

DOES HISTORY REPEAT ITSELF?
IMPACT OF CLIMATE ON FLORAL RESOURCES FOR BUMBLE BEES
THEN AND NOW

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The undersigned, appointed by the Dean of the Graduate School, have
examined the thesis entitled

DOES HISTORY REPEAT ITSELF?
IMPACT OF CLIMATE ON FLORAL RESOURCES FOR BUMBLE BEE
THEN AND NOW

Presented by James Douglas Franklin

A Candidate for the degree of Master of Art

And hereby certify that in their opinion it is worthy of acceptance

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ABSTRACT

Bumble bees require abundant floral resources that match the timing of colony establishment and growth. In alpine ecosystems, winter snowpack influences timing of flowering while summer temperature impacts retention of soil moisture to support flower production. I surveyed the seasonal timing of floral resource availability provided by nine plant species that historically received 90% of bumble bee visits at our Rocky Mountain field site. Surveys were made in years of extreme low snowpack (1977 and 2012) and years of average to high snowpack (1979-80 and 2013). Flowers were counted throughout the summer in habitats spanning an altitudinal gradient from 3500-4000 m. First and peak flowering dates were later in summers following deeper snow, and earlier under warm minimum summer temperatures. Flowering duration was shorter in the 2010s when minimum summer temperatures were 2.4 °C higher than in the late 1970s. Both seasons in the 2010s failed to support flower densities as high as those observed in 1977. Peak flowering time and duration of flowering varied significantly among habitats. Lower altitude habitats near timberline showed greater decreases in flower density than upper ones. The drought of 2012 increased overlap in the time of peak flowering among co-occurring species and especially reduced late season resources. Our model of resource intake indicates that both *Bombus balteatus* and *B sylvicola* have faced ~74-80% reductions in potential resource intake over the season. Together, these results

demonstrate strong sensitivity to climate change for resources that have been historically critical for bumble bee pollinators in the alpine.

CHAPTER 1. INTRODUCTION TO THE STUDY SYSTEM

Alpine habitats occur at high altitudes where extreme climate conditions limit the diversity of life supported (Nagy and Grabherr 2009). Growing season length is a primary limitation for the establishment of lower altitude species in the alpine and is regulated by the temperature and precipitation conditions (Billings and Bliss 1959, Chambers et al. 1990, Molau 1996). In the winter, precipitation accumulates as snow and persists in the lower temperatures associated with high altitudes. Suitable ambient temperatures and snowmelt precede active growth for plants in the alpine, limiting the growing season to summer months in temperate climates (Kudo 1991, Galen and Stanton 1995). Variation in topography, wind and vegetative cover across alpine landscapes produce patchy distribution of snow cover ranging from bare ground to deep snow drifts (Edmonds et al. 2006, Litaor et al. 2008). Insulating snow cover plays an important role in temperature regulation during winter as snow maintains a relatively warmer and constant temperature relative to exposed areas (Inouye 2008). However, snow delays the initiation of growth in summer months by blocking most sunlight and producing cooler soil temperatures. At higher altitudes solar radiation reaching the ground travels through less atmosphere and therefore receives higher intensity ultraviolet and infrared radiation than lower altitudes. Plants display special adaptations to harmful ultraviolet, but also benefit from the warmer ground conditions which can differ dramatically from ambient conditions only cm above the ground (Nybakker and Wolfgang 2007, Dietrich and Körner 2014). The dynamic topography of mountain landscapes

where alpine habitats are typically found produces high spatial variation in the local experience of regional climate conditions yielding variation in habitat suitability over small spatial scales (Ashcroft 2010). Altitude, slope, and slope-aspect drive this variation in the climate experience through their effects on wind, water and light conditions (Dobrowski 2011). Snow accumulation supports alpine communities both by moderating temperature conditions and by providing moisture as it melts (Wied and Galen 1998).

The overall diversity of communities in alpine systems is lower relative to lower altitude habitats. Notably, tree species are absent from alpine systems, a phenomenon which is part of the ecological definition of the alpine zone. The harsh climate conditions alpine habitats present organisms with limits to physiological processes while the patchy distribution of abiotic resources additionally limits an organism's dispersal and establishment (Nagy and Grabherr 2009). The special conditions in the alpine zone support only a subset of lower altitude species that demonstrate special adaptations that allow them to persist in these areas. Long-lived perennial dwarf shrubs, grasses and forbs communities occupy the alpine habitat with annual plants representing fewer than 1% of alpine plant communities (Nagy and Grabherr 2009). Some individual plants occupying the alpine have been shown to be more than 1000 years old demonstrating extreme examples of the more general trend for long-lived, slow growing life histories of alpine plants (de Witte et al. 2012). Growth rates are limited by short growing seasons due to persistent snow cover and freezing temperatures which cue dormancy of plants for the majority of the year (Bliss et al. 1984, Shaver et

al. 1992). Nutrient poor soils and water limitation are also common in alpine habitats, and reduce growth rates during the growing season (Antúnez et al. 2001). Species occupying the alpine display life histories that are capable of tolerating winter conditions but are also capable of responding with relatively rapid growth once the short period of suitable temperature conditions arise in the summer months (Sørensen 1941).

While abiotic conditions have been demonstrated to be a primary determinant of species distribution in the alpine zone, it is also clear that a variety of biotic interactions can further define distributions through their mitigating effects on climate stressors (Cavieres and Quiroz 2008, Becklin and Galen 2009, Cavieres et al. 2014). In addition to adaptations that allow alpine plant communities to persist in alpine habitat, changes in biotic interactions such as competition with different plant functional types can lead to shifts between alpine plant community types (Wookey et al. 2009) and can also facilitate colonization of the alpine by lower altitude plant species (Sturm et al. 2001, Dona and Galen 2006).

Phenology in the alpine is crucial as the availability of suitable conditions is limited over time in these systems (Rathcke and Lacey 1985, Miller-rushing et al. 2010). In the alpine, for example, mistiming emergence with suitable conditions will have a proportionally larger impact on total yearly resource exploitation compared to the same mistiming in a longer growing season found in lower altitude habitats. Organisms respond to environmental cues to trigger the initiation of active portions of their life-cycle, though the precise cues vary across

taxa (Kochmer and Handel 1986, Cleland et al. 2007a, Pau et al. 2011). While few studies have examined the relative importance of different environmental cues that guide alpine phenology across different species, it is generally believed that alpine species respond to the similar cues as lower altitude populations (Iler et al. 2013). Temperature, day length, and the number of days above physiological temperature thresholds have each been identified as important environmental cues for the phenology of alpine organisms (Hulber et al. 2010). However, the highly variable climate experience of mountain systems suggests that relying on a single environmental cue would produce phenological responses that could desynchronize life histories from the suite of suitable climate conditions. Plants, for instance, would encounter unsuitable temperature conditions if they were to only respond to day length as the likelihood of frost events and snowmelt on a given date are highly variable from year to year (IPCC 2007).

The persistence of alpine communities is dependent on a variety of biological interactions that support organisms through mitigation of the harsh conditions. Appropriate phenological responses are therefore crucial to efficient biotic resource exploitation in the alpine and may represent important co-evolutionary responses (Rathcke and Lacey 1985). Under consistent climate conditions, complex alpine communities should be able to use different suites of environmental cues to produce coordinated phenologies. However, if climate change decouples once correlated suites of cues, physiological responses that have historically yielded beneficial schedules of growth and reproduction may

now separate organisms in time from their necessary biotic resources (Stenseth and Mysterud 2002). Winter snowpack in the Colorado Rocky Mountains is highly variable year to year, but temperatures have followed the global warming trend in alpine systems over the past 35 years which are large relative to all global systems (PRISM Group, Oregon State University, Corvallis Oregon, USA, IPCC 2007). As a result, organisms that respond to temperature cues now likely display different temporal distributions, though long term data to support this are rare (Cleland et al. 2007, Miller-Rushing et al. 2007, Miller-Rushing and Primack 2008, Burkle et al. 2013, CaraDonna et al. 2014). Insects are one group of organisms whose phenology responds primarily to temperature and which have responded to warmer temperatures (Hodgson et al. 2011). Plants are a diverse group represented in the alpine which respond to other cues in addition to temperature. For instance, some plants are responsive primarily to day length (Cleland et al. 2007, Mouradov et al. 2011).

Alpine bumble bees and bumble bee pollinated plants represent a prominent mutualism in the alpine whose temporal overlap may now be decreasing under changing climate conditions. In order to maintain colony growth through the summer growing season, alpine bumble bees require a variety of ephemeral floral resources throughout the summer growing season (Heinrich 2004, Williams et al. 2012). Coordinating phenology with a variety of flower species may buffer bumble bees from phenology changes in any one plant mutualist, but increases the likelihood that a portion of alpine bumble bee diet may now display a different temporal distribution (Willis et al. 2008, CaraDonna

et al. 2014). While it is unlikely that all alpine flowering plants will display the same phenological response, it is possible that changes in the phenology of flowering plants or bumble bees or both will produce phenological mismatches between partners that can affect the demographic transitions for both (Miller-rushing et al. 2010). Additionally, the density of pollinator and flower resources in this mutualism may also respond to climate conditions and affect the benefits each partner receives across the growing season and from year to year (Feldman 2006). Sub-alpine habitats have shown periods of low floral resources due to phenology response in sub-alpine plant communities, though it is unclear if this pattern exists in the alpine (Aldridge et al. 2011a).

This study takes advantage of the research history at a field site in the front range of the Colorado Rocky Mountains, USA to document the phenology and density responses in bumble bee pollinated plants over a 35 year period. In the 1970s, permanent study plots were established to document the weekly flowering phenology of the alpine plant community on Pennsylvania Mountain, Park County, Colorado, USA. Phenology and floral density data were collected in the 2010s when summer minimum temperatures had risen by 2.4°C from 1970s baselines, (CHAPTER 2, Figure 1). In both decades flower phenology and density data were collected during growing seasons following high and low winter snowpack, allowing me to examine differences in phenology that are associated with different environmental cues. Bumble bee foraging data collected at this site during the 1970s also allow me to address the question of whether alpine bumble bees can use foraging strategies exhibited in the 1970s to

exploit resources efficiently in the 2010s, or whether floral resources that together produced continuous foraging resources for bumble bees in the 1970s now show temporal gaps that could affect alpine bumble bee colony development through the growing season.

CHAPTER 2. SHIFTS IN THE PHENOLOGY OF ALPINE BUMBLE BEE RESOURCES IN RESPONSE TO CLIMATE EVENTS AT INTER- ANNUAL AND INTER-DECADAL TIME SCALES

CHAPTER SUMMARY

Bumble bees require abundant floral resources that match the timing of colony establishment and growth. In alpine ecosystems, winter snowpack influences timing of flowering while summer temperature impacts retention of soil moisture to support flower production. I surveyed the seasonal timing of floral resource availability provided by nine plant species that historically received 90% of bumble bee visits at my Rocky Mountain field site. Surveys were made in years of extreme low snowpack (1977 and 2012) and years of average to high snowpack (1979-80 and 2013). Flowers were counted throughout the summer in habitats spanning an altitudinal gradient from 3500-4000 m. First and peak flowering dates were later in summers following deeper snow, and earlier under warm minimum summer temperatures. Flowering duration was shorter in the 2010s when minimum summer temperatures were 2.4 °C higher than in the late 1970s. Peak flowering time and duration of flowering varied significantly among habitats. The drought of 2012 increased overlap in the time of peak flowering among co-occurring species and especially reduced late season resources. Together, these results demonstrate strong sensitivity to two aspects of climate change, warming and variance in snow pack, in resources that have been historically critical for bumble bee pollinators in alpine ecosystems.

INTRODUCTION

A central focus of ecology is to understand organisms' response not only to changing abiotic conditions, but also to changing biotic interactions. The timing of biological events, termed phenology, determines temporal overlap of species with both the abiotic and biotic resources they require to accomplish their lifecycles (Rathcke and Lacey 1985). Phenological responses to climate change have implications for biotic interactions (Fitter and Fitter 2002, Cleland et al. 2007a, Diez et al. 2012). In particular, dissimilar phenological responses may disrupt biotic interactions by reducing temporal overlap of associated species (Miller-rushing et al. 2010). Several studies have made use of long term archival data to characterize past phenology, while current ecological studies serve to document changes in response to global warming moving forward (Sparks et al. 2000, Primack et al. 2004, Miller-Rushing et al. 2007, Miller-Rushing and Primack 2008, Miller-rushing and Inouye 2009, Hodgson et al. 2011, Robbirt et al. 2011, Iler et al. 2013).

Species respond in different ways to environmental cues associated with climate change, but some generalities are clear such as an advancement of distributions to higher altitude and toward poles (Parmesan and Yohe 2003, Parolo and Rossi 2008). Alpine and arctic ecosystems have experienced the largest temperature increases and are predicted to respond more strongly to future climate change (IPCC 2007). Snowmelt timing limits these systems and depends on both temperature and precipitation. Additionally, the alpine zone contains many species living at their altitude range boundaries where organisms

are typically stressed by extreme abiotic conditions and respond strongly to climate events (Parsons 1990, Abeli et al. 2011). A recent synthesis of warming experiments under the International Tundra Experiment (ITEX) at arctic and alpine sites indicates that organisms occupying these habitats will show site specific responses of varying degree, despite the general pattern of an earlier and longer growing season (Oberbauer et al. 2013).

Bumble bee pollinators and flowering plants represent a prominent mutualism in the alpine zone that may be susceptible to phenological mismatches. Insect pollinators respond primarily to temperature cues for lifecycle events, while plants can cue their biological processes by day length (Visser and Both 2005, Primack et al. 2009, Thackeray et al. 2010, Mouradov et al. 2011). A decoupling of these cues caused by climate change can produce novel mismatches between the timing, abundance or location of flowering plants and their insect pollinators with the potential to affect demographic transitions and species persistence (Miller-rushing et al. 2010, Burkle et al. 2013b). While some evidence suggests that phenological distributions of bumble bees and floral resources may shift together (Bartomeus et al. 2011) other studies have shown a variety of responses in insect and flowering plant communities including periods of low flower production during sensitive times of colony growth (Aldridge et al., 2011; Cook et al., 2012; Ellwood et al., 2012; Miller-rushing & Inouye, 2009; Primack et al., 2009). This broad range of responses leaves the nature and direction of changes in plant pollinator mutualisms unclear. Additionally, regional climate trends vary in their impact across landscapes, especially on mountains,

translating into a more varied set of microclimates at the landscape scale (Walker et al. 1995, Stanton et al. 1997, Dobrowski 2011).

In this study I observed the date of first flowering, peak flowering and total flowering duration for a guild of alpine plant species that has historically comprised the most important food resources for bumble bees in the central Colorado Rocky Mountains. Over a 35 year span there has been a 2.4 °C increase in average summer minimum temperatures at this site ($R^2=0.45$, $P<0.001$; Figure 1, A). Additionally, extremes of snow pack with contrasting dry and wet winters have occurred during both the 1970s and the past decade (Figure 1, B). These circumstances allow me to explore how the timing of resource availability for bumble bee pollinators changes with weather events at two time scales: inter-annual, and inter-decadal. Additionally with rich data for a subset of species I evaluated the relative importance of winter snowpack and summer temperature regimes for the timing of floral resource availability. Further, I characterize flower timing in a variety of alpine habitats to understand how spatial heterogeneity in mountain systems may influence landscape scale resources for bumble bees.

METHODS

Study System

Original flower censuses were conducted by Peter Kevan and collaborators from June through August in 1977, 1979, 1980, and repeated by me in 2012 and 2013 at sites ranging from 3500-3965m in altitude on

Pennsylvania Mountain (Park Co., Colorado, USA, 39°015' N, 106°003' W).

This area contains an extensive krummholz (KRUM) transition zone (3600-3650 m altitude) comprised of a willow-spruce-meadow mosaic and a variety of tundra microhabitats ranging from bare rock to alpine meadow (Figure 2). Two south and south-east facing slopes (SLOPE; 3700-3800 m altitude) support large dry alpine meadows with a dominant forb community. In contrast, north and northwestern slopes (SCREE) are steep (30.8 degrees average slope) with little plant cover. Pennsylvania Mountain has two peaks at 3897 m (FSUM) and 3965 m (SUM) separated by a wide moist drainage or swale at about 3888 m. This topography creates a broad saddle-like summit with true tundra soils as well as pockets of deep soil within exposed boulder fields. The swale (SWALE) holds deep snowpack in winter months and remains wet as snow melts through the summer leaving shallow pools of standing water that drain eastward.

Pennsylvania Mountain is characterized by fine scale spatial variation in altitude, slope, and slope-aspect within broader habitat zones typical of alpine sites (Barry 2008). In snow-covered areas, water content of soil tracks snowmelt over time (Stanton et al. 1994). In bare sites, timing of summer monsoon rains coupled with solar angle, soil temperature and ground cover play a more pronounced role in the retention of soil moisture (Wied and Galen 1998; J. Nies and J. Franklin unpubl.). Vegetative growth ceases in September when soils dry and temperatures regularly drop below freezing.

Species surveyed

I monitored the timing of flowering for nine alpine plant species which historically have provided major food resources for *Bombus balteatus* (Dahlbom) and *B. sylvicola* (Kirby), two resident bumble bees above timberline in the Colorado Rocky Mountains, (Geib et al. *in press*, Byron 1980; Macior 1974). Key floral resources for these species were identified through extensive surveys conducted at three alpine sites over four years. Macior (1974) observed flower visitation by *Bombus balteatus* and *B. sylvicola* on 51 plant species at Mount Evans, Idaho Springs, CO, USA (39°35' N, 105°38' W; 57 km NE from Pennsylvania Mountain) and Niwot Ridge (40°03' N, 105°35' W; 100 km NE from Pennsylvania Mountain) in 1968 and 1969. Using his records, I identified 27 species that each received greater than 0.6% of total visits. Of these, eight species also received high levels of bumble bee visitation (> 85% total, average 1978-1979) on Pennsylvania Mountain (Byron 1980). *Polemonium viscosum* was also designated an important food resource since it received an average of 10% of bumble bee visits on Pennsylvania Mountain over two years (Byron 1980). Together these 9 species received nearly 90% of all flower visits by resident alpine bumble bees on Pennsylvania Mountain in 1978-79 (Byron 1980; Table 1). Observers conducting flower surveys in the 1970s had variable expertise in distinguishing close congeners. For this reason, I pooled counts for *Mertensia lanceolata* and *M. viridis*. All other plants were reliably identified to species (C. Galen, pers. comm).

Sampling design

In the 1970s P. G. Kevan (pers. comm.) established 91 10m x 2m permanent plots to observe the progression of summer flowering in the alpine forb community on Pennsylvania Mountain. Plots were stratified across major habitat gradients and placed to maximize local species richness. Original plots were established in 1976 before GPS was available and their locations were archived by hand using a line to mark the 10 m edge of each plot on a “field map”. Although plots were marked in the field with wooden stakes at the vertices, most markers were lost between 1980 and 2012. Thus, I estimated their original positions using the annotated field map, Geographic Information Systems (GIS) processing and Global Positioning Systems (GPS).

I used ArcMap 10 GIS to spatially rectify the original field map with a projected coordinate system. I then translated plot locations into GPS coordinates. Assigning field map locations to GPS coordinates and using these to estimate the physical sites of original plots accumulates the inherent errors of mapping, GIS processing and GPS. The original field maps were accurate to roughly 2 m as corroborated by the accuracy of designations for permanent landmarks also indicated on the map. However, these maps indicate only one 10 m edge of each plot. Similar to the binding of a book, the side of that line (left or right “page”) containing the original plot was not noted. Additionally, once rectified in GIS, penciled lines indicating plot boundaries typically represented a distance closer to 20 m (range 14-24 m). The resolution of the modern aerial photograph was 1 m. Finally, the SXBlue II GPS unit used to locate the GPS

coordinates in the field was accurate to <1 m. I ensured that each relocated plot (hereafter termed the “plot domain”) included the historic plot, by adding a buffer area around the re-located “edge” to account for sources of error in identifying its original position. . Including this buffer area increased the original 2 m dimension to 10 m and expanded the 10 m edge to a range of 24 -34 m.

The relocation process necessary to make use of the 1970s data produced several limitations. Expanding the size of study plots could produce sampling bias for phenological events. Plot domains may include individual plants in more heterogeneous microsites. Thus, they may capture a higher variance of phenological traits. I expect that size discrepancy would bias modern data towards earlier first flowering date, later last flowering date and overall longer flower duration. I sub-sampled all large plots sampled in the 2010s to identify all possible non-overlapping 2 by 10m sub plots. I then corrected for scale discrepancy by calculating averages for these parameters from all included 2 by 10m plots. Flowering duration for each species in each plot was calculated from these averages (see statistical analysis, below). No directional bias at the full plot scale was found for peak flowering date and so whole plot data were used for 2012-13.

Changes in winter snowpack and summer minimum temperature

Snowpack and the timing of snowmelt are the two primary climate variables that limit the start of the summer growing period for alpine plants (Billings and Bliss 1959) Low winter precipitation and warm spring days advance the timing of snowmelt leading to an earlier date of first flowering at high altitudes

(Inouye 2008). I used PRISM (Precipitation-altitude Regressions on Independent Slopes Model) to estimate precipitation and temperature at a 1 km scale from 1895 to 2013 on Pennsylvania Mountain since local winter precipitation and summer temperature data were unavailable at this site before 1980. PRISM data use an interpolation model that incorporates a variety of climate variables as well as topography to estimate temperature and precipitation data from surrounding weather stations (PRISM Group, Oregon State University, Corvallis Oregon, USA). In 1977 and 2012, winter precipitation fell below the 22th percentile and in 1979, 1980 and 2013 winter precipitation was higher (85th, 96th and 69th percentile, respectively; Figure 1). Since winter precipitation was similar in 1979 and 1980 (Figure 1, B) I compared flower densities in heavy and light snowpack years using 1980 flowering data for two species (*Mertensia* and *Polemonium*; missing in 1979) and 1979 data for the remainder. Minimum monthly summer temperatures have risen on Pennsylvania Mountain over the past 35 years (Figure 1, A). The difference in the average summer minimum temperatures between years of sampling in the 1970s and in the 2010s is 1.62 °C. A regression of summer minimum temperature on calendar year from 1970 to 2013 indicates a similar increase of 2.4 °C ($R^2=0.45$, $P<0.001$; Figure 1).

Statistical analyses

In each plot, first flowering dates in the 1970s were noted as the first date open flowers were observed for a given species. In 2010s plots, first flowering dates represent the average date of first open flowers for a given species in all possible 2 by 10m plots contained within the plot domain (see sampling design

above). Similarly, last flowering dates represent the last day open flowers were observed for a given species in the 1970s and its average based on the 2 by 10 m plots in that plot domain in the 2010s. The total duration of flowering for each species in each plot was calculated as the number of weeks between the first and last flowering dates. Peak flowering times were estimated as the week in which the highest number of flowers was counted in the plot. While all plots were censused weekly, census often spanned several days due to poor weather. The timing of peak flowering was analyzed on a weekly basis so that data from plots sampled on sequential days could be pooled. All phenology responses were analyzed separately using mixed-model Analysis of Variance (ANOVA; PROC Mixed in SAS 9.2 (2012)). Plot and plant species were treated as random effects in the model with plot nested within habitat and, decade, winter snow accumulation (low or high), and their interactions treated as fixed effects. If a given species did not flower in a plot during a year, the zero counts for that species were not included in the analyses. To analyze whether the synchrony of peak flowering for co-occurring species is sensitive to temperature and snowpack, I performed a mixed-model ANCOVA on the total number of unique weeks in which peak flowering for any species occurred within each plot. Plot species richness, decade, and snowpack (low or high) and the interaction of decade with snowpack were treated as fixed effects and plot was included as a random factor (Proc Mixed in SAS 9.2 (2012)). For species observed in all five years of sampling (three *Trifolium* congeners and *P. viscosum*) I performed an ANCOVA to explore the effects of winter snowpack and summer minimum

temperature on day of first flower and week of peak flowering with species and plot as random effects using the using the mixed procedure in SAS 9.2 (2012).

RESULTS

Onset of flowering

Average onset of flowering varied between decades and in low versus high snowpack years, for the species comprising bumble bee floral resources on Pennsylvania Mountain ($F_{1,261} = 19.6$, $p < 0.0001$ and $F_{1,261} = 117.78$, $p < 0.0001$, respectively; Figure 3). Snowier winters delayed the onset of flowering an average of 15 days. Flowering started an average of six days earlier in the 2010s than in the 1970s. Average first flowering date did not vary significantly among habitats ($F_{4,19} = 2.30$, $P > 0.0966$). ANCOVA analysis of flower initiation for *Trifolium* spp. and *Polemonium* over five years indicated a significant effect of winter snowpack ($F_{1,14} = 5.09$, $P < 0.04$) with heavier snow accumulation delaying flowering (Figure 4). Winter snowpack explained 26% of the variance in first flowering day (partial r^2 , based on type II sums of squares).

Peak flowering

Average timing of peak flowering depended on winter snowpack ($F_{1,227} = 228.67$, $p < 0.0001$), decade ($F_{1,227} = 74.32$, $p < 0.0001$), and habitat ($F_{4,18} = 5.37$, $p < 0.005$). Peak flowering in years of low snowpack occurred an average of 2.7 ± 0.18 weeks earlier than in years of average to high snowpack (Figure 3). In the 1970s, flowering peaks averaged 1.6 ± 0.18 weeks earlier than in the 2010s (Figure 3). The average week of peak flowering ranged from June 12-26 and varied significantly among habitats ($F_{4,18} = 4.26$, $P < 0.013$). The order

of peak flowering did not match the altitudinal distribution of habitats. For example, peak flowering was similar for plants on the false summit (3920 m) and in the krummholz (3550-3600 m; Figure 5).

Minimum summer temperature ($F_{1,14}=6.52$, $P<0.02$) and snowpack ($F_{1,14}=22.26$, $P<0.0003$) had significant and opposing effects on the timing of peak flowering. Together the two climate variables explained 80% of the residual variation in peak flowering date after removal of variance associated with differences among species and plots. Regression showed that variation in week of peak flowering was explained largely by minimum summer temperature (partial $r^2 = 64\%$, $P<0.0001$) and more modestly by winter snowpack (partial $r^2 = 33\%$, $P<0.011$). Warm, dry conditions advanced peak flowering time (Figure 4).

The impact of winter snowpack on the synchrony of peak flowering among co-occurring species varied between decades ($F_{1,61}=5.9$, $P<0.018$, Figure 6). In the 1970s, snowpack had little influence on the synchrony of co-flowering (planned contrast, $t = 0.37$, $P>0.70$). Conversely, under current conditions, co-flowering is more likely after winters of low snowpack than after winters of average to high snowpack (planned contrast, $t = 5.21$, $P<0.0001$). Species flower more synchronously in dry years now than they did in dry years of the 1970s (planned contrast, $t = 5.03$, $P<0.0001$). Average to high winter snowpack eliminates this trend (planned contrast, $P> 0.16$; Figure 6).

Duration of flowering

The impact of snowpack on average flowering span varied between decades (interaction $F_{1,261}=3.98$, $p<0.047$; Figure 7). In neither decade was the

difference in duration of flowering between snowy and dry years significant (planned contrasts, $P > 0.09$ for both). Dry conditions tended to lengthen average time in flower for bumble bee host plants in 1977 (planned contrast, $t = 1.69$, $P < 0.091$), but not 2012 (Figure 7).

On average, species varied in flowering span among habitats ($F_{4, 19} = 3.61$, $P < 0.02$, Figure 5). Plants on the summit exhibited prolonged flowering compared to those in lower krummholz, slope and swale habitats (planned contrasts, all $p < 0.01$) and tended to flower for longer than those at similar altitude on the false summit ($t = 2.02$, $P < 0.06$, Figure 5).

DISCUSSION

Onset of flowering

On Pennsylvania Mountain, snowpack influences the timing of flowering for bumble bee host plants. This is consistent with observations across multiple arctic and alpine sites and also in the subalpine where snow is a prominent climate factor (Abeli et al. 2011, Semenchuk et al. 2013, CaraDonna et al. 2014). Snow pack in the Rocky Mountains has high inter-annual variation, as is clear in climate models going back to 1895. Year to year differences in snowpack in both decades of this study had comparable influences on the onset of flowering. Similarly, in five species for which more extensive phenological data were available, decreases in winter snowpack advanced flowering in a linear manner. Species vary in their response to temperature and precipitation across sub-alpine, alpine and arctic sites leaving it unclear whether patterns demonstrated in

this small subset of four species apply broadly to bumble bee host plants (Oberbauer et al. 2013, CaraDonna et al. 2014). However, the strong effect of snowpack on the onset of flowering across all of nine species surveyed (90% of the diet for alpine bumble bees on Pennsylvania Mountain) indicates that the less snowy winters expected with climate change in the Rocky Mountain region (Saunders and Maxwell 2005) will cause earlier and more synchronous flowering, reducing late season resources to support bumble bee reproduction.

Peak flowering

Temperature and snowpack together influenced the timing of peak flowering for plants representing predominant bumble bee food resources. Whereas onset of flowering was largely a function of snow accumulation over the winter months, most of the variation in peak flowering time was explained by minimum summer temperature. Alpine habitats of the central Rocky Mountains have been described as high altitude deserts (Bliss 1985). As the growing season progresses, soil moisture from melting snow is depleted, while seasonal warming increases evaporation rate. Peak flowering occurs weeks after snowmelt when water to support plant growth and reproduction is largely held in soil reserves. Higher temperatures in late June and July reduce this soil water, limiting flower expansion and in the extreme causing bud abortion (Wied and Galen 1998, Galen 2000). Plants respond to drought stress by advancing their flowering schedules or aborting buds later in the season, each producing an earlier peak flowering date (Primack 1987). Additionally, flower development depends on cumulative temperature input and is accelerated when temperature

increases (Gillooly et al. 2002). The extent of overlap in peak flowering times of co-flowering alpine species varied between decades consistent with a driving role of warmer temperatures in synchronizing flower development in recent summers. Later flowering species show greater advancement, indicating a trend that could, in extreme years (e.g., 2012), lead to the collapse of late season resources for alpine pollinators.

Duration of flowering

Flowering duration of the nine bumble bee host plants monitored in this study was extremely abbreviated in the dry year of 2012. Yet in 1977, similarly low winter precipitation allowed for the longest average flowering span observed in my study. All else being equal, less snow in alpine habitats should mean earlier snow melt and more snow free days for flowering (Körner 1999). I hypothesize that historically cooler temperatures reduced soil evaporation rate, prolonging moisture reserves to support flower production and allowing for longer flowering intervals. In contrast, in the summer of 2012, the combination of early and reduced snowmelt with warmer summer temperatures may have depleted soil water balance and thus indirectly shortened flower duration (Giblin 2005). Jonas et al. (2008) also found that warmer temperatures following snowmelt decrease flowering span. ITEX data shows a variety of responses to warming in alpine and arctic environments, but general trends indicate a lengthening of the growing season (Oberbauer et al. 2013). At some ITEX sites, flowering duration decreased with warming, but did so because of delayed onset of flowering (Oberbauer et al. 2013). Studies in relatively mesic sub-alpine sites also

support the trend of increased flowering duration (CaraDonna et al. 2014). My results suggest that as climate warms, the fate of alpine resources for pollinators may hinge on habitat aridity.

Synthesis and implications for bumble bee foraging in alpine ecosystems

Alpine bumble bees face earlier availability of floral resources when winter snowpack is low. While lower altitude systems have shown a variety of phenological responses in insects, some bees seem to have advanced in seasonal activity at similar rates relative to their floral resources, while other bee populations have declined due to temporal mismatching (Williams et al. 2009, Cameron et al. 2011). In sub-alpine, alpine and arctic systems, inter-annual variation in snowmelt predominates. Bumble bee queens emerging and foraging in the spring are likely to be most sensitive to these yearly shifts in the onset of flowering. Because bumble bees are ground nesters, emergence of queens in subalpine species also tracks snowmelt (B. Barr, unpubl. data) though the precise environmental cues that drive this phenomenon are unclear (Way et al. 2011). Similar trends are likely in alpine habitats: dwarf willow shrubs (*Salix*) that form large stands in the krummholz flower at the start of the growing season and attract high bumble bee visitation (Mosquin 1971). These early season resources could buffer bumble bees establishing nests from shifts in the onset of flowering for alpine forbs monitored in my study.

Bumble bee colony development and worker production respond to resource availability at the landscape scale (Williams et al. 2007). Bumble bees likely move among patches tracking peak flowering resources (Heinrich 2004).

Habitats across the mountain landscape exhibited significant variation in the timing of peak flowering. This heterogeneity may buffer against inter-annual and inter-decadal phenology shifts at smaller spatial scales by moderating the degree of plant sensitivity to drought (Litaor et al. 2008). Synthesis of ITEX experiments also show that local site characteristics are important in determining the phenological response of plants to climate change (Oberbauer et al. 2013).

In 2012 peak flowering dates of co-occurring species converged within plots, substantially shortening the period of floral resource abundance. Such temporal restrictions on resources could impact crucial demographic transitions for bumble bee colonies. Late season resources are associated with reproductive output in bumble bee colonies at lower altitudes, as this is the period when new queens and reproductive males are produced (Williams et al. 2012). If similar patterns apply to alpine bumble bee populations, synchronized episodes of early flowering have the potential to negatively affect colony reproduction.

Bumble bee populations follow annual cycles that establish nests early in the season (Goulson 2003). Paradoxically, nest searching at the onset of snowmelt above timberline likely restricts colonies to snow free microhabitats. Thus, alpine bumble bee colonies are likely concentrated in dry portions of the landscape where phenological advancement in their host plants is strongest and late season resource deficit probable. I predict that warming, by exacerbating the gap between nesting habitat and late season resources will contribute to foraging costs for alpine bumble bees and ultimately, to population decline.

Figure Legends

Figure 1. (A) Minimum summer temperatures ($^{\circ}\text{C}$) and (B) total winter precipitation (mm) for Pennsylvania Mountain, Colorado, USA. Points represent interpolated averages of (A) monthly mean minimum temperatures from June-August and (B) the sum of monthly precipitation from January-May (PRISM Climate Group Oregon State University). In (B), years of low snowpack are shown by grey symbols and high snowpack shown by white symbols. Minimum temperature and snowpack change significantly since 1977 ($R^2=0.45$, $P<0.0001$ and $R^2=.424$, $P<0.001$, respectively).

Figure 2. Aerial Map of Pennsylvania Mountain, Park County, Colorado, USA, $39^{\circ}15'$ N, $106^{\circ}03'$ W. Habitat regions are outlined in white and are labeled with abbreviations described in *Study System* section. Locations of permanent study plots are shown by white rectangles.

Figure 3. Means for (A, B) day of first flowering, and (C, D) week of peak flowering in years with different levels of winter snowpack (A, C) and in different decades (B, D). Day of year 155 corresponds to the calendar date June 4th and day 210 corresponds to July 29th. Different letters above bars indicate groups differing significantly at $p < 0.05$.

Figure 4. Average first flowering day (A,B) and peak flowering week (C,D) in bumble bee host plants as a function of total winter snow accumulation (A,C) and June-August mean minimum temperature (B,D). Symbols indicate species: blue diamonds, *Trifolium dasyphyllum*, red squares *T. nanum*; green triangles, *T. parryi*, and purple X's, *P. visocum*. Day 150 corresponds to the calendar date May 30 and week 0 begins on calendar date, June 12. Lines indicate best fit from linear regression (all, $P<0.05$).

Figure 5. Variation among habitats in (A) mean week of peak flowering and (B) mean duration of flowering for nine bumble bee host plants. Habitat abbreviations are as described in text (*Study System*). Day of year 155 corresponds to the calendar date June 4th and day 210 corresponds to July 29th. Different letters above bars show differences between groups, significant at $p < 0.05$.

Figure 6. Mean duration of flowering in snowy and dry years of the 1970s and 2010s. The interaction between decade and winter snowpack is significant ($F_{1,261}=3.98$, $P<0.047$). Different letters above bars show significant differences between groups at $P<0.05$.

Figure 7. Duration of peak resource abundance in plots during the 1970s and 2010s: the number of weeks in which peak flowering was sustained by the assemblage of co-occurring species in plots, standardized by the number of species per plot, S . Open bars show averages in years following deep winter snowpack while grey bars show averages following low winter snowpack. The interaction for decade and snowpack is significant ($F_{61}=5.9$, $P<0.018$). Different letters above bars show significant differences between groups at $P<0.05$.

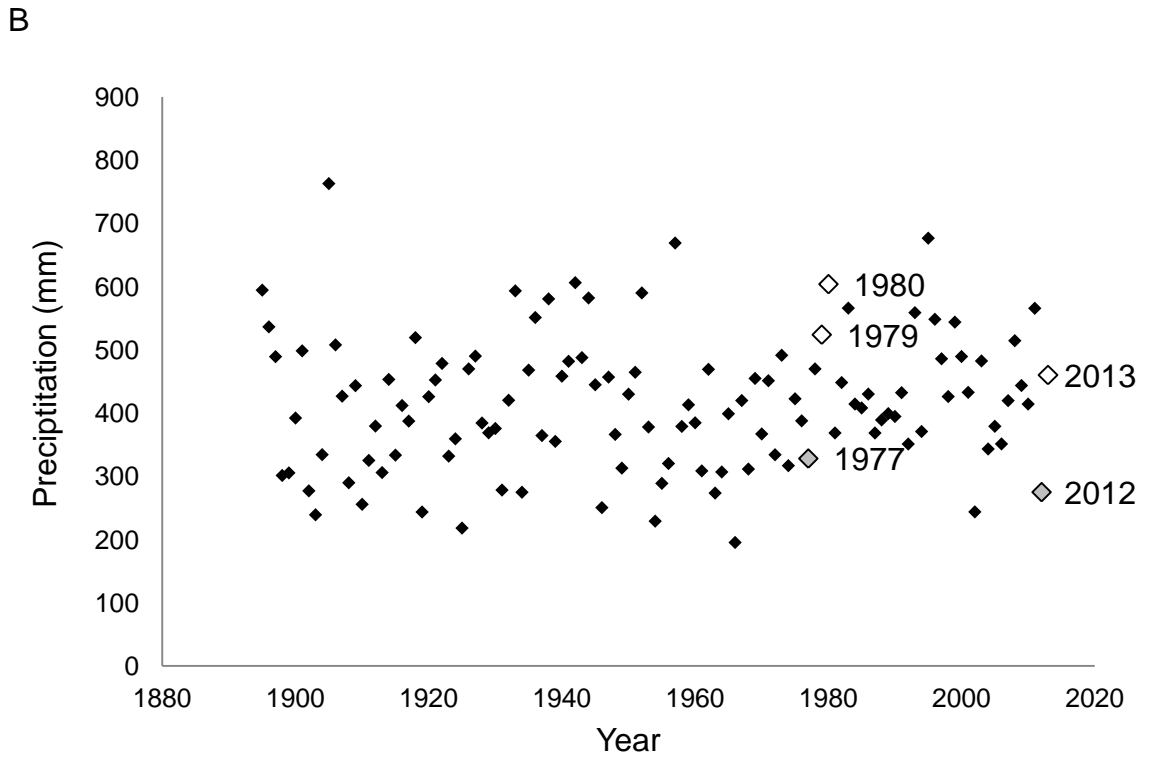
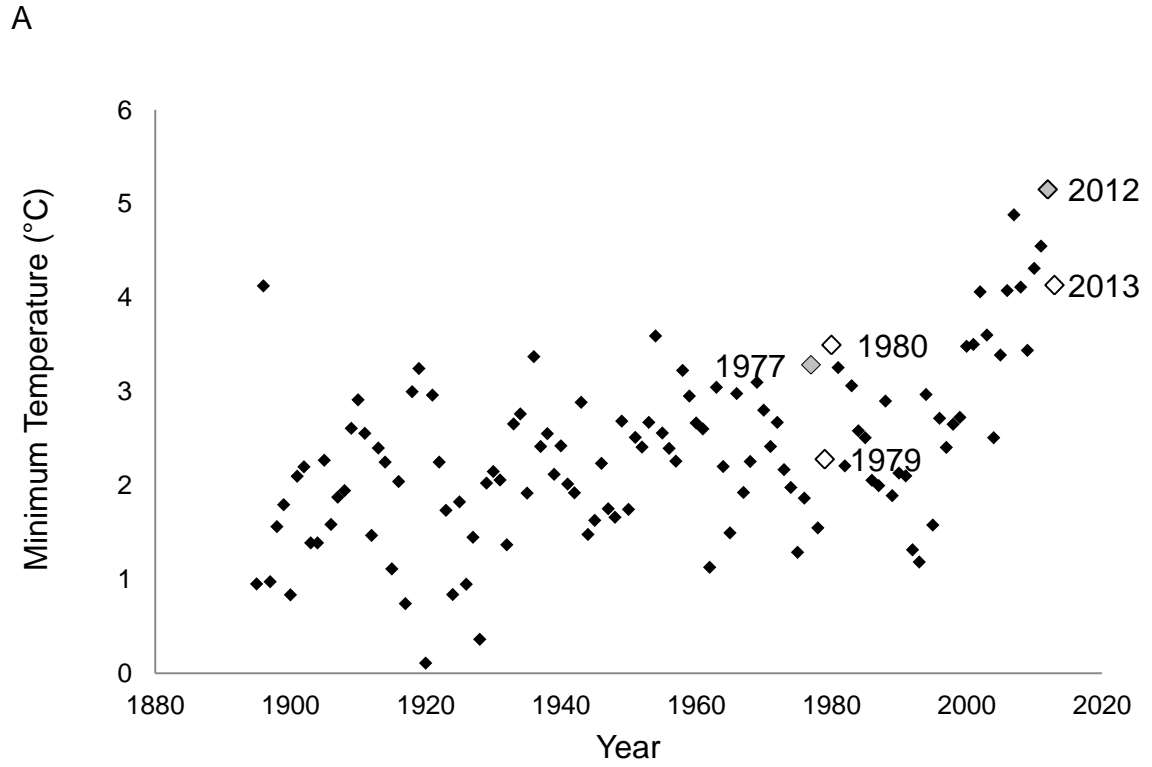


Figure 1

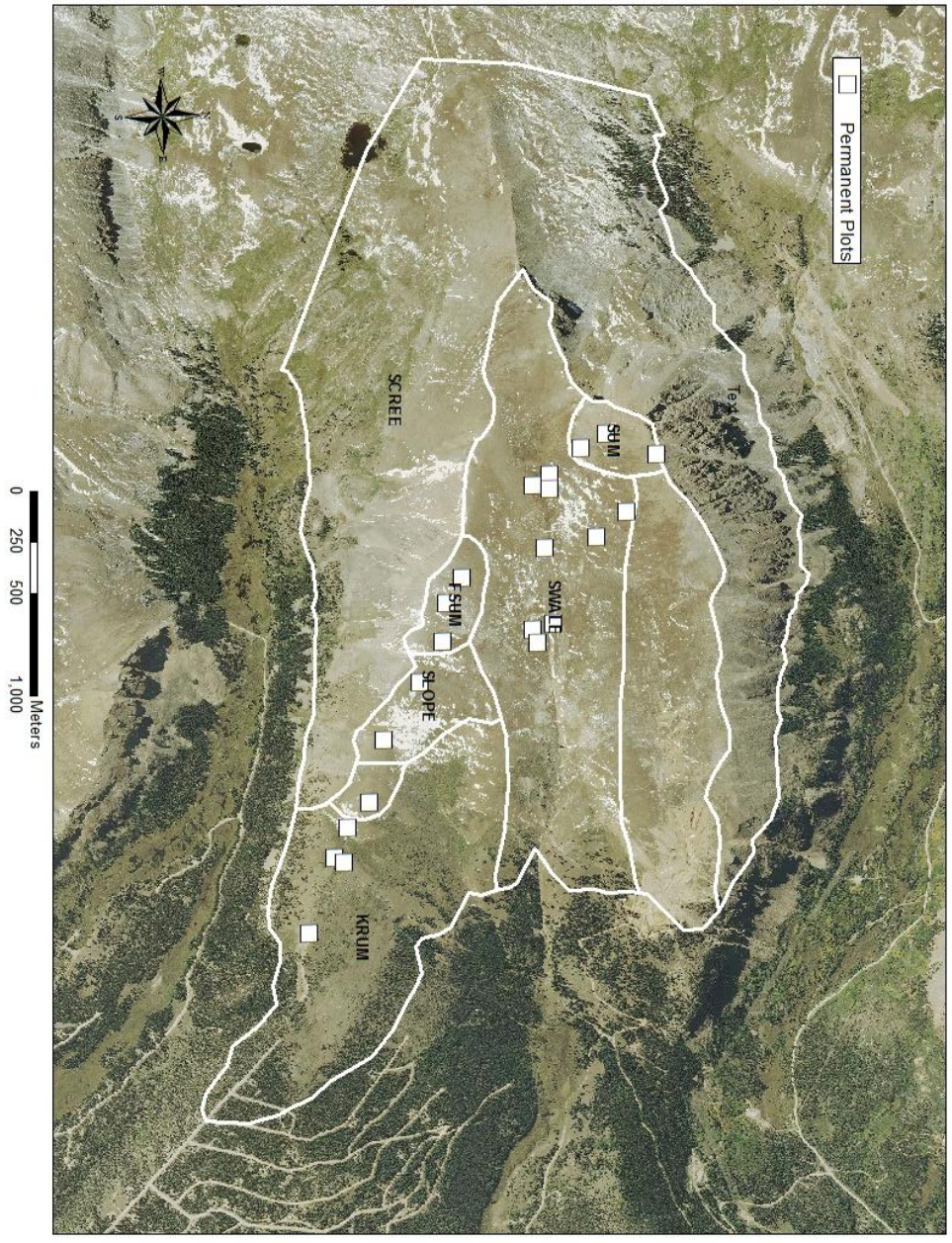


Figure 2

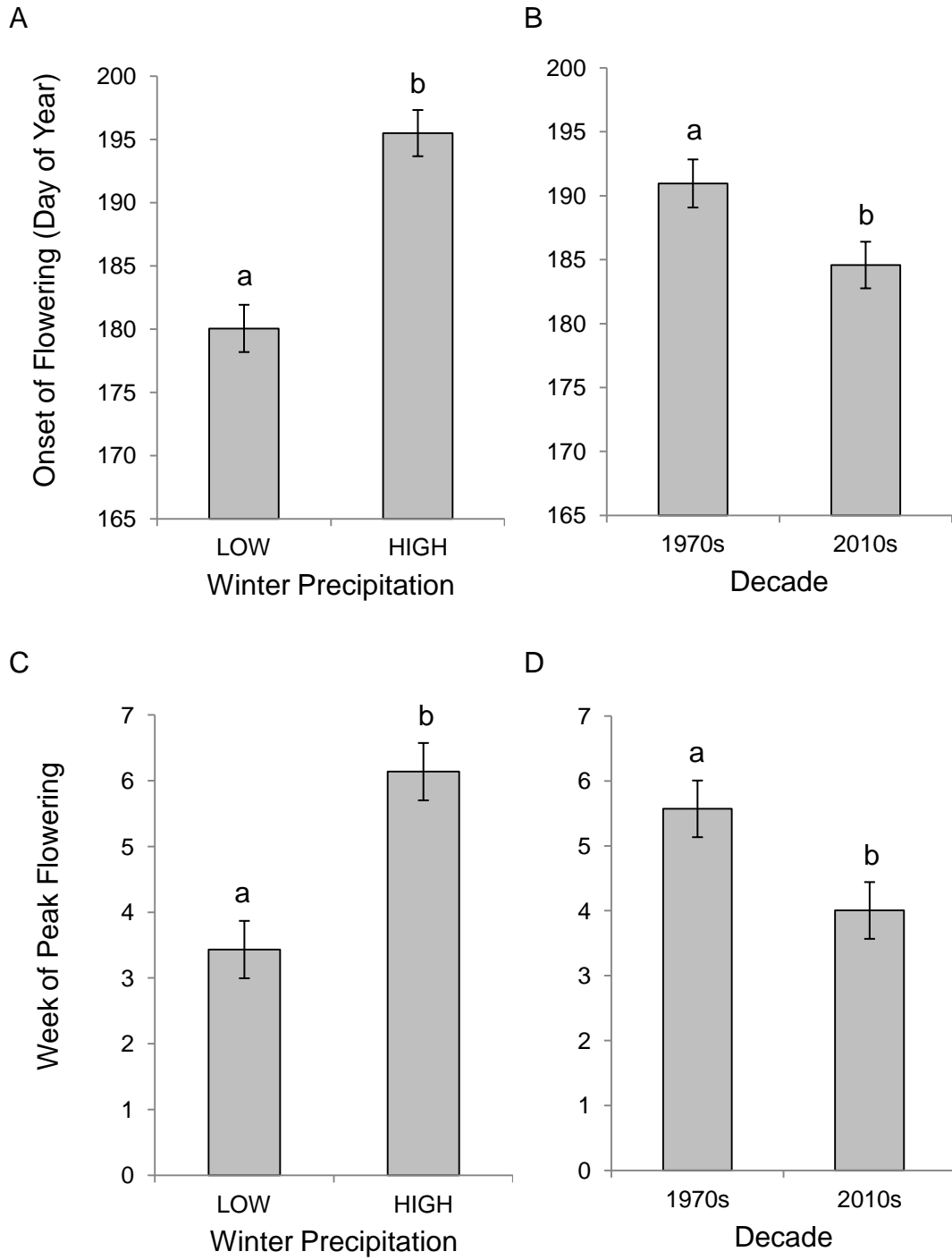


Figure 3

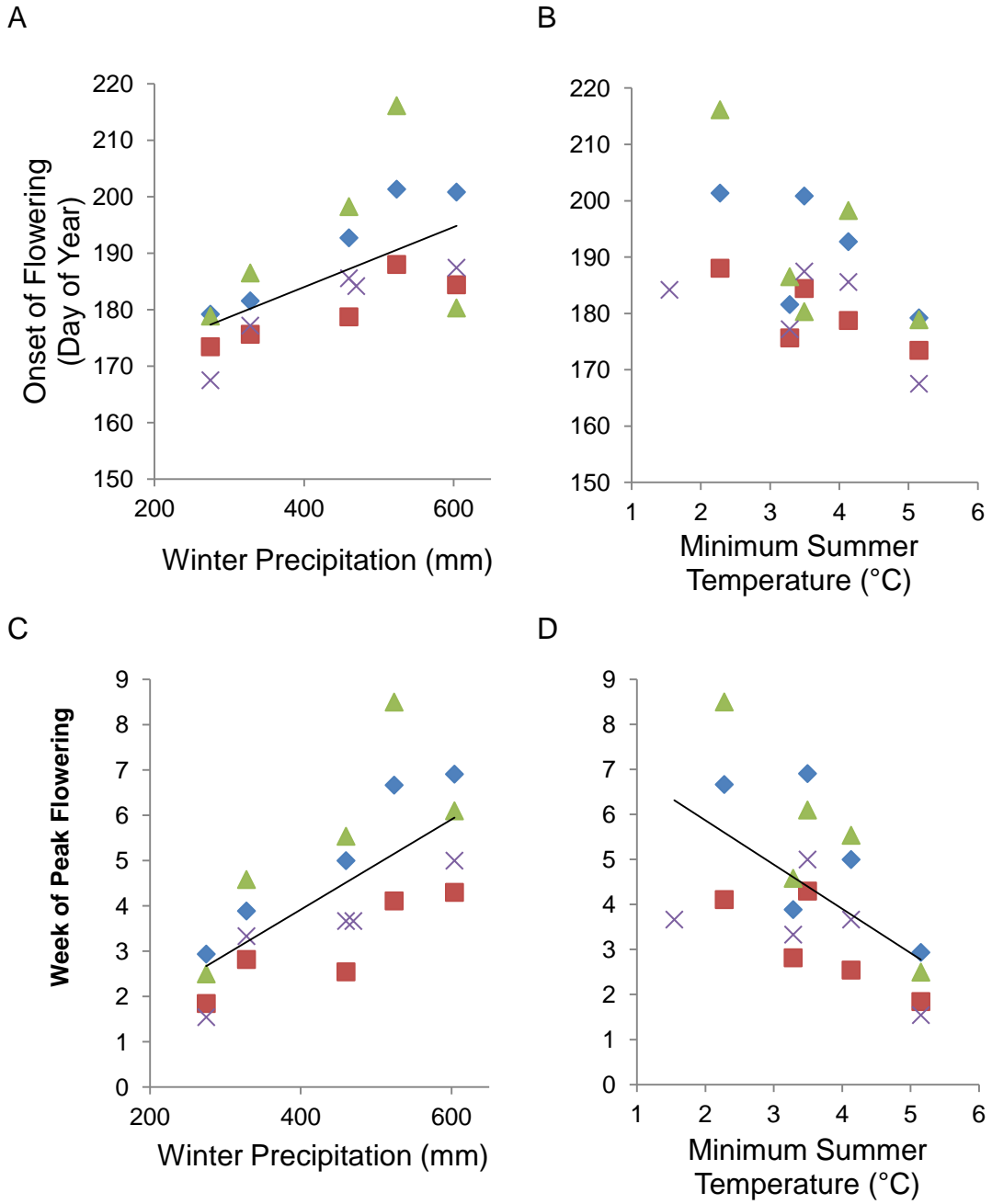


Figure 4

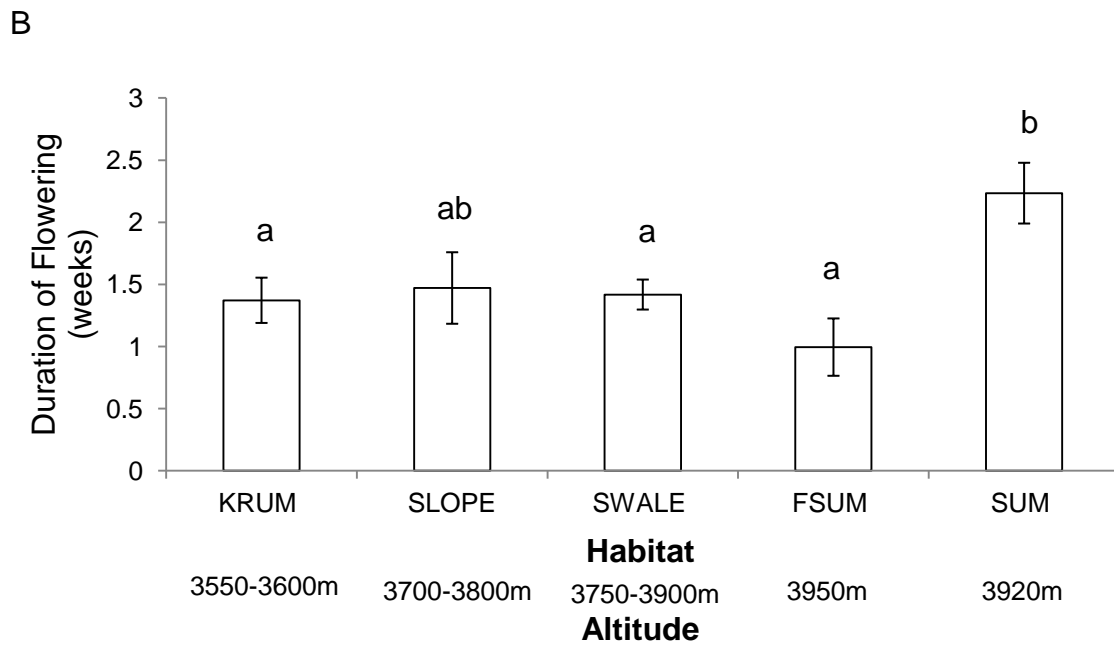
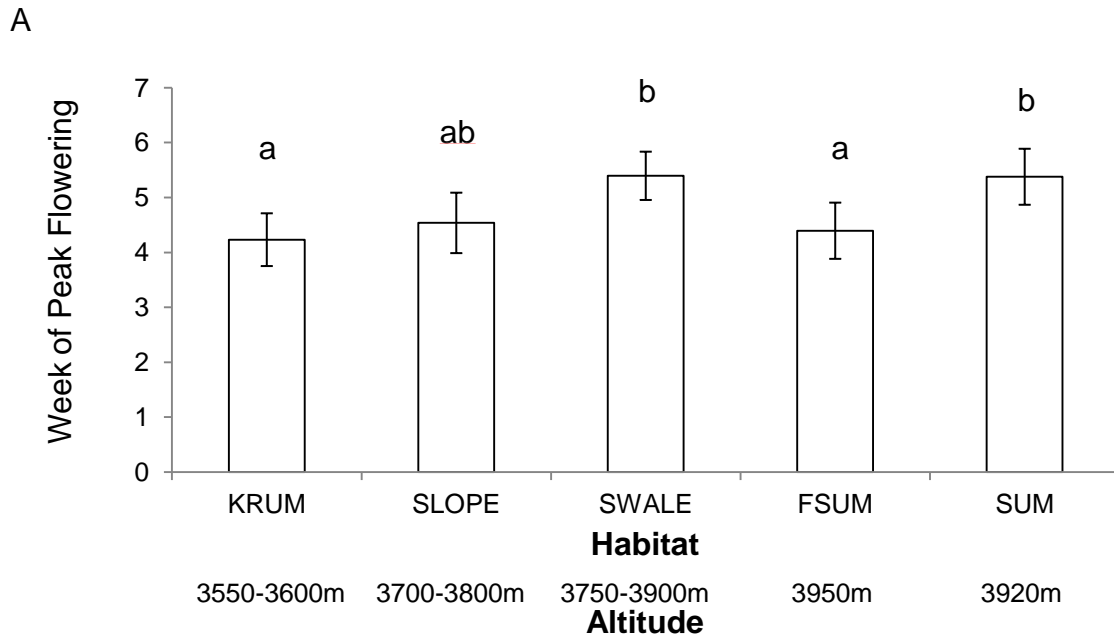


Figure 5

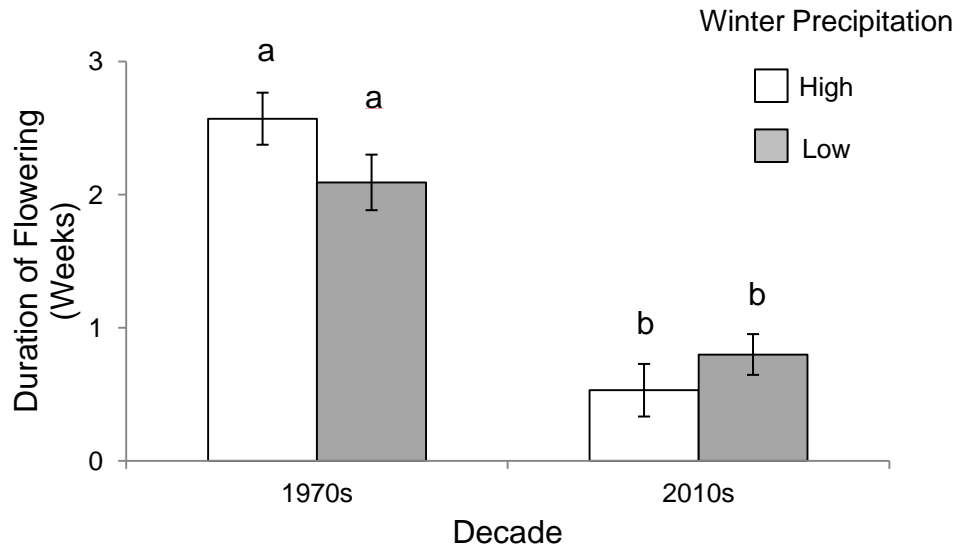


Figure 6

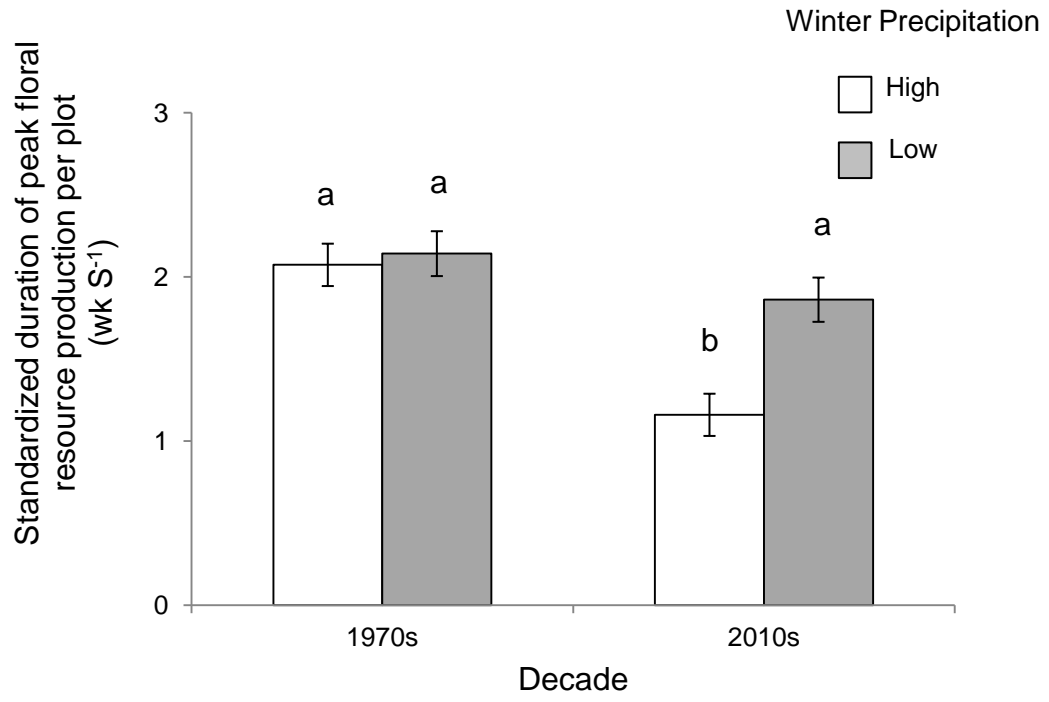


Figure 7

Table 1. Plant species that provide floral resources for bumble bees on Pennsylvania Mountain. The observed visitation rates of *B. balteatus* and *B. sylvicola* are averaged over all years given in Macior (1974) and Byron (1980). Habitat designations in bolded caps indicate those with peak abundance for that species historically (1977-80) while habitat designations in underlined caps indicate those with peak abundance currently (2012-13).

Family	Genus	Species	Macior		Byron		Habitats occupied	
Asteraceae	<i>Hymenoxis</i>	<i>grandiflora</i>	0	0	KRUM	<u>SLOPE</u>	swale	
Polemoniaceae	<i>Polemonium</i>	<i>viscosum</i>	0.4	10	krum	slope	SWALE	fsum
Scrophulariaceae	<i>Penstemon</i>	<i>whippleanus</i>	1.1	0	krum	SLOPE		fsum
Crassulaceae	<i>Rhodiola</i>	<i>rhodanthenum</i>	2.1	0			SWALE	
Fabaceae	<i>Trifolium</i>	<i>dasyphyllum</i>	2.2	14.3	KRUM	slope	swale	fsum sum
Scrophulariaceae	<i>Castilleja</i>	<i>occidentalis</i>	2.3	0.8	krum	slope	SWALE	fsum SUM
Boraginaceae	<i>Mertensia</i>		3.5	34.3	krum	slope	SWALE	fsum sum
Fabaceae	<i>Trifolium</i>	<i>parryii</i>	17.7	0.5	krum	SLOPE	<u>SWALE</u>	fsum sum
Fabaceae	<i>Trifolium</i>	<i>nanum</i>	31.6	31.8	krum	slope	swale	fsum SUM

CHAPTER 3. BLOOM AND BUST: ALPINE BUMBLE BEES FACE MAJOR DECLINES IN FLORAL RESOURCES WITH CLIMATE CHANGE

CHAPTER SUMMARY

Bumble bees require abundant floral resources that match the timing of colony establishment and growth. In alpine ecosystems, winter snowpack influences timing of flowering while summer temperature impacts retention of soil moisture to support flower production. I surveyed the seasonal abundances of floral resources provided by nine plant species that historically received 90% of bumble bee visits at the Rocky Mountain field site. Surveys included years of extreme low snowpack (1977 and 2012) and years of average to high snowpack (1979-80 and 2013). Flowers were counted throughout the summer in habitats spanning an altitudinal gradient from 3500-4000 m. Regardless of winter snow accumulation, both seasons in the current decade failed to support flower densities as high as those observed in 1977. Lower habitats near timberline showed greater decreases in flower density than upper ones, consistent with the concept of high altitude refugia from climate change. I used a simple analytical model to estimate how maximum possible bumble bee resource intake has changed from the 1970s assuming that resident bumble bees retain their historical floral preferences. This model suggests that when floral resource abundances are averaged over both wet and dry years, the foraging specialist *Bombus balteatus* and the generalist *B sylvicola* have faced ~74-80% reductions in potential resource intake over the season. Results imply that regardless of

foraging strategy, resident alpine bumble bees are under strong pressure to shift to new resources or expand their foraging ranges. Such scenarios could favor host plants from lower altitudes as they expand upward into alpine habitats with climate change.

INTRODUCTION

The influence of regional climate patterns may vary at small spatial scales producing a range of abiotic conditions across a landscape. The term refugia describes area of relatively suitable conditions within regions of generally adverse climate patterns. Refugia allow restricted populations to persist through adverse climate events that can then act as a source for re-colonization when conditions become more broadly suitable (Davis and Shaw 2001, Dobrowski 2011). The identification of refugia and smaller scale microrefugia informs species response under current climate change and helps set priorities for conservation of biodiversity (Primack et al. 2009, Ashcroft 2010). Because temperature declines with altitude, mountain landscapes may provide refugia for lower altitude populations as warming occurs. Similarly, current alpine communities may become restricted to sites where combinations of slope, slope aspect and vegetation create suitable microrefugia (Wundram et al. 2010).

Bumble bees and flowering plants represent a prominent mutualism that interacts across alpine landscapes. Alpine bumble bees forage for pollen and nectar on flowers near annually-established nest sites (Goulson 2010). Colony growth is limited by pollen and nectar intake and so nest site location and the

associated costs of flight to forage from broadly distributed patches of flowers influence colony reproduction (Heinrich 2004). As alpine habitats warm globally alpine plant community response depends on habitat specific factors producing variation in flower resources across a landscape (Oberbauer et al. 2013). It is unclear whether current alpine floral resources are sufficiently dense over the foraging landscape and throughout the summer foraging season to support bumble bee colony growth and reproduction under established mutualist partnerships (CaraDonna et al. 2014). Habitat variation in plant response may therefore produce foraging refuge in some habitats while others decrease in floral resources.

In this study I observed total seasonal flower density for a guild of alpine plant species that has historically comprised the most important food resources for resident bumble bee species at high altitudes in the central Colorado Rocky Mountains. Over the 35 year span of my study there has been a 2.4°C increase in average summer minimum temperatures at this site ($R^2=0.45$, $P<0.001$; Chapter 2 Figure 1). The first two goals of my study were to explore (1) how floral resource availability for bumble bee pollinators has responded to extreme weather events at two time scales: inter-annual, and inter-decadal and (2) to characterize flower production in a variety of alpine habitats in order to understand whether spatial heterogeneity in mountain systems gives rise to resource rich micro-refugia for bumble bees.

Recent models of pollinator foraging in relation to resource abundance suggest that specialists and generalists should exhibit different sensitivity to

declining flower production (Essenberg 2013). My data provide a unique opportunity to address this idea for two resident alpine bumble bee species with contrasting foraging strategies, *Bombus sylvicola* and *B. balteatus*. Although multiple bumble bee species occur currently above timberline in the Colorado Rocky Mountains, these two species represent the sole *Bombus* to nest above timberline in the Rocky Mountain alpine historically (Byron 1980, Miller-Struttman & Galen, 2014). In the 1970s *B. sylvicola* exhibited a generalist foraging strategy with diet composition tracking floral abundance ($r = 0.93$, $P < 0.005$ for the correlation between the proportion of bumble bee visits received and the flower density of the host plant species; Figure 1). Conversely, flower visitation by longer-tongued *B. balteatus* exhibited little relationship to flower abundance ($r = 0.27$, ns; Figure 1; Byron 1980). Thus, a third goal of my study is to explore the potential impact of climate driven changes in flower abundance on resource consumption by specialist and generalist pollinator species using a simple analytical model to ask whether differences in their foraging strategies might alter the impact of variation in flower abundance on potential food intake.

METHODS

Flower counts

Methods for plot selection, temporal sampling, correction for changes in sampling scale between decades and description of the topography and habitat configuration for the Pennsylvania Mountain study site are described in Chapter 2. Here I include additional detail on techniques for estimation and analysis of

flower density. As inflorescence structure varies among plant species, I used open flowers·m⁻² as a common metric of floral resource density. Counts were made during weekly phenology surveys (CHAPTER 2, Sampling Design) from the onset to the end of flowering in each plot. In 1977-80 flowers were counted for all species on a weekly basis and total season flower counts were divided by the 20 m² area. In 2012-13 the larger plot scale necessitated use of more rapid estimation techniques. Large study plots were sampled as a contiguous grid of 1 x 2 m cells. I counted inflorescences per m² in every third row (10 m dimension of plot) and estimated flowers per inflorescence from a single individual in the center and two edge cells of each counted row (30 per plot domain or less if fewer than 30 individuals were available). Flower per inflorescence data for *T. dasyphyllum* and *T. parryi* were taken from Geib *et al.* (*in press*) collected on Pennsylvania mountain in previous years, while flower per inflorescence data for *C. occidentals* were taken from Miller-Struttmann (unpubl.) collected at Mount Evans and Niwot Ridge in the Colorado Rockies.

Statistical analyses

Inter-annual and inter-decadal variation in flower density

For 1970s plots, total seasonal flower densities were calculated in each plot by summing the total number of flowers for each species over the growing season and dividing by the total area of the plot. Because I was interested in total seasonal resource availability, I did not compute average flower density on a daily or weekly basis. 2010s flower counts were taken over larger plots (CHAPTER 2, Sampling Design). To compare flower densities in the 2010s and

1970s, I calculated flower density separately in each independent 2 x 10 m area included in the larger 2010s plot and then averaged these values. Flower species that were absent from plots were included in the analysis as zero values.

Seasonal flower densities (average number of flowers observed per m² per season) for each species in each plot were analyzed with mixed model analysis of variance (ANOVA) using PROC Mixed in SAS 9.2 (2013). To meet assumptions of normality and reduce heteroscedacity, seasonal flower densities were log-transformed prior to analysis. Plot and plant species were included as random effects in the model while decade, winter snowpack and habitat were included as fixed effects.

Impact of temporal change in flower abundance on potential bumble bee resource intake

To explore how recent seasons of low floral abundance (Figure 2) impact the maximum possible food intake for resident bumble bee species I calculated the relative decline d in flowering for each host plant species i as

$$d_i = (HF_i - CF_i) / HF_i$$

where HF_i and CF_i are respectively the average flower density of species i per m² in the 1970s (historic) and 2010's. I then calculated the resource loss that a bumble bee of species j experiences from foraging on species i as:

$$c_{ij} d_i$$

where c_{ij} represents the consumption rate of species j on species i or the fraction of flower visits made to i historically (CHAPTER 2, Table 1). The total reduction R_j in consumption if species j retains its historical diet is given as:

$$R_j = \sum_{i=1}^{i=n} c_{ij}d_i$$

This model assumes that flower resources are currently of similar value both in reward quality and reward type (e.g., pollen vs. nectar) to historical norms.

RESULTS

Inter-annual and Inter-decadal variation in flower density

The change in flower density associated with climate depended on the decade ($F_{1,720}=8.54$, $P<0.0036$). Flowering of bumble bee resources was more prolific in 1977 with an average of 4.9 ± 1.12 flowers·m⁻² over the season than in any other year (range of flower density 0.79-2.07 flowers·m⁻²; planned comparisons based on least squares means, all $P<0.0048$). Average seasonal flower densities were low in both the 2012 and 2013 seasons (Figure 2).

The recent decline in flower density varies in magnitude among habitats ($F_{4,720}=3.29$, $P<0.0109$; Figure 3). Current declines in flower density of an order of magnitude have occurred in the krummholz ($t=3.95$, $P<0.0001$) southeast facing slopes ($t=3.34$, $P<0.0009$) and in the swale habitat ($t=2.67$, $P<0.0078$). However, flower density has not changed over time on the false summit ($P>0.35$; 3920m) or summit habitats ($P>0.30$ for both; Figure 3).

Impact of current low seasonal flower production on bumble bee resource intake

For *B. balteatus* and *B. sylvicola* expected reductions in potential consumption of floral resources from individual host species vary from 83-100% (Figure 4). When summed across the full complement of species used historically, these incremental reductions add up to substantial losses in potential dietary resources of 74% and 79% respectively. Historical differences in foraging niche breadth do not appear to alter the impact of declines in flower availability.

DISCUSSION

Seasonal floral resources for bumble bees are less abundant within the current alpine landscape on Pennsylvania Mountain than they were in the 1970s. My results are consistent with the view that declines are primarily driven by a combination of winters of low snowfall followed by warmer summers. Growth and flowering of alpine plants in the central Rocky Mountain are largely drought limited (Galen 2005) Yet in 1977, dry winter conditions promoted relatively high flower density in alpine habitats. In alpine habitats, low snow pack favors earlier snowmelt, potentially lengthening the growing season. Under this scenario, higher flower production over the season is expected (Inouye 2008). Many have predicted that warmer temperatures and reduced snow pack associated with climate change will increase the total length of the growing season in alpine ecosystems and thus increase flower resources for insect pollinators (Molau and Shaver 1997, Klanderud 2005). However, my results indicate that warmer

summers are reducing seasonal flower production for alpine plants because of a mismatch between time available for growth and flowering and sufficient soil moisture to support flower production (Galen 2000).

Soil drying under warmer summer conditions such as those observed on Pennsylvania Mountain in 2012, can reduce reproductive effort for plants as water availability limits flower production (Primack 1987). Soil drying is a proposed mechanism for shortening plant reproductive intervals across arctic and alpine sites especially in dry conditions (Oberbauer et al. 2013). I have also observed an overall shortening of the flowering season on Pennsylvania Mountain in recent years ($F_{1,227}=, p<0.0001$; CHAPTER 2, Figure 7) which was especially pronounced in 2012. Flower number and size are sensitive to water availability (Galen 2000). Frost damage to reproductive structures also increases when snowpack melts early and could reduce seasonal resources for bumble bees in alpine habitats (Inouye et al. 2002, Inouye 2008).

Decreased flower density over time is most pronounced in low altitude habitats (Figure 3). This trend conforms to the view of high alpine habitat as a climatic refuge for populations from lower altitudes during historic and current warming events (Parmesan and Yohe 2003, Parolo and Rossi 2008). Flower resources for bumble bee pollinators may provide an early signal of future distributional shifts for these plant species.

Over the past 35 years, woody, dwarf shrubs have expanded their distributions in alpine and arctic sites (Sturm et al. 2001, Cannonel et al. 2007). This process of “habitat conversion” may have indirect effects on resident

pollinators, if shrubs displace key floral resources. On Pennsylvania Mountain, dwarf shrubs are dominated by willow (*Salix*; Dudley 2006). While willows provide abundant resources for bumble bees at the onset of the growing season, they exclude nearly all later-flowering forbs that have historically provided floral resources for bumble bees (CHAPTER 2, Table 1). *Salix* may provide an important pollen source for early emerging queens, but reduce later flowering plants that support reproductive output for bumble bee colonies (Williams et al. 2012). For example, one krummholz plot in this study that contained over 1200 flowers in the 1970s is now dominated by *Salix* and contained only 12 flowers in 2012-13. Genetic studies show some dwarf shrubs alive today are 1500 years old and respond quickly to novel climate conditions (de Witte et al. 2012). Thus, increasing cover of dwarf shrubs may have lasting impacts on plant-pollinator interactions and pollination services in alpine ecosystems.

Flower resources were estimated to have been prolific in the 1970s with roughly 100,000 flowers for every bumble bee (Byron 1980). If I assume similar populations of bumble bees currently, the ratio of bumble bees to floral resources after the dry winter of 2012 drops to 1:460. Use of supplementary sources may over estimate flower number early and late in flowering because observations were typically made when plants were in full bloom. In this case, current density estimates could be artificially inflated relative to historical counts in the field, making my estimate of decline conservative. Alpine flowering plants have historically exhibited strong pollinator limitation (e.g., García-Camacho and Totland 2009) and it is unclear whether total flower abundance has fallen low

enough to limit bumble bee population growth. Optimal foraging theory suggests that reduced flower density should increase energetic costs for foraging bumble bees (Heinrich 2004). Williams et al. (2012) found that low floral density accompanying anthropogenic disturbance decreased colony production for *Bombus* at the landscape scale independent of local conditions. If these findings apply to alpine bumble bees, declining flower density near timberline could reduce bumble bee colony productivity at large altitudinal scales and favor a shift to pollinating taxa with lower search costs (Essenberg 2013).

My model relating declining floral abundance to bumble bee resource consumption suggests that differences in past foraging strategy should have little direct impact on the sensitivity of bumble bees to recent and future changes in flower abundance. Essentially, none of the host plant species that bumble bees used historically represents a “good bet” for a stable floral resource under climate change. Neither the generalist forager *B. sylvicola* or specialist forager *B. balteatus* showed a strong historical preference for plant species experiencing the largest decrease in flower density. However, decreases in flower production for all species exceed 80%. For both resident alpine bumble bees, including novel host plants in their diet or switching between co-flowering species opportunistically should be favored as colony output becomes increasingly resource limited. Kleijn and Raemakers (2008) demonstrated persistent populations of bumble bees foraged on a greater variety of plant species than did declining populations and that their preference tracked changes in flower availability at the landscape scale. At my site, the inability of bumble bees to rely

on historic foraging preferences favors the upward spread of subalpine and exotic plants that offer rich resources to bumble bee pollinators (e.g., *Chaemanerion angustifolium*, *Taraxacum officinale*, Brock 2004, Dona and Galen 2006) and are currently expanding into high alpine habitats.

Figure Legends

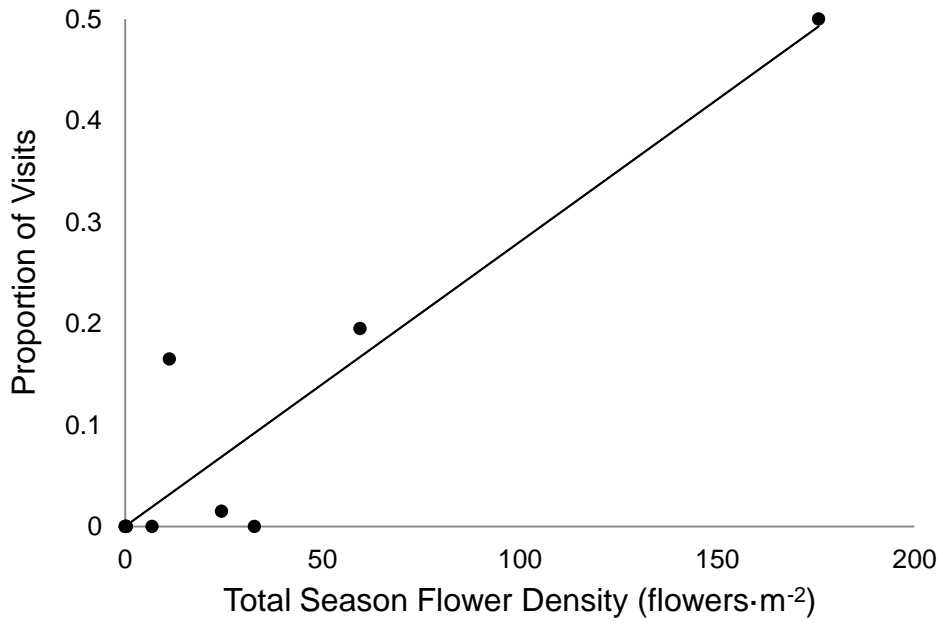
Figure 1. Correlation of bumble bee flower visitation rate (Byron 1980) with average seasonal flower density for each host plant species in the 1970s for (A) *B. sylvicola* and (B) *B. balteatus*. The correlation is significant for *B. sylvicola* ($r = 0.93$, $P < 0.005$) but not *B. balteatus* ($r = 0.27$, ns)

Figure 2. Seasonal flower density for bumble bee host plants (least squares means from mixed model ANOVA) taken from 2 x 10 m plots sampled in the 1970s and using the average of independent 2 x 10 m plots contained within 2012-13 sampling domains surrounding each original plot. Means for years of low snowpack are shown by open bars and years of high snow pack by solid bars. For the interaction of decade and snowpack, $F_{1,342} = 3.65$, $p < 0.057$. Bars with different letters indicate means significantly different at $P < 0.05$.

Figure 3. Average seasonal flower density for bumble bee host plants (least squares means from mixed model ANOVA). For the 1970s, open bars show average flower densities over the growing season within original 2 X 10 m plots and for the 2010s solid bars show average density from independent 2 x 10 m subplots in a plot domain centered on the original plot (see methods, CHAPTER 2.) For the interaction of decade and habitat, $F_{1,720} = 3.29$, $p < 0.01$. Habitat abbreviations (ordered by altitude) are defined in the text, *Study System*,* indicates a significant difference between means ($p < 0.01$).

Figure 4. The relative decline in flower availability (d_{ij}) of each plant species from its historical flower density on Pennsylvania Mountain. Historic preference of (a) *B. sylvicola* and (b) *B. balteatus* based on the proportion of total flower visits observed to that species in 1978 and 1979 (Byron 1980) is shown on the x-axis. For both bumble bee taxa, constancy to historically preferred host plants should reduce maximum floral resources by more than 90%.

A



B

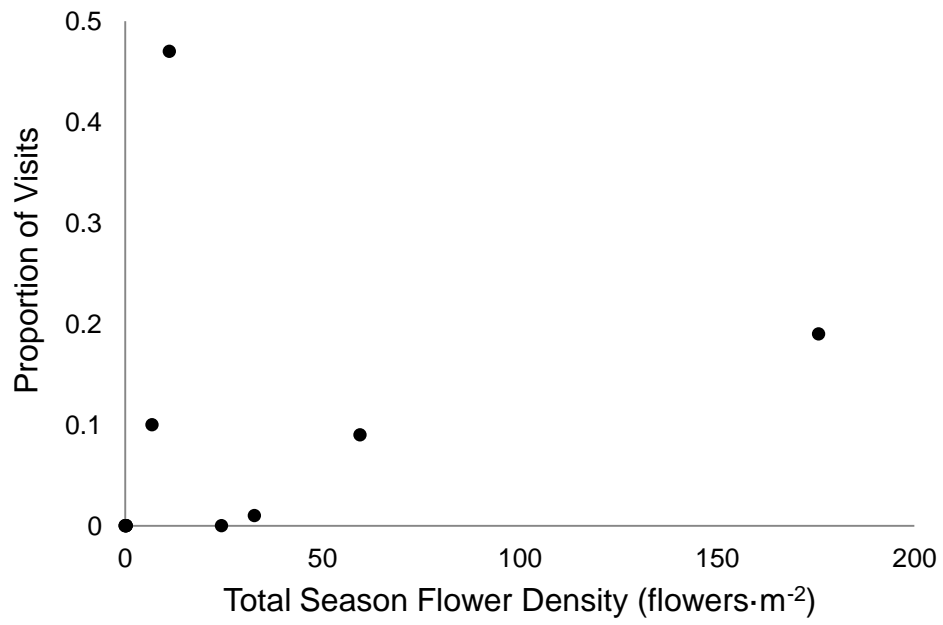


Figure 1

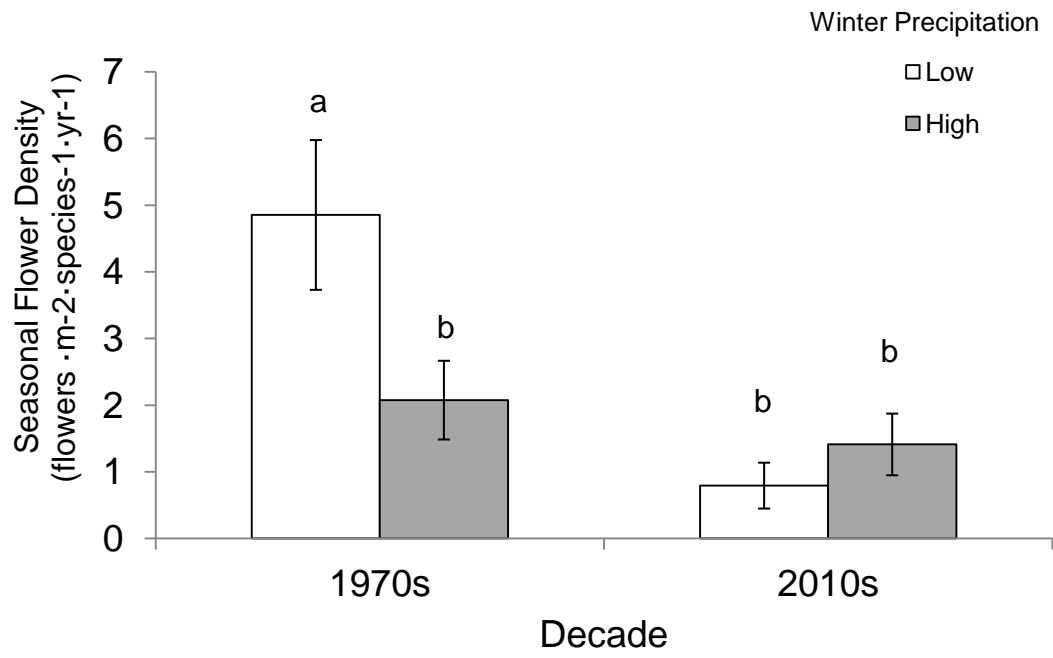


Figure 2

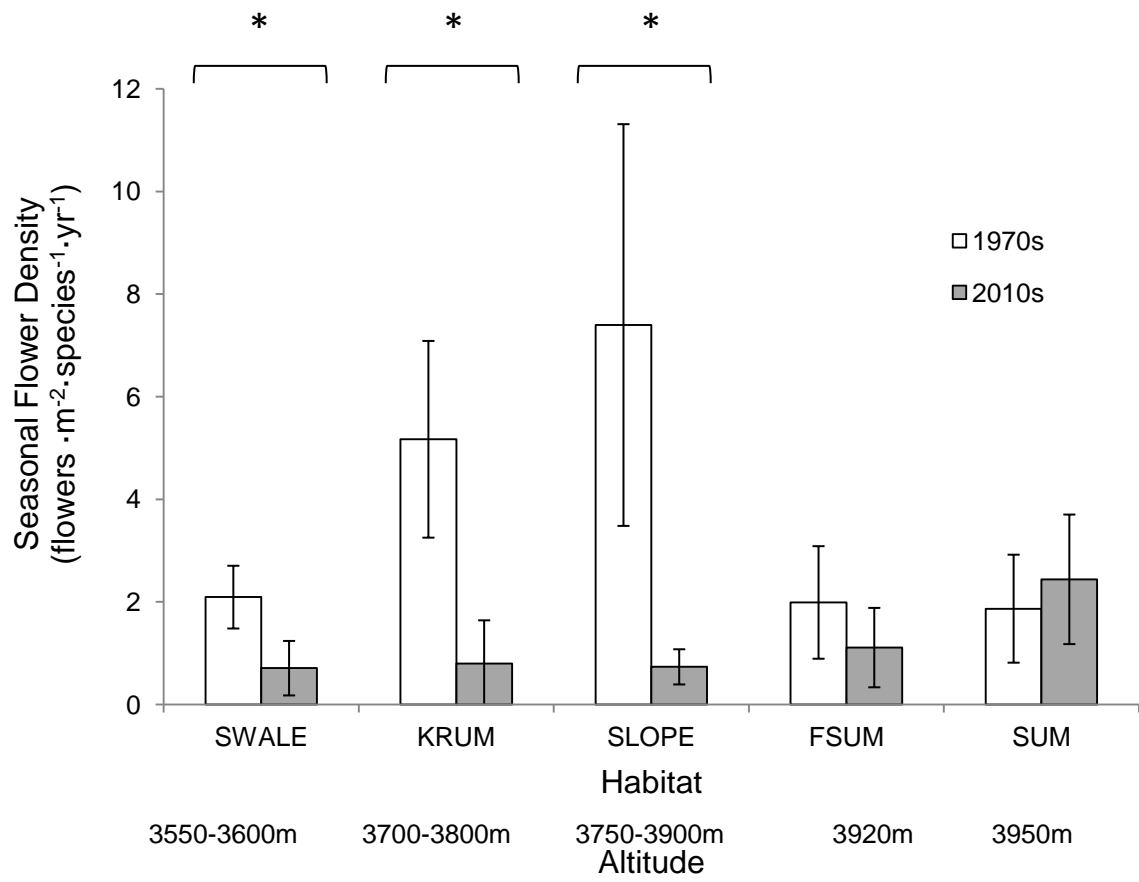
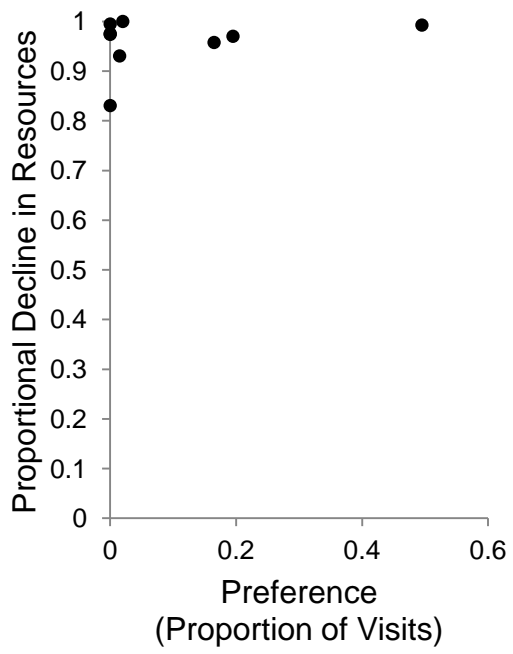


Figure 3

A



B

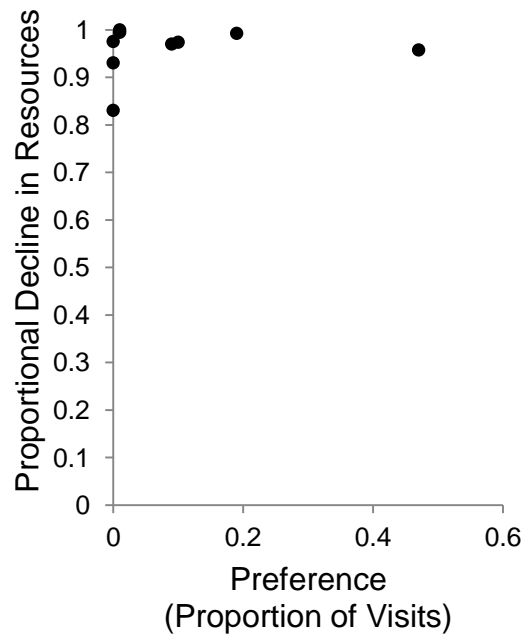


Figure 4

CHAPTER 4. CONCLUSIONS

As a baseline, the 1970s phenological surveys show that lower temperatures and less winter precipitation on Pennsylvania Mountain produced the highest density and longest duration of floral resources for alpine bumble bees. Both seasons in the 2010s produced significantly lower availability of flower resources. For the *Trifolium* species and *Polemonium* where additional years of data are available, I observed a strong correlation between both onset of flowering and peak flowering with winter precipitation and summer minimum temperatures respectively, indicating that timing of flowering in these plant species is responding to the same environmental cues in the 2010s as the 1970s. The increase in temperature at this site over the past 35 years has produced a higher likelihood for the coincidence of low winter precipitation events with higher summer minimum temperatures, a situation in which sparser and more ephemeral floral resources observed in the warmer 2010s are further restricted in time by synchrony among peak flowering by different species within a plot. Our data suggest that warmer temperatures are associated with reduced resources for alpine bumble bees promoting demographic and possibly evolutionary responses in these charismatic consumer species.

The results of our resource intake model, suggest that declines in density of flowers across historically important flower species will drive alpine bumble bees to alter foraging strategies from the 1970s. Alpine bumble bees may establish new mutualist partnerships with resident alpine flower species or with invading lower altitude plant species (Dona and Galen 2006). Further studies of

alpine bumble bee foraging decisions at this site are necessary to address how the composition of plant-pollinator mutualisms has changed over this period. Alternatively, alpine bumble bee populations may decline in response to the landscape scale reduction in flower availability (Williams et al. 2012). It is unclear whether alpine bumble bee colony growth is limited by the lower availability of floral resources observed in the 2010s, especially since current flower densities are similar to those observed in the 1970s following high winter snowpack (CHAPTER 3, Figure 2). In the 1970s the ratio of flowers to individual bumble bees was 100,000:1 and overall pollinator limitation was demonstrated in some bumble bee pollinated plants indicating an abundance of flowers relative to bumble bee populations (Byron 1980). Alpine bumble bees follow annual reproduction cycles and the absence of a season with flower densities comparable to 1977 in the 2010s may affect boom and bust dynamics and the long term persistence of resident alpine bumble bee populations. The foraging range of alpine bumble bees is unclear and it is possible that surrounding alpine habitat could support colonies. However, optimal foraging theory suggests that increased flight distance between patches of flowers should produce a larger energetic cost for bumble bee colonies (Heinrich 2004). Most forecasts of pollinator decline are based on decreases in resource benefits rather than increases in foraging costs. Developing models that consider both costs and benefits of foraging could improve our understanding of bumble bee responses to climate change.

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