snowfall measured in one year at Mammoth Mountain Ski Area Main Lodge from 2012 to 2023. The Day of Year (DOY) is the first day in which flowers were observed on an individual of each of the following species, *Arctostaphylos patula, Heracleum maximum, Lupinus polyphyllus, and Purshia tridentata*, at Valentine Camp each year from 2012 to 2023. Snowfall was correlated with delaying the DOY of *A. patula* (p = 0.0416, R^2 = 0.13), *H. maximum* (p = 0.0249, R^2 = 0.45), and *P. tridentata* (p = 0.0008, R^2 = 0.31), and had no effect on *L. polyphyllus* (p = 0.3678, R^2 = 0.03).

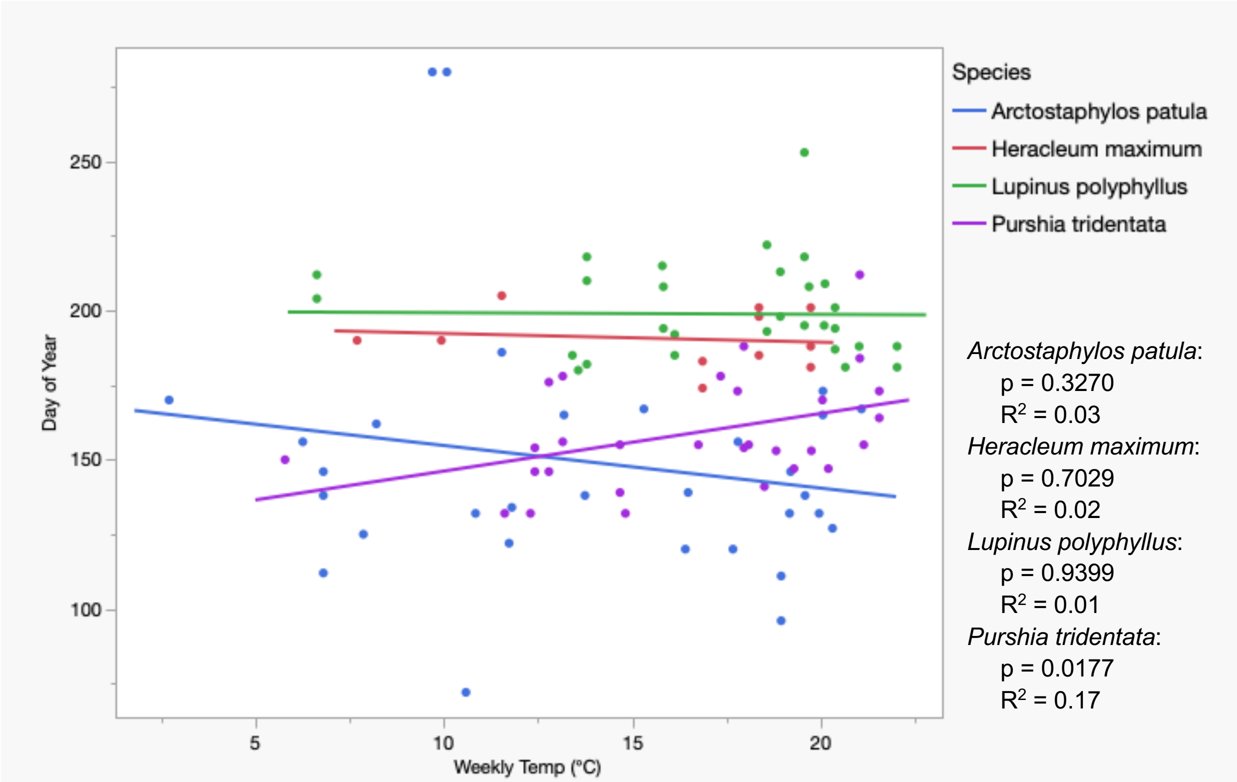

Figure 3. The effect of temperature on the bloom timing of plants. The Weekly Temperature represents the temperature of the weeks corresponding with the first week flowers are reported in each season for each species. The Day of Year (DOY) is the first day in which flowers were observed on an individual of each of the following species, *Arctostaphylos patula, Heracleum maximum, Lupinus polyphyllus, and Purshia tridentata*, at Valentine Camp each year from 2012 to 2023. Temperature was not correlated with the DOY of *A. patula* (p = 0.3270, R^2 = 0.03), *H. maximum* (p = 0.7029, R^2 = 0.02), and *L. polyphyllus* (p = 0.9399, R^2 = 0.01), but had a small effect on delaying the DOY of *P. tridentata* (p = 0.0177, R^2 = 0.17).