

Effects of altitude on co-flowering phenology in a montane wildflower community

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Abstract:

Phenology is an important life history trait. As altitude increases in alpine environments, the growing season shortens and flowering phenology is more compressed. Co-flowering could occur more at higher elevations as a compensation for the shorter growing season. However, interspecific competition is another force that could result in no change in co-flowering as altitude changes. I examined whether co-flowering changes as altitude changes. I censused wildflower species throughout the 2010 growing season in Virginia Basin outside of Gothic, Colorado. I found that co-flowering does not change significantly as over an altitudinal gradient from 2900 m to 3700 m above sea level. Instead, all species may shorten their flowering periods. Other changes in plant phenology and community did occur. Examining this question over an altitudinal gradient could serve as a proxy for long-term climate change studies.

Keywords: Co-flowering, flowering phenology, plant communities, altitude gradient

Introduction:

Phenology, the timing of various events in a species's life cycle, is an important life history trait. In alpine communities, timing of specific events is especially important because of the short growing season. As altitude increases in the Rocky Mountains, temperatures tend to decrease and snowmelt date progresses later into the spring and summer (Clow 2010). Extensive phenological research has shown that snowmelt date is a predominant environmental parameter that determines the growing season and flowering phenology of subalpine plants of the West Elk Mountains of central Colorado, USA (Inouye et al. 2002). While snowmelt date, and thus the beginning of the growing season, generally occurs later as altitude increases, the end of the growing season, as defined by the first hard freeze, may remain relatively constant along an altitudinal gradient. The result is a shortening of the growing season as altitude increases.

Because snowmelt controls the flowering phenology of many subalpine plants in this region, species have a shorter time to develop and flower at higher altitudes. Specifically, early-flowering species's phenologies have generally demonstrated a stronger relation to snowmelt date than late-flowering species's (Dunne et al. 2003). However, subsequent research suggests that such trends are species dependent. Overall, broad trends suggest that early-flowering species are

reacting more drastically to rising temperatures than are late-flowering ones (Miller-Rushing and Inouye 2009).

Thus, species's flowering phenologies may change differently as altitude changes depending on what time of the season they usually flower. The flowering phenologies of early-flowering species should change more drastically as altitude changes than the phenology of mid and late-flowering species. In addition, in years of later snowmelt date, early-flowering species such as *Lathyrus leucanthus* exhibited more co-flowering with more other species and for longer periods of time than in early-snowmelt years (Forrest et al. 2010).

Many species of flowering plants select for different pollinators via the depth of flowers as determined by the corolla length. At the Rocky Mountain Biological Laboratory (RMBL), different species of bumblebees visited flower species for varying periods of time depending on their success in entering the flower (according to corolla length) (Inouye 1980). Species with similar corolla morphologies or phylogenetic similarities may depend upon the same pollinators and increased competition between these plant species could result where they co-flower. As a result they could exhibit character trait displacement as found in previous sympatric studies (Miyake and Inoue 2003). Alternatively, competition could lead to temporal niche partitioning (according to flowering phenology) and or the disappearance of one of the competing species.

Finally, studying co-flowering over an altitudinal gradient can serve as a proxy for studying how rising temperatures will affect high-altitude systems. Lower-altitude systems may reflect what will happen to higher altitudes as the snowmelt date continues to become earlier and the growing season becomes longer. Phenology studies are important in both the short-term and the long-term data they can yield. Studies like this can provide data about flowering during a single season, but sustained monitoring can yield important data associated with topics such as

community change and climate change (e.g. Inouye 2008). It can also provide insights across different plant communities, allowing the comparison of different communities' responses to change.

Altitude affects co-flowering in subalpine wildflower communities (by influencing snowmelt date). I hypothesized that more co-flowering should occur at higher altitudes due to a shorter growing season. Specifically, early-flowering species should alter their flowering phenologies to a later date than at lower altitudes, accounting for higher co-flowering. More co-flowering may lead to more interspecific competition because similar species may flower simultaneously at higher altitudes. Alternatively, wildflower diversity could decrease as altitude increases as a consequence of interspecific competition. Or, all species could compress their flowering time as a result of the shorter growing season.

Methods:

Site Selection

I conducted my study at the Rocky Mountain Biological Laboratory (RMBL) in the Colorado Rocky Mountains. RMBL is located approximately 2886 m elevation in the East River valley approximately 9.5 km north of Crested Butte, CO.

I haphazardly selected phenology plots of 2 x 2 m in montane meadow habitats at regular altitudinal intervals from 3145 m around Gothic townsite to 3672 m at the top of Virginia Basin (Figure 1).

Flower Censusing

Beginning July 2, 2010, flowering abundance for all flowering plant species in the Virginia Basin altitudinal plots was collected twice per week for the remainder of the summer until August 5, 2010. The number of open flowers of each species was counted each day for each

plot. Depending on species, censusing was conducted differently. For example, for *Pseudocymopterus montanus*, an umbel, each umbel was counted as a single flower unit. In contrast, for a species like *Delphinium barbeyi*, the number of flowers per stalk was the counting unit. Whenever practical, the number of individual flowers per stalk was recorded.

Data Analysis

When conducting statistical analyses of my dataset, I employed parameters including initial flowering date for each species at each altitude, proportion of flowering species flowering on any single sampling date. I calculated the coefficient of variability of first flowering date across species at each altitude and the mean proportion of species flowering on any single day for each altitude. I then ran linear regressions of each of these parameters (mean proportion of flowering species and coefficient of variability) as dependent variables on altitude. I created linear models for these regressions, conducting t-tests of the slopes of the lines and examining r-squared values. I used Microsoft Excel and R statistical computing software with a significance threshold of 0.05 to analyze my data.

Results:

For each altitude, the proportion of species flowering on any given day generally has a bell-shaped curve. Plots at 3340 m do not follow this trend. In addition, the peak date generally becomes later as altitude increases and the peak itself becomes greater. (Figures 2, 3, 4, 5)

A linear regression of the mean proportion of flowering species across all species over altitudes yielded a line with a positive and insignificant relationship with a low R-squared value. (Table 1, Figure 7)

A similar linear regression of the coefficient of variability of initial flowering date across all species over altitude yielded a line with negative slope and an insignificant p-value. It yielded

a marginally better R-squared value. (Figure 6)

Discussion:

Community flowering dynamics and phenology:

First of all, higher elevations generally exhibited a lower overall species richness of flowering plants. 3145 m, the lowest altitude with plots, does not follow this pattern. A possible explanation for the lower species richness is the theory of temporal niche partitioning. At higher elevations, the later snowmelt date leads to a shorter growing season. Competition among species could have led to the evolution of the diverse flower timing of species. But, when growing season shortens enough, some species's temporal niche completely disappears, meaning they must compete with other species in a similar or the same temporal niche. Thus, the less fit species cannot compete and disappears from the community.

For example, *Noccaea montana* and *Draba* sp. both flowered in my plots, but at different elevations. These two species are both Brassicaceae and look very similar: inflorescences of small flowers with four petals. I observed the first flower of these two species on the same day and they exhibited similar flowering durations. This temporal likeness suggests that the two species could inhabit the same temporal niche and have partitioned to different elevations as a result of interspecific competition. To explain the unexpected result seen in the species richness at 3145 m, I would argue that the plant community is inherently different. These plots were located in a very rocky, dry meadow. The other elevations's sites are located in less rocky, moister soil that has approximately 100 percent ground cover.

The higher peak proportion of species observed as altitude increased does suggest that even if co-flowering was not significant, it did occur with a greater proportion of species at higher altitudes. In addition, the temporal shift to peak proportion of species flowering as altitude

increases may be a result of the later start to the growing season at higher altitudes. The small sample size makes these parameters difficult to analyze statistically.

Co-flowering does not change over elevations:

The results suggest that there is no significant change in the amount of co-flowering as altitude increases. First of all, the mean proportion of flowering species that are flowering on any one date did not increase as altitude increased suggests that though the higher elevations exhibit a shorter growing season, on average, no more species flower simultaneously. However, it is important to note that each altitude characterized a plant community with a different number of species.

In addition, the variability of initial flowering date of all species at each altitude fails to change significantly as a function of altitude. To support the hypothesis that more co-flowering occurs at higher elevations, the coefficient of variability would have decreased as altitude increased. Instead, I observed that coefficient of variability and altitude were negatively correlated, but only showed a weak relationship. Thus, the coefficient of variability does not support the hypothesis that more co-flowering occurs at higher altitude. But, nor does it reject the other alternative hypothesis that instead of more co-flowering occurring at higher elevations, a species's flowering duration decreases. An explanation for the compression of flowering to avoid co-flowering could be competition and temporal niche partitioning. Competition for pollinators could be especially fierce at higher altitudes where the pollinator community is smaller and less diverse. Thus, competition for pollinators could have resulted in the aversion to co-flowering and compression of flowering duration.

First flowering date data can reveal how, at the community level, the date of first flowering becomes more or less restricted and more or less variable with changes in altitude, thus

indicating more or less co-flowering. These data do not indicate whether or not species-specific flowering duration or flowering curves change as altitude changes. A complete data set of the entire flowering season would help to test this hypothesis.

Implications for Climate Change Research

Alpine ecosystems could be especially responsive to climate change due to a suite of unique characteristics that include their occurrence at high elevation, short growing season, and range restrictions. As such, trying to learn how climate change will affect these ecosystems before the changes actually occur can be highly useful. Changes in plant communities and flowering phenology of montane plants has already been observed and documented in previous studies (Inouye 2008). Many of these studies have been used over longitudinal gradients, but conducting them over altitude allows for research on a more microcosmic scale. In addition, changes in the flowering distribution of plants have also been observed as higher altitudes warm (Crimmins et al. 2009). Thus, by studying the plant phenologies over altitudinal gradients, I hope to elucidate what may happen at higher elevations as temperatures continue to rise. Whether plants will be able to adapt quickly enough at higher elevations to continue to occupy their same relative temporal niches if the growing season lengthens is an important ecological question.

Potential for Invasive Species

If the growing season continues to lengthen as other studies have found (Inouye et al. 2002) and the montane plant communities I studied do not evolve quickly enough to fill the longer growing season, new temporal niches may appear. Recent research has shown that invasive species in the Mediterranean have exploited open temporal niches by flowering when other species are not, thus gaining an advantage over them (Godoy 2009). A similar invasion could occur in montane communities if evolution occurs more slowly than the lengthening of the

growing season.

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Tables:

Table 1: Summary statistics of regression of mean proportion flowering species over altitude.

Slope	t-value	F-statistic	p-value	Significant?	R-squared
0.0000352	0.173	0.0298	0.8788	no	0.01468

Table 2: Summary statistics of regression of coefficient of variability of initial flowering date over altitude.

Slope	t-value	F-statistic	p-value	Significant?	R-squared
-0.0004789	-0.817	0.6676	0.4997	no	0.2503

Figures:

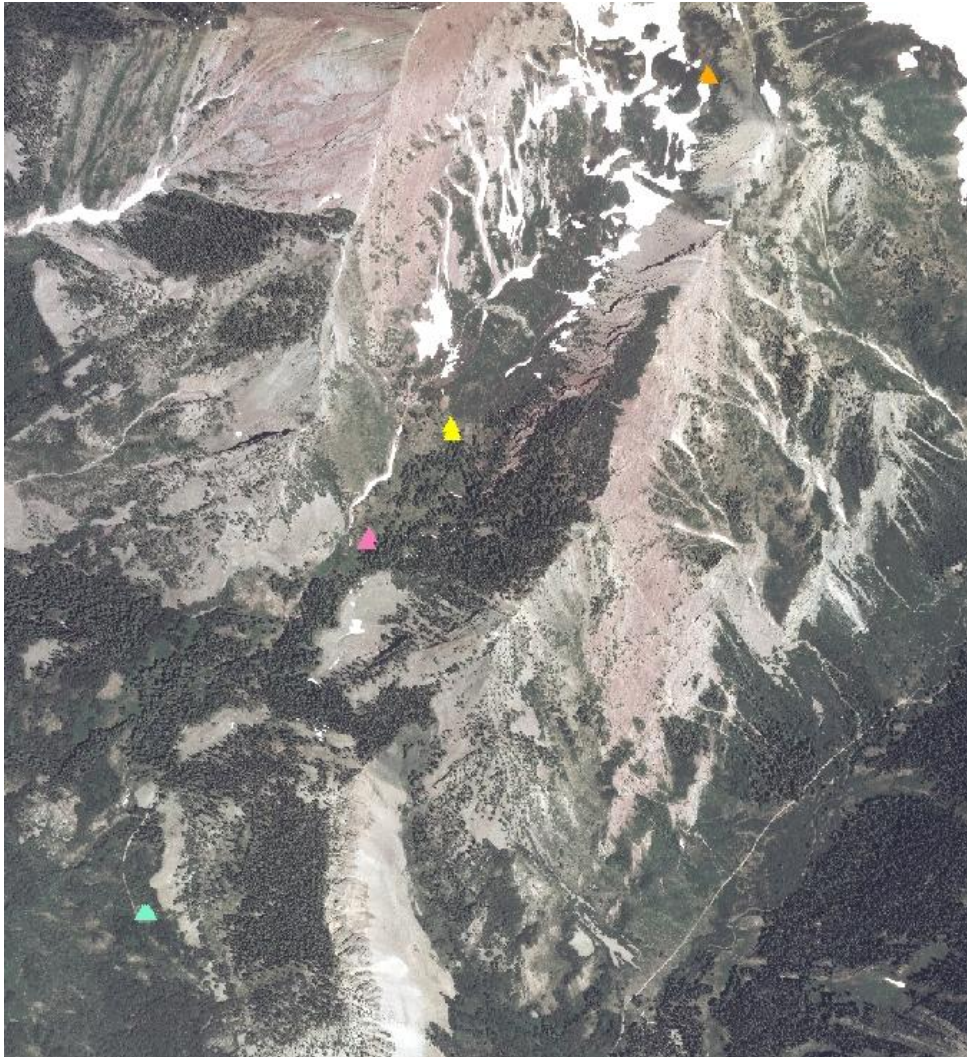


Figure 1. Map of study sites in Virginia Basin. Altitude decreases from the triangles in the upper right (top of Virginia Basin) to the lower left set of triangles (above Gothic).

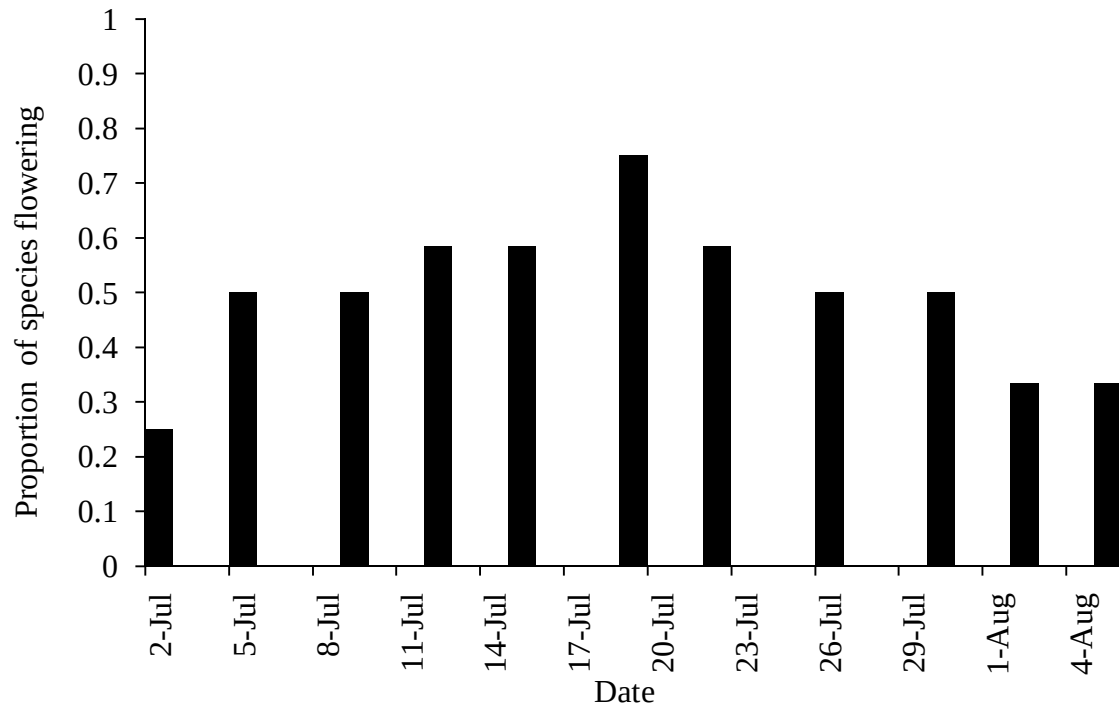


Figure 2. Proportion of flowering species in bloom by date at 3145 m altitude. In this figure, the x-axis is organized by date. The y-axis is the proportion of flowering species in bloom of the total number of flowering species at that altitude.

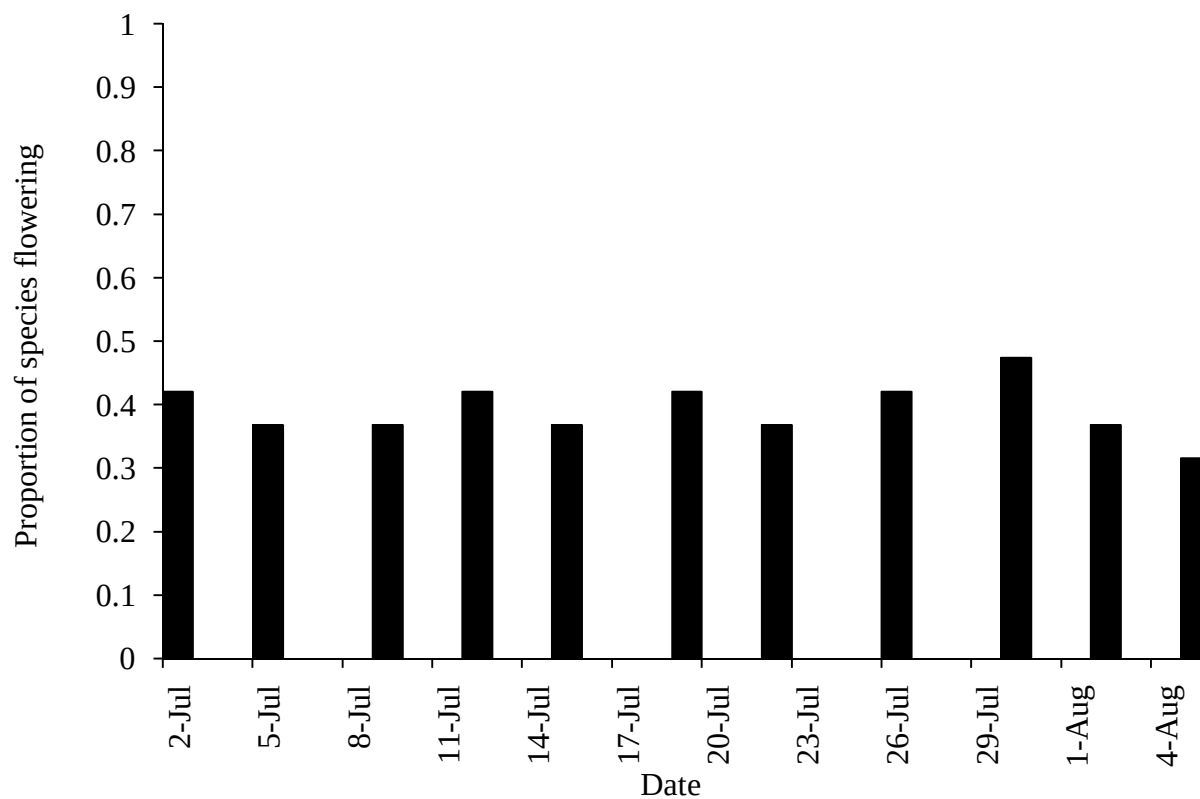


Figure 3. Proportion of flowering species in bloom by date at 3340 m altitude. In this figure, the x-axis is organized by date. The y-axis is the proportion of flowering species in bloom of the total number of flowering species at that altitude.

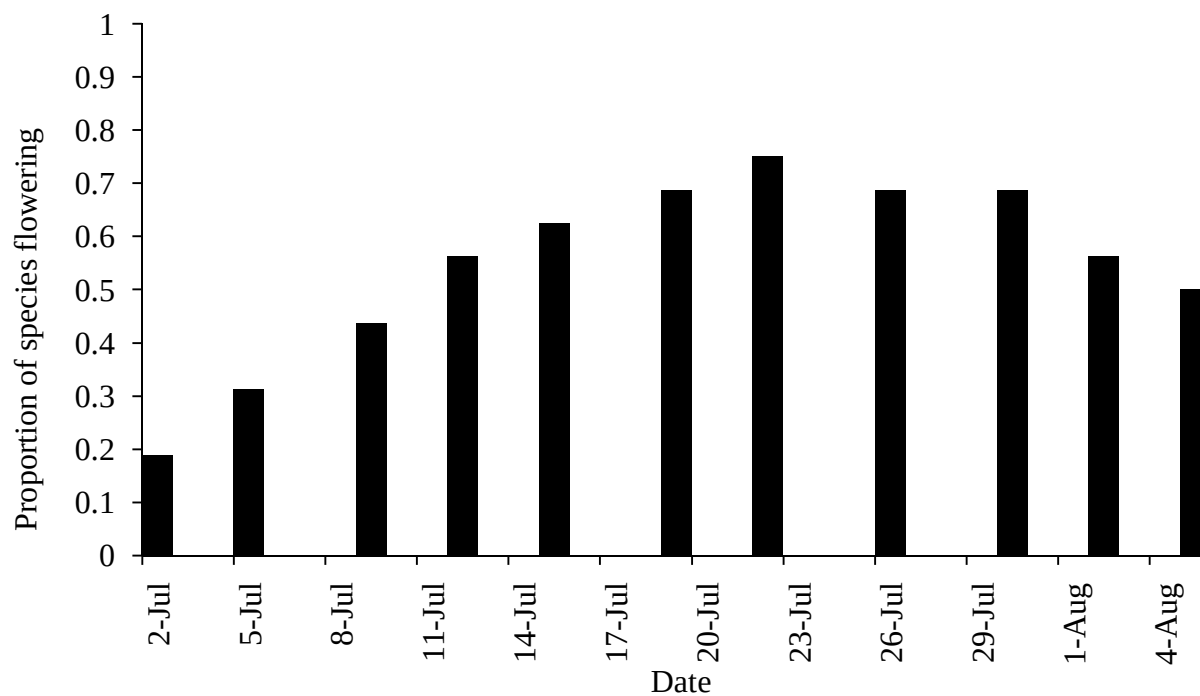


Figure 4. Proportion of flowering species in bloom by date at 3450 m altitude. In this figure, the x-axis is organized by date. The y-axis is the proportion of flowering species in bloom of the total number of flowering species at that altitude.

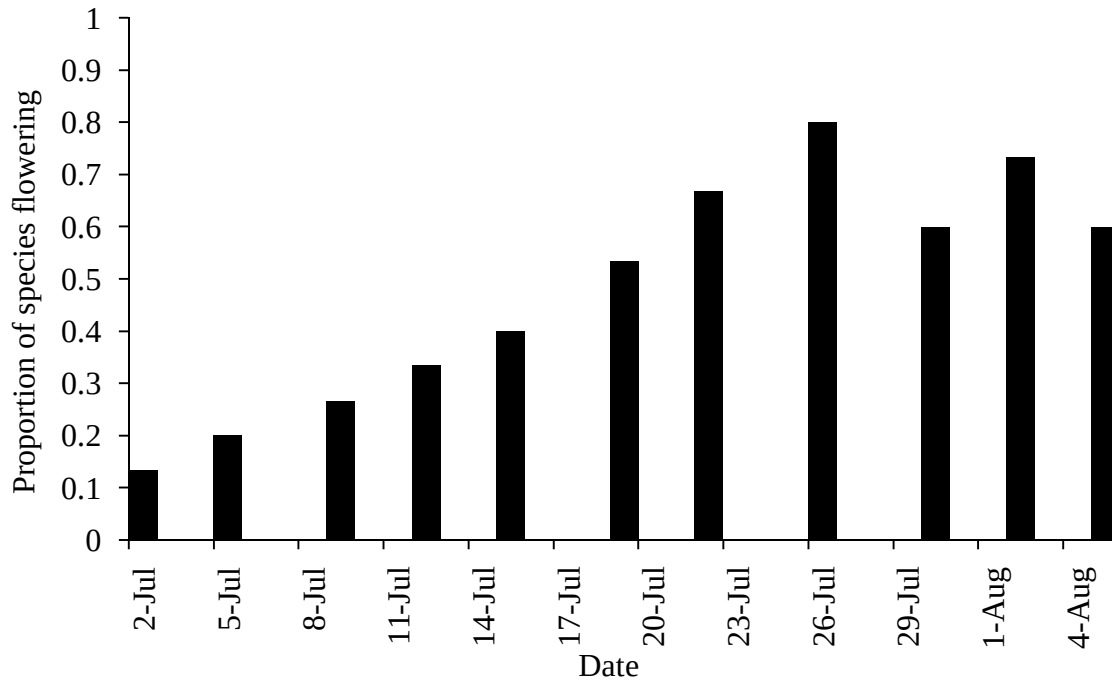


Figure 5. Proportion of flowering species in bloom by date at 3672 m altitude. In this figure, the x-axis is organized by date. The y-axis is the proportion of flowering species in bloom of the total number of flowering species at that altitude.

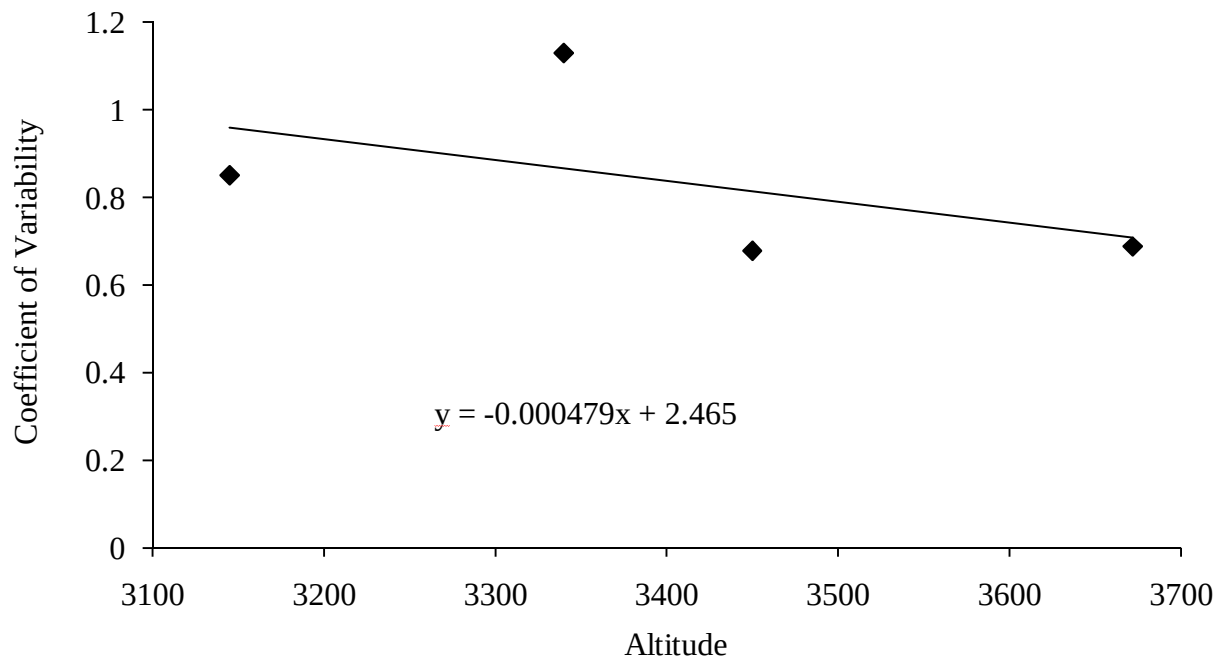


Figure 6. Coefficient of variation of initial flowering over altitude. The x-axis is the altitude and the y-axis is the coefficient of variability of initial flowering date across all species for that elevation.

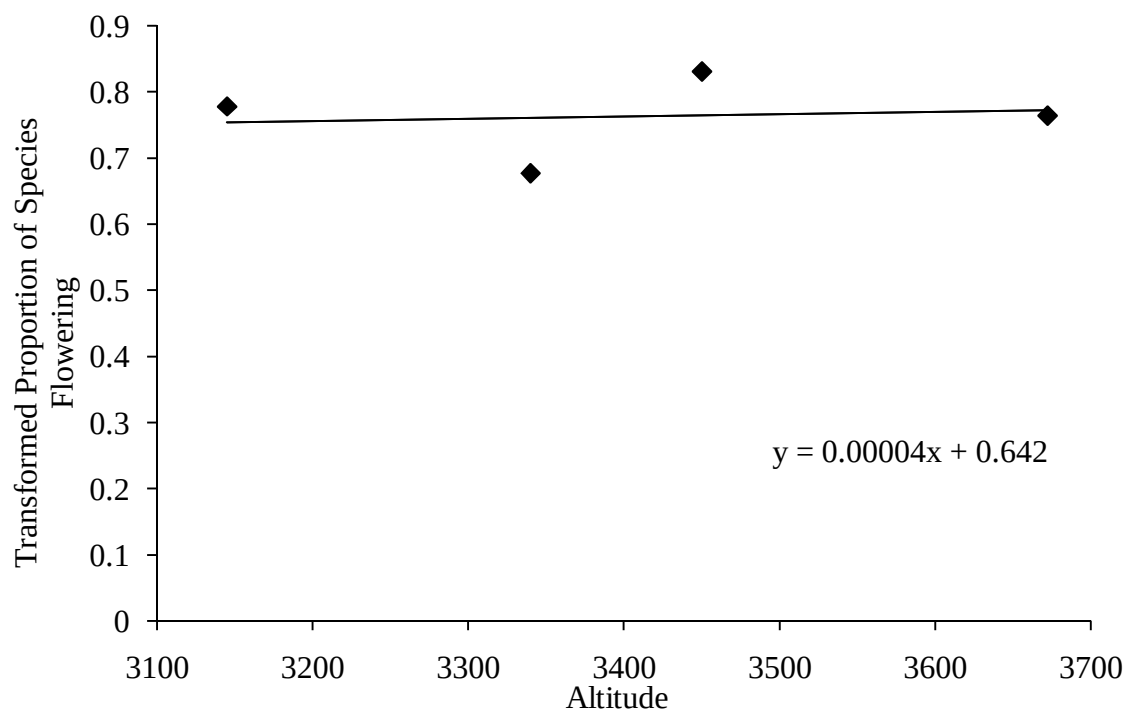


Figure 7. Mean proportion of flowering species over altitude. The x-axis is the altitude, and the y-axis is the arcsine-square root transformation of mean proportion of species in bloom across all dates for that altitude.