EARLIER SNOWMELT TIMING IS ASSOCIATED WITH SPECIES-SPECIFIC SHIFTS IN FLOWERING SYNCHRONY AND REPRODUCTION IN THREE ALPINE PLANTS

by

EMMA HORNE

(Under the Direction of Megan DeMarche)

ABSTRACT

Earlier spring warming temperatures induced by climate change are projected to advance snowmelt in the alpine tundra, resulting in changes to plant flowering regimes which have the potential to interrupt reproductive processes. In this study, I investigate the effect of snowmelt timing on the flowering synchrony and reproductive success of three co-flowering species across four sites with various mean snowmelt timing in an alpine meadow ecosystem. I find distinct responses to earlier snowmelt within my study species. Changes to snowmelt timing may have detrimental impacts on reproduction in some species, but positive effects in others. My results suggest that changes to flowering synchrony among and within species in response to snowmelt can have species and interaction specific consequences for reproduction in future climate scenarios.

INDEX WORDS: Synchrony, Flowering, Snowmelt, Pollen Deposition, Climate Change

EARLIER SNOWMELT TIMING IS ASSOCIATED WITH SPECIES-SPECIFIC SHIFTS IN FLOWERING SYNCHRONY AND REPRODUCTION IN THREE ALPINE PLANTS

by

EMMA HORNE

BSc, University of Georgia, 2021

A Thesis Submitted to the Graduate Faculty of The University of Georgia in Partial Fulfillment of the Requirements for the Degree

MASTER OF SCIENCE

ATHENS, GEORGIA
2024

EARLIER SNOWMELT TIMING IS ASSOCIATED WITH SPECIES-SPECIFIC SHIFTS IN FLOWERING SYNCHRONY AND REPRODUCTION IN THREE ALPINE PLANTS

by

EMMA HORNE

Major Professor:	Megan DeMarche
Committee:	Jill Anderson
	Julian Resasco

Electronic Version Approved:

Ron Walcott
Vice Provost for Graduate Education and Dean of the Graduate School
The University of Georgia
August 2024

DEDICATION

I dedicate this thesis to my moms

ACKNOWLEDGEMENTS

To start, I collected all of my data at the Niwot Mountain Research Station, and I would like to acknowledge that this station resides in occupied territory of Núu-agha-tʉvʉ-pʉ̱ (Ute), Hinono’ei (Arapaho), Tséstho’e (Cheyenne) peoples. I thank them for their stewardship of this land.

A huge thank you to my advisor, Megan DeMarche. Though there were a lot of setbacks during my degree, Megan did a wonderful job helping me get through them. She is a great mentor, and I feel very lucky to have been in her lab.

Thank you to all my committee members, Jill Anderson and Julian Resasco, for your guidance and assistance. Thank you to Shu-Mei Chang for this as well, and for first introducing me to the joys of scientific research.

Thank you to my wonderful lab mates, for all your feedback and for letting me help out with your field work when I needed a break. I feel so lucky to have shared a space with such wonderful and kind people. I would especially like to thank Emma Chandler and Meredith Zettlemoyer for all your help during field work. I would also like to thank Natalie Chaine and Claire Stufflebeam for their assistance during fieldwork.

I would also like to thank Chelsea Hargroves and Wolfgang Lukowitz for helping me figure out all my logistic and administrative needs surrounding my degree. Thank you to John Burke for letting me use his microscope.

Thank you to my moms, who were there for me when I needed them. Thank you to all my wonderful friends for being so kind and understanding, and providing some extra fun during my time here.

Finally, a special thank you to my partner, Jacob Simon. I don’t think I would have been able to do this without your kindness and support. You are such a light in my life. I love you so much.

TABLE OF CONTENTS

Page

CHAPTER

LIST OF TABLES

Page

LIST OF FIGURES

CHAPTER 1

LITERATURE REVIEW

Flowering phenology can be signaled by multiple different aspects of the environment, and the signals utilized often vary between species (Wilczek et al 2010, Kudo 2020). Many of these cues are expected to shift with climate change (Chmura et al 2018). In the alpine tundra, one of the most important phenological cues to instigate flowering is snowmelt because alpine environments have relatively short summer growing seasons, and consequently short time periods in which to flower (Inouye and Wielgolaski 2013, Kudo 2020). Plant responses to snowmelt can be related to different environmental variables, including moisture and temperature. Increases in soil moisture can cue plants into the start of the growing season as melting snow increases soil moisture, which can instigate plant growth and flowering (Holway and Ward 1963, Holway and Ward 1965). Cumulative increases in daily temperatures can contribute to snowpack thawing and cue plants to flower (Hulber et al 2010). Soil warming therefore is an important cue for the start of the growing season (Inouye 2019). Nonetheless, not all phenological cues in the alpine tundra are related to snowmelt timing. Daylength, or photoperiod, has been shown to influence phenology in alpine plants, and can even buffer plants from emerging too early after warm spells in late winter or early spring (Keller and Korner 2003, Bannister et al 2005).

The effects of climate change likely will have increasingly important impacts for flowering phenology in alpine ecosystems. One of the aspects of climate change that impacts alpine ecosystems is earlier warming temperatures and reduced snowpack in the spring, which result in earlier snowmelt timing (Wipf et al 2009, Vorkauf et al 2021). Additionally, temperatures are becoming more variable, which some studies suggest will result in reduced phenological sensitivity in plants (Wang et al 2013). Previous research has shown that advanced snowmelt timing has caused earlier flowering in alpine plants (Petragalia et al 2014, Winkler et al 2018). These shifts in phenology in response to snowmelt timing could therefore have consequences for alpine plant reproduction.

An important aspect of plant phenology is synchrony, or the amount of overlap in timing of events. Flowering synchrony can be thought of as the temporal overlap in flowering distributions, or times when plants put out flowers (Augspurger 1983). Flowering synchrony is important because it can influence plant reproduction via several factors. At the individual level, flowering at the same time as conspecific neighbors can increase the chances of receiving and getting fertilized by outcrossing pollen (Tachiki et al 2010, Feldman 2008). On the other hand, individuals flowering synchronously with heterospecific neighbors can increase the chances of heterospecific pollen deposition (Morales and Traveset 2008, Smith et al 2021). At the community level, competition for pollinators may also be higher when flowering synchronously with heterospecifics; however large and attractive floral displays created by multiple flowering species blooming together may also act facilitatively and attract more pollinators to the community than a single species, increasing pollination rates for all species (Hurtado et al 2023, Johnson et al 2022, Hegland and Totland 2012). As discussed before, phenological cues that initiate flowering vary among plants. As spring temperatures continue to warm and snowmelt times become earlier, some plants may adjust their phenology to match snowmelt, but others that use different phenological cues may not. This is one key way in which shifting phenology can impact alpine reproduction.

Another key component of synchrony is that between plants and pollinators. Flowering synchrony with pollinators is often necessary for plant reproduction, as most flowering alpine plant species rely on insect visitors for pollination services (Ollerton et al 2011). The main pollinating insects in this ecosystem are bees and flies, followed by butterflies, moths, and some beetles (Inouye 2019). Pollinator diversity is lower in the alpine compared to lower elevations due to the harsher conditions that some animals cannot tolerate, though many insect taxa specialize in alpine pollination (Inouye 2019). Furthermore, pollinators are a relatively scarce resource due to the harsh climate (Kearns 1992, Bingham 1999). Thus, synchrony between plants and pollinators is likely very important for increasing the chances of a given pollinator encounter.

Nonetheless, it is important to note that plant reproductive success depends not only on pollinator abundance, but also on their effectiveness at pollination (Herrera 1989, Kehrberger et al 2019, Willcox et al 2017). Flowering species often have floral morphological traits that select for the most effective types of pollinators, known as pollination syndromes (Fishman and Wyatt 1999). In addition to floral anatomy, pollinators have different behaviors that work to collect and spread pollen between flowers, and this can influence their effectiveness in pollination services. Floral constancy is the idea that pollinators use a search image approach to finding flowers (Waser 1986). Floral constancy was originally found in bees, but evidence exists for constancy in flies, beetles, and lepidopteran foraging behaviors as well (Amaya-Marquez 2009). Pollinators that exhibit floral constancy are more likely to visit flowers with similar traits

(e. g. color, morphology, scent). This can lead to greater outcrossing rates through higher rates of conspecific pollen deposition (Montgomery 2009). However, pollinators don't always visit the same species within a given foraging event, and therefore heterospecific pollen may end up on stigmas as well (Ashman 2013).

High heterospecific pollen loads can negatively affect plant reproduction by clogging receptive stigmas and thus reducing the chance of fertilization by conspecific pollen (Galen and Gregory 1989, Bell et al 2005). Heterospecific pollen can also be allelopathic, releasing chemicals that inhibit germination, tube growth, or ovule development (Ashman and Arceo-Gomez 2013). The amount of heterospecific pollen deposited on stigmas of a given plant species depends on multiple factors. Past research on 29 species occupying a prairie community show that flowers with restrictive morphologies received less heterospecific pollen than those with unrestrictive morphologies (Montgomery and Rathcke 2012). Additionally, the amount and diversity of heterospecific flowers within a flowering community can affect the number of heterospecific pollen grains deposited on stigmas (Levin and Anderson 1970). With this in mind, if earlier snowmelt alters flowering synchrony between heterospecific plants, the amount of heterospecific pollen deposited on stigmas may change. Although, plant-plant flowering and plant-pollinator synchrony may not respond to snowmelt congruently.

Both plants and their pollinators can respond to earlier snowmelt in different ways, either advancing, delaying, or maintaining their phenology. In many cases, pollinators are not shifting their phenology in the same way their plant counterparts are (McKinney et al 2012, Kudo 2014) leads to plant-pollinator mismatch, which can negatively affect plant reproduction by reducing the co-occurrence of effective pollinators available for pollen transfer (Hegland et al 2009, Miller-Struttmann et al 2015, Gerard et al 2020). For example, one study found that solitary nesting bees and wasps are less likely than plants to advance their phenology due to spring warming (Forrest and Thomson 2011). Nonetheless, the researchers posit that this alone is unlikely to significantly affect either plants or pollinators because both members of the relationship likely respond to the same phenological cues, given survival and reproduction are closely tied into the interaction. This supports the notion that plant-pollinator interactions may be resilient to the effects of climate change due to the nested structure of their interactions and plasticity of generalist pollinators (Memmott et al 2007, Gerard et al 2020). In alpine ecosystems, plant pollinator interactions may be conserved through microclimate differences, interannual climate variation, and the generalist foraging behavior of alpine pollinators throughout the flowering season (Iler et al 2013, Hall 2018, Inouye 2020). Therefore, the effects of earlier snowmelt and changes in flowering synchrony have implications for alpine plant-pollinator interactions and fertilization.

Understanding how snowmelt timing influences flowering synchrony and plant reproduction in alpine environments will bring researchers to a greater understanding of how plant fitness will be affected by changes in climate. Though plant phenological responses to climate change have been well documented, less research has explored the impact of snowmelt on flowering synchrony, particularly in alpine regions. In this thesis, I aim to elucidate how snowmelt timing influences flowering synchrony within and between three alpine cushion plants, and whether variation in synchrony has impacts on pollen deposition and fruit production.

CHAPTER 2

EARLIER SNOWMELT TIMING IS ASSOCIATED WITH SPECIES-SPECIFIC SHIFTS IN FLOWERING SYNCHRONY AND REPRODUCTION IN THREE ALPINE PLANTS[1]

---

[1] Horne, E.C. To be submitted to a peer-reviewed journal

ABSTRACT

With earlier spring warming temperatures brought on by climate change, snowmelt timing is also becoming earlier in the alpine tundra. Earlier snowmelt timing in this ecosystem has the potential to shift flowering regimes throughout the growing season. However, not all plants shift their flowering timings at the same rate, both within and among species, resulting in changes to flowering synchrony and potentially novel floral neighborhoods. Changes in flowering synchrony can have impacts on plant-plant interactions, particularly in the context of pollination and reproduction. This study aims to determine the effect of snowmelt timing on the conspecific and heterospecific flowering synchrony between three alpine cushion plant species, *Silene acaulis*, *Minuartia obtusiloba*, and *Phlox condensata*. Additionally, I investigated the effect of conspecific floral display on conspecific pollen deposition as well as the effect of conspecific and heterospecific flowering synchrony on fruit set. I compared these results with the overall effect of snowmelt on fruit production and pollen deposition. I measured floral display size, fruit set, and pollen deposition across four sites with varying mean snowmelt timing in an alpine meadow ecosystem. I find that responses to earlier snowmelt within these three species are distinct. The earlier flowering species, *Phlox* and *Silene*, showed less synchrony with heterospecifics with earlier snowmelt timing. The later flowering species, *Minuartia*, showed more conspecific and heterospecific synchrony with earlier snowmelt timing. I find that conspecific synchrony increased fruit production in Minuartia and Phlox, and heterospecific synchrony increased and decreased fruit production in Silene and Phlox, respectively. Nonetheless, I find that the overall effect of snowmelt timing seems to be a stronger driver of reproductive success than plant-plant interactions.

INTRODUCTION

Many plants that reside in the alpine tundra adjust their phenology to the timing of snowmelt (Inouye and Wielgolaski 2013). One aspect of phenology that is particularly important for plants is flowering time. Flowering time influences the number of potential mates available for outcrossing, and how many pollinators are available to reach those potential mates (Weis et al 2014, Shelton et al 2023). Due to climate change, earlier snowmelt is occurring in the alpine with the rise of warmer and more variable spring temperatures (Wipf et al 2009, Vorkauf et al 2021). Thus, many plant species are expected to shift their flowering times with earlier snowmelt, if they haven't already, given that this is a common phenological cue for flowering in alpine regions (Winkler 2018, Inouye and Wielgolaski 2013). Nonetheless, some plants rely on other cues, such as photoperiod, temperature, and water availability to induce flowering (Keller and Korner 2003, Bannister et al 2005). Shifts in flowering time, or the lack thereof, can have consequences for plant reproduction.

Within a single plant species, shifting phenology may have negative impacts for plant reproduction through a variety of mechanisms. Phenological mismatch between pollinators and plants induced by climate change may negatively affect pollination within plant species (Hegland et al 2009, Miller-Struttmann et al 2015, Gerard et al 2020). However, phenological mismatch may be buffered in alpine environments by microclimate differences, interannual climate variation, and the adaptability of generalist pollinators throughout the flowering season (Iler et al 2013, Hall 2018, Inouye 2020). Another way shifting flowering regimes can influence plant reproduction is via changes in plant-plant interactions. Flowering synchrony is the amount of overlap between flowering periods, and can be measured within and between plant species

(Ims 1990). Shifting phenology can affect flowering synchrony, resulting in consequences that can influence reproduction.

In particular, changes in flowering time can alter synchrony within a single species, or conspecific synchrony, which can have positive and negative effects on plant reproduction depending on community context. If plants are flowering at the same time as their conspecific neighbors, this can increase outcrossing rates due to increased chances of pollinators visiting plants of the same species and spreading pollen between individuals (Feldman 2008). Additionally, a higher number of the same plant species flowering together increases the chance for conspecific pollen deposition, increasing the chance of fertilization (Duffy and Stout 2011). Nonetheless, competition can still have a strong influence on the amount of pollination services received among conspecifics. Individuals flowering at the same time as other conspecific individuals might reduce visitation rate by decreasing the ratio of pollinators to plants, thus increasing the demand for pollinators (Bergamo 2020, Ward 2013). In this case, flowering less synchronously with conspecifics would increase reproductive output, though not necessarily outcrossing.

Dynamics between plants and pollinators become more complicated when considering plant communities as a whole, and how heterospecific flowering synchrony influences reproduction. Individuals flowering together with their heterospecific neighbors to create large, showy displays might be more attractive to pollinators, facilitatively increasing pollinator visitation (Moeller 2004, Tachiki et al 2010). However, more heterospecific synchrony also creates a higher chance for heterospecific pollen deposition (Ashman 2013). High heterospecific pollen loads can reduce the chance of fertilization by clogging receptive stigmas and reducing conspecific pollen germination (Galen and Gregory 1989, Bell et al 2005). Low pollinator fidelity, unrestrictive floral morphology, and high diversity of flowering communities all have the potential to increase heterospecific pollen deposition (Montgomery 2009, Fishman and Wyatt 1999, Levin and Anderson 1970). However, pollinators are unlikely to visit plant species randomly with respect to their frequency, and instead may rely on a search image to temporarily specialize on one or a few plant species while foraging. This pattern of floral constancy in pollinator behavior can reduce heterospecific pollen load (Levin and Anderson 1970).

The strength of competition or facilitation within a flowering neighborhood depends on community composition and structure. Plants tend to experience more heterospecific pollinator competition when surrounding plants are visited by the same pollinators and have similar pollination syndromes, and this competition is thought to structure communities so that a diversity of pollination syndromes are present (Sargent and Ackerly 2008). However, Sargent and Ackerly (2008) also note that, in communities structured by pollinator facilitation, more similar pollination syndromes are expected since plant species that share pollinators are more likely to persist when coexisting in these communities. Pollinator resources can also vary in different communities, where overall pollinator abundance, visitation rate, pollinator effectiveness, and floral constancy may also play a role in driving reproductive success (Hegland et al 2009, Miller-Struttmann et al 2015, Gerard et al 2020, Montgomery 2009, Willcox et al 2017). In alpine ecosystems, pollinators are a relatively scarce resource due to the harsh climate (Kearns 1992, Bingham 1999). A lack of readily available pollinators might drive more competitive plant interactions owing to lower visitation rates by effective pollinators (Chittka and Schurkens 2001). Nonetheless, other research hints to the importance of facilitative pollination interactions (Moeller 2004, Gurung et al 2018). In the case of flowering synchrony in alpine communities, it is unclear whether competition or facilitation is a more powerful driver of reproductive success.

Research that seeks to disentangle the effects of earlier snowmelt on coflowering synchrony and plant reproduction could better inform how climate change will impact flowering community persistence in alpine environments. In this study, I examine the dynamics of flowering synchrony in three alpine cushion plants: *Silene acaulis* (Carophyllaceae), *Minuartia obtusiloba* (Carophyllaceae), and *Phlox condensata* (Polemoniaceae). I explore whether snowmelt timing affects flowering synchrony both within and between species. I also investigate how local conspecific and heterospecific floral displays influence patterns of pollen deposition over the flowering season. Lastly, I test whether conspecific or heterospecific synchrony influences reproductive success.

Flowering earlier increases the length of the potential flowering period, creating greater opportunity for plants to flower asynchronously. Therefore, I hypothesize that individual variation and variation between species in response to snowmelt will induce more asynchrony in conspecific and heterospecific flowering in sites with earlier snowmelt (Figure 1). Given the most common alpine pollinators likely exhibit some floral constancy and the relative scarcity of pollinators in alpine tundra habitats (Waser 1986, Bingham 1999, Amaya-Marquez 2009), I predict that greater conspecific synchrony will result in higher reproductive success through facilitation, and the presence of more outcrossing opportunities. In contrast, I predict that greater heterospecific synchrony will result in lower reproductive success due to competition for pollinators and higher rates of heterospecific pollen deposition. Alternatively, I could find that heterospecific synchrony could confer a fitness advantage by aiding in an overall more attractive floral display, or that the competitive and facilitative effects of synchrony combine to show no net effect (Figure 2).

METHODS

Study System and Species

I collected data at the Niwot Ridge LTER (40.05411, -105.5891, 3022-3790m, Colorado, USA) from June 19th through August 1st of 2023. Niwot ridge is an alpine meadow along the east face of the front range of the Rocky Mountains. I conducted this study at four previously marked sites at varying elevations (Table 1) and exposure to maximize variation in snowmelt timing (Figure 3). I expected that two sites, Early 1 and Early 2, would have earlier snowmelt because they are more exposed and slightly higher in elevation compared to the other two sites, Late 1 and Late 2. Sites at higher elevations are more exposed to winds that prevent the formation of heavy snowpack, thus snow melts more readily than sites where snowpack is thicker. These sites are part of a demography and phenology study established in 2021 (DeMarche, *unpubl. data*). Each site contains one transect where plants of all three study species were mapped and marked (Figure 4).

Three alpine cushion species were chosen for this study: *Silene acaulis*, *Minuartia obtusiloba*, and *Phlox condensata*. All three species are long-lived herbaceous perennials mainly found in alpine tundra environments, and they all flower between June and August. Cushion plants are characterized by their short, dense growth pattern, forming mats that spread radially along the ground. Foliage consists of densely packed stems that end with a rosette. These three species commonly cooccur, often with overlapping foliage, and flower at approximately the same time, making them good candidates for studying effects of synchrony in the wild (Figure 5).

Silene acaulis produces small flowers ranging from light to dark pink, with reproductive structures presented openly. *Silene acaulis* individuals can live for hundreds of years, with some of the oldest plants being over 300 years old (Morris and Doak 1998). This plant is gynodioecious, where some individuals only produce female (pollen-sterile) flowers and some individuals produce hermaphrodite flowers. *Silene acaulis* females have been shown to produce more fruits and higher quality seeds than their hermaphroditic counterparts (Morris and Doak 1998). *Minuartia obtusiloba* is also gynodioecious. This species produces smaller, white flowers with reproductive structures presented openly. Life expectancy for *M. obtusiloba* is around 200 years (Forbis and Doak, 2004). *Minuartia obtusiloba* and *S. acaulis* share similar pollinators, including insects from Coleoptera, Diptera, Hemiptera, Hymenoptera, and Lepidoptera (Resasco unpubl. data). *Phlox condensata* flowers range from white to pale purple, and reproductive parts remain inside the corolla tube, with stigmas underneath anthers (Locklear 2011). They are generally larger than *S. acaulis* and *M. obtusiloba* flowers. Little is known about *P. condensata* pollinators, though in observations I made, I noted visits from ants (Formicidae) and flies (Tachinidae, Syrphidae). Another study from Niwot ridge also observed ant and fly visitors to *Phlox* (Rose-Person et al 2023). One study suggests they are visited at night by moths (Kendall et al 1981).

Snowmelt

To estimate snowmelt timing, I used data on soil surface temperatures recorded by three HOBO 64k temperature data loggers (®Onset Computer Corporation) at the beginning, middle, and end of each transect. Temperature data is recorded every 2-4 hours across the entire year. I averaged data across the three loggers to get an estimate of mean plot conditions. I estimate last snow cover date by finding the first spring day with mean temperature >2°C and >1°C difference between maximum and minimum daily temperatures, indicating that a sensor is no longer insulated by snowpack (Zettlemoyer et al, 2024). When snowpack is present, soil temperature remains constant due to insulation from the snow. Thus, I can use a combination of the soil temperature and its variation to estimate snowmelt.

Floral Display Over Time

I counted the number of open flowers for the three species at each transect throughout the season to measure the overlap in flowering distributions. I used photographs of 0.5x0.5m quadrats along the transect to count flowers after the flowering season ended (Figure 6). Photographs were taken three days per week. This method allowed me to maximize my time in the field, given some individuals of each species can produce hundreds of flowers. At each site, I placed a quadrat made of PVC piping against a transect tape running along the transect. If flowers of either of the three focal species were present in the transect, I would take a photo of the quadrat; otherwise, I recorded 0 open flowers for that quadrat at that time. Cameras were positioned so that the PVC quadrat's top and bottom edges lined up with the photograph's edges. Once a photo was taken, I moved the quadrat to the next 50cm location. If there were no flowers from the three focal species in a quadrat, that quadrat was skipped. After the field season had passed, I went through every photo and quantified the number of flowers of each species that were present in each quadrat. Flowers were not counted if they were early (buds), senesced, or overlapped with other quadrats. When I found overlap in quadrats, I counted them in the first quadrat where they were observed, and ignored them in later ones.

Synchrony Estimates

I calculated a synchrony index for each focal species in each quadrat of a site by comparing the flowering distribution of that species within a quadrat to the site-level flowering distribution of each of the three focal species. This resulted in quadrat-level estimates of both conspecific and heterospecific synchrony for each of the three focal species. The synchrony index quantifies the amount of overlap between two flowering distributions (Hall et al 2018), as:

$$\mathrm{SI_q} = 1 - 0.5 \sum_{d=1}^{D} | \frac{\mathrm{F_{qd}}}{\mathrm{F_{qs}}} - \frac{\mathrm{F_{sd}}}{\mathrm{F_{ss}}} | \, (1)$$

where F_{qd} and F_{sd} are the total number of open flowers on day d for a quadrat q or for the site s, *and* F_{qs} and F_{ss} are the total number of flowers produced across all D census days for a quadrat q or for the site s, respectively. This index ranges from 0, where there is no overlap in flowering between a quadrat and the site, and 1, where there is perfect overlap between the quadrat and the site. Conspecific synchrony quantifies the overlap between a species' flowering distribution within a quadrat to the site level flowering distribution of the same species. Heterospecific synchrony, similarly, quantifies the overlap between a species' flowering distribution within a quadrat to the site level floral display of each of the other two species, resulting in two estimates of heterospecific synchrony per species (ex. *Silene* vs*. Minuartia*, and *Silene* vs. *Phlox*).

Pollen Deposition

At each of the four sites, I collected stigmas from each plant species and sex (when applicable) to observe the composition and quantity of pollen deposited on receptive flowers. Throughout the flowering season (6/19-7/28), we visited each site twice per week and collected 10 stigmas from haphazardly selected individuals of each species. For gynodioecious species, I aimed to collect 5 stigmas from individuals of each sex. I collected all stigmas from 4-10 individuals per species per sampling date, with no more than three flowers collected from a single individual. *Silene acaulis* and *Minuartia obtusiloba* produced three stigmas per flower and *Phlox condensata* produced one per flower. I did not record the identity of plant individuals when collecting stigmas, and therefore cannot include this as a covariate in analyses. Stigmas were preserved in microcentrifuge tubes filled with a mixture of acetic acid and ethanol, then transferred to tubes filled with 75% ethanol after 24 hours (Kearns and Inouye 1993). In order to identify pollen grains of particular species, I also collected anthers of each of the three focal species as well as other co-flowering plant species found within a given site to form a pollen library. Anthers were preserved similarly to stigmas by storing first in acetic acid and ethanol for 24 hours, then transferring to 75% ethanol until ready to be mounted.

Anthers were mounted on slides and observed under a microscope (Accu-Scope® EXI-310) and imaged to create a pollen library for future reference. Stigmas were mounted on slides using a 20% glycerin solution. All stigmas from an individual flower were mounted on the same slide. Pollen grains were viewed under a (get exact brand and model) microscope. I used the pollen library as a reference to visually identify pollen grains found on the collected stigmas based on size and morphology. At this stage, I noted that *S. acaulis* pollen and *M. obtusiloba* pollen grains were indistinguishable based on morphology and size. I attribute this to these species being in the same family. Pollen grains that were unfamiliar or not present in the pollen library were categorized based on shape. The number of heterospecific pollen grains and conspecific pollen grains were recorded. *S. acaulis* pollen and *M. obtusiloba* pollen were categorized as Carophyllaceae pollen.

Fruit Set

Towards the end of the field season (7/21 –8/1), demographic data were collected for all mapped plants in a transect. Among other measurements, this includes fruit count and plant size, which were used in this study. Plant size for *M. obtusiloba* and *S. acaulis* was determined by calculating the area of the plant as an ellipse (Morris and Doak 2010). I measured the plant's length along the longest axis and then the length perpendicular to the longest. The percentage of the plant missing from the ellipse was estimated as well. These measurements were used to calculate the final area of the plant. Plant size for *P. condensata* was assessed using rosette count. Fruit count consisted of the total fruits produced by a single plant.

Statistical Analyses

All analyses were performed using R Statistical Software (v4.1.3; R Core Team 2021). All model assumptions were met before running analyses.

Synchrony and snowmelt: I tested patterns of flowering synchrony across sites by fitting separate general linear models for each species. For each species, I used synchrony as the response variable and included site, comparison species, and their interaction as predictors. Comparison species refers to which species' flowering distribution – *S. acaulis, M. obtusiloba*, or *P. condensata* - at the site level was being compared to the species at the quadrat level. For example, *S. acaulis* at the quadrat level had three comparisons: *S. acaulis* at the site level (conspecific synchrony), and *M. obtusiloba* and *P. condensata* at the site level, (heterospecific synchrony). Thus, including comparison species as a predictor allowed me to test for differences in conspecific vs. heterospecific synchrony both as a main effect and as an interaction with site. I used a similar approach to assess the effect of snowmelt time on synchrony. I again fit separate general linear models for each species with synchrony as the response variable, and included mean snowmelt date, comparison species, and their interaction as predictors. I tested the significance of predictors with type III F-tests using the Anova function in the car package (Fox and Weisberg 2019) and calculated estimated marginal means and confidence intervals using the emmeans package (Lenth 2023).

Pollen deposition: To determine whether floral display influences conspecific pollen deposition, I tested for a relationship between the total number of conspecific flowers within a transect on a particular sampling day and the percentage of conspecific pollen grains found on nearby stigmas collected the following day. I fit generalized linear models for each species, using the quasibinomial family to account for large variation in the data. I used the number of conspecific flowers, site, and the interaction between conspecific flowers and site as predictor variables. I tested for effects of sex for *Silene* and *Minuartia*, but sex was not significant so I excluded it from my analyses. I tested the significance of predictors with type III F-tests using the Anova function in the car package (Fox and Weisberg 2019).

Using a similar method to testing the effects of floral display, I tested the effect of snowmelt timing on conspecific pollen percentage using the mean snowmelt date as a predictor variable. I fit generalized linear models for each species using the quasibinomial family. I tested the significance of predictors using type II F-tests using the Anova function in the car package (Fox and Weisberg 2019).

Reproductive success: To assess whether flowering synchrony influences reproductive success, I tested for a relationship between the fruit production of individual plants and the synchrony values calculated for the quadrat in which that plant occurred. This allowed me to relate reproductive success, which I measured at the level of individuals, with patterns of local flowering synchrony measured at the level of quadrats. I fit negative binomial models to account for overdispersion in fruit count data, and fit separate models for each species. I used quadrat-level summed fruit number as the response variable and included each of the three measures of synchrony (conspecific plus both heterospecific comparisons), plant size (log transformed plant area for *S. acaulis* and *M. obtusiloba*, log transformed rosette count for *P. condensata*), plant sex, and site as predictor variables. I fit negative binomial generalized linear models for each species, using the log link function to account for overdispersion. I then ran a type II F-test with the Anova function in the car package (Fox and Weisberg 2019) on each of the models to determine significance of predictors.

Using a similar method to testing the effects of synchrony, I tested the effect of snowmelt timing on fruit set using the mean snowmelt date as a predictor variable. I also included plant size and site as predictors. I fit negative binomial generalized linear models for each species, using the log link function to account for overdispersion, and ran a type II F-test with the Anova function in the car package (Fox and Weisberg 2019) on each of the models to determine significance of predictors.

RESULTS

Synchrony and Snowmelt Timing

Early 1 experienced the earliest average snowmelt, followed by Early 2, Late 1, and Late 2, respectively (Figure 6). Snowmelt timing differences were slight between sites Early 2, Late 1, and Late 2.

Across sites, I see distinct differences in the flowering distributions of the three species. *P. condensata* flowers first at most sites, with a short and narrow flowering window (Table 2, Figure 7). *Phlox condensata* generally produces the largest floral display at peak flowering compared to the other species, with the exception of Early 1. *S. acaulis* flowering peaks in between the other two species, with flowering window varying between sites. *M. obtusiloba* peaks latest of the three, and has a long flowering window. Peak flowering dates for *P. condensata* and *M. obtusiloba* were earlier in the more exposed sites compared to the sheltered sites. *Silene acaulis* peak flowering dates were inconsistent between sites, however Late 1 peak flowering date was later than the other three. (Table 2, Figure 7).

There was a significant interaction effect of site with comparison species, indicating that synchrony differed among sites, but this depended on the type of synchrony for all three species (Table 3). All three species consistently had higher conspecific synchrony than heterospecific synchrony across sites. *Phlox condensata* and *M. obtusiloba*, were least synchronous with each other (Figure 8).

The interaction between comparison species and snowmelt date was significant for all three species (Table 4), indicating that the effect of snowmelt timing varies depending on species and species comparison. For *P. condensata,* heterospecific synchrony with both *S. acaulis* and *M. obtusiloba* decreased significantly with earlier snowmelt date, whereas conspecific synchrony remained stable and high (~0.75) regardless of snowmelt conditions (Figure 9). For *M. obtusiloba*, conspecific synchrony and synchrony with *S. acaulis* increased significantly with earlier snowmelt (Figure 9). In *S. acaulis*, there was significantly less synchrony with *P. condensata* with earlier snowmelt (Figure 9).

Pollen Deposition

Carophyllaceae pollen percentage in *M. obtusiloba* appears to be lowest early in the flowering season across all sites, and in *S. acaulis* in most sites except Late 2 (Figure 10). Contrastingly, in *P. condensata*, the percentage of conspecific pollen appears to remain consistently high throughout the flowering season (Figure 10).

The interaction between the number of conspecific flowers and site was a significant predictor of the proportion of conspecific pollen and Carophyllaceae pollen deposited on stigmas in both *P. condensata* and *S. acaulis,* respectively (Table 5). In *M. obtusiloba*, main effects of floral display and site were significant, but not the interaction, indicating floral display is an effective predictor of Carophyllaceae pollen deposition regardless of site (Table 5). The effect of floral display was positive in *M. obtusiloba* across sites, but negative in *P. condensata* in Early 1 and Late 1 (Figure 11). In *S. acaulis*, Carophyllaceae pollen percentage increased with conspecific floral display in Early 2 and Late 1, but decreased in Late 2 (Figure 11). Earlier mean snowmelt date significantly decreased Carophyllaceae pollen deposition in *Silene acaulis* and *Minuartia obtusiloba*, but had no effect on *Phlox condensata* conspecific pollen deposition (Table 6, Figure 12).

Fruit Production

Conspecific synchrony was a significant predictor of fruit production in both *M. obtusiloba* and in *P. condensata* (Table 6). For both of these species, conspecific synchrony increased fruit production (Figure 13). There was no significant effect of conspecific synchrony on fruit production in *S. acaulis* (Table 6). Interestingly, *S. acaulis* synchrony with *M. obtusiloba* significantly increased fruit production in *S. acaulis*, whereas synchrony with *S. acaulis* significantly decreased fruit production in *P. condensata* (Table 6, Figure 13). In all three species, both site and plant size also significantly influence fruiting (Table 6). Earlier mean snowmelt date significantly decreased fruit production in *M. obtusiloba* and *P. condensata*, but significantly increased fruit set for *S. acaulis* (Table 7, Figure 14).

DISCUSSION

Changes in flowering synchrony of plant communities due to climate change could have profound impacts on pollinator visitation and reproductive success. In this study, I compared conspecific and heterospecific synchrony, pollen deposition, and reproductive success of three co-flowering alpine plants in sites that vary in the timing of snowmelt. I found that flowering synchrony varies significantly with snowmelt date, but this depends on the type of synchrony. I find that conspecific floral density lowers conspecific pollen deposition in *Phlox condensata*, increases it in *Minuartia obtusiloba*, and mixed results depending on site for *S. acaulis*. Fruit set is influenced by conspecific and heterospecific synchrony depending on the species and comparison species. Earlier snowmelt timing overall decreases fruit set in *M. obtusiloba* and *P. condensata*, but increases fruit set in *S. acaulis*. Overall, plant phenological responses to environmental changes like snowmelt timing appear to be species specific, as are the consequences for reproduction.

Snowmelt and Synchrony

The effect of snowmelt timing on flowering synchrony differed in magnitude and even direction depending on the species involved (Figure 9). Overall, conspecific synchrony values were consistently higher than the heterospecific synchrony values for all three species, regardless of snowmelt. This is consistent with another study examining snowmelt effects on synchrony within populations of *Empetrum hermaphroditum*, an alpine dwarf shrub (Bienau et al 2015), and another study investigating synchrony across multiple species (Carbognani et al 2016). I find the largest effects of snowmelt date are on heterospecific synchrony (Figure 9). The two earlier flowering species were less synchronous together with earlier snowmelt, indicating that climate change may reduce synchrony between these species as regular spring snowmelt times become earlier. In other research, Chen et al (2022) noted reduced heterospecific synchrony in warmed plots compared to untreated plots, consistent with what I see in *P. condensata* and *S. acaulis*. This trend is also seen in Fisogni et al (2022), where heterospecific synchrony decreased across an elevation gradient due to warming temperatures across four decades of sampling. Perhaps these two species rely on different phenological cues to flower, given that phenological responses to climate change are often species specific, and even if species respond to the same factor, they can respond in different directions (Arft et al 1999, Galen and Stanton 1995, Hulber et al 2010).

Conversely, I find in later flowering species, heterospecific synchrony increases with earlier snowmelt. Earlier snowmelt also induced greater conspecific synchrony in later flowering species. If conspecific synchrony is greater with earlier snowmelt in *M. obtusiloba*, this might provide greater outcrossing opportunities under climate warming. Carbognani et al

(2016) saw greater synchrony between both conspecifics and heterospecifics in experimentally warmed plots compared to untreated plots, which is consistent with most of my observations in *M. obtusiloba. Minuartia obtusiloba* flowering has a greater spread throughout the season and peaks later than the other species. Moore and Lauenroth (2017) find that earlier flowering species are more phenologically responsive to warming, whereas in later flowering species with longer flowering durations, flowering phenology is driven more by precipitation. Perhaps species like *Minuartia* that have a general strategy of flowering for longer time periods will show less shifts in flowering time in response to snowmelt.

Reproductive Success

Synchrony and floral display influence strong effects on conspecific pollen deposition and fruit set, however these effects indicate a mix of competitive and facilitative interactions. In *P. condensata*, conspecific floral display decreases the proportion of conspecific pollen deposition, and this is dependent on site (Figure 11). This finding is especially interesting, given that I found flowering synchrony with conspecifics in *P. condensata* increases fruit set. A study looking at heterospecific pollen deposition in a hummingbird pollinated community found increased reproductive success with greater amounts of heterospecific pollen, and they suggest the negative consequences of heterospecific pollen deposition may be overcome by sufficient deposition of conspecific pollen (Lopes et al 2021). I find mixed results in Silene acaulis, where the effect of conspecific floral display on the percentage of conspecific pollen deposited on stigmas is site dependent. In two sites, there is a positive relationship, and in one site, I find a negative relationship. This indicates there may be site differences in either pollinator interactions or selfing in this species. In *Minuartia*, I see that a greater floral display size increases the percentage of conspecific pollen deposited on stigmas regardless of site, indicating that fertilization is more likely with larger conspecific floral displays. This is consistent with what I see in fruit production as well for this species.

I found evidence for conspecific synchrony to be an important driver of reproductive output in the form of fruit set in two of my three study species (Figure 13). *Silene acaulis* did not exhibit a relationship between conspecific synchrony and fruit set, contradictory to my hypothesis and results of other studies on conspecific synchrony in this species (Hall et al 2018, Kempe 2014). Higher conspecific synchrony is thought to increase outcrossing potential, and therefore increase reproductive output (Tachiki et al 2010, Feldman 2008). However, there is a possibility that competition for pollinators can nullify the facilitative effect of attracting pollinators, as exemplified in Schiffer et al (2022), where flowering before or after the peak blooming period increased plant fecundity through escaping conspecific competitors. In *Minuartia obtusiloba* and *Phlox condensata*, I find that higher conspecific synchrony increases fruit set, which is consistent with my hypothesis and supports conspecific facilitation. In *M. obtusiloba*, earlier snowmelt increases conspecific synchrony, indicating that climate change may increase reproduction through this mechanism.

Flowering synchronously with *M. obtusiloba* increased fruit set in *S. acaulis*, a result consistent with the hypothesis of facilitation between heterospecifics (Figure 13). This could be because the facilitative effect of attracting pollinators is stronger than the competitive effect of sharing pollinators between these two species. This may be driven by the fact that *S. acaulis* and *M. obtusiloba* are closely related and share similar pollination syndromes (Moeller 2004). Furthermore, pollinator observations of both species show they are often visited by the same species, and thus both species' compounded floral display may attract pollinators beneficial to both species (Resasco unpubl. data). In contrast, I find that flowering synchronously with *S. acaulis* decreased fruit set in *P. condensata*, consistent with the prediction that heterospecific plants compete for pollinator resources. In this case, perhaps pollinator competition is stronger than facilitation between these two species. Given that synchrony with *Silene acaulis* decreases *Phlox* fruit production, earlier snowmelt may benefit reproduction this species.

Climate Change Implications

All of my study species are long-lived plants. Plants that utilize this strategy generally tend to put more energy into survival rather than recruitment (Forbis and Doak 2004). Nonetheless, particularly in future climate scenarios where warming threatens survival, reproduction is an important demographic factor contributing to population persistence in long-lived species. For example, populations in *Silene acaulis'* southern range are increasingly limited by the effects of climate warming on reproduction (Morris and Doak 2010). Thus, it is important to study the effects of climate change on reproduction in long-lived plants as well as shorter-lived plants.

I find that snowmelt timing has overall effects on reproduction in my study species, and these effects appear to be disconnected from my findings on species interactions (Figure 15). Though we see earlier snowmelt has positive effects on fruit production indirectly in *M.*

obtusiloba via increases in conspecific synchrony, earlier snowmelt appears to decrease fruit production (Figure 13). In *Phlox condensata*, we see a release of competition from *S. acaulis* in early snowmelt conditions, but still we see an overall negative effect of earlier snowmelt on reproduction. These results indicate positive changes in plant-plant interactions in these species may not be enough to compensate for the other negative effects of earlier snowmelt on reproductive output. For example, earlier snowmelt can expose flowers to more frost events, which can decrease reproduction (Inouye 2008, Wheeler et al 2014). Earlier snowmelt timing has a positive effect on fruit set overall in *Silene acaulis*, though the mechanisms behind this finding are unclear.

CONCLUSION

I find evidence for species specific responses to synchrony with earlier snowmelt between both conspecifics and heterospecifics in my three study species. Based on my results, these responses likely will have species dependent impacts on reproductive success. These species-specific responses may be driven by factors such as main pollinator species and pollinator sharing among plant species, typical flowering duration, and phenological cues, to name a few. Nonetheless, the plant-plant responses I investigate here appear to have relatively little impact on the overall effects that earlier snowmelt have on reproduction in my study species. Future research should consider the interplay between direct and indirect effects of earlier snowmelt timing on plant reproduction.

Table 1: Information regarding the four sites used in this study. Elevation is shown in meters. For each flowering species, the number of tagged individuals of that species present at the site is shown.

Site	**Latitude**	**Longitude**	**Elevation (m)**	***S. acaulis***	***M. obtusiloba***	***P. condensata***	**Quadrats**
Early 1	40.05312103	-105.57557530	3514	23	104	102	46
Early 2	40.05400306	-105.57878193	3503	98	179	112	54
Late 1	40.05304495	-105.57698180	3493	48	101	113	54
Late 2	40.05610614	-105.58080640	3501	46	103	105	56

Table 2: Table showing the onset, peak and last day of year (DOY) in which flowering occurred for each species at each site.

Species	Site	Onset DOY	Peak DOY	Last DOY
Silene	Early 1	178	187	210
	Early 2	178	187	>210
	Late 1	175	185	203
	Late 2	178	192	208
Phlox	Early 1	171	185	201
	Early 2	166	180	203
	Late 1	166	180	201
	Late 2	173	185	210
Minuartia	Early 1	178	194	>210
	Early 2	175	194	>210
	Late 1	171	192	>210
	Late 2	175	199	>210

Table 3: Results of the Anova to assess the effect of site on flowering synchrony across the three focal species. Comparison species refers to which species' flowering distribution at the site level is being compared to the species at the quadrat level.

Site ANOVA *Silene*				
Factor	Df	F value	P	**Significant?**
Site	3	2.4577	0.06282	.
Comparison species	2	12.4385	6.17E-06	***
Site:Comparison species	6	2.7592	0.01246	*
Site ANOVA *Phlox*				
Factor	Df	F value	P	
Site	3	5.0206	1.92E-03	**
Comparison species	2	241.606	< 2.2E-16	***
Site:Comparison species	6	19.9249	< 2.2E-16	***
Site ANOVA *Minuartia*				
Factor	Df	F value	P	
Site	3	2.624	4.97E-02	*
Comparison species	2	66.5706	< 2.2E-16	***
Site:Comparison species	6	9.0251	1.88E-09	***

Table 4: Results of the Anova to assess the effect of snowmelt day of year (DOY) on flowering synchrony across the three focal species. Comparison species refers to which species' flowering distribution at the site level is being compared to the species at the quadrat level.

Snowmelt ANOVA *Silene*				
Factor	Df	F value	P	**Significant?**
Mean Snowmelt DOY	1	1.3979	0.2379	
Comparison species	2	4.3432	1.37E-02	*
Mean Snowmelt DOY: Comparison species	2	4.4025	0.01295	*
Site ANOVA *Phlox*				
Factor	Df	F value	P	
Mean Snowmelt DOY	1	13.147	3.13E-04	***
Comparison species	2	25.048	3.71E-11	***
Mean Snowmelt DOY: Comparison species	2	23.913	1.06E-10	***
Site ANOVA *Minuartia*				
Factor	Df	F value	P	
Mean Snowmelt DOY	1	6.1541	1.34E-02	*
Comparison species	2	16.6893	8.86E-08	***
Mean Snowmelt DOY: Comparison species	2	15.869	1.93E-07	***

Table 5: Results of the Anova to assess the effect of conspecific floral density on the proportion of conspecific pollen deposited on stigmas across the three focal species.

Pollen Deposition ANOVA *Silene*				
Factor	**Df**	**Chisq**	**P**	**Significant?**
Conspecific Flowers	1	0.5378	0.463334	
Site	3	5.5764	1.34E-01	
Conspecific Flowers:Site	3	13.875	0.003081	**
Pollen Deposition ANOVA *Phlox*				
Factor	**Df**	**Chisq**	**P**	
Conspecific Flowers	1	4.3886	0.03618	*
Site	3	1.8772	5.98E-01	
Conspecific Flowers:Site	3	8.0873	0.0442421	*
Pollen Deposition ANOVA *Minuartia*				
Factor	**Df**	**Chisq**	**P**	
Conspecific Flowers	1	9.9258	1.63E-03	**
Site	3	19.1658	2.53E-04	***
Conspecific Flowers:Site	3	4.446	0.2171	

Table 6: Results of the Anova to assess the effect of mean snowmelt DOY on conspecific pollen percentage across the three focal species.

Pollen Deposition vs Snowmelt ANOVA ***Silene***				
Factor	Df	Chisq	P	**Significant?**
Mean Snowmelt DOY	1	4.64	7.44E-06	***
Pollen Deposition vs Snowmelt ANOVA ***Phlox***				
Factor	Df	Chisq	P	
Mean Snowmelt DOY		33.281	6.03E-01	
Pollen Deposition vs Snowmelt ANOVA ***Minuartia***				
Factor	Df	Chisq	P	
Mean Snowmelt DOY	3	6.117	1.74E-02	*

Table 7: Results of the Anova to assess the effect of flowering synchrony on fruit set across the three focal species.

Fruit vs Synchrony ANOVA *Silene*

Factor	Df	Chisq	P	**Significant?**
Silene-Silene Synchrony	1	0.33	0.56549	
Silene-Phlox Synchrony	1	3.3	6.93E-02	.
Silene-Minuartia Synchrony	1	6.212	0.01295	*
logArea	1	57.726	3.01E-14	***
Sex	1	0.682	0.40899	
Site	3	28.154	3.37E-06	***

Fruit vs Synchrony ANOVA *Phlox*

Factor	Df	Chisq	P	
Phlox-Phlox Synchrony	1	18.102	2.09E-05	***
Phlox-Silene Synchrony	1	15.752	7.22E-05	***
Phlox-Minuartia Synchrony	1	1.741	0.187	
logRosette	1	313.323	< 2.2E-16	***
Site	3	73.028	9.59E-16	***

Fruit vs Synchrony ANOVA *Minuartia*

Factor	Df	Chisq	P	
Minuartia-Minuartia Synchrony	1	10.632	0.001112	**
Minuartia-Silene Synchrony	1	0.99	3.20E-01	
Minuartia-Phlox Synchrony	1	0.057	0.810498	
logArea	1	149.16	< 2.2E-16	***
Sex	1	0.886	0.346448	
Site	3	8.826	3.17E-02	*

Table 8: Results of the Anova to assess the effect of mean snowmelt DOY on fruit set across the three focal species.

Fruit vs Snowmelt ANOVA *Silene*				
Factor	Df	Chisq	P	**Significant?**
Mean Snowmelt DOY	1	4.64	3.12E-02	*
Sex	1	1.133	0.28723	
logArea	3	61.766	3.87E-15	***
Fruit vs Snowmelt ANOVA *Phlox*				
Factor	Df	Chisq	P	
Mean Snowmelt DOY		33.281	7.98E-09	***
logRosette	1	287.581	< 2.2E-16	***
Fruit vs Snowmelt ANOVA *Minuartia*				
Factor	Df	Chisq	P	
Mean Snowmelt DOY	3	6.117	1.34E-02	*
Sex	1	0.928	0.33537	
logArea		189.573	< 2.2E-16	***

Figure 1: Conceptual diagram of hypotheses for question 1.

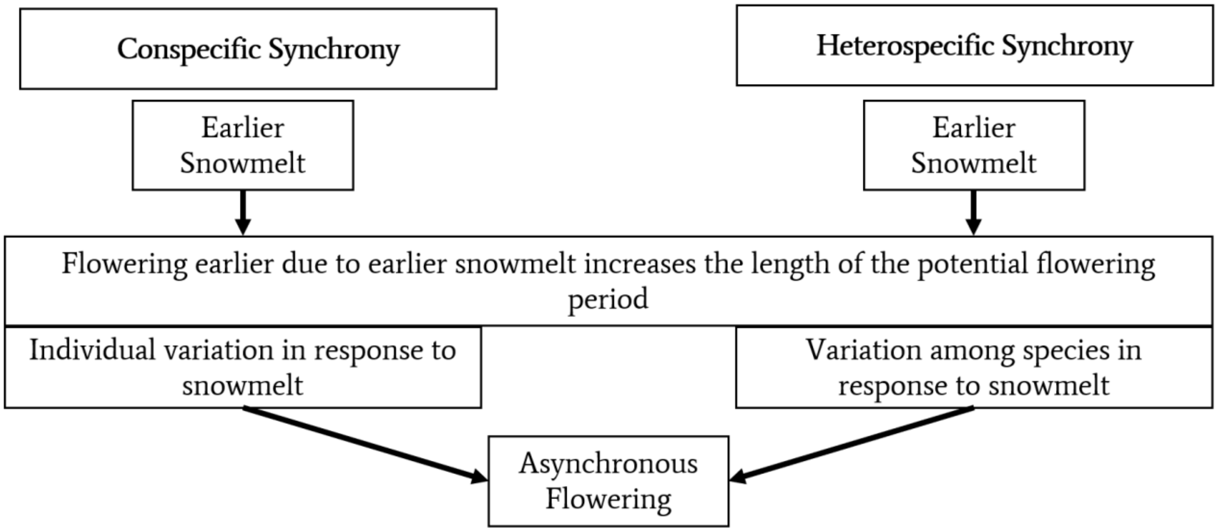


Figure 2: Conceptual diagram of hypotheses for question 2.

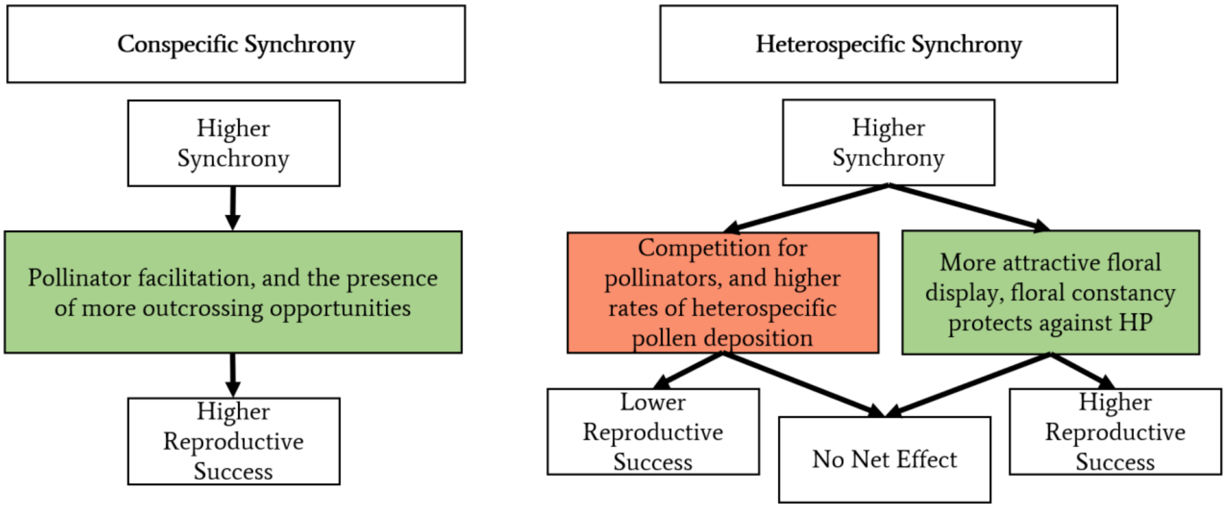


Figure 3: Map showing topography and elevation of the four sites used in my study

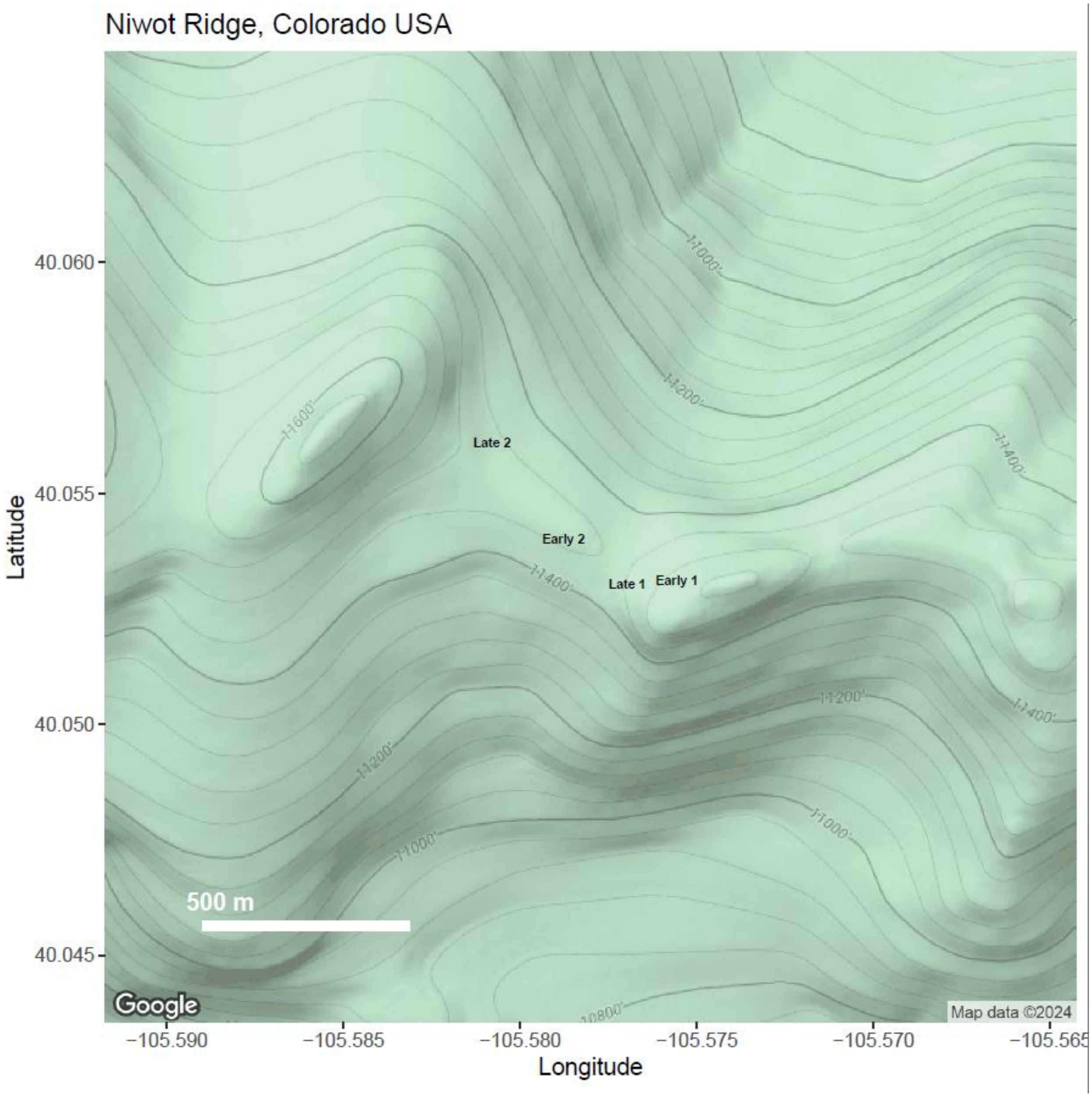


Figure 4: Diagram showing transect layout. Transect length varies by site, with the shortest being 11.5m long and the longest being 14m long. Each transect is delineated by a positive and negative side in order to map plants using an x,y coordinate.

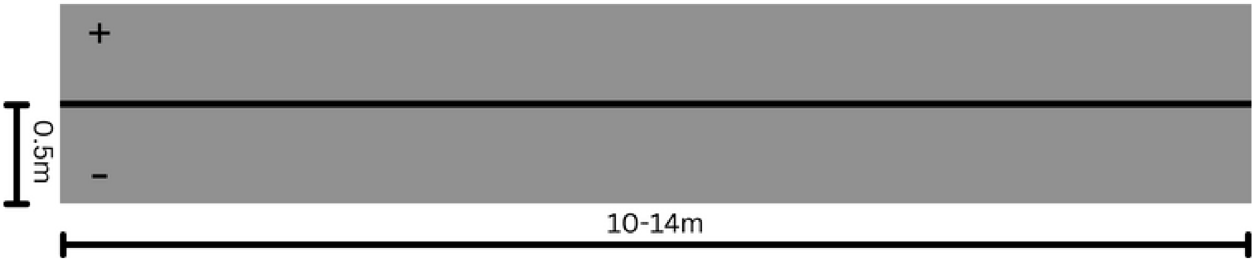


Figure 5: Graphic showing three study species. From top to bottom on the left: *Phlox condensata*, *Minuartia obtusiloba*, *Silene acaulis*. Photo on the right shows an example of the three species flowering together. *Phlox* and *Minuartia* photo courtesy of Southwest Colorado Wildflowers

Figure 6: Boxplot showing the distribution of snowlelt time at each site. Averages, calculated from the 2-3 temperature loggers per site, are shown with red dots. Snowmelt was collected using HOBO temperature loggers placed in varying locations along the focal transect.

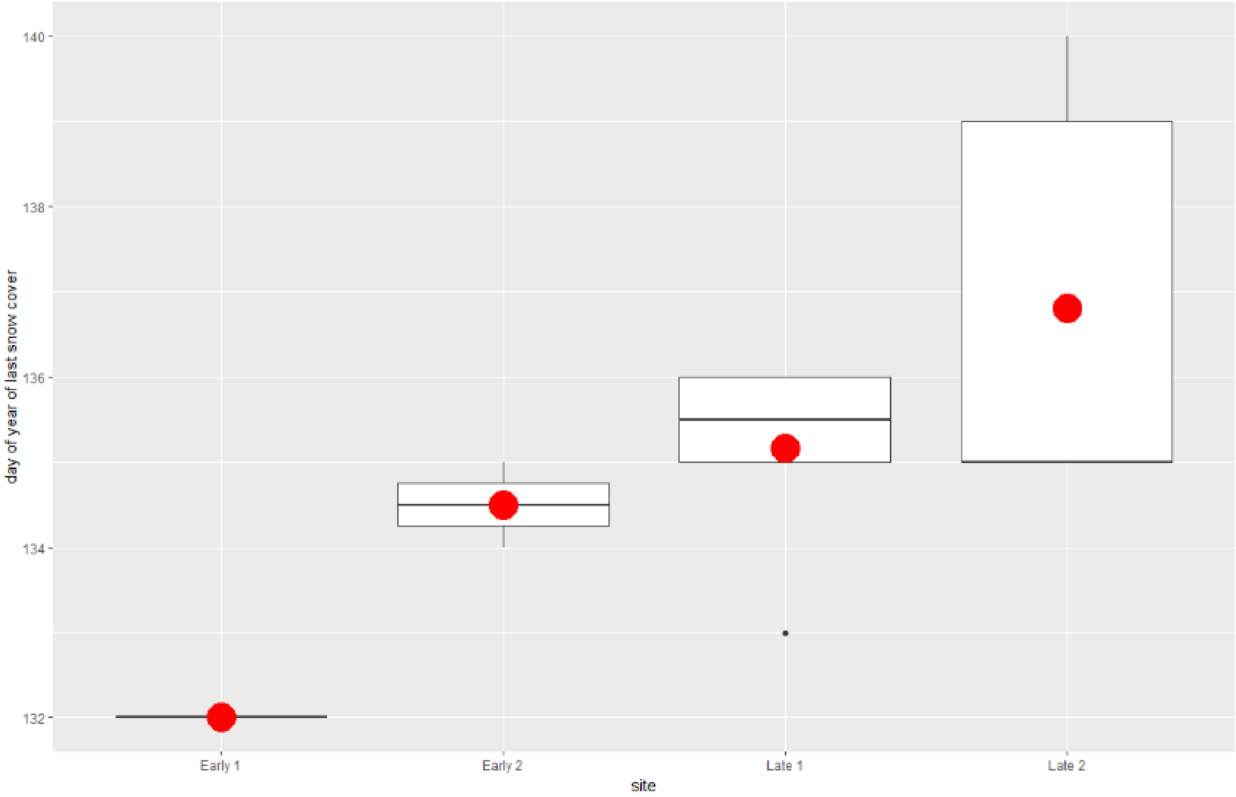


Figure 7: Plots showing the distribution of flowering time for each species. Julian day is shown on the x axis, and flower count is shown on the y axis. Flower counts were collected by manually counting flowers captured in photographs along each transect.

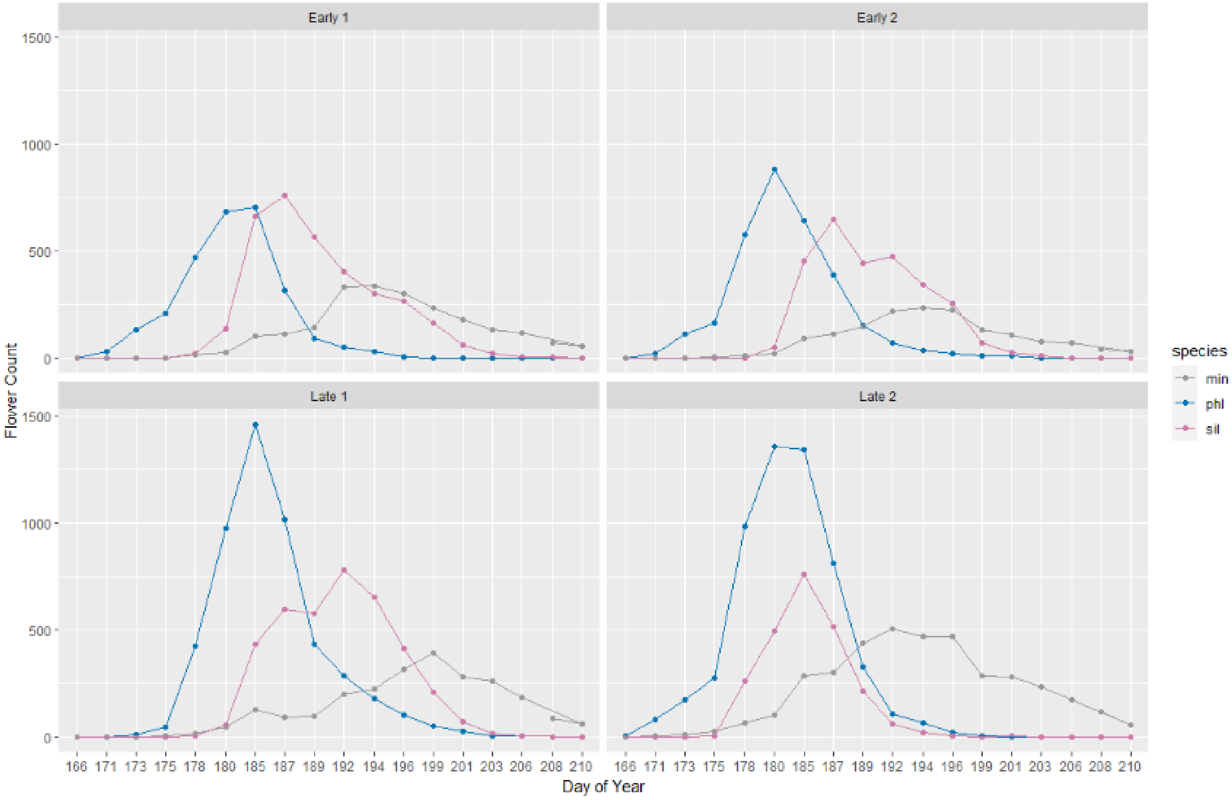


Figure 8: Bar plots showing estimated marginal mean synchrony values at each site organized by quadrat level species. X axis shows comparison species, and y axis shows synchrony index. Black lines show confidence intervals.

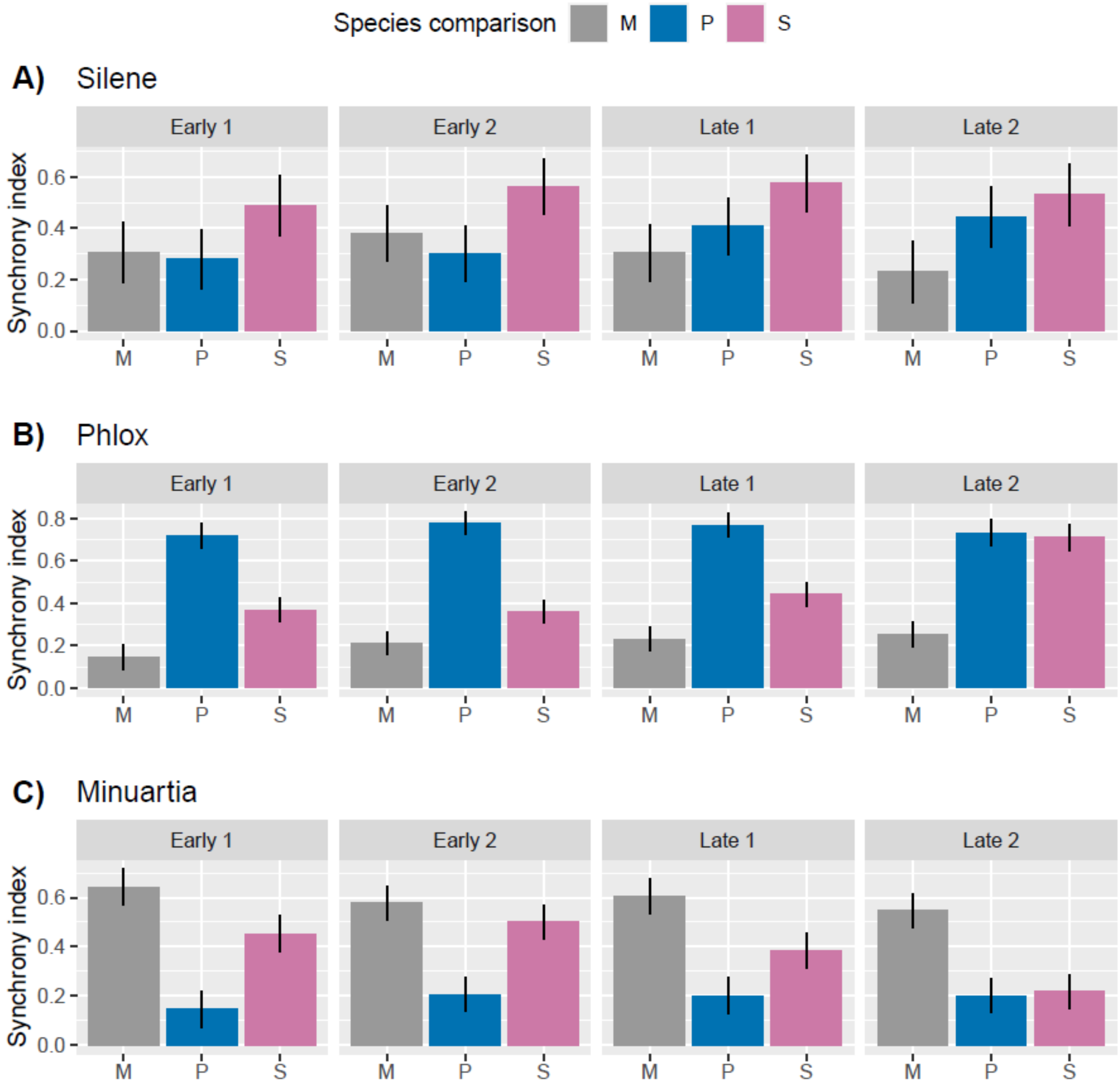


Figure 9: Scatterplots showing the effect of snowmelt timing on heterospecific and conspecific synchrony organized by quadrat level species. Lines show slope of relationship with grey confidence intervals.

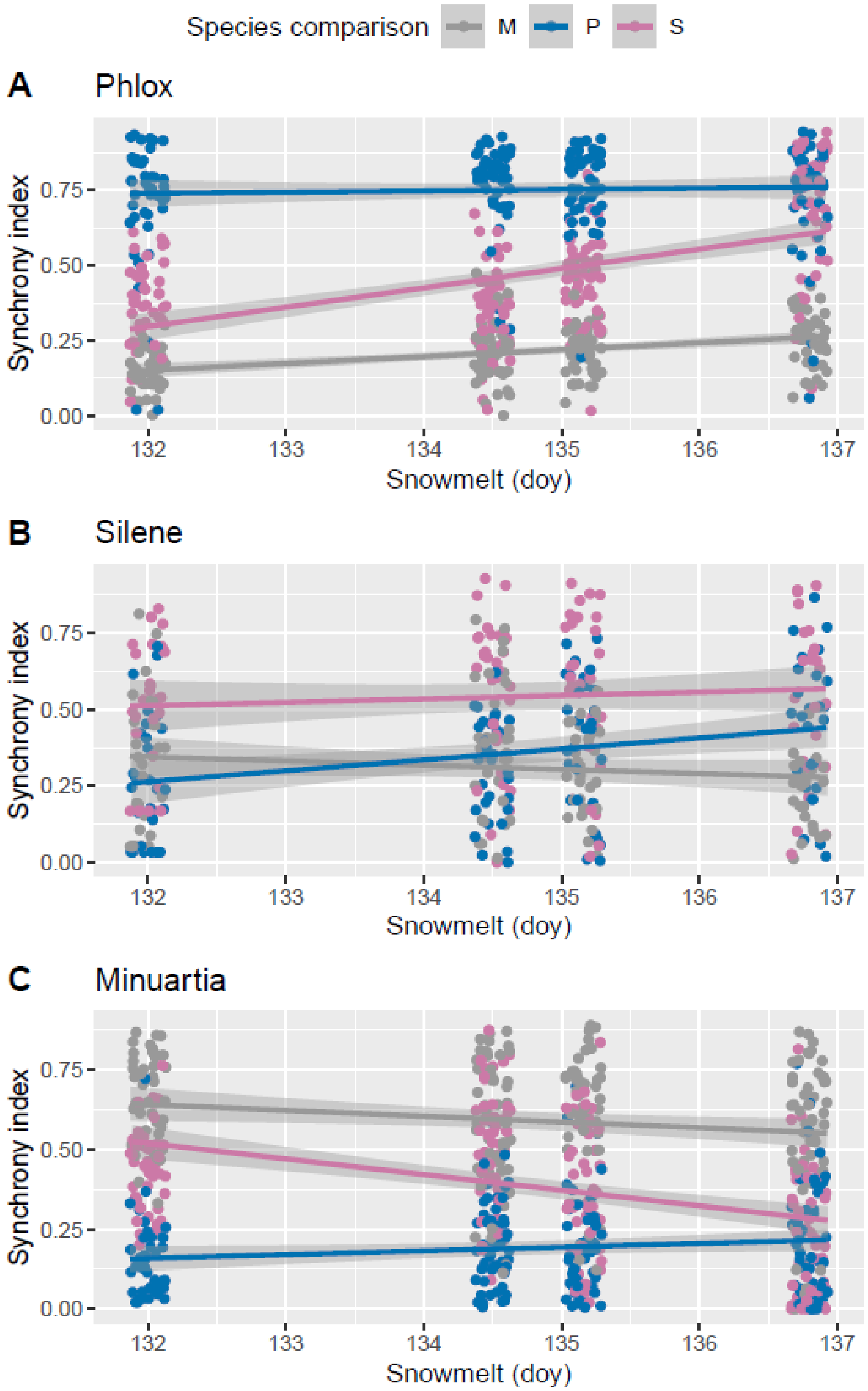


Figure 10: The percent conspecific pollen deposited on stigmas of each of the three species at each site across the growing season.

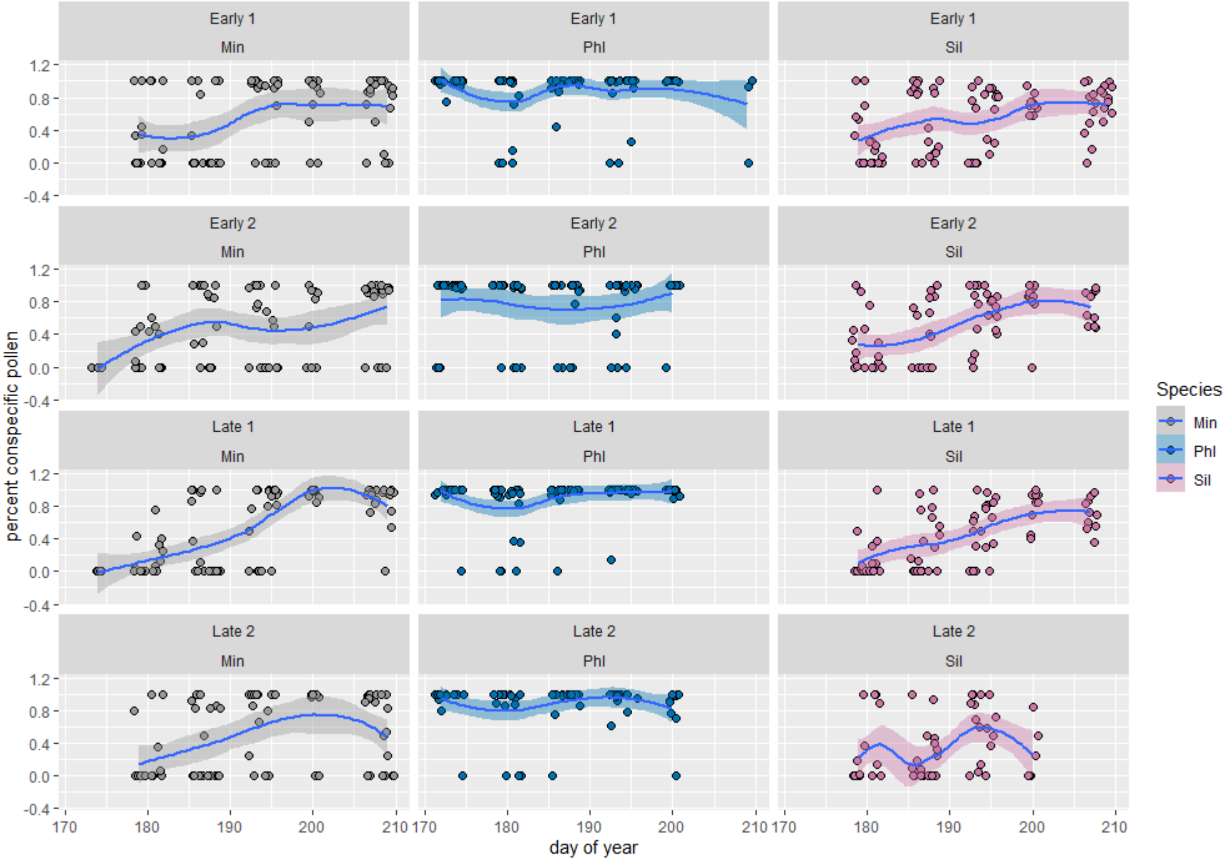


Figure 11: Predicted relationships of conspecific floral display and the proportion of conspecific pollen deposition. Predictions generated using the model.

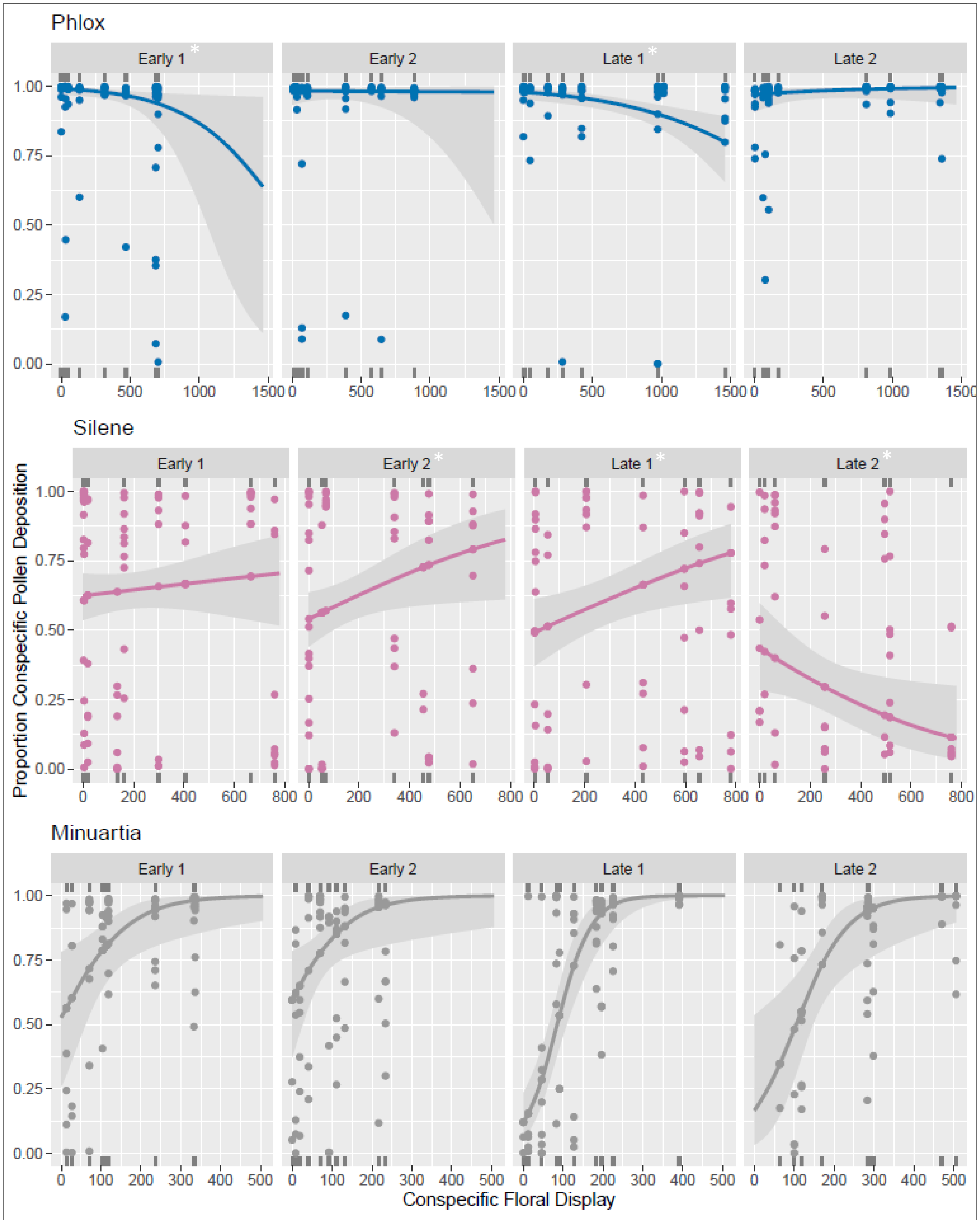


Figure 12: The effect of mean snowmelt day of year (DOY) on the percentage of conspecific pollen deposited on stigmas of the three study species.

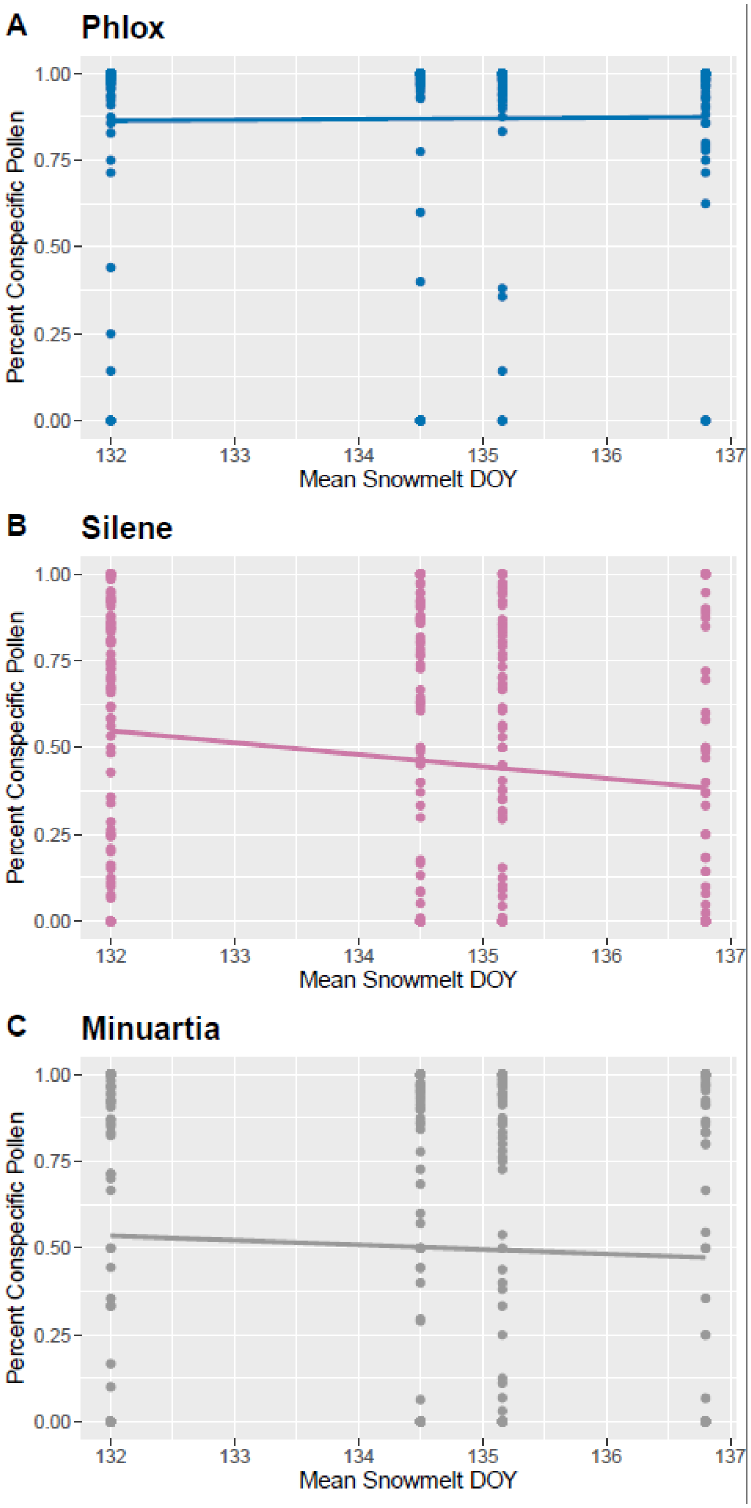


Figure 13: Predicted relationships of conspecific and heterospecific synchrony with fruit set in each of the three species. Asterisks indicate significance of synchrony as a predictor. Predictions generated using the model

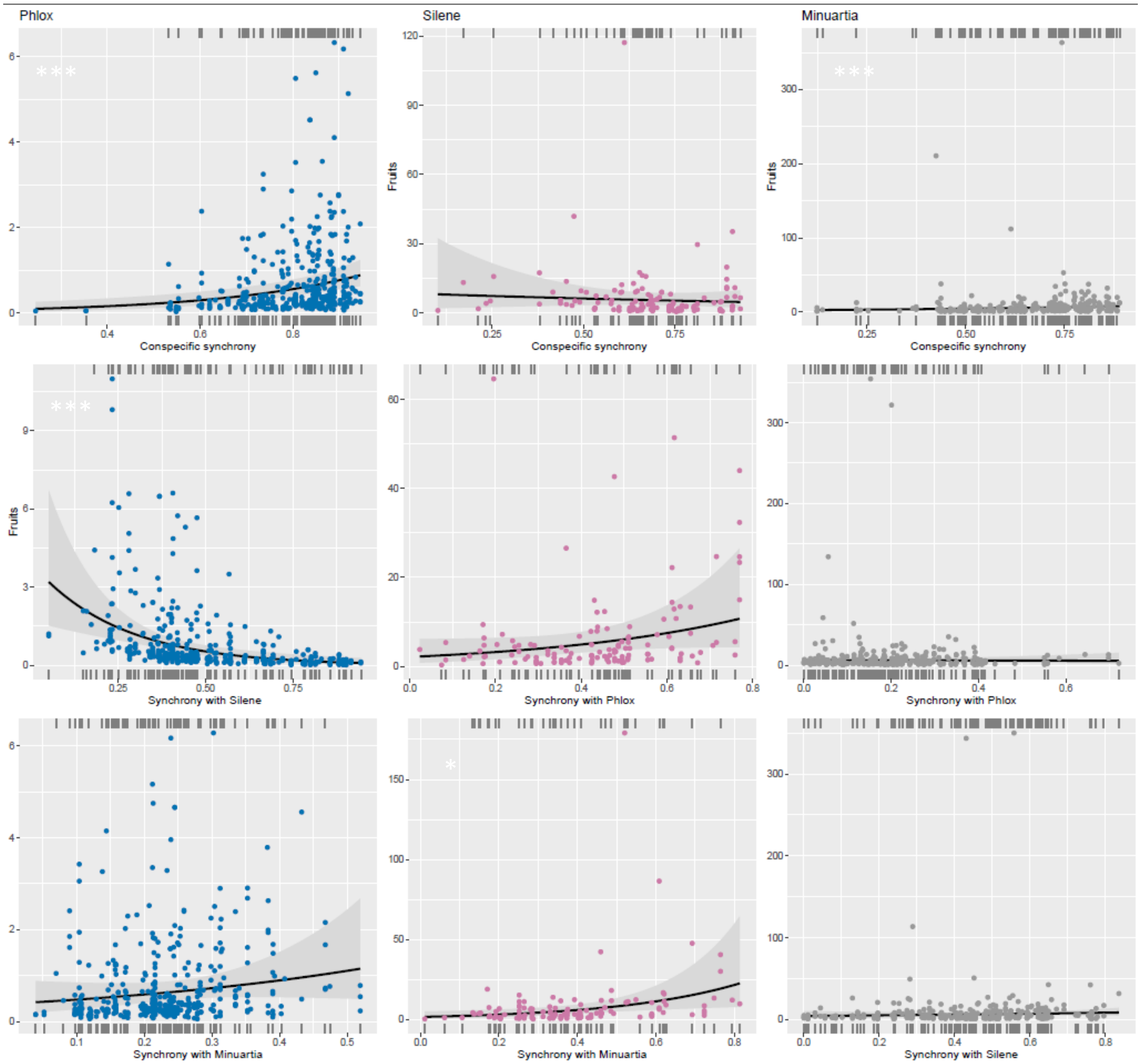


Figure 14: Effect of mean snowmelt day of year (DOY) on the number of fruits produced by the three study species.

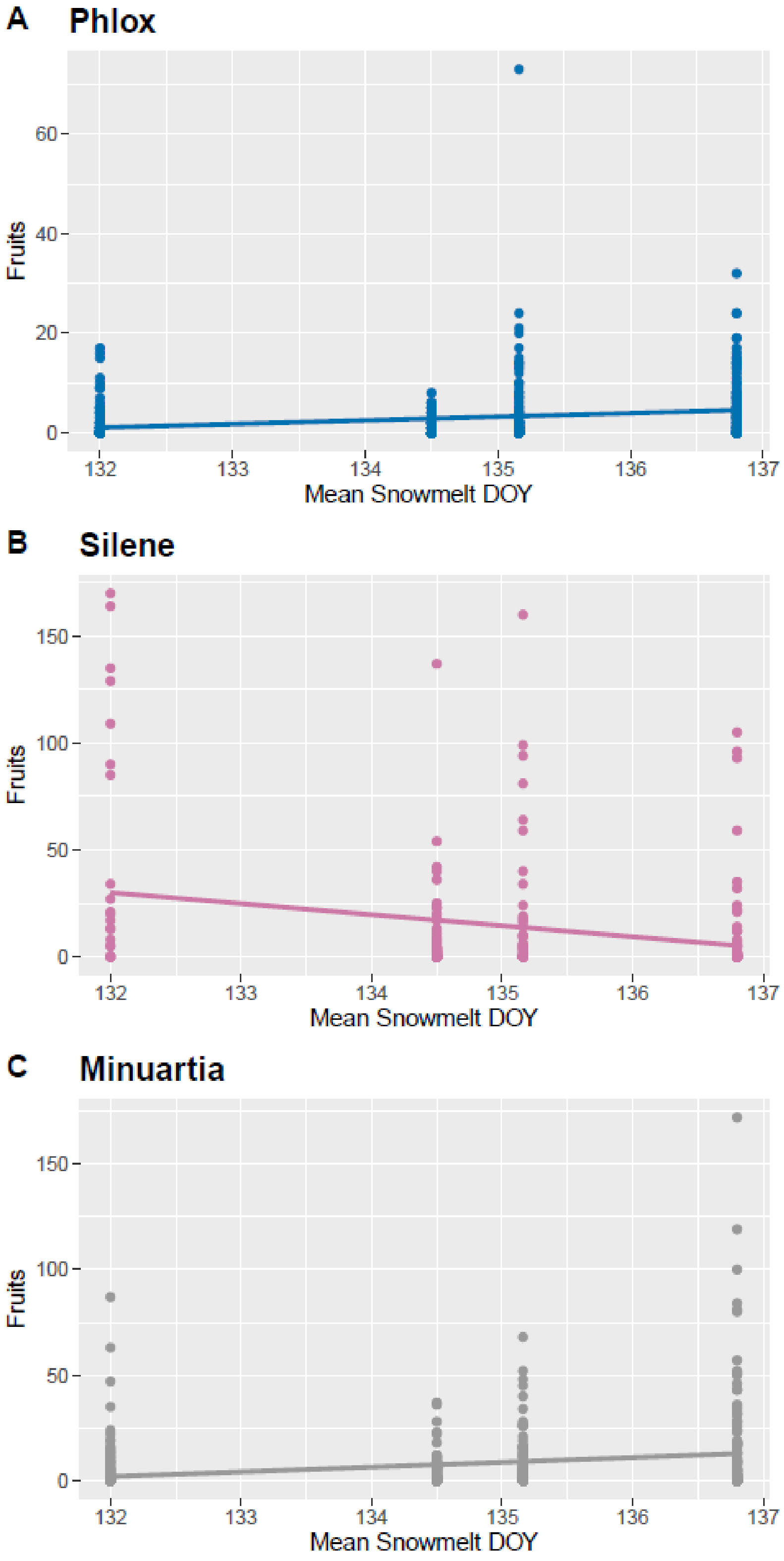
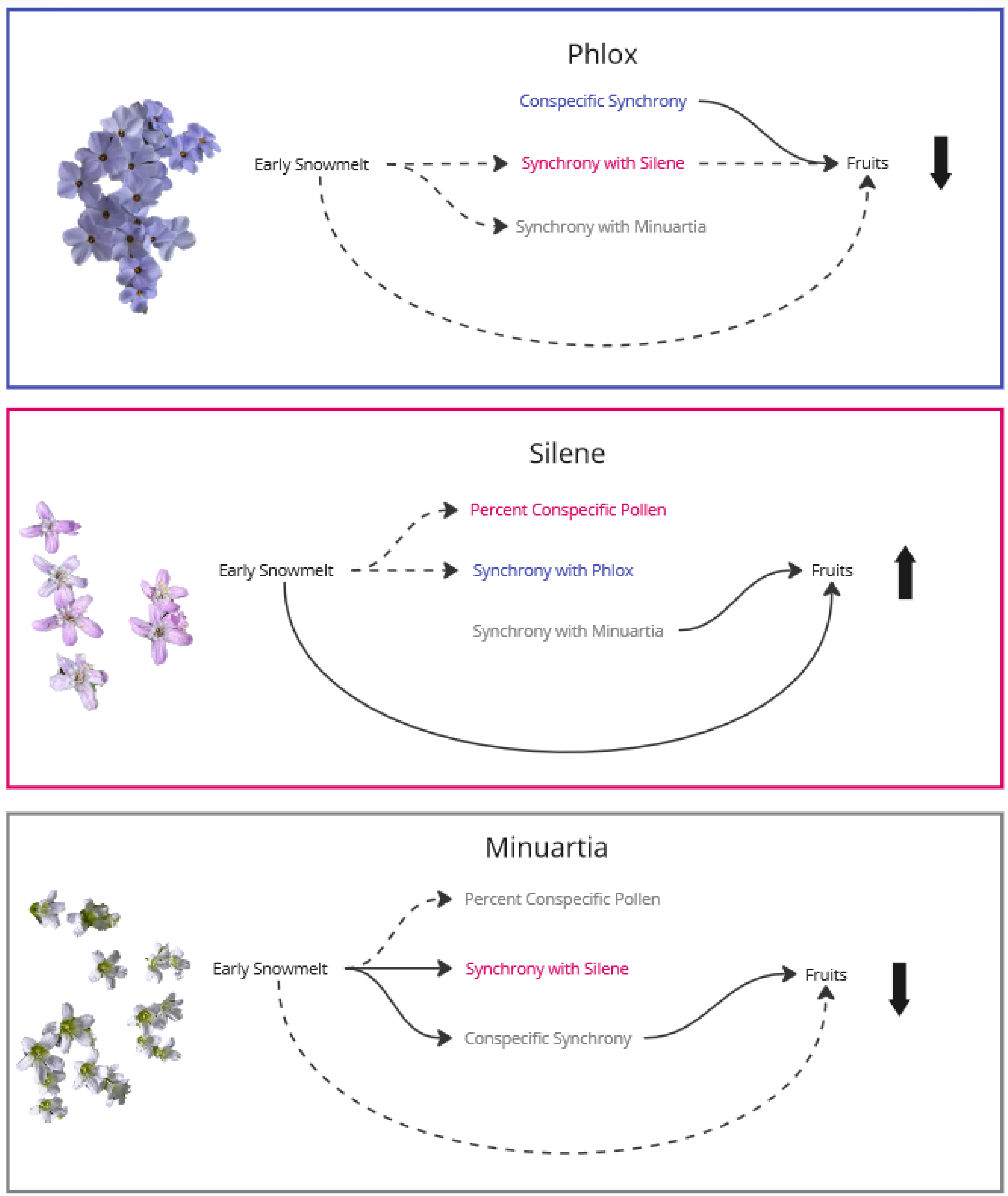


Figure 15: Diagram showing main results for each species. Solid lines indicate a positive effect, whereas dashed lines indicate a negative effect



CHAPTER 3

CONCLUSIONS AND LIMITATIONS

Conclusions

Overall, I find evidence that changes to synchrony may occur with earlier snowmelt timing within my three study species. These responses appear to be species specific between both conspecifics and heterospecifics. These responses likely will have species dependent and interaction dependent impacts on reproductive success, where some species benefit and others fare worse.

In *Phlox condensata*, one of the earlier flowering species, I find no effect on conspecific synchrony with earlier snowmelt, however earlier snowmelt reduced synchrony with *S. acaulis* and *M. obtusiloba*. *Phlox condensata* produced more fruit with higher conspecific synchrony, which will likely remain the case in earlier snowmelt scenarios, given snowmelt timing has no effect on conspecific synchrony. *Phlox condensata* produced less fruits when flowering synchronously with *S. acaulis*, indicating competition between these species for pollinators may occur. With earlier snowmelt, this detriment may be reduced via less synchrony with *S. acaulis*. Nonetheless, snowmelt had an overall negative effect on *P. condensata* fruit production. In this case, escape from pollinator competition with *S. acaulis* is likely not enough to overcome other detriments of earlier snowmelt on reproduction in this species.

Silene acaulis conspecific synchrony showed weaker responses to snowmelt timing, contrary to previous studies, though synchrony with *P. condensata* decreased with earlier snowmelt. Conspecific synchrony had no effect on fruit production, however synchrony with *M. obtusiloba* positively affected fruit production. This effect will likely be preserved in earlier snowmelt scenarios, given that synchrony with *M. obtusiloba* was unaffected by earlier snowmelt timing. Earlier snowmelt timing also reduced the percentage of conspecific pollen on *S. acaulis* stigmas, which may work to reduce fruit set in this species as well. The overall effect of earlier snowmelt increases fruit production, indicating reproduction in *S. acaulis* might actually improve.

I find that in *Minuartia obtusiloba*, earlier snowmelt predicts greater conspecific synchrony and greater synchrony with *Silene acaulis*. Greater conspecific synchrony was found to increases fruit production and percent conspecific pollen deposition in this species. Though this indicates this species may have higher fecundity in future warming scenarios, I find that overall earlier snowmelt has a negative effect on *M. obtusiloba*, indicating that increases in conspecific synchrony are not enough to compensate for other negative effects of earlier snowmelt.

Limitations

As Wolkovitch et al (2012) points out, there are often two ways researchers determine the effects of climate change on plants: space for time substitutions and warming experiments. I used a natural variation in snowmelt for this study, however other researchers have used snowmelt manipulations to observe effects on flowering phenology and synchrony (Carbognani et al 2016). One major caveat to my study is that my observations may be attributed to site level adaptation rather than exclusively snowmelt differences. The more sheltered, lower elevation sites I observed as having later snowmelt likely have historically had later snowmelt than the more exposed, earlier snowmelt sites. Thus, perhaps attributing effects of different snowmelt times from each site on fruit number are not transferable to the effects of climate change (Lovell et al 2023). Nonetheless, warming experiments have the potential to alter other environmental factors that can influence plant responses. In fact, Wolkovitch et al (2012) finds that experimental warming often underpredicts plant responses to warming compared to long term observational trends. Future studies in this system would benefit from experimental snowmelt treatments as well as natural variation in order to disentangle site level effects.

I collected my data in a relatively short time period, over only one growing season. Other synchrony research generally spans more than one flowering season (Bienau et al 2015, Hall et al 2018). In particular, Waananen et al (2018) find that inter-annual variation in synchrony explained 39% more of the variation in daily mating potential compared to variation within one year. Variation may come from interannual differences in pollinator availability and visitation, which may influence reproductive success. Additionally, changes in weather patterns have the potential to alter fruit production, such as frost events and the amount of precipitation (Korner 2011, Dolezal et al 2020). Future studies in this system that observe effects for multiple seasons might be better informed as to the interannual variation in synchrony among and within species. Additionally, other studies looking into the effects of snowmelt and synchrony on reproduction in other alpine plants would inform other plant responses to climate change. I only analyze three species within a diverse flowering community; thus, I only observe a fraction of heterospecific synchrony effects likely taking place in this community. Including more plants into the study, particularly plants with varying phenologies, pollination syndromes, and pollinators, would provide a more comprehensive view of heterospecific synchrony, competition, and facilitation.

To measure pollen deposition, I collected stigmas outside of the transects where floral display was measured to avoid affecting fruit production estimates. Thus, my results regarding the effect of floral display size on conspecific pollen deposition may not be as accurate as they could have been if I measured the site level floral display of the larger surrounding area. Additionally, collecting floral display size of the plants I collected from may have provided more information on the importance of individual level floral display. Pollinators often visit multiple flowers on one plant, and individual display size can influence conspecific pollen deposition (Mitchell et al 2004). This may be particularly important in *P. condensata* and hermaphroditic *S. acaulis* and *M. obtusiloba* individuals who are capable of producing pollen and selfing.

When examined under the microscope, *Silene acaulis* and *Minuartia obtusiloba* pollen grains appeared identical, and thus could not be distinguished from each other. Thus, I used Carophyllaceae pollen as my measure of conspecific pollen deposition. My results regarding conspecific pollen deposition between these species could be improved by a more rigorous method to determine pollen species under the microscope.

Based on my research, it appears that reproduction related responses to earlier snowmelt vary between species, and that variation has consequences that work to help or hinder reproduction. Nonetheless, the plant-plant interactions that I study here don’t appear to be as important as other effects that earlier snowmelt may have on alpine plant reproduction. My research helps to inform how climate change impacts interactions between flowering plants, and the relative importance of these interactions for reproduction. Future research could benefit from considering the connections between direct and indirect effects of earlier snowmelt timing on plant reproduction. Additionally, work focusing on long term effects of snowmelt timing on flowering synchrony and reproduction may provide a clearer picture of how climate change will impact this system.

REFERENCES

Arceo-Gómez, G., Abdala-Roberts, L., Jankowiak, A., Kohler, C., Meindl, G. A., Navarro-Fernández, C. M., ... & Alonso, C. (2016). Patterns of among-and within-species variation in heterospecific pollen receipt: The importance of ecological generalization. *American Journal of Botany*, *103*(3), 396-407.

Arft, A.M., Walker, M.D., Gurevitch, J., Alatalo, J.M., Bret-Harte, M.S., Dale, M., Diemer, M., Gugerli, F., Henry, G.H.R., Jones, M.H., Hollister, R., Jónsdóttir, I.S., Laine, K., Lévesque, E., Marion, G.M., Molau, U., Mølgaard, P., Nordenhäll, U., Rasvhizin, V., Robinson, C.H., Starr, G., Stenstro¨m, A., Stenström, M., Totland, Ø., Turner, L., Walker, L., Webber, P., Welker, J.M. & Wookey, P.A. (1999) Responses of Tundra plants to experimental warming: a meta-analysis of the international tundra experiment. *Ecological Monographs*, 69, 491–511.

Ashman, T. L., & Arceo-Gómez, G. (2013). Toward a predictive understanding of the fitness costs of heterospecific pollen receipt and its importance in co-flowering communities. *American Journal of Botany*, *100*(6), 1061-1070.

Augspurger, C. K. (1983). Phenology, flowering synchrony, and fruit set of six neotropical shrubs. *Biotropica*, 257-267.

Avise, J. C. (2000). *Phylogeography: the history and formation of species*. Harvard university press.

Bannister, P., Maegli, T., Dickinson, K. J., Halloy, S. R., Knight, A., Lord, J. M., ... & Spencer, K. L. (2005). Will loss of snow cover during climatic warming expose New Zealand alpine plants to increased frost damage?. *Oecologia*, *144*, 245-256.

Bell, J. M., Karron, J. D., & Mitchell, R. J. (2005). Interspecific competition for pollination lowers seed production and outcrossing in Mimulus ringens. *Ecology*, *86*(3), 762-771.

Bergamo, P.J., Susin Streher, N., Traveset, A., Wolowski, M. and Sazima, M. (2020), Pollination outcomes reveal negative density-dependence coupled with interspecific facilitation among plants. Ecol Lett, 23: 129-139.

Bertness, M. & Callaway, R.M. (1994) Positive interactions in communities. *Trends in Ecology and Evolution*, 9, 191–193.

Bienau, M. J., Kröncke, M., Eiserhardt, W. L., Otte, A., Graae, B. J., Hagen, D., ... & Eckstein, R. L. (2015). Synchronous flowering despite differences in snowmelt timing among habitats of Empetrum hermaphroditum. *Acta oecologica*, *69*, 129-136.

Bingham, R. A. (1999). Pollinator limitation in arctic alpine environments: myth or fact of life above treeline?. *Science Progress*, *82*(2), 103-112.

Bingham, R. A., & Orthner, A. R. (1998). Efficient pollination of alpine plants. *Nature*, *391*(6664), 238-239.

Bingham, R., Orthner, A. Efficient pollination of alpine plants. Nature 391, 238–239 (1998).

Carbognani, M., Bernareggi, G., Perucco, F., Tomaselli, M., & Petraglia, A. (2016). Micro-climatic controls and warming effects on flowering time in alpine snowbeds. *Oecologia*, *182*, 573-585.

Chen, Y., Collins, S. L., Zhao, Y., Zhang, T., Yang, X., An, H., ... & Ma, M. (2023). Warming reduced flowering synchrony and extended community flowering season in an alpine meadow on the Tibetan Plateau. *Ecology*, *104*(1), e3862.

Chittka L, Schurkens S (2001) Successful invasion of a floral market—an exotic Asian plant has moved in on Europe's river-banks by bribing pollinators. *Nature* 411:653

Chmura, H. E., Kharouba, H. M., Ashander, J., Ehlman, S. M., Rivest, E. B., & Yang, L. H. (2019). The mechanisms of phenology: the patterns and processes of phenological shifts. *Ecological monographs*, *89*(1), e01337.

Dolezal, J., Kurnotova, M., Stastna, P., & Klimesova, J. (2020). Alpine plant growth and reproduction dynamics in a warmer world. *New Phytologist*, *228*(4), 1295-1305.

Duffy, K. J., & Stout, J. C. (2011). Effects of conspecific and heterospecific floral density on the pollination of two related rewarding orchids. *Plant Ecology*, *212*, 1397-1406.

Fabbro, T., & Körner, C. (2004). Altitudinal differences in flower traits and reproductive allocation. *Flora-Morphology, Distribution, Functional Ecology of Plants*, *199*(1), 70-81.

Fazlioglu, F., & Wan, J. S. (2021). Warming matters: alpine plant responses to experimental warming. *Climatic Change*, *164*(3-4), 56.

Feldman, T. S. (2008). The plot thickens: does low density affect visitation and reproductive success in a perennial herb, and are these effects altered in the presence of a co-flowering species?. *Oecologia*, *156*(4), 807-817.

Fishman, L., & Wyatt, R. (1999). Pollinator-mediated competition, reproductive character displacement, and the evolution of selfing in Arenaria uniflora (Caryophyllaceae). *Evolution*, *53*(6), 1723-1733.

Fisogni, A., de Manincor, N., Bertelsen, C. D., & Rafferty, N. E. (2022). Long-term changes in flowering synchrony reflect climatic changes across an elevational gradient. Ecography, 2022(2).

Forbis, T. A., & Doak, D. F. (2004). Seedling establishment and life history trade-offs in alpine plants. American Journal of Botany, 91(7), 1147-1153.

Forrest, J. R., & Thomson, J. D. (2011). An examination of synchrony between insect emergence and flowering in Rocky Mountain meadows. *Ecological Monographs*, *81*(3), 469-491.

Fox J, Weisberg S (2019). _An R Companion to Applied Regression_, Third edition. Sage, Thousand Oaks CA. <URL: https://socialsciences.mcmaster.ca/jfox/Books/Companion/>.

Galen, C., & Stanton, M. L. (1995). Responses of snowbed plant species to changes in growing-season length. *Ecology*, *76*(5), 1546-1557.

Galen, C., and T. Gregory. 1989. Interspecific pollen transfer as a mechanism of competition: consequences of foreign pollen contamination for seed set in the alpine wildflower, *Polemonium viscosum*. *Oecologia* 81: 120–123.

Galen, C., and T. Gregory. 1989. Interspecific pollen transfer as a mechanism of competition: consequences of foreign pollen contamination for seed set in the alpine wildflower, *Polemonium viscosum*. *Oecologia* 81: 120–123.

Ganjurjav, H., Gornish, E. S., Hu, G., Schwartz, M. W., Wan, Y., Li, Y., & Gao, Q. (2020). Warming and precipitation addition interact to affect plant spring phenology in alpine meadows on the central Qinghai-Tibetan Plateau. Agricultural and Forest Meteorology, 287, 107943.

Gérard, M., Vanderplanck, M., Wood, T., & Michez, D. (2020). Global warming and plant–pollinator mismatches. *Emerging topics in life sciences*, *4*(1), 77-86.

Gurung, P. D., Ratnam, J., & Ramakrishnan, U. (2018). Facilitative interactions among co-flowering Primula species mediated by pollinator sharing. *Plant ecology*, *219*, 1159-1168.

Hall, E.S., Piedrahita, L.R., E Waddle, Kendziorski, G., Doak, D.F., DeMarche, M.L. (2018). Climate and synchrony with conspecifics determine the effects of flowering phenology on reproductive success in *Silene acaulis*. Arctic, Antarctic, and Alpine Research 50: e1548866

Hegland, S. J., & Totland, Ø. (2012). Interactions for pollinator visitation and their consequences for reproduction in a plant community. *Acta Oecologica*, *43*, 95-103.

Hegland, S. J., Nielsen, A., Lázaro, A., Bjerknes, A. L., & Totland, Ø. (2009). How does climate warming affect plant-pollinator interactions?. *Ecology letters*, *12*(2), 184-195.

Herrera, C.M. Pollinator abundance, morphology, and flower visitation rate: analysis of the “quantity” component in a plant-pollinator system. *Oecologia* **80**, 241–248 (1989). https://doi.org/10.1007/BF00380158

Holway, J. G., & Ward, R. T. (1965). Phenology of alpine plants in northern Colorado. Ecology, 46(1-2), 73-83.

Holway, J. G., and R. T. Ward. 1963. Snow and melt-water effects in an area of Colorado alpine. *Am. Midland Naturalist* 69: 189-197.

Hülber, K., Winkler, M., & Grabherr, G. (2010). Intraseasonal climate and habitat-specific variability controls the flowering phenology of high alpine plant species. Functional ecology, 24(2), 245-252.

Hurtado, M., Godoy, O., and Bartomeus, I.: Plant spatial aggregation modulates the interplay between plant competition and pollinator attraction with contrasting outcomes of plant fitness, *Web Ecology*., 23, 51–69, https://doi.org/10.5194/we-23-51-2023, 2023.

Iler, A. M., Inouye, D. W., Høye, T. T., Miller-Rushing, A. J., Burkle, L. A., & Johnston, E. B. (2013). Maintenance of temporal synchrony between syrphid flies and floral resources despite differential phenological responses to climate. *Global Change Biology*, *19*(8), 2348-2359.

Ims, Rolf (1990). "The ecology and evolution of reproductive synchrony". *Trends in Ecology and Evolution.* **5** (5): 135–140.

Inouye, D. W. (2008). Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. *Ecology*, *89*(2), 353-362.

Inouye, D. W., & Wielgolaski, F. E. (2013). Phenology at high altitudes. In *Phenology: An integrative environmental science* (pp. 249-272). Dordrecht: Springer Netherlands.

Inouye, D.W. (2019), Effects of climate change on alpine plants and their pollinators. Ann. N.Y. Acad. Sci., 1469: 26-37.

Johnson, C. A., Dutt, P., & Levine, J. M. (2022). Competition for pollinators destabilizes plant coexistence. *Nature*, *607*(7920), 721-725.

Kearns, C. A. (1992) Anthophilous fly distribution across an elevational gradient. Am. Midland Nat. 127, 172-182.

Kearns, C. A., & Inouye, D. W. (1993). *Techniques for pollination biologists*. University press of Colorado.

Kehrberger, S., & Holzschuh, A. (2019). How does timing of flowering affect competition for pollinators, flower visitation and seed set in an early spring grassland plant?. *Scientific Reports*, *9*(1), 15593.

Kempe, K. 2014. The effect of flowering synchrony on reproductive success in the tundra cushion plant *Silene acaulis*. M.S. thesis, Uppsala University.

Kendall, D. M., Kevan, P. G., & LaFontaine, J. D. (1981). Nocturnal flight activity of moths (Lepidoptera) in alpine tundra. *The Canadian Entomologist*, *113*(7), 607-614.

Körner, C. (2003). *Alpine plant life: functional plant ecology of high mountain ecosystems; with 47 tables*. Springer Science & Business Media.

Kudo, G. (2014). Vulnerability of phenological synchrony between plants and pollinators in an alpine ecosystem. Ecological research, 29, 571-581.

Kudo, G. (2020). Dynamics of flowering phenology of alpine plant communities in response to temperature and snowmelt time: Analysis of a nine-year phenological record collected by citizen volunteers. *Environmental and experimental botany*, *170*, 103843.

Levin, D. A., & Anderson, W. W. (1970). Competition for pollinators between simultaneously flowering species. *The American Naturalist*, *104*(939), 455-467.

Locklear, J. H. (2011). *Phlox: a natural history and gardener's guide* (pp. 103-107). Timber Press.

Lopes, S. A., Bergamo, P. J., Najara Pinho Queiroz, S., Ollerton, J., Santos, T., & Rech, A. R. (2022). Heterospecific pollen deposition is positively associated with reproductive success in a diverse hummingbird-pollinated plant community. *Oikos*, *2022*(1).

Lovell, R. S., Collins, S., Martin, S. H., Pigot, A. L., & Phillimore, A. B. (2023). Space-for-time substitutions in climate change ecology and evolution. *Biological Reviews*, *98*(6), 2243-2270.

Maestre, F. T., Callaway, R. M., Valladares, F., & Lortie, C. J. (2009). Refining the stress-gradient hypothesis for competition and facilitation in plant communities. *Journal of ecology*, *97*(2), 199-205.

McKinney, A. M., CaraDonna, P. J., Inouye, D. W., Barr, B., Bertelsen, C. D., & Waser, N. M. (2012). Asynchronous changes in phenology of migrating Broad-tailed Hummingbirds and their early-season nectar resources. Ecology, 93(9), 1987-1993.

Memmott, J., Craze, P. G., Waser, N. M., & Price, M. V. (2007). Global warming and the disruption of plant–pollinator interactions. *Ecology letters*, *10*(8), 710-717.

Miller-Struttmann, N. E., Geib, J. C., Franklin, J. D., Kevan, P. G., Holdo, R. M., Ebert-May, D., ... & Galen, C. (2015). Functional mismatch in a bumble bee pollination mutualism under climate change. *Science*, *349*(6255), 1541-1544.

Mitchell, R. J., Karron, J. D., Holmquist, K. G., & Bell, J. M. (2004). The influence of Mimulus ringens floral display size on pollinator visitation patterns. *Functional Ecology*, 116-124.

Moeller, D. A. (2004). Facilitative interactions among plants via shared pollinators. *Ecology*, *85*(12), 3289-3301.

Moore, L. M., & Lauenroth, W. K. (2017). Differential effects of temperature and precipitation on early-vs. late-flowering species. *Ecosphere*, *8*(5), e01819.

Morales, C. L., & Traveset, A. (2008). Interspecific pollen transfer: magnitude, prevalence and consequences for plant fitness. *Critical Reviews in Plant Sciences*, *27*(4), 221-238.

Morris, W. F., & Doak, D. F. (1998). Life history of the long-lived gynodioecious cushion plant *Silene acaulis* (Caryophyllaceae), inferred from size-based population projection matrices. American Journal of Botany, 85(6), 784-793.

Morris, W. F., & Doak, D. F. (2010). Demographic compensation and tipping points in climate-induced range shifts. Nature 467: 959–962.

Ollerton, J., Winfree, R., & Tarrant, S. (2011). How many flowering plants are pollinated by animals?. *Oikos*, *120*(3), 321-326.

Pauli, H., Gottfried, M., & Grabherr, G. (2003). Effects of climate change on the alpine and nival vegetation of the Alps. *Journal of mountain ecology*, *7*(Suppl), 9-12.

Petraglia, A., Tomaselli, M., Petit Bon, M., Delnevo, N., Chiari, G., & Carbognani, M. (2014). Responses of flowering phenology of snowbed plants to an experimentally imposed extreme advanced snowmelt. Plant Ecology, 215, 759-768.

R Core Team (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Rosas-Guerrero, V., Aguilar, R., Martén-Rodríguez, S., Ashworth, L., Lopezaraiza-Mikel, M., Bastida, J. M., & Quesada, M. (2014). A quantitative review of pollination syndromes: do floral traits predict effective pollinators?. *Ecology letters*, *17*(3), 388-400.

Rose-Person, A., M. Spasojevic, C. Forrester, W. Bowman, K. Suding, M. Oldfather, and N. Rafferty. (2023). Pollinator visitation, flower count, and seed set in Black Sand plots, 2020. ver 2. Environmental Data Initiative. https://doi.org/10.6073/pasta/eab9ada640979e96e08a407cab6f534b (Accessed 2024-05-21).

Russell V. Lenth (2023). emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.9.0. https://CRAN.R-project.org/package=emmeans

Sargent, R. D., & Ackerly, D. D. (2008). Plant–pollinator interactions and the assembly of plant communities. *Trends in Ecology & Evolution*, *23*(3), 123-130.

Schiffer, A., Loy, X., Morozumi, C., & Brosi, B. J. (2023). Differences in individual flowering time change pollen limitation and seed set in three montane wildflowers. *American Journal of Botany*, *110*(3), e16123.

Shelton, W. R., Mitchell, R. J., Christopher, D. A., Jack, L. P., & Karron, J. D. (2024). Among-individual variation in flowering phenology affects flowering synchrony and mating opportunity. *American Journal of Botany*, *111*(1), e16269.

Smith, G. X., Swartz, M. T., & Spigler, R. B. (2021). Causes and consequences of variation in heterospecific pollen receipt in Oenothera fruticosa. *American Journal of Botany*, *108*(9), 1612-1624.

Tachiki, Y., Iwasa, Y., & Satake, A. (2010). Pollinator coupling can induce synchronized flowering in different plant species. *Journal of Theoretical Biology*, *267*(2), 153-163.

Vorkauf, M., Marty, C., Kahmen, A., & Hiltbrunner, E. (2021). Past and future snowmelt trends in the Swiss Alps: the role of temperature and snowpack. *Climatic Change*, *165*, 1-19.

Waananen, A., Kiefer, G., Ison, J. L., & Wagenius, S. (2018). Mating opportunity increases with synchrony of flowering among years more than synchrony within years in a nonmasting perennial. *The American Naturalist*, *192*(3), 379-388.

Wang, T., Ottlé, C., Peng, S., Janssens, I. A., Lin, X., Poulter, B., ... & Ciais, P. (2014). The influence of local spring temperature variance on temperature sensitivity of spring phenology. Global Change Biology, 20(5), 1473-1480.

Ward, M., Johnson, S.D. & Zalucki, M.P. (2013). When bigger is not better: intraspecific competition for pollination increases with population size in invasive milkweeds. Oecologia 171, 883–891.

Weis, A. E., Nardone, E., & Fox, G. A. (2014). The strength of assortative mating for flowering date and its basis in individual variation in flowering schedule. *Journal of Evolutionary Biology*, *27*(10), 2138-2151.

Wheeler, J. A., Hoch, G., Cortés, A. J., Sedlacek, J., Wipf, S., & Rixen, C. (2014). Increased spring freezing vulnerability for alpine shrubs under early snowmelt. *Oecologia*, *175*, 219-229.

Wilczek, A. M., Burghardt, L. T., Cobb, A. R., Cooper, M. D., Welch, S. M., & Schmitt, J. (2010). Genetic and physiological bases for phenological responses to current and predicted climates. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1555), 3129-3147.

Willcox, B. K., Aizen, M. A., Cunningham, S. A., Mayfield, M. M., & Rader, R. (2017). Deconstructing pollinator community effectiveness. *Current Opinion in Insect Science*, *21*, 98-104.

Winkler, D.E., Butz R.J., Germino M.J., Reinhardt K., Kueppers L.M. (2018). Snowmelt Timing Regulates Community Composition, Phenology, and Physiological Performance of Alpine Plants. Frontiers in Plant Science

Wipf, S., Stoeckli, V., & Bebi, P. (2009). Winter climate change in alpine tundra: plant responses to changes in snow depth and snowmelt timing. *Climatic change*, *94*(1-2), 105-121.

Wirth, L. R., Waser, N. M., Graf, R., Gugerli, F., Landergott, U., Erhardt, A., ... & Holderegger, R. (2011). Effects of floral neighborhood on seed set and degree of outbreeding in a high-alpine cushion plant. *Oecologia*, *167*, 427-434.

Wolkovich, E. M., Cook, B. I., Allen, J. M., Crimmins, T. M., Betancourt, J. L., Travers, S. E., ... & Cleland, E. E. (2012). Warming experiments underpredict plant phenological responses to climate change. Nature, 485(7399), 494-497.

Zettlemoyer, M.A., Conner, R.J., Seaver, M.M., Waddle, E., DeMarche, M.L. 2024. A long-lived alpine perennial advances flowering under warmer conditions but not enough to maintain reproductive success. *American Naturalist*, accepted.