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# Climate Change Impacts in Alpine Plant Communities

By

Meredith D. Jabis

A dissertation submitted in partial satisfaction of the

requirements for the degree of

Doctor of Philosophy

in

Environmental Science, Policy and Management

in the

Graduate Division

of the

University of California, Berkeley

Committee in charge:

Professor John Harte, Chair

Professor Lara M. Kueppers

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Climate Change Impacts in Alpine Plant Communities

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By

Meredith Diana Jabis

Abstract

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Mountains have been warming faster than lower elevation ecosystems, and because of tight coupling between organisms and a compressed growing season, the impacts of change may be more pronounced in high elevation systems. Further, in the climatically extreme alpine environment, biotic interactions between neighboring species may be important to alpine species persistence or colonization by lower elevation species. For species whose upper distributional range is within or near the alpine-treeline ecotone, climate change will likely relieve cold temperature limitations to higher elevation establishment. Taken together, climate change is likely to impact alpine plant phenology, species interactions, and may cause species range shifts. However because many alpine plants are long-lived, they may persist in the midst of change resulting in disequilibrium with climate. In the first chapter, I examine the effects of experimental warming and watering on alpine plant phenology and evaluate the mechanisms driving change. I ask does warming act directly through temperature or indirectly through snowmelt or drier soils to influence community flowering? I found that earlier snowmelt, not warmer temperature, drives advances in alpine plant community flowering. Because of strong synchrony of alpine phenology to a short growing season, community level flowering duration was conserved. Early flowering species with strong coupling to snowmelt timing responded most strongly along with forbs and graminoids, while longer lived cushion plants and succulents were more resistant to change and did not take advantage of a prolonged growing season. My second chapter examines the role of species interactions between native alpine vegetation and subalpine conifers, which have the potential to migrate into the alpine ecosystem. Consistent with the stress gradient hypothesis, which would predict greater benefits from neighbors at higher elevations, a shade and moisture tolerant conifer requires neighbors to establish in the alpine, while a sun and drought tolerant conifer Is equally likely to establish aside neighbors or in vegetation gaps. Contrary to the stress gradient hypothesis however, a native alpine herb benefits from the presence of neighbors even at the low elevation end of an environmental stress gradient. In the final chapter, I use a decade long observational dataset from four mountain summits, at four

elevations, as part of the Global Observation Research Initiative in Alpine Environments. Over a longer, 40-year time period, maximum and minimum temperatures have risen, while snowmelt date advanced at a nearby weather station. On the summits, community-wide vegetation cover decreased while richness increased over the decade of observations. Long-lived alpine plants were generally slow to respond, but there is some evidence for colonization of the lowest elevation, the most rugged, and the highest elevation summit. Long-lived alpine species may be able to resist change resulting in disequilibrium with climate but continued rising temperature and decreased snow duration will likely have an impact on future composition, performance and persistence of plant species in alpine tundra communities.

## DEDICATION

This dissertation is dedicated to my dear cousin, Christopher Molinaro, who left this earthly form much too young, but who understood the value of learning a lesson the hard way, dusting yourself off and simply moving on as he would say "*to the next chapter*".

Chris's memory lives on in these pages since he inspired me to complete something that seemed overwhelming and impossible. He was the reason, outside of myself, that I persevered.

*If you can't fly then run, if you can't run then walk, if you can't walk then crawl, but whatever you do you have to keep moving forward.*

*Only in the darkness can you see the stars.*

Martin Luther King Jr.

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## Acknowledgements

My dissertation began in a small meadow in the southern Sierra Nevada Mountains of California while crouched over a range restricted endemic plant with an undetermined fate given climatic change. This final work was made possible, however, because of the inspiration, dedication, and insight of my advisor, Lara Kueppers. It was both her foresight in developing a complicated and important experiment that allowed me to investigate a subject I have been impassioned about for some time, and her dedication to the subject and her students that allowed me to finish. I am also indebted to the instructors I met along the way – Tina Ayers and Thomas Whitham who guided me in my formative path as a scientist. John Harte provided me with the opportunity to study at UC Berkeley, and Katherine Suding, Todd Dawson, and David Ackerly all shared their wisdom. Ethan Brown gave hours of computing encouragement, and Meagan Oldfather endured the process with me. Also to my father who let me give up on gymnastics as a kid but wouldn't let me give up on this larger pursuit of knowledge, and to my mother who was with me every step of the way.

# INTRODUCTION

The composition of alpine plant communities is driven, as in many other systems, by a combination of biotic and abiotic elements. In the alpine, extreme abiotic conditions include long periods of snow cover, strong wind scouring, large temperature fluctuation, poor soil development, early- and late-season frosts and soil moisture dry-down during the growing season. Organisms must be adapted to this short growing season and strongly seasonal regime in order to successfully emerge, grow and reproduce. Alpine plant communities are composed of largely perennial species cued to this seasonally extreme environment. Alpine plant lifeforms include forbs, graminoids, mat-forming cushion species, succulents, and low-lying shrubs. Although species are tightly adapted to their environment, in the context of climate change, it is unclear how alpine species will respond. The rate of climate change will certainly play a role, and even though steep climatic gradients exist within small spatial scales in the alpine (Loarie et al., 2009), range filling following the last glacial period was not complete (Dullinger et al., 2012*b*). Several key concepts inform how this system may respond to climate change including the stress gradient hypothesis (Callaway and Walker, 1995), the concept of disequilibrium dynamics (Svenning and Sandel, 2013), extinction and establishment lags (Alexander et al. 2017) and persistence in microhabitat refugia (Opedal et al., 2015).

The stress gradient hypothesis describes the continuum of interactions, namely competition and facilitation, between species under various abiotic conditions. It posits that under conditions of high abiotic stress, neighboring plants can facilitate germination, establishment, or growth of neighbors due to protection from environmental extremes such as reducing wind desiccation, providing shade from intense solar radiation and protection from soil moisture loss. Conversely at the low end of a stress gradient, which in the alpine would be at relatively lower elevations nearer the subalpine zone, species are more likely to compete for resources including light, nutrients, and soil moisture. Therefore at higher elevations, plants are more likely to facilitate one another and at lower elevations, competition is expected to be the predominant interaction. This hypothesis is relevant in the context of a changing climate as cold temperature limitations are expected to be relieved for montane and treeline species, potentially allowing movement upward in elevation into higher stress environments. Reciprocally, alpine endemics will also experience relief of abiotic stress but novel interactions occurring at the low end of their alpine stress gradient will occur where competition would be expected to be predominant. Thus, changes in abiotic stress at both ends of a species range will inform how species interact and whether competition or facilitation will predominate in community assembly.

Other conceptual frameworks that may describe how alpine plant communities respond to climate change include disequilibrium dynamics, migration and extinction lags or extinction debt. Depending on the rate of climatic alteration, long-lived species may tolerate slowly changing climatic trends for a period of time before responding. This may be particularly true for alpine species already adapted to daily weather extremes throughout the growing season. Thus, these species may persist in a modified climate even when it no longer suits their establishment niche (Jackson and Overpeck, 2000). Such remnant populations (Eriksson, 2000) would thus be

out of equilibrium with climate creating a local extinction debt (Dullinger et al., 2012a) through an extinction lag (Alexander et al., 2018). On a smaller scale, infilling of local species may modify current dominance patterns (Dullinger et al., 2012b). Although relatively short distances are required for dispersal between montane and alpine environments, the relative pace of alpine plant community transformation will be informed by a combination of infilling of locally adapted species, actual dispersal (Engler et al., 2009) and establishment of lower elevation montane species into the alpine, of alpine species into un-colonized mountain summits, and extinction of alpine residents.

Finally, the alpine ecosystem displays micro-topographic relief that has historically structured communities on a relatively small scale. Distinct community types may exist in relatively close proximity based on small-scale differences in aspect, slope, or depressions which accumulate snow; thus producing dry meadow, wet meadow, or snowbed communities (Bliss, 1962; Opedal et al., 2015). That such small-scale topography already structures communities demonstrates the potential for this structure to provide refugia under climate change (Sherrer and Korner, 2011). Thus microhabitat refugia may further allow species to persist, at least for some time, in the face of a changing overall climate, which could provide time for local genetic adaptation (Ashcroft, 2010), albeit the timeframe may not be reasonable for long-lived species.

Since alpine environments are expected to experience relatively rapid rates of environmental change compared to lower elevations, the alpine environment presents a conundrum of relatively fast environmental change, with long-lived species that could be slow to respond. To more completely understand the ways alpine plant communities may respond to climatic change, my dissertation addressed three main topics: *i)* alpine flowering phenology, which investigated how species with tight environmental coupling respond in the short term to a warmer environment using an actively heated experiment, *ii)* species interactions between introduced establishing conifers in the alpine environment and their alpine plant neighbors in the context of a warmer environment, and *iii)* a long-term observational study of alpine community change on several mountain summits.

# 1 Warming acts through earlier snowmelt to advance but not extend alpine community flowering

*Abstract*

Large-scale warming will alter multiple local climate factors in alpine tundra, yet very few experimental studies examine the combined yet distinct influences of earlier snowmelt, higher temperatures and altered soil moisture on alpine ecosystems. This limits our ability to predict plant species and community responses. To address this gap, we used infrared heaters and manual watering in a fully factorial experiment to determine the relative importance of these climate factors on plant flowering phenology, and response differences among plant functional groups. Heating advanced snowmelt and flower initiation, but exposed plants to colder early-spring conditions in the period prior to first flower, indicating that snowmelt timing alone, not temperature advances flowering initiation in the alpine community. Flowering duration was largely conserved; most plants in heated plots did not extend flowering into the latter part of the growing season but instead completed flowering ahead of the unheated plots, again indicating no proximal effect of temperature on community phenology. Although passive warming experiments have resulted in warming-induced soil drying suggested to advance flower senescence, supplemental water did not counteract the community-scale advance in flowering cessation caused by heating or extend flowering in unheated plots, indicating no effect of soil moisture on length of the flowering period. Functional groups differed in sensitivity to earlier snowmelt, with flower initiation most advanced by early-season species and flowering duration lengthened only by graminoids and forbs. We conclude earlier snowmelt, driven by increased radiative heating, is the most important factor altering alpine flowering phenology. Studies that only manipulate summer temperature will err in estimating the sensitivity of alpine flowering phenology to large-scale warming. The wholesale advance in flowering phenology with earlier snowmelt suggests the alpine community will track the warming climate, but only alpine forbs and graminoids appear able to take advantage of an extended snow-free season.

## 1.1 Introduction

Plant phenology is an indicator of ecosystem response to climate change and affects gas exchange, energy balance, and species interactions (Cleland et al., 2007; Sherry et al., 2007: Bonan, 2008). Long-term monitoring and remote sensing data suggest that plant phenology has already advanced in the spring and extended in the fall due to historical warming (Myneni et al., 1997, Parmesean & Yohe 2003; Root et al., 2003; Wolkovich et al., 2012). In combination, these adjustments have created a longer growing season that appears to have triggered increased primary production (Edwards & Richardson, 2004; Nemani et al., 2003) resulting in a greater draw down of atmospheric $CO_2$ during the growing season, amplifying the seasonal peaks and troughs of atmospheric $CO_2$ (Keeling et al., 1996; Ernakovich et al., 2014). Changes in plant phenology can also alter reproductive synchronicity, which could have cascading impacts on pollinator interactions (Memmott et al., 2007; Liu et al., 2011), or on birds and small rodents that depend on vegetative matter or seeds (Inouye et al., 2000; Moritz et al., 2008).

Climate observations hint that high-elevation mountain regions are warming faster than lower elevations (Giorgi et al., 1997; Theurillat & Guisan, 2001; Rangwala & Miller 2012; MRI, 2015), although this pattern has not been confirmed globally (Oyler et al., 2015). If this is occurring, alpine ecosystems may be exposed to more rapid and larger climate changes than lowlands. Alpine plants are adapted to alpine climate, often flowering and reproducing relatively quickly after snowmelt to take advantage of the short snow-free season, growing close to the ground to avoid strong winds, and harboring physiological adaptations to prevent tissues from freezing and to cope with intense solar radiation (Korner, 1999). Because of these adaptations to alpine climate, and the greater relative sensitivity of biological and chemical processes occurring in colder temperatures (Kirschbaum, 1995), even small environmental changes could theoretically elicit a large response, which would make tundra systems sensitive gauges of environmental change (Petralgia et al., 2014; Prevéy et al., 2017).

Temperature and photoperiod influence spring growth initiation in the alpine (Korner, 1999; Chuine, 2010); however, once a photoperiod threshold has been exceeded (Korner, 1999; Keller & Korner, 2003), primary drivers for the initiation of growth and flowering for arctic, alpine and subalpine species are the timing of snowmelt (access to visible and infrared spectra) and temperature in the period directly following (Dunne et al., 2003; Hulber et al., 2010; Iler et al., 2013; Oberbauer et al., 2013; Petraglia et al., 2014; Wang et al., 2014). When the snow melts completely, solar input rapidly raises soil temperature above zero during the day, melting water, promoting root activity and enhancing soil nutrient cycling. Earlier phenology takes advantage of these conditions and increases the time available for seed maturation, the potential for reproductive success, and the time to build reserves for the next growing season (Bliss, 1962b; Korner, 1999; Kimball et al., 2014). Perennial alpine and subalpine plants, however, must trade the benefits of earlier leafing, fruiting, and flowering with the risk of damage from late spring, early-summer freeze events or summer water stress, which can retard root and plant growth and destroy reproductive potential for the entire year (Inouye, 2008; Gezon et al., 2016).

Despite potential negative consequences, most research in alpine and arctic tundra ecosystems finds an advance in flowering phenology in response to warming (Suzuki & Kudo, 1997; Abeli et al., 2012; Barrett & Hollister, 2016; Bjorkman et al., 2015) via change in temperature (Kopp & Cleland, 2015) or an advance in snowmelt (Wipf et al., 2009; Iler et al., 2013; Petralgia et al., 2014). Conversely snow addition delays phenology (Cooper et al., 2011; Smith et al., 2012). For some species, however, earlier snowmelt via snow removal without additional warming did not significantly advance flowering phenology due to low ambient temperature (Petralgia et al., 2014), and in one study, cooler temperatures following early snowmelt caused frost damage (Wipf et al., 2009). Some studies have found multiple drivers of phenology; over a 22-year period in arctic control plots Bjorkman et al. (2015) observed an increase of 1°C in ambient temperature as well as later trending snowmelt and flowering. Yet passive warming after the snow melted advanced flowering (Bjorkman et al. 2015), suggesting that snowmelt and temperature both influence phenology but their relative importance under future climate change is not clear. In the subalpine, earlier snowmelt via snow removal and due to active warming has advanced flowering time (Gezon et al., 2016; Dunne et al., 2004) but duration of flowering was unaffected by experimental warming even though years with earlier snowmelt were associated with extended flowering periods and greater overlap in co-flowering species (Price & Wasser, 1998). While it is clear that the influence of warming in the subalpine advances phenology through earlier snowmelt and that flowering duration is not modified by extension of the growing

season (*but see* CaraDonna et al., 2014), it is unclear how flowering phenology will respond in the alpine tundra where species may track climate even more closely since they face a sharper trade-off between risk of reproductive failure due to frost and opportunity for greater reproductive success with a longer snow-free season.

Most subalpine or tundra phenology studies (Alatalo & Totland, 1997; Welker et al., 1997; Arft et al., 1999; Wipf et al., 2009; Liu et al., 2011; Cooper et al., 2011; Buizer et al., 2012; Smith et al., 2012; Dorji et al., 2013; Oberbauer et al., 2013; Petraglia et al., 2014; Bjorkman et al., 2015; Kopp & Cleland, 2015; Carbognani et al., 2016; Ganjurav et al., 2016; Gezon et al., 2016; Livensperger et al., 2016; Semenchuk et al., 2016; Zhu et al., 2016) use long-term observations, open–topped warming chambers following snowmelt, or snow addition/removal. With real climate change, temperature and snowmelt will be altered simultaneously. Therefore all of these methods are incomplete in simulating climate change and may yield misleading information regarding responses and underlying mechanisms. In particular, long-term temperature trends cannot reveal cause and effect, as they are not controlled, and passive warming after snowmelt provides information about post-snowmelt sensitivity to temperature and wind reduction but no evidence for the impact of changes in snowmelt. Further, snow addition or removal provides information about sensitivity to snowmelt timing alone but not full effects of warming. Though less commonly used in the subalpine and alpine tundra, active warming (Price & Wasser, 1998; Dunne et al., 2004; Suonan et al., 2016) both advances snowmelt and warms plants and soils following snowmelt. This combination allows quantification of the relative importance of snowmelt timing and temperature within a common framework, to examine which of these two mechanisms drives alpine plant response to changes in climate.

Even less is known about the effects of soil moisture or its interactions with warming on alpine plant phenology. Additional precipitation had little effect in a temperate grassland, although active warming advanced phenology (Sherry et al., 2007). In the alpine, however, ambient temperature, snow depth, snow persistence and soil moisture all interact. For example, snow cover reduces temperature variability (Henry, 2008; Brown & DeGaetano, 2011), more snow and slower snowmelt can result in higher soil moisture when solar input is high, and warmer temperatures cause earlier snowmelt, and can lead to earlier soil dry-down (Dorji et al., 2013). Soil moisture influence on alpine and subalpine phenology has been indirectly investigated via snow manipulation aimed at studying impacts of earlier snowmelt on phenology thus studies often only measure temperature variation or heat accumulation. This approach does not separate the effects of snowmelt timing from soil moisture, however, and therefore cannot determine which is responsible for phenological change. By drying soils, passive warming actually delayed reproductive phenology and reduced the number of inflorescences of *Kobresia pygmaea*, a shallow-rooted alpine plant (Dorji et al., 2013; Zhu et al., 2016) which was a departure from advancement in two herbs; while concomitantly additional snow delayed phenology for another herb in the study. Warming-induced soil drying during the growing season could also cause early senescence (Oberbauer et al., 2013). Moisture can limit the response of subalpine, arctic and alpine abundance and productivity to warming (Elmendorf et al., 2012; Winkler et al., 2016), but it remains unclear how flowering phenology will respond to warming if soil moisture concurrently declines.

Differences in species or functional group responses to changes in resources including climate, soil moisture, energy, nutrients and pollinators will affect their persistence in the community.

Species-specific or functional group strategies prevalent among alpine plants, such as belowground storage and preformation of buds could decouple plant demand from current resource availability and temporarily buffer their sensitivity to changes in climate. Also, plants active earlier in the growing season have been more responsive to changes in climatic conditions than later-blooming species (Price & Wasser, 1998; Dunne et al., 2003; Sherry et al., 2007; Wolkovich et al., 2012; Petralgia et al., 2014). This may enhance the likelihood of temporal mismatch with pollinators because even with a warming-driven extension in the flowering period a mismatch in timing can still lead to a decline in reproductive success (Petanidou et al., 2014). Responses of other functional groups to warming have been investigated but are less understood. In a review of the International Tundra Experiment (ITEX), Arft et al. (1999) found warming advanced anthesis for both woody and herbaceous arctic species, with forbs and graminoids exhibiting the greatest reproductive effort in response to warming. In a subsequent ITEX review, evergreen shrubs and graminoids showed larger advances in flowering than deciduous shrubs and forbs in warmed plots but all life-form types senesced at similar heat sum values (Oberbauer et al., 2013). In an alpine ecosystem in the Front Range of the Rockies, forbs (particularly *Geum rossii*) flowered earlier with summer warming, and later with snow addition, while a dominant graminoid flowered slightly earlier with higher temperature (Smith et al., 2012). Responses by lifeform group have appeared inconsistent making community shifts hard to predict, however early season species (Petralgia et al., 2014), graminoids (Oberbauer et al., 2013) and forbs (Smith et al., 2012), are likely to be more sensitive to warming than other community members.

To quantify the combined effects of multiple proximal climate factors on alpine plant phenology (Park et al., 2018), and to disentangle the relative importance of each, we conducted a fully crossed heating and watering experiment in alpine tundra at Niwot Ridge, CO, USA. We used infrared heaters to induce earlier snowmelt and warm plants and soil, and manual watering to offset warming-induced decreases in soil moisture. We use 4 years of flowering phenology observations to address four questions: *1)* How does radiative warming that can affect snowmelt timing, ecosystem temperature and soil moisture alter flowering phenology (onset, cessation, duration) across an entire alpine community? Based on studies using multiple experimental and observational methods (*e.g.,* Price & Wasser, 1998; Dunne et al., 2004; Liu et al., 2011; Smith et al., 2012; Gezon et al., 2016), we expected that warming would advance flowering onset, thereby extending flowering duration. *2)* Will warming advance onset of spring flowering phenology through increased temperature, advanced snowmelt or drier soils? Based on findings in the subalpine (Dunne et al 2003), we expected that snowmelt timing would be the primary driver of flowering onset. *3*) Does the effect of warming on flowering senescence and duration depend on soil moisture status? Because the snowmelt pulse of soil moisture is depleted at end of the growing season, we expected heating to delay flower senescence and extend flowering duration only under increased soil moisture (Reyes-Fox et al., 2014). *4)* How do phenologies of functional groups, lifeforms and species differ in their sensitivity to warming? We expected early season species (Petralgia et al., 2014), graminoids and forbs, specifically the dominant forb *Geum rossii* (Smith et al., 2012), to be more sensitive to warming than other community members.

## 1.2 Materials and methods

### *1.2.1 Study site and experimental design –*

Our study was conducted on Niwot Ridge in the Colorado Rocky Mountains (40°3' 14.84"N, 105°35'37.71" W; 3540 m), on a shallow (15°) south-southeast facing slope 400 m above timberline. The growing season is approximately 3–4 months (June-September; Greenland 1989) and average annual precipitation and temperature are 966 mm and -2.15°C, with a majority of precipitation falling as snow (Blanken et al., 2009). Variability in local snow depth is determined by westerly winds and local topography (Liator et al., 2008).

In 2009 we established twenty 3 m-diameter plots within the alpine tundra and assigned them to four treatment groups: control (C), heated (H), watered (W), and heated + watered (HW). Each plot was divided into four 1x1 $m^2$ quadrats for observations. Six infrared heaters (Mor Electric Heating, Comstock Park, MI, USA) were suspended 1.2 m aboveground in hexagonal arrays surrounding each H and HW plot (Kimball et al., 2007). Heaters were activated in October 2009 and delivered 215 $W/m^2$ to the ground in plots under low wind conditions which was expected to increase temperature +4°C; high wind speeds diminished heating efficiency (Kimball, 2005) and limited overall warming effects to +1.5°C at 5-10 cm depth in the soil. Winkler et al. (2016) describes the heating treatment in more detail. Infrared radiation (IR) is absorbed by surfaces so our aim was to increase growing season plant and soil temperatures - and not to modify air temperature. While they do not elevate air temperature except very near the ground surface, IR heaters are advantageous as compared with passive heating designs (Elmendorf et al., 2012, Oberbauer et al., 2013) because they preserve the ambient wind regime and advance the timing of snowmelt (Aronson & McNulty, 2009). We applied 2.5 mm of water weekly to the HW and W groups when soil moisture dropped below ~0.2 $m^3/m^3$ (2-3 weeks after snowmelt), to offset soil drying due to heating, and to study the impacts of increased growing season soil moisture. Annual water addition totaled ~ 30 mm, which is roughly 20% of mean June–September precipitation from 1951–1980 on Niwot Ridge (Greenland, 1989).

### *1.2.2 Phenology observations –*

We conducted weekly flowering phenology surveys of 39 species in the community starting when a quadrat was at least 50% snow free, as determined by weekly snow surveys. Each week, the phenological stage of each species was recorded as one of the following: (1) vegetative bud, (2) flower (defined by the presence of visible stamen or stigmatic surfaces), (3) senescence, (4) bud and flower, (5) bud and senescence, (6) flower and senescence, (7) bud, flower and senescence. A stage was recorded when at least one individual of a species in a quadrat entered that stage. Records typically included individuals in multiple phenological phases (i.e. stages 4, 5, 6, 7). Data collection ended when all plants in a species had reached phenological stage 3, 6 or 7, typically mid-late August. Surveys were conducted each growing season from 2009 (pre-treatment) through 2013. Day of flower initiation (first flower) and cessation (last flower) were determined by the first flower occurrence and the last flower senescing for each species across all plots and quadrats, respectively; and flowering duration was calculated as the period between first and last flower.

### *1.2.3 Climate and microclimate observations –*

Air temperature, relative humidity (HMP45C; Vaisala, Helsinki, Finland) and wind speed were measured at 2 m height via a meterological tower erected at the center of the site (03101-L; RM Young, Traverse City, MI, USA). Precipitation was measured at a nearby LTER meteorological station approximately 500 m away, elevation 3528 m (NWCC 2014). Soil moisture and

temperature were recorded every 15 min averaged over a 5–10 cm probe depth (ECTM or 5TM; Decagon Devices, Pullman, WA, USA) at the center of each quadrat. Soil probes were calibrated in the laboratory to volumetric water contents ($m^3/m^3$) ranging from dry to saturated using soil collected adjacent to plots. We determined meltdate of plots as days with greater than 0.5°C diel soil temperature variability, and confirmed that these temperature-based snow cover determinations were consistent with bi-weekly field snow surveys. Mean daily (diel) soil temperature (5−10 cm) was calculated between day of snowmelt and: i) day of first flower, ii) day of last flower, and iii) day of peak flowering (also the day of peak aboveground biomass) for each species in the community and for each quadrat. Adequate soil moisture days were calculated as the total number of days when mean daily volumetric water content was above a threshold of $\Theta_v > 0.13$ $m^3/m^3$, which corresponded to midday water potentials of approximately −1.5 MPa for limber pine seedlings at our site (Moyes et al., 2013) and to decreased productivity in another alpine community (Billings & Bliss, 1959). We used the same time periods described above for mean soil temperature. Each of these variables were used for analyses of *first flower*, *last flower* and *flowering duration* respectively.

### *1.2.4 Statistical analysis –*

We examined effects of heating and watering on flowering phenology for 33 species (with 6 species excluded from statistical analyses because they were represented by only a few individuals at the site, or were not present in control plots) in the community. We used linear mixed effects models to predict mean date of first flower, last flower and flowering duration for all species. To quantify the full, combined effects of warming on phenology, our first model included the main effects of heat, water, year, lifeform, and all 2-way interactions. The lifeform category included 4 groups – cushion plants (all mat-forming, prostrate forbs and true cushions), forbs (all other forbs not mat-forming), graminoids, and succulents. We previously found that the community-wide aboveground productivity response most closely matched that of the dominant forbs (Winker et al., 2016), so the model was designed so that all other groups would be compared against forbs (the dominant lifeform) in contrast summaries. We also included pretreatment (2009) day of first and last flower and flowering duration as covariates in the models to control for pre-existing variation across plots. Random effects included plot, quadrat nested within plot, and species. Our sample size of 4,259 observations was reduced from a potential 20 plots x 4 quadrats x 33 species over 4 years (10560 potential observations) because not all species were present in all plots or quadrats.

To determine whether warming alters flowering phenology via increases in growing season temperature, earlier snowmelt and/or changes in soil moisture, we constructed a second model which included continuous environmental variables standardized by their standard deviations. The second model included lifeform, mean temperature (Tmean), snow meltdate, adequate soil moisture days (AdqMoist), and all 2-way interactions as main fixed effects, and the same random effects as the categorical model. This model did not include the fixed effect 'year' or the 'pretreatment' covariate because we are leveraging variation among years and across plots in climate variables, such as snowmelt timing (which varied by ~3 weeks across years) and growing season temperature, to glean universal relationships between phenology and climate factors. We also ran mixed effects models to determine how the heating and watering treatments affected each of the microclimate variables described above.

To assess which lifeforms were more sensitive to combined direct and indirect effects of warming, we used model 1. To assess whether these lifeform-level phenological responses were more cued to changes in temperature, snowmelt or moisture we used model 2. To compare response differences among flowering functional groups we ran the same linear mixed effects models (1 and 2), but coded species as early, mid or late flowering. Species that initiated flowering (on average) in May or June were designated as "early", those that commenced in July were designated as "mid", and those that initiated in August, past peak productivity for most species, were designated as "late". Lifeform and phenological functional group (early, mid or late season species) were not included in the same models. To examine warming effects on phenology across individual species, we ran linear mixed models as described above (model 1) for each species separately, but only for species that were present in at least 16 plots (15 species of the 33 included in other analyses).

Models were built using the lme4 package and all graphics were developed in R (Bates et al. 2015, R Core Team 2014). We summarized the models using restricted maximum likelihood, t-tests via Satterthwaite approximations for degrees of freedom. Significance levels were estimated using Wald $\chi^2$ tests (car::Anova in R). To gauge the amount of variation explained by each model, we computed both marginal and conditional $R^2$ values following the method of Nakagawa & Schielzeth (2013). Marginal $R^2$ is a measure of variance explained only by fixed factors, whereas conditional $R^2$ is a measure of variance explained by both fixed and random factors.

## 1.3 Results

### *1.3.1 Direct effects of heat –*

Heating advanced the timing of snowmelt by approximately 11 days (+/- 5), but did not significantly increase mean soil temperature during periods directly relevant to phenological observations (**Tables 1.1, 1.2**). In fact, mean temperature between snowmelt and day of first flower was lower in heated plots on average compared to unheated plots (**Tables 1.1, 1.2**). Soil moisture, calculated as adequate soil moisture days, was not significantly affected by heating and there was no effect of watering on soil moisture during periods relevant to flowering phenology (**Table 1.2**).

Mean duration of flowering across all species in this perennial alpine community was approximately three weeks (20 +/- 0.5 days, ***Supplemental Table 1.1***), with the mean date of first flower for control treatments occurring in mid-July, day-of-year (DOY) 196.75 (+/- 0.68 days), and the mean last flower initiating senescence in early August DOY 216 (+/- 0.8 days). Experimental heating advanced flowering initiation community-wide by approximately 8 days (**Table 1.3, Figure 1.1**). Contrary to our expectation that flowering cessation would be delayed, it was instead advanced approximately 7 days by heating (**Table 1.3, Figure 1.1**), resulting in the entire flowering period shifting earlier in the season (**Table 1.3, Figure 1.1**). Thus, also contrary to our expectation, alpine community flowering duration was unaffected by heating. Models explained approximately 90 percent of the variation in flowering phenology (***Supplemental Table 1.4***).

### *1.3.2 Indirect effects of heat and water –*

As expected, variation in snowmelt had a greater effect than the variation in temperature or moisture on flowering onset. Meltdate had a larger standardized coefficient (*16*); nearly three times that of mean soil temperature (*6.2*), and about five times greater than that of soil moisture (*3.3*) (**Table 1.4**). The temperature effect on first flower was also positive – opposite the expected earlier flowering with higher temperature (**Table 1.1**). Finally, mean pre-flowering soil temperature in heated plots was actually *cooler* than in unheated plots likely because heating advanced snowmelt by 11 days (**Table 1.2**), exposing heated plots to cooler nighttime temperatures earlier in the growing season.

Evidence for warming-driven effects on alpine phenology via soil moisture are ambiguous at best. Contrary to our expectation that adding water to warmed plots would delay senescence and extend the flowering season, our watering treatment did not affect flowering initiation, cessation or duration overall, nor was there a significant interaction between heating and watering (**Table 1.3**). However, after accounting for snowmelt date and temperature, community wide flowering initiation and cessation were both later in wetter soils, with no effect of soil moisture on flowering duration (**Table 1.4**).

### *1.3.3 Lifeform and species responses –*

Lifeform responses differed only slightly, but in important ways, from the full community response. Specifically, while warming similarly advanced forb and graminoid flowering initiation, cushions and succulents advanced less (**Table 1.3**). All lifeforms had similar sensitivity of flowering cessation to heating. Heating shortened only cushion flowering duration, but had no effect on the rest of the community (**Table 1.3**). Microclimate relationships revealed a slightly different perspective. With an earlier meltdate, date of first flower advanced more strongly for cushion and forb species, with weaker responses by graminoids and succulents (**Table 1.4, Figure 1.2a**). For last flower, cushions and succulents had a stronger response to meltdate than forbs and graminoids (**Figure 1.2d**). Ultimately, graminoid and forb flowering duration was lengthened by earlier meltdate while cushion and succulent duration was not (**Table 1.4, Figure 1.2g**). Soil temperature, with coefficients less than half as strong as meltdate, had no differential effect on flower initiation across lifeforms, but higher soil temperature was associated with later flower senescence most strongly for graminoids, with weaker effects on forbs, cushions and succulents (**Table 1.4, Figure 1.2e**). Ultimately, soil temperature was inversely correlated with flowering duration in cushions and succulents but positively correlated with duration for graminoids (**Table 1.4, Figure 1.2e, h**). Soil moisture, with coefficients ~one fifth as strong as meltdate, had a strong positive relationship with first and last flower in cushion species, and weaker, but still positive effects on other lifeforms (**Table 1.4, Figure 1.2c, f**). Variation in soil moisture did not explain variation in flowering duration of any group (**Table 1.4, Figure 1.2i**).

Contrary to predictions, early flowering species were not more sensitive to heating than mid- or late-season species in terms of flowering initiation, cessation or duration (**Table 1.5**). This may be due to the fact that there is not large variation in the flowering season across species at our alpine site; there was substantial overlap in the flowering period amongst species (**Figure 1.1**). However, consistent with our expectations, flowering onset by early-season species was more sensitive to snowmelt timing than by mid-season species (**Table 1.6, Figure 1.3a**). Surprisingly, earlier snowmelt advanced and later snowmelt delayed cessation more strongly for mid- and late-

season species (**Figure 1.3b**). Flowering duration was not differentially associated with meltdate for any phenological functional group.

With respect to soil temperature, mid-season species had the strongest positive relationship between temperature and flowering initiation (**Table 1.6, Figure 1.3d**), which is consistent with less dependence of mid-season phenology on snowmelt date. Increasing soil temperature correlated with later flower senescence for early-season species but earlier senescence for late-season species (**Figure 1.3e, Table 1.6**), which suggests these groups respond distinctly to temperature once snowmelt cues have subsided. Flowering initiation and cessation were both later with increasing adequate moisture days for all three phenological functional groups, but effects were strongest for early season species and weakest for late season species (**Figure** 1.**3c, f**). Ultimately, flowering duration was longer with increasing soil moisture for early season species (**Table 1.6**), which suggests once the snow melts and soils begin to dry down, early species benefit most from enhanced moisture. Surprisingly, greater moisture correlated with shortened duration in mid-season species (**Figure 1.3i***),* perhaps due to a stronger delay in flower initiation than cessation. Models explained over 90% of the variation in flowering phenology (***Supplemental Table 1.5***).

Regarding warming effects on individual species, when the fifteen species with adequate representation across plots and treatments are considered individually, the response is similar to that of the entire community. Heating advanced flowering onset and senescence for almost all individual species (**Table 7**, **Figure 1**). Other community-level expectations were borne out for a few individual species: first, in one early-season forb, *Lloydia serotina*, heating significantly expanded the duration of the flowering season by almost 7 days. Second, watering delayed flower initiation for the mid-season forb, *Erigeron simplex*. Lastly, the addition of water in heated plots appeared to *i*) counter the heat-induced advance in flowering initiation in the mid-season succulent, *Lewisia pygmaea* and *ii*) offset the heat-induced advance in senescence and expanded duration in the early-season forb, *Geum rossii.* With added moisture, this dominant forb was able to take advantage of the extended growing season.

**Table 1.1** Microclimate variables measured 2010-2013 and averaged by treatment group; *Trt* (treatment), *Meltdate, TmeanF* (mean temperature to day of first flower, *°C*)*, TmeanL* (mean temperature ~ last flower, *°C*)*, TmeanD* (mean temperature ~ peak flowering, *°C*)*, AdqF* (adequate soil moisture days ~ to day of first flower)*, AdqL* (adequate soil moisture days ~ to last flower)*, AdqD* (adequate soil moisture days ~ peak flowering), *+/-se* (plus or minus standard error).

| Trt | Meltdate | *+/- se* | TmeanF | *+/- se* | TmeanL | *+/- se* | TmeanD | *+/- se* | AdqF | *+/- se* | AdqL | *+/- se* | AdqD | *+/- se* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| C | 162.3 | 0.80 | 9.61 | 0.08 | 11.03 | 0.05 | 10.73 | 0.05 | 26.56 | 0.48 | 40.8 | 0.66 | 37.45 | 0.39 |
| H | 148.5 | 1.19 | 8.58 | 0.09 | 10.72 | 0.07 | 10.03 | 0.06 | 33.21 | 0.60 | 47.5 | 0.70 | 40.13 | 0.37 |
| HW | 154.4 | 0.88 | 9.09 | 0.09 | 11.08 | 0.06 | 10.50 | 0.05 | 30.33 | 0.52 | 46.3 | 0.65 | 41.53 | 0.50 |
| W | 163.4 | 0.77 | 9.51 | 0.07 | 10.87 | 0.05 | 10.46 | 0.05 | 27.31 | 0.50 | 44.3 | 0.70 | 35.65 | 0.45 |

**Table 1.2** Treatment effects on microclimate variables. Linear mixed effects model parameter estimates for each microclimate variable explored in the continuous model as described in Table 1: *Meltdate, TmeanF, TmeanL, TmeanD, AdqF, AdqL, AdqD*. Wald $\chi^2$ tests and P-values, $P(\chi^2)$, were calculated for effects of: Year, Water, Heat, and the interaction of Heat*Water.

| | | Coef | SE | $\chi^2$ | df | $P(\chi^2)$ |
|---|---|---|---|---|---|---|
| **Meltdate** | Intercept | 162.45 | 3.48 | | | |
| | Heat | -10.72 | 4.90 | 7.50 | 1 | **0.006** |
| | Water | 1.56 | 4.90 | 0.65 | 1 | 0.42 |
| | Heat x Water | 2.46 | 6.93 | 0.13 | 1 | 0.72 |
| | Year | | | 15535.48 | 3 | **< 2e-16** |
| | 2011 | 28.10 | 0.53 | | | |
| | 2012 | -33.94 | 0.51 | | | |
| | 2013 | 8.44 | 0.52 | | | |
| **TmeanF** | Intercept | 8.93 | 0.30 | | | |
| | Heat | -0.75 | 0.41 | 3.79 | 1 | **0.05** |
| | Water | -0.04 | 0.41 | 0.25 | 1 | 0.62 |
| | Heat x Water | 0.36 | 0.58 | 0.39 | 1 | 0.53 |
| | Year | | | 2910.87 | 3 | **< 2e-16** |
| | 2011 | 2.81 | 0.08 | | | |
| | 2012 | -1.31 | 0.08 | | | |
| | 2013 | 1.28 | 0.08 | | | |
| **TmeanL** | Intercept | 10.81 | 0.26 | | | |
| | Heat | -0.03 | 0.36 | 0.15 | 1 | 0.70 |
| | Water | -0.12 | 0.36 | 0.001 | 1 | 0.98 |
| | Heat x Water | 0.25 | 0.51 | 0.23 | 1 | 0.63 |
| | Year | | | 3066.72 | 3 | **<2e-16** |
| | 2011 | 1.83 | 0.06 | | | |
| | 2012 | -1.19 | 0.06 | | | |
| | 2013 | 0.38 | 0.06 | | | |
| **TmeanD** | Intercept | 10.50 | 0.29 | | | |
| | Heat | -0.42 | 0.41 | 0.37 | 1 | 0.54 |
| | Water | -0.26 | 0.41 | 0.004 | 1 | 0.95 |
| | Heat x Water | 0.49 | 0.58 | 0.69 | 1 | 0.41 |
| | Year | | | 4598.28 | 3 | **<2e-16** |
| | 2011 | 2.16 | 0.05 | | | |
| | 2012 | -0.72 | 0.05 | | | |
| | 2013 | -0.30 | 0.05 | | | |
| **AdqF** | Intercept | 25.75 | 2.97 | | | |
| | Heat | 5.46 | 4.17 | 1.98 | 1 | 0.16 |
| | Water | 1.07 | 4.17 | 0.01 | 1 | 0.94 |
| | Heat x Water | -2.62 | 5.90 | 0.20 | 1 | 0.66 |
| | Year | | | 854.89 | 3 | **<2e-16** |
| | 2011 | -8.08 | 0.62 | | | |
| | 2012 | 9.16 | 0.60 | | | |
| | 2013 | -1.78 | 0.61 | | | |
| **AdqL** | Intercept | 38.72 | 3.61 | | | |
| | Heat | 5.25 | 5.07 | 0.92 | 1 | 0.34 |
| | Water | 4.07 | 5.06 | 0.40 | 1 | 0.53 |
| | Heat x Water | -3.63 | 7.16 | 0.26 | 1 | 0.61 |
| | Year | | | 462.53 | 3 | **<2e-16** |
| | 2011 | -7.62 | 0.85 | | | |
| | 2012 | 10.08 | 0.83 | | | |
| | 2013 | 1.37 | 0.85 | | | |
| **AdqD** | Intercept | 38.29 | 2.53 | | | |
| | Heat | 3.42 | 3.57 | 3.38 | 1 | 0.07 |
| | Water | -1.27 | 3.57 | 0.001 | 1 | 0.98 |
| | Heat x Water | 2.44 | 5.05 | 0.23 | 1 | 0.63 |

| | | | | | |
|---|---|---|---|---|---|
| Year | | | 3728.61 | 3 | **< 2e-16** |
| 2011 | -4.50 | 0.38 | | | |
| 2012 | 9.70 | 0.38 | | | |
| 2013 | -12.46 | 0.37 | | | |

**Table 1.3** Linear mixed effects model parameter estimates for main effects and all two-way interactions for day of first flower, day of last flower and flowering duration in the categorical model (1). Wald $\chi^2$ tests and P-values, $P(\chi^2)$, were calculated for effects of treatments, year, lifeform and their interactions. For effects with only two levels, the coefficient for the level not shown is the same magnitude but opposite sign as the coefficient shown. Random effects included: plot, quad nested within plot, and species. Probabilities <0.05 are given in bold type. Complete results provided in ***Supplemental Table 1.2***.

| | *First flower* | | | *Last flower* | | | *Duration of flowering* | | |
|---|---|---|---|---|---|---|---|---|---|
| | Coef | $\chi^2$ | $P(\chi^2)$ | Coef | $\chi^2$ | $P(\chi^2)$ | Coef | $\chi^2$ | $P(\chi^2)$ |
| Intercept | 168.21 | | | 178.11 | | | 16.11 | | |
| H | -7.67 | 48.23 | **3.79e-12** | -7.04 | 48.37 | **3.53e-12** | 0.66 | 0.00 | 0.98 |
| W | -1.77 | 0.02 | 0.90 | 0.17 | 0.18 | 0.67 | 1.39 | 0.45 | 0.50 |
| H x W | 1.44 | 0.86 | 0.35 | 1.87 | 1.40 | 0.24 | 0.37 | 0.12 | 0.73 |
| Pre-phenol | 0.12 | 56.07 | **6.99e-14** | 0.14 | 19.56 | **9.73e-06** | 0.11 | 28.72 | **8.35e-08** |
| Year | | 13543.84 | **< 2.2e-16** | | 6229.73 | **< 2.2e-16** | | 175.39 | **< 2.2e-16** |
| 2011 | 19.88 | | | 19.02 | | | -1.32 | | |
| 2012 | -21.86 | | | -16.92 | | | 4.51 | | |
| 2013 | 4.12 | | | 5.65 | | | 1.18 | | |
| Lifeform | | 3.55 | 0.31 | | 2.46 | 0.48 | | 0.40 | 0.94 |
| cushions | 1.01 | | | 3.70 | | | 2.83 | | |
| graminoids | 6.97 | | | 9.48 | | | 2.67 | | |
| succulents | 6.82 | | | 7.48 | | | 0.30 | | |
| Lifeform x H | | 11.31 | **0.01** | | 6.65 | 0.08 | | 9.97 | **0.02** |
| cushions x H | 1.68 | | | -1.76 | | | -3.67 | | |
| graminoids x H | 0.50 | | | -0.09 | | | -0.50 | | |
| succulents x H | 2.47 | | | 1.48 | | | -0.75 | | |
| Lifeform x W | | 0.37 | 0.95 | | 0.52 | 0.91 | | 0.64 | 0.89 |
| cushions x W | 0.10 | | | 0.42 | | | 0.68 | | |
| graminoids x W | 0.12 | | | -0.01 | | | -0.41 | | |
| succulents x W | -0.42 | | | -0.49 | | | -0.26 | | |
| Year x Heat | | 68.64 | **8.36e-15** | | 13.31 | **4.02e-03** | | 8.29 | **0.040** |
| 2011 x H | 4.71 | | | 2.91 | | | -1.65 | | |
| 2012 x H | -1.35 | | | 0.08 | | | 1.56 | | |
| 2013 x H | 0.33 | | | 0.06 | | | -0.28 | | |
| Year x Water | | 5.63 | 1.31E-01 | | 2.33 | 0.506648 | | 3.37 | 0.33842 |
| 2011 x W | 1.09 | | | -1.21 | | | -1.62 | | |
| 2012 x W | 1.79 | | | -0.61 | | | -1.85 | | |
| 2013 x W | 1.04 | | | -1.27 | | | -1.46 | | |

**Table 1.4** Linear mixed effects model parameter estimates for main effects and all two-way interactions for day of first flower, day of last flower and flowering duration in the continuous model (2). Wald $\chi^2$ tests and P-values, $P(\chi^2)$, were calculated for effects of lifeform, meltdate, mean soil temperature (*MeanTemp*), adequate soil moisture (*AdqMoist*), and their interactions. Explanatory variables were calculated differently for each response variable, see the methods section for a full explanation. Random effects included: plot, quad nested within plot, and species. Probabilities <0.05 are given in bold type. Complete results provided in ***Supplemental Table 1.3***.

| | *First flower* | | | *Last flower* | | | *Duration of flowering* | | |
|---|---|---|---|---|---|---|---|---|---|
| | Coef | $\chi^2$ | $P(\chi^2)$ | Coef | $\chi^2$ | $P(\chi^2)$ | Coef | $\chi^2$ | $P(\chi^2)$ |
| Intercept | 187.77 | | | 207.90 | | | 20.44 | | |
| Lifeform | | 2.08 | 0.56 | | 1.06 | 0.79 | | 0.62 | 0.89 |
| cushion | 0.18 | | | 1.47 | | | 1.74 | | |
| graminoid | 3.58 | | | 5.66 | | | 1.14 | | |
| succulent | 5.48 | | | 5.72 | | | -2.15 | | |
| Meltdate | 16.19 | 3104.83 | **< 2.2e-16** | 15.13 | 1987.32 | **< 2.2e-16** | -2.90 | 39.14 | **3.944e-10** |
| MeanTemp | 6.28 | 629.32 | **< 2.2e-16** | 3.98 | 99.49 | **< 2.2e-16** | 0.37 | 1.90 | 0.17 |
| AdqMoist | 3.30 | 589.62 | **< 2.2e-16** | 3.96 | 502.52 | **< 2.2e-16** | -0.14 | 0.04 | 0.83 |
| Lifeform x Meltdate | | 29.69 | **1.60e-06** | | 100.22 | **< 2.2e-16** | | 30.67 | **9.98e-07** |
| cushion x Meltdate | -0.08 | | | 1.52 | | | 3.42 | | |
| graminoid x Meltdate | -2.84 | | | -5.44 | | | -2.29 | | |
| succulent x Meltdate | -1.41 | | | 1.26 | | | 3.75 | | |
| Lifeform x MeanTemp | | 4.87 | 0.18 | | 27.60 | **4.41e-06** | | 18.53 | **3.42e-04** |
| cushion x MeanTemp | 0.06 | | | -1.16 | | | -2.01 | | |
| graminoid x MeanTemp | 1.31 | | | 2.44 | | | 1.10 | | |
| succulent x MeanTemp | 0.29 | | | -1.93 | | | -2.25 | | |
| Lifeform x AdqMoist | | 45.42 | **7.53e-10** | | 27.58 | **4.44e-06** | | 2.53 | 0.47 |
| cushion x AdqMoist | 2.15 | | | 1.39 | | | -0.38 | | |
| graminoid x AdqMoist | -0.97 | | | -0.93 | | | 0.82 | | |
| succulent x AdqMoist | -0.89 | | | -1.11 | | | -0.32 | | |
| Meltdate x AdqMoist | -3.05 | 668.61 | **< 2.2e-16** | -2.33 | 140.39 | **< 2.2e-16** | -0.33 | 1.72 | 0.19 |
| Meltdate x MeanTemp | 1.53 | 221.47 | **< 2.2e-16** | 2.15 | 416.67 | **< 2.2e-16** | -0.62 | 5.62 | **0.02** |
| AdqMoist x MeanTemp | 2.43 | 226.29 | **< 2.2e-16** | 2.09 | 88.63 | **< 2.2e-16** | -0.24 | 0.63 | 0.43 |

**Tables 1.5 and 1.6.** Linear mixed effects model parameter estimates for main effects and all two-way interactions for *5)* the categorical and *6)* the continuous model with *phenological functional group (PhenFG)* instead of *lifeform* included in the model. Wald $\chi^2$ tests and P-values, $P(\chi^2)$, were calculated for effects of treatment, year, phenological functional group (*PhenFG*) and their interactions. In Table 6, explanatory variables were calculated differently for each response variable, see the methods section for a full explanation. For effects with only two levels, the coefficient for the level not shown is the same magnitude but opposite sign as the coefficient shown. Random effects included: plot, quad nested within plot, and species. Probabilities <0.05 are given in bold type. Complete results provided in ***Supplemental Tables 1.7 & 1.8***.

***Table 1.5***

| | *First flower* | | | *Last flower* | | | *Duration of flowering* | | |
|---|---|---|---|---|---|---|---|---|---|
| | Coef | $\chi^2$ | $P(\chi^2)$ | Coef | $\chi^2$ | $P(\chi^2)$ | Coef | $\chi^2$ | $P(\chi^2)$ |
| Intercept | 161.24 | | | 171.53 | | | 15.91 | | |
| Heat | -6.86 | 51.24 | **8.17e-13** | -6.27 | 45.87 | **1.27e-11** | 0.65 | 0.00 | 0.97 |
| Water | -1.92 | 0.02 | 0.90 | 0.21 | 0.12 | 0.73 | 1.69 | 0.30 | 0.58 |
| Heat x Water | 1.45 | 0.93 | 0.34 | 1.81 | 1.26 | 0.26 | 0.27 | 0.06 | 0.80 |
| Pre-phenology | 0.12 | 62.30 | **2.96e-15** | 0.14 | 20.36 | **6.40e-06** | 0.11 | 30.19 | **3.92e-08** |
| Year | | 13496.83 | **< 2.2e-16** | | 6229.50 | **< 2.2e-16** | | 175.75 | **< 2.2e-16** |
| 2011 | 19.88 | | | 2.92 | | | -1.36 | | |
| 2012 | -21.84 | | | 0.13 | | | 4.42 | | |
| 2013 | 4.08 | | | 0.08 | | | 1.16 | | |
| PhenFG | | 52.57 | **3.84e-12** | | 20.12 | **4.29e-05** | | 0.72 | 0.70 |
| mid | 10.15 | | | 11.36 | | | 1.12 | | |
| late | 23.95 | | | 28.55 | | | 5.27 | | |
| PhenFG x H | | 0.31 | 0.85 | | 3.18 | 0.20 | | 1.79 | 0.41 |
| mid x H | -0.10 | | | -1.24 | | | -1.15 | | |
| late x H | -0.74 | | | -1.74 | | | -1.17 | | |
| PhenFG x W | | 0.75 | 0.69 | | 0.15 | 0.93 | | 1.10 | 0.58 |
| mid x W | 0.14 | | | -0.16 | | | -0.42 | | |
| late x W | 1.21 | | | 0.42 | | | -2.14 | | |
| Year x H | | 67.80 | **1.26e-14** | | 13.14 | **0.004** | | 8.63 | **0.035** |
| 2011 x H | 4.68 | | | 2.92 | | | -1.61 | | |
| 2012 x H | -1.40 | | | 0.13 | | | 1.66 | | |
| 2013 x H | 0.40 | | | 0.08 | | | -0.32 | | |
| Year x W | | 5.28 | 0.15 | | 2.23 | 0.53 | | 3.05 | 0.38 |
| 2011 x W | 1.10 | | | -1.16 | | | -1.58 | | |
| 2012 x W | 1.73 | | | -0.63 | | | -1.76 | | |
| 2013 x W | 0.99 | | | -1.26 | | | -1.35 | | |

***Table 1.6***

| | *First flower* | | | *Last flower* | | | *Duration of flowering* | | |
|---|---|---|---|---|---|---|---|---|---|
| | Coef | $\chi^2$ | $P(\chi^2)$ | Coef | $\chi^2$ | $P(\chi^2)$ | Coef | $\chi^2$ | $P(\chi^2)$ |
| Intercept | 183.64 | | | 203.52 | | | 20.35 | | |
| PhenFG | | 62.67 | **2.46e-14** | | 29.26 | **4.43e-07** | | 0.11 | 0.94 |
| mid | 5.55 | | | 6.88 | | | -0.08 | | |
| late | 19.62 | | | 25.77 | | | 1.46 | | |
| Meltdate | 16.66 | 2889.47 | **< 2.2e-16** | 12.84 | 2028.15 | **< 2.2e-16** | -2.43 | 39.16 | **3.91e-10** |
| MeanTemp | 6.24 | 754.04 | **< 2.2e-16** | 7.59 | 134.52 | **< 2.2e-16** | 0.53 | 1.51 | 0.22 |
| AdqMoist | 5.15 | 613.55 | **< 2.2e-16** | 6.66 | 568.41 | **< 2.2e-16** | 1.12 | 0.11 | 0.74 |
| PhenFG x Meltdate | | 16.74 | **0.0002** | | 60.45 | **7.49e-14** | | 0.40 | 0.82 |
| mid x Meltdate | -1.87 | | | 2.24 | | | 0.35 | | |
| late x Meltdate | -0.19 | | | 6.38 | | | -0.34 | | |
| PhenFG x MeanTemp | | 12.62 | **0.0018** | | 134.84 | **< 2.2e-16** | | 5.11 | 0.08 |
| mid x MeanTemp | 1.21 | | | -4.41 | | | -1.06 | | |
| late x MeanTemp | -1.07 | | | -10.49 | | | 0.66 | | |
| PhenFG x AdqMoist | | 98.56 | **< 2.2e-16** | | 112.87 | **< 2.2e-16** | | 11.81 | **0.003** |
| mid x AdqMoist | -1.57 | | | -2.67 | | | -1.83 | | |
| late x AdqMoist | -4.66 | | | -5.50 | | | -0.88 | | |
| Meltdate x AdqMoist | -3.57 | 741.80 | **< 2.2e-16** | -3.74 | 340.65 | **< 2.2e-16** | -0.42 | 2.66 | 0.10 |
| Meltdate x MeanTemp | 1.41 | 151.05 | **< 2.2e-16** | 2.05 | 365.41 | **< 2.2e-16** | -0.53 | 4.00 | **0.05** |
| AdqMoist x MeanTemp | 3.19 | 310.99 | **< 2.2e-16** | 3.70 | 265.73 | **< 2.2e-16** | -0.18 | 0.36 | 0.55 |

**Table 1.7** Results of linear mixed effects models for individual species with data across most (at least 16) plots. A – indicates an advance in date of first flower (doff) or last flower (dolf) and a reduction in duration. A + indicates a delay in doff or dolf and an extension of flowering duration. A *o* indicates no change (coefficients between -1 and 1). The column *CMean* provides average control-plot day of first and last flower and flowering duration. Earliest flowering species are at the top of the list and descend with increasing doff. Species scientific names are denoted in *Supplemental Table 8*, and complete results provided in ***Supplemental Table 1.9***. Probabilities <0.05 are given in bold type.

| | *First* | | | | *Last* | | | | *Duration* | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Species | *C Mean* | Heat | Water | H*W | *C Mean* | Heat | Water | H*W | *C Mean* | Heat | Water | H*W |
| GERO | 185.21 | **-** | o | o | 218.78 | **-** | - | **+** | 33.56 | - | - | **+** |
| CARU | 188.00 | **-** | - | + | 212.79 | - | o | o | 24.79 | + | + | - |
| LLSE | 188.83 | **-** | - | + | 199.11 | - | + | o | 10.28 | **+** | + | **-** |
| SIPR | 189.32 | **-** | - | + | 204.81 | **-** | o | - | 15.49 | + | + | - |
| PODI | 191.68 | **-** | o | + | 211.56 | - | o | + | 19.88 | + | **-** | - |
| LEPY | 192.22 | **-** | - | **+** | 205.20 | **-** | + | - | 12.98 | + | + | **-** |
| ARSC | 193.28 | **-** | - | + | 212.57 | **-** | - | + | 19.28 | + | o | o |
| MIOB | 193.76 | - | o | + | 227.89 | **-** | + | - | 34.13 | **-** | + | - |
| ERSI | 196.87 | **-** | **+** | + | 211.63 | **-** | + | o | 14.76 | **-** | **+** | **-** |
| SIAC | 198.20 | **-** | - | + | 214.47 | **-** | - | + | 16.27 | - | + | + |
| BIBI | 198.49 | **-** | o | o | 215.79 | **-** | o | o | 18.53 | o | - | o |
| CHJA | 199.03 | **-** | o | - | 217.53 | **-** | + | - | 18.50 | o | + | o |
| LUSP | 199.17 | **-** | - | + | 214.38 | **-** | o | + | 15.21 | + | + | - |
| ARFE | 200.13 | **-** | - | o | 234.40 | **-** | o | + | 34.27 | **-** | + | + |
| TRSP | 207.57 | **-** | o | + | 228.29 | **-** | o | - | 23.33 | o | - | o |

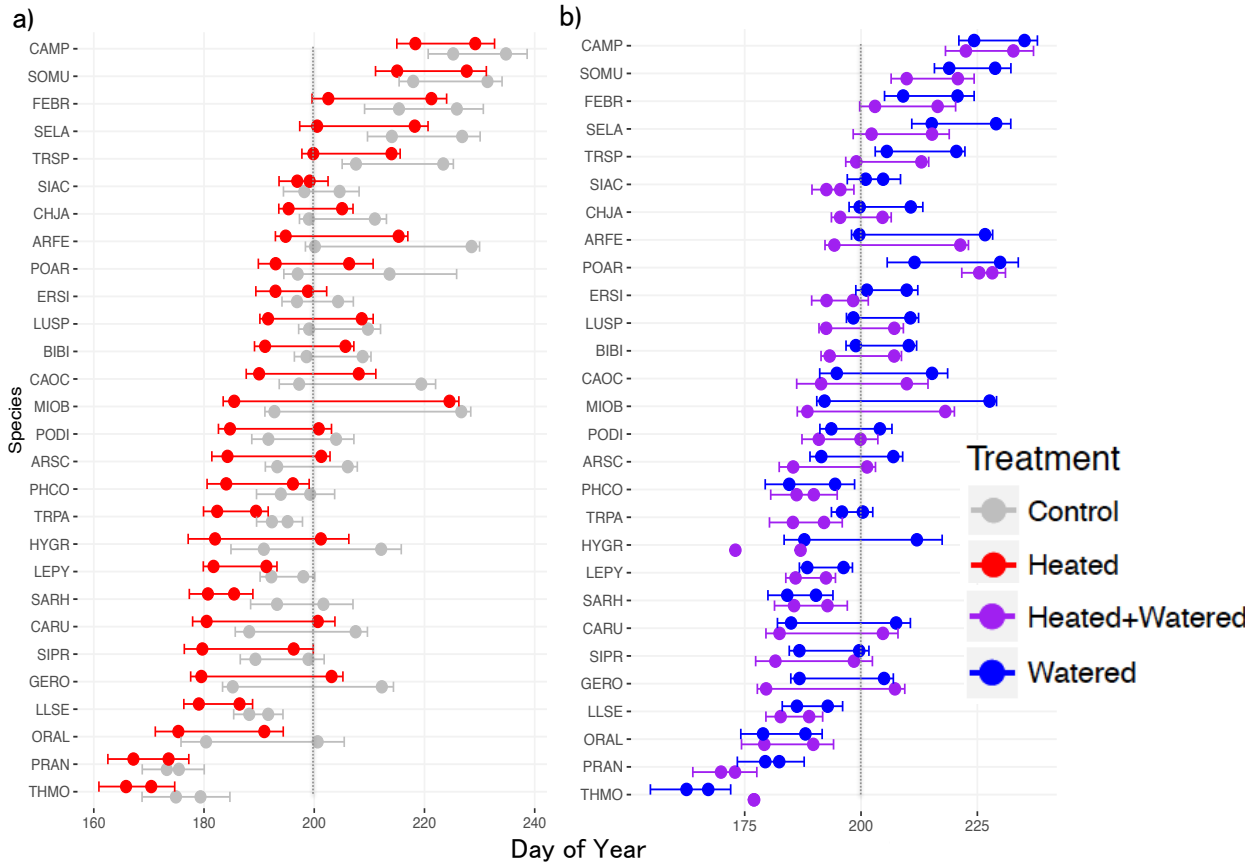


**Figure.** 1.1 Duration of flowering for 28 species present in at least 1 of each of 4 treatments (color-coded by treatment), species names provided in *Supplemental Table 6*. Panel a) represents control and heated plots while b) represents heated + watered and watered plots. The leftmost point represents the mean date of first flowering with its lower standard error; the rightmost point represents the date of last flowering with its upper standard error for each species. The vertical line at DOY 200 was added for ease of comparison between the two panels.

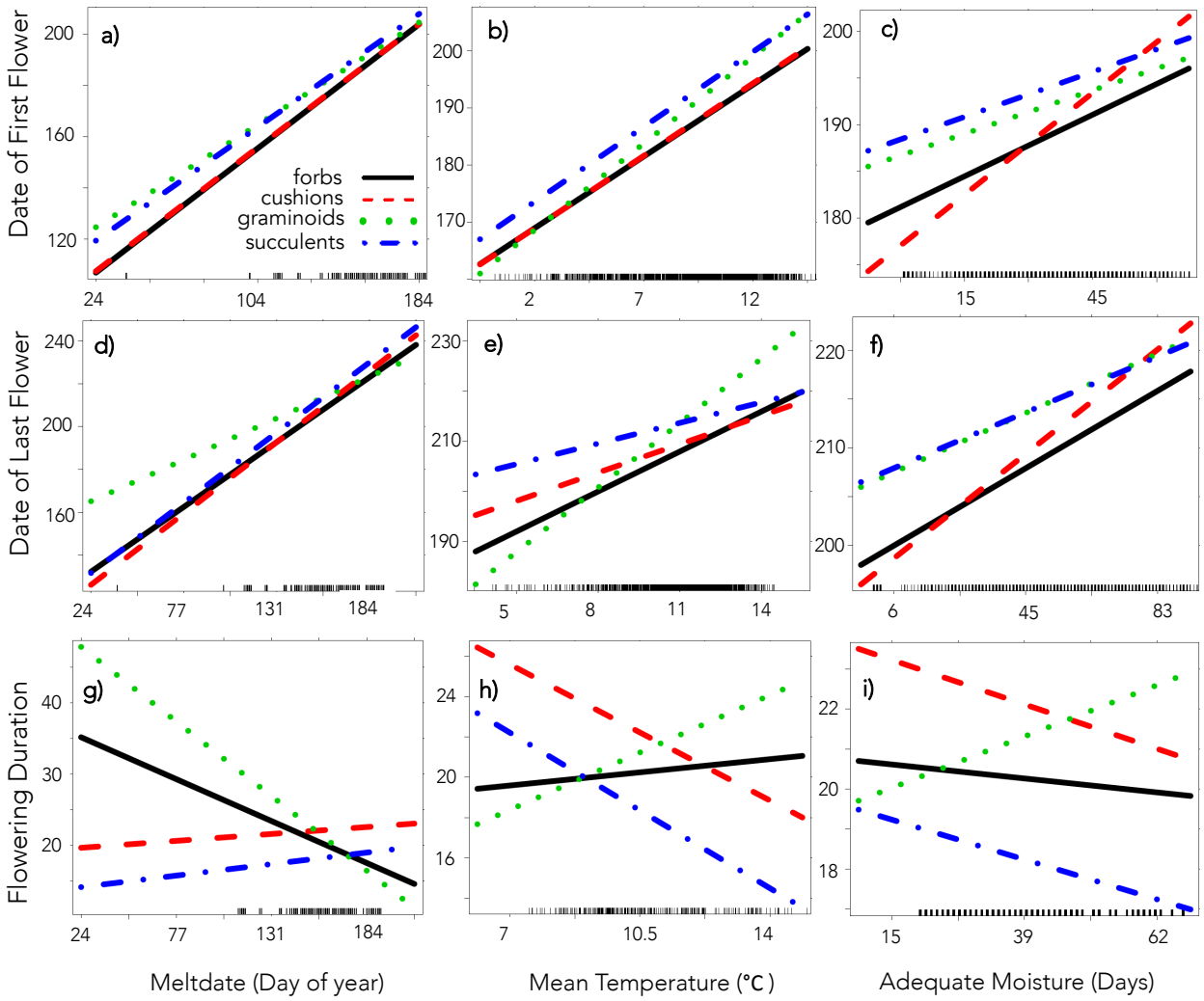


**Figure 1.2** Interaction plots of lifeform-level date of first (top row), last flower (middle row) and flowering duration (bottom row). Model estimates of: lifeform x meltdate (plots *a*, *d*, and *g*), lifeform x mean temperature (plots *b*, *e*, and *h*), and lifeform x adequate moisture (plots *c*, *f*, and *i*), on the x-axis, and first, last flower and flowering duration on the y-axis. Model estimates are corrected for random effects. A black-solid, red-dashed, green-dotted and blue-dot-dashed lines indicate *forbs, cushions*, *graminoids*, and *succulents* respectively. Predictor variables have been converted from units of standard deviation into native measurement units for clarity.

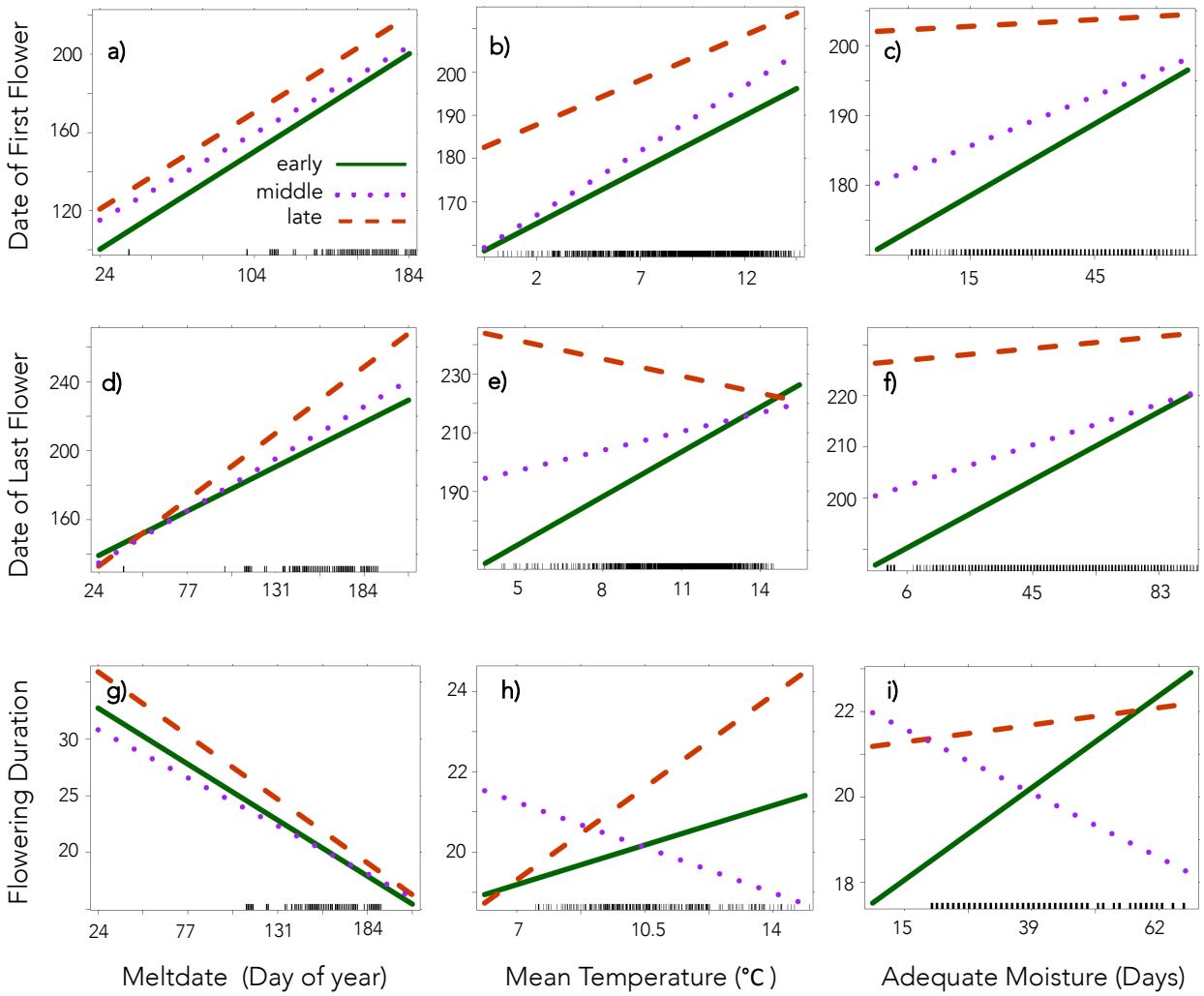


**Figure 1.3** Interaction plots of phenological functional group (PhenFG) for timing of first (top row), last flower (middle row) and flowering duration (bottom row). Model estimates of: phenFG x meltdate (plots *a*, *d*, and *g*), PhenFG x mean temperature (plots *b*, *e*, and *h*), and PhenFG x adequate moisture (plots *c*, *f*, and *i*), on the x-axis, and first, last flower and flowering duration on the y-axis. Model estimates are corrected for random effects. A solid green, dotted purple and dot-dashed orange line represents *early*, *mid* and *late* flowering species respectively. Predictor variables have been converted from units of standard deviation into native measurement units for clarity.

## 1.4 Discussion

In our active infrared heating experiment at Niwot Ridge, CO, warming advanced the flowering season due to earlier snowmelt, not warmer temperatures. Heating advanced snowmelt approximately 12 days, but reduced mean preflowering soil temperature, likely due to heated plot exposure to greater diel temperature variation or a larger number of colder nights in the early spring. Contrary to our expectations, warming did not extend the flowering season for most functional groups and species, and watering did not counter the advance in flowering cessation caused by warming. Finally, in some cases, lifeform and phenological functional groups showed distinct mean responses to changing climate. Earlier meltdate lengthened graminoid and forb flowering duration while cushion and succulent duration were less sensitive. Onset of flowering in early season species responded more strongly to warming-induced advances in snowmelt than it did in later flowering species.

### *1.4.1 Heating and advanced alpine flowering phenology –*

Consistent with our expectations, flowering initiation and cessation occurred earlier with active warming, for the entire alpine plant community over the 4 years of our study. The heating treatment caused a mean temperature rise of 1.5°C in the heated plots over the snow-free growing season, and a flowering advance of approximately 7 days. This result is consistent with other active experiments (Sherry et al., 2007, Dunne et al., 2003) and with the findings of Wolkovich et al. (2012), who found an advance of approximately 4.6 days per °C temperature rise in an analysis of 1,558 species in various ecosystems in response to inter-annual temperature variation. This suggests that extrapolations based on realistic experimentation have the potential to replicate plant species responses to non-experimental climate changes (Dunne et al., 2004).

Across the community, flowering duration did not expand despite an imposed warmer growing season because flowering initiation and cessation both advanced – by 8 and 7 days respectively. It appears that duration is a conserved trait for most alpine species, or is at least insensitive to temperature. We therefore did not find any support for our prediction that early flowering would allow a longer community flowering period and more time to complete the reproductive cycle as it has in a temperate grassland (Reyes-Fox et al., 2009). This result is consistent with observations along an elevational gradient in the Canadian arctic that revealed high phenotypic plasticity in flowering time but evolutionary conservatism in duration (Lessard-Therrien et al., 2014; Semenchuk et al., 2016). Experimental warming also had no detectable effect on duration of flowering or fruiting in a subalpine meadow (Price & Wasser, 1998). However, contrasting evidence from warmed alpine communities on the Tibetan Plateau (Yu et al., 2010), from ITEX experiments (Oberbauer et al., 2013), and from long-term observations (CaraDonna et al., 2014) have resulted in shorter and longer reproductive seasons respectively; the former as a result of winter warming preventing chilling requirements from being met.

### *1.4.2 Factors driving alpine phenology advance –*

To determine the relative importance of the proximal factors through which heating could have advanced alpine flowering phenology, we examined whether changes were more strongly cued by advanced snowmelt, post-snowmelt temperature or changes in soil moisture. Timing of snowmelt emerged as the dominant factor to advance flowering. In our study warming advanced snowmelt by 11 days (**Table 1.2**), which advanced flowering initiation and cessation by 8 and 7

days (**Table 1.3**), respectively. This dominant effect of snowmelt is consistent with a study in the Alps that reduced snow depth and advanced snowmelt timing, which concluded that snowmelt timing had stronger effects than snow depth on phenology and reproduction (Wipf et al., 2009). Other studies have found the same relationship between earlier snowmelt and advanced flowering (Dunne et al., 2003; Abeli et al., 2012; Bjorkman et al., 2015), although exposure of plants to extreme spring temperatures caused frost damage and reduced reproductive capacity in some high arctic and subalpine species (Wipf et al., 2009; Cooper et al., 2011; Gezon et al., 2016). Carboganni et al. (2016) found differential flowering triggers based on timescale of investigation; at the scale of an individual growing season (following snowmelt), air temperature surrounding plants prompted blooming; but at the annual timescale (across years) variation in snowmelt date was the dominant predictor for peak flowering time. The strong correlation of flowering with snowmelt timing is also consistent with local alpine community assemblage patterns; in which species generally organize along a snowpack depth (and therefore snowmelt timing) gradient (Korner, 1999), and phenological phases both vegetative and reproductive generally follow snowmelt patterns (Semenchuk et al., 2016).

Temperature appears to have little direct effect on flowering phenology. Between snowmelt and the date of flower initiation, we found soil temperature in warmed plots was colder than in controls. This is because earlier snowmelt results in greater subsequent exposure to short days, spring frost and generally colder nighttime temperatures that were not fully compensated by active warming. A similar pattern of exposure to cold early season temperatures was found in a snow removal study in the high arctic (Wipf et al., 2009). While Hulber et al. (2010) concluded that temperature sums were an important catalyst initiating flowering phenology for ten alpine species, in our study, temperature was not more important than snowmelt date as a flowering trigger as it 1) had a weaker standardized coefficient as compared with snowmelt date, and 2) does not appear to have caused the advance in community flowering detected from the heating treatment since soils were actually cooler in heated than control plots. While temperature was a significant factor explaining variation in timing of first and last flower, the coefficient is positive, suggesting that as soils warmed later in the growing season, more species in this alpine community commenced (or ceased) flowering (**Figure 1.2b**) as would be expected under unmanipulated conditions. In a subarctic plant community, lagged effects of plant phenology in response to temperature suggest that shifts can take several years to develop particularly due to preformation of buds (Mulder et al., 2017).

While water addition did not significantly alter soil moisture or community flowering phenology, spatial and temporal variation in soil moisture revealed that increased soil moisture was correlated with delayed onset of flowering and flowering termination, but was uncorrelated with flowering duration. This is consistent with studies that 1) added snow in plots to increase moisture and delay snowmelt (Smith et al., 2012; Dorji et al., 2013; Legault et al., 2015), or 2) analyzed inter-annual variation and found increased winter snowfall (Bjorkman et al., 2015) resulted in the delay of at least one plant phenophase (budding, flowering or fruiting), although these studies could not distinguish effects of greater soil moisture from later snowmelt. While our multivariate model did account for variation in snowmelt timing, it is possible that melt-water from upslope areas of the site that kept late-melting plots moist longer resulted in some second order snowmelt-driven variation being absorbed by the soil moisture variable in the model. That the controlled watering experiment revealed no significant effect suggests, at best, an ambiguous proximal effect of soil moisture on alpine community phenology.

### *1.4.3 Watering does not modulate phenological responses to heating –*

Additional soil moisture did not counter any warming-driven advance in cessation of flowering. This is consistent with two active heating experiments: Dunne et al. (2003) found that soil moisture played a surprisingly small role in the timing and duration of flowering in a subalpine meadow, and in a temperate grassland warming advanced flowering phenology but water addition had little effect (Sherry et al., 2007). However, it contrasts with the suggestion that shortened growing seasons could be a result of early senescence caused by warming induced soil drying (Oberbauer et al., 2013). Warming-induced drier soils have also resulted in delayed flower initiation with warming (Dorji et al., 2013). Further, Reyes-Fox et al. (2014) found additional $CO_2$ reduced moisture stress and delayed the graminoid growing (though not flowering) season. In our experiment, however, either we did not add water sufficient to elicit a response or the effect was small relative to variability among species, years, and plots. Although our watering treatment did not significantly modify alpine soil moisture quantified by adequate moisture days (**Table 1.2**) it did affect alpine productivity (Winkler et al., 2016) and first year tree seedling recruitment (Kueppers et al., 2017), suggesting that phenology may simply be less sensitive to surface soil moisture than other biological processes in the alpine.

### *1.4.4 Lifeform, phenological functional group, and species-level differences –*

We tested whether commonly used lifeform classes, such as forbs (Smith et al., 2012; Zhu et al., 2016) and graminoids (Oberbauer et al., 2013), were more sensitive to warming than other groups such as cushions and succulents, which are longer lived and could perhaps be less sensitive to climate change (Eriksson, 2000). Indeed, we found succulent and cushion flowering initiation to be less flexible with imposed warming than forbs and graminoids. Cushion and succulent flowering durations were shorter with higher temperatures in general, and cushions were the only lifeform with a shorter flowering duration as a result of warming; although with earlier snowmelt, cushion and succulent duration remained relatively constant. Taken together, this suggests cushion and succulent species may be less able to take advantage of climatic warming and are more at risk for reduced reproductive success than other groups (Petanidou et al., 2014). This could compound cushion species' decline in productivity with warming, as detected in the same experiment (Winkler et al., 2016), putting this archetypal alpine lifeform at risk of population contraction. Finally, moisture availability most strongly affected date of first and last flower for cushion species, indicating that dry soils would most significantly advance cushion flowering phenology (**Figures 1.2c and 1.2f**).

Of all lifeform groups, graminoids responded most strongly to soil temperature, with increasing temperature extending the end of the flowering season – delaying senescence and extending duration but not affecting initiation. This disagrees with prior work finding that warmer temperatures cause earlier flowering phenology of graminoids (Oberbauer et al., 2013). Unlike graminoids, forb flowering duration was insensitive to temperature, but both graminoid and forb flowering duration were ultimately lengthened with earlier snowmelt suggesting these groups are better able to take advantage of future climatic changes. This result disagrees with a shortened flowering season for graminoids in response to earlier snowmelt (Zhu et al., 2016) and the mean reproductive period for *Kohleria macrantha,* an alpine grass (growing in a temperate grassland), shortening due to warming (Reyes-Fox et al., 2014). That forbs responded to earlier meltdate with earlier flowering onset, but did not respond to temperature, disagrees with earlier bud break for forb species following post-snowmelt warming in a meta-analysis of tundra species (Arft et

al., 2009). Two different effects of warming – earlier snowmelt and warmer temperatures – appeared to yield longer flowering periods for forbs or graminoids and a shorter period for cushions and succulents respectively, but via different proximal factors (*compare* **Figures 1.2g and 1.2h**). This suggests that these groups may respond to different climate drivers and reinforces the importance of simultaneously increasing temperature and advancing snowmelt to understand drivers and anticipate effects of climate change on alpine plant phenology.

Since prior studies have found that early-season species are highly cued to snowmelt date (Korner, 1999; Dunne et al., 2003 *and references therein*), we asked whether they were more responsive to warming than later-flowering species (*sensu* Petanidou et al., 2014). In keeping with the strong community-wide response to heating, early-season species did not advance flowering initiation or senescence more than mid- or late-season species. This is not surprising because a short window between snowmelt and first frost compresses the flowering season into an approximately 8-week week period, with flowering relatively synchronized across species within the community (**Figure 1.1**). Differential responses between early and later flowering alpine species with warming were also not seen on the Tibetan Plateau (Wang et al., 2014), indicating that the short potential growing season in alpine sites may differ from most lower elevation communities where stronger responses are typically found in earlier flowering species (Sherry et al., 2007; Wolkovich et al., 2012). Our early-onset species, however, advanced flower initiation more with earlier snowmelt (**Figure 1.3a**), delayed floral senescence more with warmer temperatures (**Figure 1.3e**); and delayed flower initiation and senescence more with higher moisture (**Figure 1.3c, i**) than occurred with later flowering species. The overall response and success of early-season species could be controlled by multiple proximal effects of climate change (Gezon et al 2016), but especially modification of snowmelt timing with the highest coefficient driving flowering initiation and senescence (**Table 1.6**). This could simply reflect the short window between snowmelt and flowering onset for early season species, which does not afford time for other factors to contribute additional variation to alter flowering phenology. However, contrary to what was found in a subalpine meadow (Dunne et al., 2003), flowering duration was not extended by earlier snowmelt. This is consistent with what we found in our alpine community as a whole; flowering duration appears to be a tightly conserved trait.

Resources are more completely used when individual species' peak demand is spread over the growing season, leading to complementary phenological strategies (*sensu* Hooper, 1998; Korner, 1999; Loreau & Hector, 2001; Ackerly, 2003; Sherry et al., 2007). Changes in climate together with species-specific phenological sensitivity and response strategies may translate to advantages for some species and disadvantages for others. At the species level, we found the same general response as the whole community; most species we examined advanced flowering onset and cessation with heating, with mixed results for flowering duration. These findings are primarily for the most dominant species in the community, as many could not be tested due to small sample size. There were some notable differences in species response, however. In the forb, *Lloydia serotina*, heating significantly expanded the duration of the flowering season, which we expected was possible if flowering onset was earlier and senescence simply remained stable. Watering appeared to counter heat-induced advancement of flowering initiation in *Lewisia pygmaea;* this result was expected if heating dried soils, triggering a stress response in plants causing them to begin the reproductive cycle. Watering reversed both the advance in senescence and shortened duration caused by heating for the dominant forb *Geum rossii*; this could be due to an extension of appropriate growing conditions provided by the treatments. In another forb,

*Erigeron simplex,* watering alone delayed flower onset and expanded flowering duration; this was an unexpected result but could be due to water-logged soils delaying initiation of bud elongation and flower development. The other 11 species examined did not change flowering duration (**Table 1.7**). If phenological responses alter reproductive success via lack of synchronization in plant-pollinator relationships or cause shortened flowering and differential reproductive success, this could result in new assemblage patterns. Similarly, increased synchronization among co-flowering species can enhance interactions with pollinators (Thompson, 1981; Forrest et al., 2010) and thus reproductive success. Remarkable consistency amongst species in this study suggests that with warming, community phenology will largely shift, and there will be little change in synchrony of flowering. Thus if pollinators can similarly advance their phenology, plant-pollinator interactions could remain intact.

### *1.4.5 Conclusions –*

Most studies to date that have attempted to understand effects of climate warming on alpine plant phenology are incomplete because they did not assess the individual and combined effects of temperature, snowmelt, and soil moisture and as a consequence could not explore the relative importance of proximal climate variables. Our findings agree with other studies that show that heating advances flowering phenology, but by using a fully factorial experiment in the alpine tundra, and measuring these distinct proximal variables, we have also shown that heating advanced alpine phenology primarily through advances in snowmelt, rather than via effects on plant and soil temperature. This informs prior global findings from warming experiments in the arctic and alpine tundra, which generally use passive chambers following snowmelt. We also found flowering duration to be a generally conserved trait in this alpine site with few species or functional groups expanding flowering duration to take advantage of a longer snow-free season. Thus, this alpine community – and likely alpine communities more generally – appear to be less able to capitalize on a longer growing season than lower elevation ecosystems. Continued advance of the flowering season could alter plant-pollinator relationships and plant reproductive success if insect pollinators respond in a different manner to environmental cues, but the largely conservative nature of species and functional group flowering duration would help to maintain flowering synchrony.

Our research demonstrates that realistic experimentation that maintains multi-factor responses to enhanced infrared radiation can, in fact, predict plant community response to natural variation in climate; the experimental warming produced similar advances in phenology as observational studies examining time-series of observations (Wolkovich et al., 2012). Yet by analyzing controlled experimental results together with observed plant sensitivity to spatial, interannual and experimental variation in multiple climate factors, we were able to determine that in the alpine, temperature is a less important predictor of phenological change. Water addition did not alter flowering initiation or cessation, nor did it moderate effects of warming, suggesting that soil drying is not as important to flowering phenology in this system as it is for productivity. Alpine systems vary in summer moisture availability so such global differences in this variable can be expected. Lifeform and species results suggest a complex community response to a changing climate; according to microclimate results, longer-lived cushion and succulent species appear to be less able to take advantage of a warmer climate and extend the flowering season, while forbs and graminoids are more elastic and could potentially enhance reproductive success. This could have implications for the community as a whole, particularly since cushion species have been

found to facilitate neighbor recruitment. Further research focusing on alpine plant-pollinator interactions and their implications for fecundity and recruitment under changing climate are needed. Differential species responses will influence the composition of future communities, which may in turn alter ecosystem structure and functions.

***Chapter 1 Acknowledgements***

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# 2 Migration of trees into the alpine tundra: Alpine neighbors assist late-seral but not early-seral conifer seedlings

*Abstract*

Climate change is projected to alter the altitude and latitude of the treeline globally, however seed germination and seedling survival is a critical local control on the expansion or contraction of treeline. The realized climatic conditions that colonizing seedlings will experience is a product of both the ambient climate and interactions with plant neighbors. Recruiting conifers may have to compete with alpine plants or they may be facilitated via protection from the intense alpine environment by neighbors during establishment. To determine whether neighboring plant species can alter the success of seedling recruitment into the alpine tundra ecosystem in the context of climate change, we conducted a controlled replicated experiment with two treeline conifer species. Within the alpine tundra on Niwot Ridge, CO, we imposed crossed active heating and watering manipulations in a common garden experiment and removed neighboring plants from emerging conifer seedlings and a naturally occurring mature alpine herb. Consistent with its late-seral status, *Picea engelmanii* seedlings showed lower survival as compared with *Pinus flexilis* three weeks following neighbor removal, and one year following only survived in watered plots. *P. engelmanii* also had the highest instantaneous water use efficiency (WUE) of all three species. Consistent with its early-seral status, limber pine seedlings were less sensitive to alpine neighbors, and responded to neighbor removal by lowering the quantum yield of photosynthesis ($\phi_{PSII}$), or reducing WUE when also heated. Contrary to expectations from the stress gradient hypothesis, at the low stress and low elevation edge of an alpine herb's range, survival of *Chionophila jamesii* was lower without neighbors regardless of climate treatment. Results suggest that *P. flexilis* has the highest invasion potential into the alpine tundra ecosystem due to its ability to tolerate warmer and drier conditions, which appears to relieve the necessity of neighbor facilitation, while Engelmann spruce will require neighbor facilitation to expand its range. Given future climate change this could mean a range expansion for limber pine and a concomitant land cover change with likely consequences for alpine plant diversity and ecosystem function.

## 2.1 Introduction

Given the expected increase in global temperatures due to rising $CO_2$ levels, and the dependence of treeline position on temperature clines globally (Korner, 1998; Paulsen et al., 2000; Korner and Paulsen, 2004; Danby and Hik, 2007; Korner, 2012), alpine and arctic treelines are expected to shift upward in elevation and latitude in the coming decades (Dullinger et al., 2004; Harsch et al., 2009). This could result in substantial modification of current alpine plant community composition and diversity, which is primarily dominated by graminoids, forbs, succulents and low stature woody species (Korner, 1999). There is evidence of trees invading subalpine meadows over the 20$^{th}$ and early 21$^{st}$ centuries (Haugo et al., 2011; Durak et al., 2015; Lubetkin et al., 2017), and of shrubs and trees beginning expand into the alpine (Harsch et al., 2009; Formica et al., 2014). Invasion of trees into the alpine environment requires seed dispersal, germination and successful establishment (Malanson et al., 2007). While temperature constraints may be primary for growth of mature trees, environmental constraints on seedling establishment

may be different from those that maintain adults; micro-scale climate factors may be more important (Germino and Smith, 1999; Maher et al., 2005; Smith et al., 2009).

Climatic conditions in the alpine such as low temperatures at night followed by high solar radiation the following day have been found to cause conifer seedling mortality in the alpine-treeline ecotone (Germino and Smith, 2000), and spring temperatures and soil moisture have emerged as key drivers for tree seedling establishment across several ecosystems (Weisberg and Baker, 1995; Ibanez et al., 2007; Walck et al., 2011; Millar et al., 2015; Loranger et al., 2016). In the alpine, however, low-stature vegetation is structured to decouple from the free atmosphere and the mat-like structure of alpine herbs therefore creates a boundary layer with a distinct climate (Korner, 1999). This layer can reflect or absorb incoming solar radiation and thus moderate daytime high temperatures, however proximity to the ground can also expose plants to cold air pooling. Greater radiative losses to a clear night sky may also expose plants to more frost events (Jordan and Smith, 1994; Jordan and Smith 1995b). Thus, the microclimate that migrating tree seedlings would experience is different than that of adult trees because of proximity to the ground and neighboring vegetation.

Assuming that viable seeds can arrive to the alpine from the treeline edge, establishment and recruitment will likely depend on very local microclimatic conditions that can be modified by the vegetation neighborhood (Germino et al., 2002; Smith et al., 2003). Interactions between species such as competition and facilitation always co-occur, however depending on environmental conditions one may predominate (Callaway and Walker, 1997). The stress gradient hypothesis states that under more stressful abiotic conditions, facilitation may be more common between co-existing species. At the highest edge of their stress gradient, germinating trees may experience competition for resources (light, water, nutrients) from alpine neighbors (Moir et al., 1999; Tingstad et al., 2015), or according to this hypothesis, alternatively may be buffered from extreme environmental conditions in the alpine such as strong and desiccating wind (Hadley and Smith, 1987), temperature extremes and intense solar radiation (Jordan and Smith, 1995a) by neighboring alpine species (Weisberg & Baker 1995, Hättenschwiler & Smith, 1999; Germino et al., 2002; Smith et al., 2003; Malanson et al., 2007; Batllori et al., 2009; Grau et al., 2013). Many studies in the alpine-treeline ecotone have thus found patterns of seedling establishment aggregated near neighboring vegetation such as grasses (Germino et al., 2002), on the leeward side of tree islands (Hättenschwiler & Smith, 1999) or underneath abiotic shelters (Germino and Smith, 1999) which may moderate temperature and soil moisture. In addition, experimental shading and nocturnal warming as would be experienced under the cover of alpine vegetation, had positive effects on photosynthesis in seedlings of *Picea engelmanii* and *Abies lasiocarpa* (Germino and Smith, 1999). Under a climate change scenario, it is unclear how these microsite biotic and abiotic interactions will be modified (Spasojevic et al., 2013) and is possible that warming trends could counteract any benefit of overhead shelter.

The expansion of a species range may place pioneer individuals in a higher stress environment. Previous work in the alpine treeline ecotone in the front range of CO has linked large-scale subalpine conifer seedling mortality with low volumetric soil water content (Reinhardt et al., 2015) and with drought stress in midday stem water potential, stomatal conductance, photosynthesis, and respiration (Moyes et al., 2013). Further, summer precipitation was at least as important as temperature in limiting growing season carbon gain in establishing subalpine conifers at and above alpine treeline (Moyes et al., 2015).

Instantaneous measurements of seedling physiology can indicate stress under recent or current environmental conditions. The efficiency of photosystem II photochemistry ($\phi_{PSII}$) provides a measure of the rate of electron transport and can be used as an indication of overall photosynthesis (Maxwell and Johnson, 2000). Under conditions of greater stress, more photons will be deflected from the photosynthetic apparatus and the efficiency of photosynthesis will decrease. Instantaneous photosynthetic water-use efficiency (WUE) is the ratio between carbon gain in photosynthesis and water loss during transpiration. It is measured as the ratio of mass of $CO_2$ fixed, to mass of water released into the atmosphere expressed as mg $CO_2$ $g^{-1}$ $H_20$ (Nobel 1980), and provides a measure of water stress. Under low stress conditions, the conductivity of a plant's vascular system and the atmospheric water demand are the main constraints on water use (Lambers et al., 2008). However, when a plant is water stressed from heat, drought or desiccation from wind (DeLucia and Schlesinger, 1991) there can be more water lost per carbon gain, hence instantaneous water use efficiency can be used to estimate one component of in situ plant stress.

The capacity to establish in a new environment depends, in part, on the life history traits and physiological properties of a species (Dullinger et al., 2004; Maher et al., 2005). In the treeline of the Colorado Front Range, Engelmann spruce (*Picea engelmanii* Parry ex. Engelm) and limber pine (*Pinus flexilis* James) are widely distributed conifers that occur at high elevation up to the treeline. Limber pine is a shade-intolerant pioneer species that can persist under conditions of high solar radiation and dry infertile soils, while Engelmann spruce is a later successional species tolerant of shade and adapted to higher moisture substrates. Lazarus et al. (2018) found that limber pine is adapted to conditions of higher moisture stress, demonstrated by higher intrinsic WUE, a slower growth rate and reliance on seed reserves as compared with Engelmann spruce.

We experimentally tested how neighboring plants influenced the ability of these two species to invade an intact alpine meadow in the context of climate change by using a climate change x common garden x removal experiment in the alpine tundra at Niwot Ridge, CO. We also compared the response of a native and mature alpine herb, Rocky Mountain snowlover (*Chionophila jamesii* Benth), restricted geographically to the alpine tundra (Weber, 1976; Ackerfield, 2015) and at the lower end of its elevational range, to the same treatments. We asked two questions: 1) How do neighboring alpine plants affect survival and ecophysiology of tree seedlings and a mature alpine plant? We predicted that the removal of neighboring alpine species would have a negative impact on seedling ecophysiology (measured using $\phi_{PSII}$ and instantaneous WUE) in the short term, and lower survival in the longer term. Further, we expected Engelmann spruce to be more sensitive to neighbor removal. 2) How do climate manipulations alter these effects? We expected warming could relieve cold temperature limitations but could also dry soils and thereby amplify the negative effects of neighbor removal but watering would offset negative effects of drier soils.

## 2.2 Materials and methods

### *2.2.1 Experimental design –*

We conducted our experiment at the alpine site within the Alpine Treeline Warming Experiment (ATWE) on Niwot Ridge in the Front Range of the Colorado Rocky Mountains (40°3' 14.84"N,

105°35'37.71" W; 3540m), on a shallow south-southeast facing slope. The site is 400m above the elevation of established trees, primarily of krummholtz (stunted trees below 3m height) form, with thin and rocky soils. The majority of precipitation falls as snow, and snow depth is locally variable due to westerly winds and topography. Average annual precipitation and temperature are 966 mm and -2.15°C respectively (Blanken et al. 2009). See Castanha et al. (2012) for more details on site and Kueppers et al. (2017) for experimental design. Our alpine site is also located at 3540 m, only 200 m above the lowest elevation range of the alpine herb, *Chionophila jamesii* (Ackerfield, 2015).

Our fully crossed design included two arrays of twenty 3m-diameter plots assigned to four treatment groups: control (C), heated (H), watered (W), and heated + watered (HW). Each plot was divided into four 1x1 $m^2$ quadrats. Six infrared (Mor Electric Heating, Comstock Park, MI, USA) heaters (1000W each) were suspended 1.2m aboveground in hexagonal arrays surrounding each heated plot (Kimball et al., 2007). The heating treatment delivered 215 $W/m^2$ under low wind conditions, but in the alpine, high wind speeds diminished heating efficiency (Kimball et al., 2007) and limited overall warming effects to +1.4°C (Kueppers et al., 2017). Once soil moisture dropped below ~0.2$m^3/m^3$ (2-3 weeks after snowmelt), we applied 2.5mm of water weekly to watered plots to compensate for soil drying due to heating, and to study the impacts of increased growing season soil moisture. Annual water addition totaled ~ 30mm, which is roughly 20% of mean June–September precipitation from 1951–1980 on Niwot Ridge (Greenland 1989).

Each plot was divided into four 1x1 $m^2$ quadrats. One array of 20 plots was seeded in the fall of 2014 with locally collected (within 8 km) seed from forest and treeline, with seed of each species and source elevation sown in a separate quadrat. In 2015, we selected 2 target individuals within one of four quadrats for each *Pinus flexilis* (PIFL), or *Picea engelmannii* (PIEN), and removed all neighboring alpine plants and spike moss within a 5cm radius around each target plant seedling. For each quadrat and for each tree species selected, we chose 2 target individuals designated for neighbor removal and 2 control individuals with neighbors intact (N = 40 per species). For the alpine herb (*Chionophila jamesii,* CHJA) neighbor removal, the protocol was the same except we used 1 target and 1 control individual (N = 20) in the second 20-plot experimental array, which was not sown with tree seed. Survival assessments were conducted twice: at three weeks for seedlings and at one-year following neighbor removal for both the alpine herb and tree seedlings.

### *2.2.2 Measurements of physiological stress –*

To determine whether experimental treatments affected the capacity of both seedlings and an alpine herb to tolerate exposure to high light, we assessed efficiency of Photosystem II *in situ* ($\phi_{PSII}$ ) using a photosynthesis chamber with a fluorometer attachment (6400-40; Li-Cor Biosciences). We measured the ratio of variable to maximum fluorescence, divided by fluorescence in light saturation $\phi_{PSII} = (F_v/F_m)/F_m$ (Maxwell and Johnson 2000). Measurements were performed at actinic red light (1500 µmol $m^{-2}$ $s^{-1}$), with an additional 10% of blue light to maximize stomatal opening, and 400 µmol CO2 $mol^{-1}$ in the cuvette. Air temperature and humidity in the chamber was set to match environmental conditions by the flow of air into the chamber. Ultimately, the PIEN seedlings were too small (short) to reach the opening of the

fluorometer chamber, so no fluorescence measurements were taken for this species. Short segments of PIFL needles and CHJA leaf material were pressed flat in the chamber for measurement. We collected fluorescence data between 9 am and 3pm during a 7-day period from August 10–17, 2015.

To quantify the level of moisture stress the plants experienced under the experimental treatments, we assessed the ratio of carbon gain during photosynthesis to water loss via transpiration as water use efficiency *in situ*. We used the same LICOR photosynthesis chamber this time analyzing gas exchange. During all gas exchange measurements, CO2 gas concentration was set to 400 µmol CO2 $mol^{-1}$ in the cuvette, and relative humidity and temperature were matched to ambient conditions as above. Instantaneous water use efficiency (WUE) was calculated as: photosynthetic rate *A* (umol C $m^{-2}$ $s^{-1}$)/transpiration *E* (mol $H_20$ $m^{-2}$ $s^{-1}$).

To quantify the influence of treatments on the microclimate directly adjacent to target plants, we collected soil temperature at the soil surface and percent volumetric soil water content over a 0-5 cm depth within a 5cm radius of each target plant within 1-2 hours of the gas exchange and fluorescence readings. These measurements were collected three weeks following removal treatments.

### *2.2.3 Statistical analysis –*

To assess survival three weeks following removal, we ran separate generalized linear mixed effects models for each seedling species, including the water*removal and heat*removal interaction terms as main fixed effects and plot as a random effect with a logit link and binomial distribution (function lme4::glmer in R3.3.2 package Matrix). For PIFL, the final model only included the fixed effect of removal (because minimal change in survival prohibited a more complex model fit). To evaluate survivorship at one year, we ran separate models for each of the three species. Models for CHJA and PIFL included the same terms as above, but the model for PIEN included only a water*removal interaction term (we separately evaluated a water*removal and a heat*removal model because very low survival in unwatered plots precluded more complex model fits). To assess effects on $\phi_{PSII}$ and instantaneous WUE of each species in various treatments, we again ran separate models for each species as above with heat*removal and water*removal as main fixed effects and plot as a random effect, but with a gaussian distribution and an identity link. Microclimate readings adjacent to plants were analyzed with a similar model as above with data for the two species of seeding combined; the alpine herb readings were analyzed in a separate model because it was located in an independent array. Models were built using the lme4 package and all graphics were developed in R (Bates et al. 2015, R Core Team 2014). We summarized the models using restricted maximum likelihood, z-tests via Laplace approximation and t-tests via Satterthwaite approximations for degrees of freedom (binomial and Gaussian distributions respectively). Significance levels were estimated using Wald $\chi^2$ tests (car::Anova in R).

## 2.3 Results

### *2.3.1 Treatment effects –*

The heating treatment increased mean 5–10 cm soil temperature +1.4°C (+/– 0.03) and reduced volumetric soil water content by –0.016 $m^3 m^{-3}$ (+/– 0.001) on average over the snow free growing seasons of 2010-2014 in the seeded alpine plots (Kueppers et al., 2017). In the unseeded plots, from 2010-2015, heating increased mean 5–10 cm soil temperature +1.2°C (+/– 0.07) and reduced volumetric soil water content by –0.012 $m^3 m^{-3}$ (+/– 0.0016) on average. The watering treatment increased 5–10 cm soil volumetric water content in seeded plots by +0.008 $m^3 m^{-3}$ (+/– 0.001) and in unseeded plots by +0.025 $m^3 m^{-3}$ (+/– 0.001). Three weeks following removals, the instantaneous microclimate around seedlings was warmer in removal plots and wetter in watered plots (**Tables 2.1a & b**). The microclimate around the native herb was cooler in the watered and water*removal plots and warmer in removal and heat*removal plots (Table 1a), and wetter in watered plots (**Table 2.1b**).

### *2.3.2 Survival –*

In partial agreement with our hypothesis that neighbor removal would negatively affect seedling survival, three weeks following alpine plant removal, PIEN survival was lower but PIFL was unaffected. PIEN experienced lower survival when neighbors were removed (92% survival with neighbors intact and 70% following removal; **Table 2.2 & Figure 2.1**) regardless of climate treatments. Survival of PIFL was essentially unaffected with 98.5% survival regardless of removal or climate treatment.

Seedling survivorship one year post-removal of neighboring plants also responded differentially between the species. In agreement with predictions that PIEN would be more impacted by treatments, the only PIEN survivors in heated plots were also watered; in fact PIEN seedlings only survived in watered plots (**Table 2.3 & Figure 2.2**) regardless of removal. In the more drought tolerant seedling species, PIFL, survivorship did not respond to any of the neighborhood or climate treatments. For the alpine herb, CHJA, removal marginally ($\alpha < 0.1$) reduced survival (Table 3); a larger sample size may provide more confidence in this result.

### *2.3.3 Physiological response –*

In agreement with our predictions that neighbor removal would reduce the efficiency of photosynthesis, $\phi_{PSII}$ was lower in PIFL seedlings with neighbors removed, but was not impacted consistently by the climate treatments (**Table 2.4, Figure 2.3**). Conversely, for the alpine herb CHJA, $\phi_{PSII}$ was unaffected by neighbor removal but was marginally reduced ($\alpha <$ 0.1) with additional heat.

Instantaneous water use efficiency was actually highest in PIEN ($t = 5.85$, $p = 1.38e^{-7}$, **Figure 2.4**) as compared with PIFL and CHJA. Contrary to our expectations for any of the species, instantaneous water use efficiency was reduced for PIFL when plants were warmed and neighbors were removed (**Table 2.5**).

**Table 2.1a** Linear mixed effects model parameter estimates for main effects and two-way interactions for instantaneous surface soil temperature (ºC) around seedlings and an alpine herb three weeks following neighbor removal and within an hour of physiology measurements.

| | *Seedlings* | | | | | *CHJA* | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Coef | SE | $X^2$ | df | $P(X^2)$ | Coef | SE | $X^2$ | df | $P(X^2)$ |
| Intercept | 16.61095 | 1.42374 | | | | 15.2339 | 1.2176 | | | |
| H | -0.01552 | 1.64277 | 0.0069 | 1 | 0.93 | -2.2478 | 1.4025 | 0.6502 | 1 | 0.42 |
| W | -1.64503 | 1.64321 | 0.4923 | 1 | 0.48 | -1.6522 | 1.4025 | 3.8061 | 1 | **0.05** |
| Removal | 0.69 | 1.07961 | 5.9755 | 1 | **0.01** | 1.32 | 0.7959 | 10.4733 | 1 | **0.001** |
| H*Removal | 0.29 | 1.21806 | 0.0572 | 1 | 0.81 | 2.35 | 0.9054 | 6.764 | 1 | **0.009** |
| W*Removal | 1.17 | 1.22308 | 0.9159 | 1 | 0.34 | -1.8748 | 0.9054 | 4.2875 | 1 | **0.04** |

**Table 2.1b** Linear mixed effects model parameter estimates for main effects and two-way interactions for instantaneous volumetric soil moisture (%) adjacent to seedlings and an alpine herb at 0-5 cm depth three weeks following neighbor removal and within an hour of physiology measurements.

| | *Seedlings* | | | | | *CHJA* | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Coef | SE | $X^2$ | df | $P(X^2)$ | Coef | SE | $X^2$ | df | $P(X^2)$ |
| Intercept | 6.21 | 0.53808 | | | | 6.46 | 0.9987 | | | |
| H | -0.08134 | 0.61659 | 1.415 | 1 | 0.23 | -1.1775 | 1.1417 | 0.0999 | 1 | 0.75 |
| W | 1.03 | 0.61746 | 11.5719 | 1 | **0.0007** | 3.86 | 1.1417 | 7.6344 | 1 | **0.006** |
| Removal | -0.43497 | 0.71031 | 0.2863 | 1 | 0.59 | 0.13 | 1.2322 | 0.0176 | 1 | 0.89 |
| H*Removal | -0.99506 | 0.80167 | 1.5407 | 1 | 0.21 | 2.92 | 1.4018 | 4.3533 | 1 | **0.04** |
| W*Removal | 1.22 | 0.80482 | 2.2859 | 1 | 0.13 | -2.7348 | 1.4018 | 3.8061 | 1 | **0.05** |

**Table 2.2** Linear mixed effects model parameter estimates for main effects and two-way interactions for three-week survival of PIEN (*Picea engelmanii*) and PIFL (*Pinus flexilis*) following neighbor removal within climate treatments. Wald $\chi^2$ tests and P-values, $P(\chi^2)$, were calculated for effects of treatments and their interactions. Effects have only two levels, so the coefficient for the level not shown is the same magnitude but opposite sign as the coefficient listed. Plot was included as a random effect. Probability <0.05 is indicated with bold type.

| | *PIEN* | | | | | *PIFL* | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Coef | SE | $X^2$ | df | $P(X^2)$ | Coef | SE | $X^2$ | df | $P(X^2)$ |
| Intercept | 2.03 | 0.83 | | | | 8.82 | 3.24 | | | |
| H | 0.36 | 0.86 | 0.60 | 1 | 0.44 | | | | | |
| W | -1.10 | 0.91 | 0.03 | 1 | 0.86 | | | | | |
| Removal | -2.87 | 1.02 | 12.04 | 1 | **0.001** | 7.10E-07 | 1.49 | 0 | 1 | 1.00 |
| H*Removal | 0.06 | 1.08 | 0.00 | 1 | 0.96 | | | | | |
| W*Removal | 1.53 | 1.12 | 1.86 | 1 | 0.17 | | | | | |

**Table 2.3** Linear mixed effects model parameter estimates for main effects and two-way interactions for one-year survivorship of PIEN (*Picea engelmanii*), PIFL (*Pinus flexilis*) and CHJA (*Chionophila jamesii*) following neighbor removal within climate treatments. Wald $\chi^2$ tests and P-values, $P(\chi^2)$, were calculated for effects of treatments and their interactions. Effects have only two levels, so the coefficient for the level not shown is the same magnitude but opposite sign as the coefficient listed. Plot was included as a random effect. Probabilities <0.1 are indicated with bold type.

| | *PIEN* | | | | | *PIFL* | | | | | *CHJA* | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Coef | SE | $X^2$ | df | $P(X^2)$ | Coef | SE | $X^2$ | df | $P(X^2)$ | Coef | SE | $X^2$ | df | $P(X^2)$ |
| Intercept | -136.60 | 316.00 | | | | -0.05 | 0.58 | | | | -0.24 | 0.51 | | | |
| H | | | | | | 0.53 | 0.68 | 0.99 | 1 | 0.32 | 0.19 | 0.58 | 0.13 | 1 | 0.71 |
| W | 124.50 | 316.00 | 0.16 | 1 | 0.69 | -0.11 | 0.68 | 1.20 | 1 | 0.27 | 0.22 | 0.58 | 1.99 | 1 | 0.16 |
| Removal | -1459.90 | 355.20 | 0.00 | 1 | 0.9901 | -1.65 | 0.91 | 2.42 | 1 | 0.12 | -1.15 | 0.61 | 2.82 | 1 | **0.09** |
| H*Removal | | | | | | -0.03 | 0.98 | 0.00 | 1 | 0.97 | -0.02 | 0.66 | 0.00 | 1 | 0.98 |
| W*Removal | 1460.00 | 355.20 | 16.90 | 1 | **3.947E-05** | 1.56 | 1.00 | 2.44 | 1 | 0.12 | 1.04 | 0.68 | 2.38 | 1 | 0.12 |

**Table 2.4** Linear mixed effects model parameter estimates for main effects and two-way interactions for $\phi_{PSII}$ in PIFL (*Pinus flexilis*) seedlings and CHJA (*Chionophila jamesii*) following neighbor removal within climate treatments. Wald $\chi^2$ tests and P-values, $P(\chi^2)$, were calculated for effects of treatments and their interactions. Effects have only two levels, so the coefficient for the level not shown is the same magnitude but opposite sign as the coefficient listed. Plot was included as a random effect. Probabilities <0.1 are indicated with bold type.

| | *PIFL* | | | | | *CHJA* | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Coef | SE | $X^2$ | df | $P(X^2)$ | Coef | SE | $X^2$ | df | $P(X^2)$ |
| Intercept | 0.31 | 0.07 | | | | 0.20 | 0.02 | | | |
| H | -0.12 | 0.08 | 2.02 | 1 | 0.16 | -0.02 | 0.03 | 2.89 | 1 | **0.09** |
| W | 0.08 | 0.08 | 0.26 | 1 | 0.61 | 0.00 | 0.03 | 0.15 | 1 | 0.69 |
| Removal | -0.09 | 0.06 | 10.48 | 1 | **0.001** | 0.03 | 0.03 | 1.46 | 1 | 0.227 |
| H*Removal | 0.02 | 0.07 | 0.10 | 1 | 0.75 | -0.02 | 0.04 | 0.14 | 1 | 0.71 |
| W*Removal | -0.10 | 0.07 | 1.63 | 1 | 0.20 | 0.02 | 0.04 | 0.33 | 1 | 0.57 |

**Table 2.5** Linear mixed effects model parameter estimates for main effects and two-way interactions for water use efficiency in PIEN (*Picea engelmanii*), PIFL (*Pinus flexilis*) and CHJA (*Chionophila jamesii*) following neighbor removal within climate treatments. Wald $\chi^2$ tests and P-values, $P(\chi^2)$, were calculated for effects of treatments and their interactions. Effects have only two levels, so the coefficient for the level not shown is the same magnitude but opposite sign as the coefficient listed. Plot was included as a random effect. Probabilities <0.1 are indicated with bold type.

| | *PIEN* | | | | | *PIFL* | | | | | *CHJA* | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Coef | SE | $X^2$ | df | $P(X^2)$ | Coef | SE | $X^2$ | df | $P(X^2)$ | Coef | SE | $X^2$ | df | $P(X^2)$ |
| Intercept | 1.51 | 0.78 | | | | 0.48 | 0.15 | | | | 0.32 | 0.07 | | | |
| H | 1.09 | 0.90 | 0.64 | 1 | 0.42 | 0.30 | 0.17 | 0.04 | 1 | 0.83 | 0.01 | 0.08 | 1.82 | 1 | 0.18 |
| W | -0.81 | 0.90 | 0.62 | 1 | 0.43 | -0.09 | 0.17 | 0.08 | 1 | 0.78 | 0.01 | 0.08 | 0.43 | 1 | 0.51 |
| Removal | 0.52 | 0.66 | 0.02 | 1 | 0.88 | 0.05 | 0.13 | 0.65 | 1 | 0.42 | 0.08 | 0.10 | 0.09 | 1 | 0.769 |
| H*Removal | -1.37 | 0.81 | 2.89 | 1 | **0.09** | -0.51 | 0.16 | 10.72 | 1 | **0.001** | -0.20 | 0.12 | 0.22 | 1 | 0.64 |
| W*Removal | 0.46 | 0.81 | 0.32 | 1 | 0.57 | 0.25 | 0.16 | 2.60 | 1 | 0.11 | 0.05 | 0.12 | 2.99 | 1 | **0.08** |

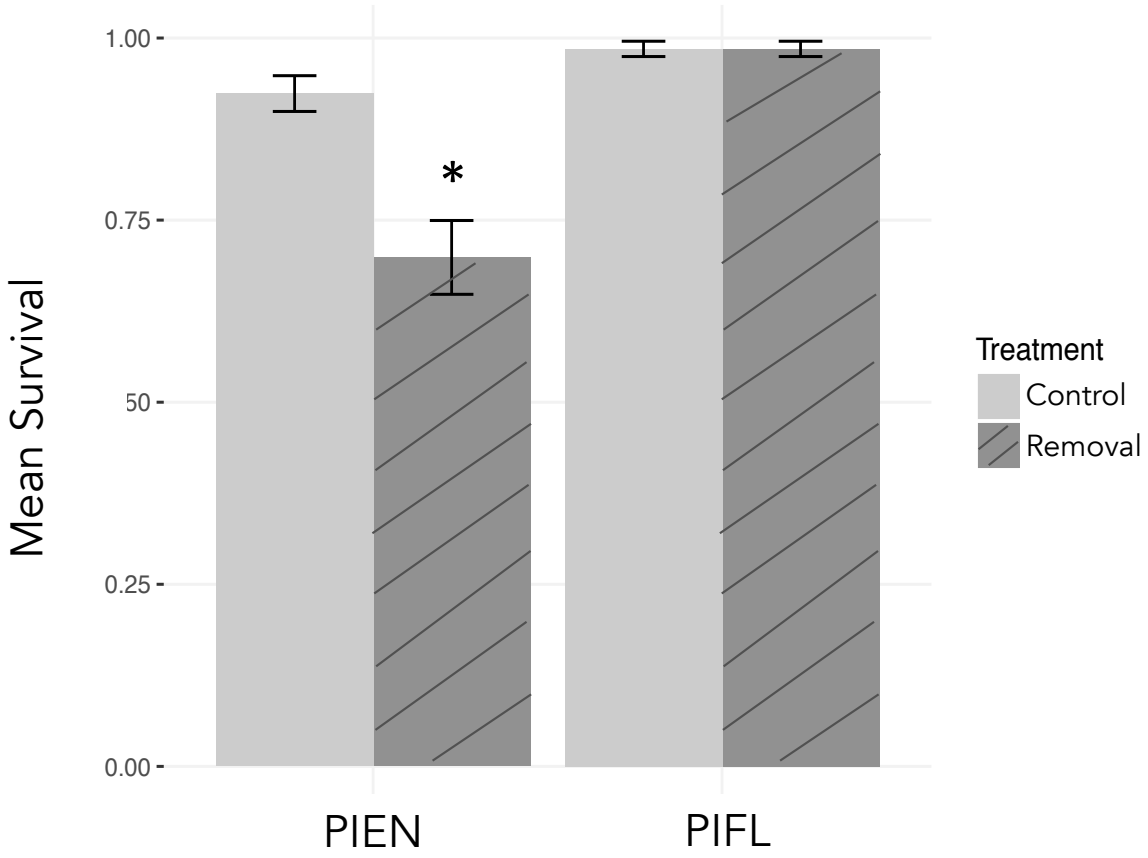


**Figure. 2.1** Mean three week survival (+/- 1 standard error) of PIEN (*Picea engelmanii*) and PIFL (*Pinus flexilis*) seedlings in the alpine following the removal of all neighboring plants within 5 cm (*see* Table 2). The removal treatment is indicated with grey hashing.

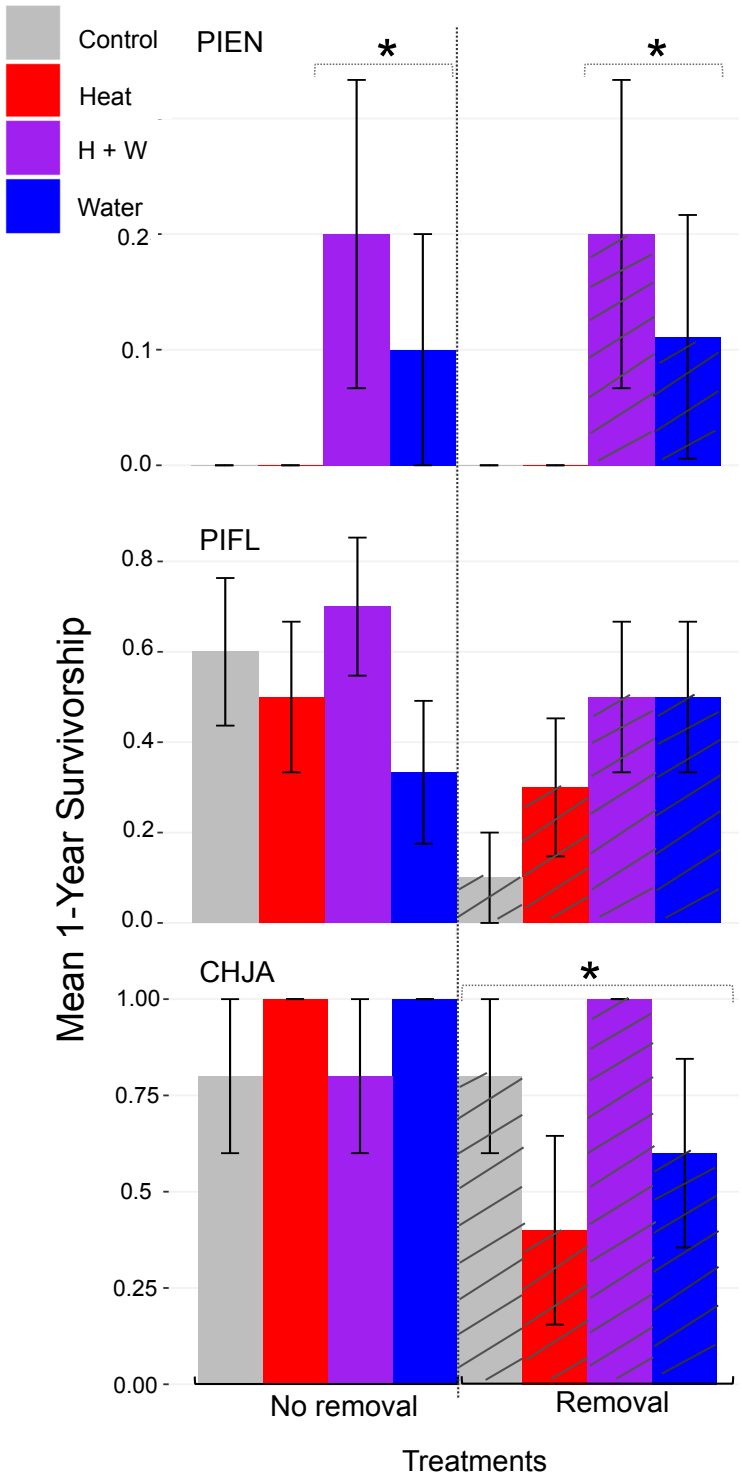


**Figure. 2.2** Figure 2. Mean 1-year survivorship (+/- 1 standard error) of the two tree species PIEN (*Picea engelmanii*) and PIFL (*Pinus flexilis*) seedlings, and an alpine herb CHJA (*Chionophila jamesii*) one year following the removal of alpine herb neighboring plants. Plots with heated treatments are depicted with red bars, blue bars depict watered plots, purple bars depict heated + watered plots and the removal treatment is indicated with grey hashing (*see* Table 3.)

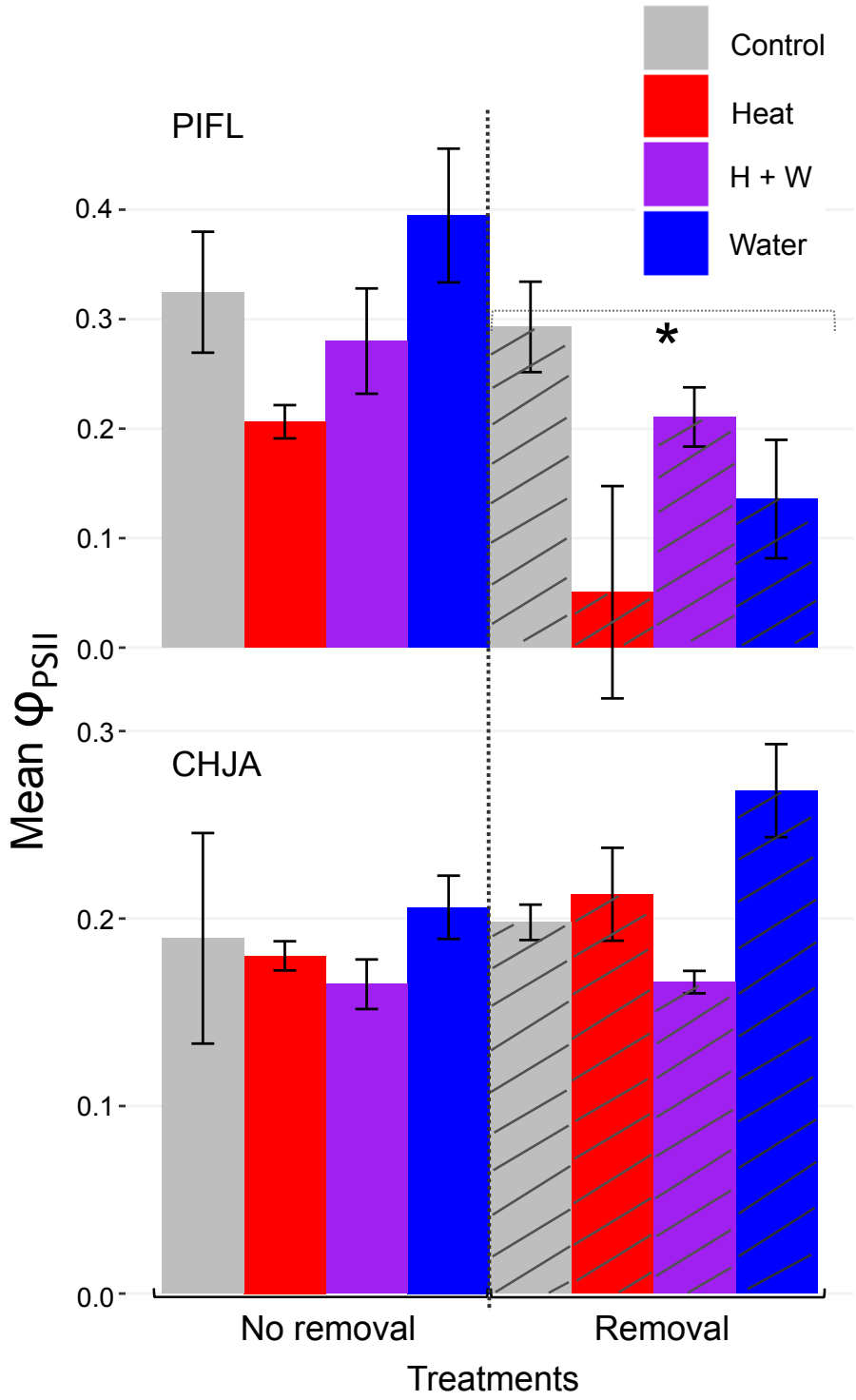


**Figure. 2.3** Mean $\phi_{PSII}$ (+/- 1 standard error) for PIFL (*Pinus flexilis*) seedlings, and an alpine herb CHJA (*Chionophila jamesii*) three weeks following the removal of neighboring alpine plants. Plots with heated treatments are depicted with red bars, blue bars depict watered plots, purple bars depict heated + watered plots and, the removal treatment is indicated with grey hashing (*see* Table 4).

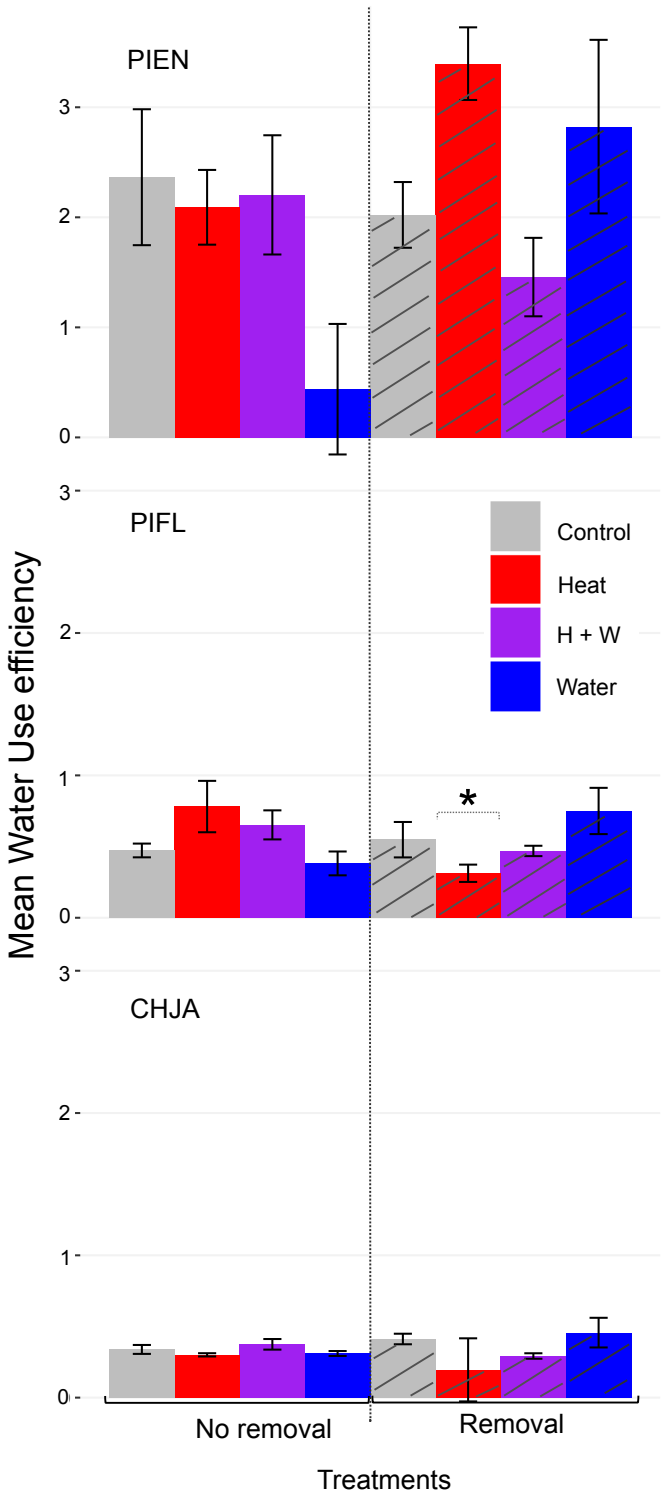


**Figure 2.4** Water use efficiency for PIEN (*Picea engelmanii*), PIFL (*Pinus flexilis*) seedlings, and an alpine herb CHJA (*Chionophila jamesii*) three weeks following the removal of neighboring alpine plants. Plots with heated treatments are depicted with red bars blue bars depict watered plots, purple bars depict heated + watered plots, and the removal treatment is indicated with grey hashing (*see* Table 5).

## 2.4 Discussion

### *2.4.1 Stress gradient hypothesis and neighbors –*

Prior studies have found seedling establishment to be idiosyncratic according to species life history and physiology (Loranger et al., 2016). While native alpine vegetation has been traditionally thought to compete with tree seedlings for resources including nutrients, light and water (Billings, 1959; Tingstad et al., 2015), relatively new evidence suggests positive associations between plant neighbors including shrubs, krumholtz trees and grasses with tree seedling density and survival (Weisberg & Baker, 1995; Hättenschwiler and Smith, 1999; Germino et al., 2002; Smith et al., 2003; Grau et al., 2013). This suggests neighbors can facilitate tree seedling recruitment through several potential mechanisms: reducing incoming IR, buffering intense and drying wind (Hattenschwiler and Smith, 1999), shading soils or enhancing soil moisture.

At the upper edge of the stress gradient for tree seedlings, the presence of plant neighbors appears to enhance survival in the alpine environment for the moisture and shade tolerant conifer species Engelmann spruce. These seedlings perform better with neighbors intact as they showed greater survival in the first 3 weeks with neighbors, which could be due to a warmer microclimate in removal plots (**Table 1a**). Engelmann spruce seedlings and saplings in the alpine-treeline ecotone of the Medicine Bow Mountains occurred most frequently near islands of adult trees (Germino et al., 2002). This could be due to protection from cold nighttime temperatures found to kill spruce seedlings (Helmers et al., 1970). In addition, Maher et al. (2005) observed that tree and herb cover had additive effects on survivorship and photosynthesis of conifer seedlings (including Engelmann spruce) except under alleviated water stress implicating soil moisture as we found in this study, discussed below.

Inconsistent with our expectations, limber pine survival was not harmed by neighbor removal, but also was not enhanced, suggesting neutral interactions with neighbors. Given its ability to tolerate xeric conditions on exposed slopes, this result is reasonable (Rebertus et al., 1991; Letts et al., 2009). Donnegan and Rebertus (1999) also found solitary pines with no spruce or fir neighbors had a greater chance of survival than individuals within clumps of six or more trees. Despite its clear tolerance for high light, because this conifer species has not yet invaded the alpine, we presumed that neighbors would provide some moderation of the harsh alpine environment. Indeed, neighbor removal reduced photosynthetic efficiency indicating seedlings experienced some elevated level of stress but not enough to cause mortality. Perhaps its high survival rate is due to its capacity to engage in photo-protective mechanisms as has been demonstrated for low temperature tolerance in other conifers (Germino and Smith, 1999; Germino and Smith, 2000). Second, when limber pine seedlings were heated and neighbors were removed seedling water use efficiency was lower which could indicate a lowered stress environment. Since this is unlikely, lowered photosynthesis could explain reduced water use efficiency consistent with the in situ $\phi_{PSII}$ response (**Figure 2.3**). In another study at this site, Moyes et al. (2013) found lower rates of growth and maintenance respiration at high temperature in warmed plots, which suggested respiratory but not photosynthetic acclimation to warmer growing temperatures.

Situated just above treeline our site was ideal for testing the low-elevation edge of the alpine stress gradient on Niwot ridge for the native herb mountain snow lover. Our alpine site is located at 3540 m, only 200 m above the species lowest elevation range (Ackerfield, 2015). Contrary to expectations from the stress gradient hypothesis, which would predict benefits from neighbor removal in the lower elevation alpine (Callaway 1995, Callaway and Walker 1997, Callaway 1997), we found no benefits, and even negative effects of removal on survival of this alpine herb. Presence of neighbors was important for survival of Rocky mountain snowlover regardless of climate treatment even at this low elevation edge of its altitudinal range, suggesting facilitation is still the predominant interaction.

### *2.4.2 Microclimate and climate change –*

Engelmann spruce success in the alpine ecosystem also appears to be influenced by the local microclimate. Of all species studied, we predicted Engelmann spruce would be most affected by the alpine environment due to its tolerance of high soil moisture and shade (Kauffman and Eckard, 1977; Gill et al., 2015). In comparison, limber pine displays an adaptive response to drier conditions by maintaining a generally high intrinsic WUE (Lazarus et al., 2017). Symptomatic of severe water stress, three weeks following neighbor removal, Engelmann spruce displayed the highest instantaneous water use efficiency of all three species. In order to conserve water Engelmann spruce seedlings maintained higher WUE than expected based on prior measurement over lifetime of a seedling of this species in the alpine and treeline environments (Lazarus et al., 2017). Thus soil moisture availability is likely limiting Engelmann spruce in the alpine. Further, spruce only survived in watered plots, regardless of other treatments, over the one-year timeframe of the study. Since these plots were also moister (**Table 2.1b**), greater survival in moister plots is also consistent with water limitation. In another study at this site, warming reduced Englemann spruce recruitment above the treeline primarily due to soil drying (Kueppers et al., 2017). Similarly, photosynthesis and respiration were highest for potted spruce seedlings at moisture deficits less than 10% (Ronco, 1970). Indeed, in other subalpine forests, spruce was less drought-tolerant than pines and therefore expected to require amelioration of the environment before it could colonize (Donnegan and Rebertus, 1999).

Zurbriggen et al. (2013) found that seedling success of a number of tree species was not limited by current climate above treeline. In our study, local climatic modification did not significantly alter limber pine seedling survival over one year, reinforcing the idiosynchratic nature of species responses and suggesting that limber pine may possess adaptive mechanisms to deal with the alpine environment particularly in the context of climate change. Limber pine seedlings are generally larger and have deeper roots than Engelmann spruce (Lazarus et al., 2017), which may allow them to better tolerate both drying associated with warming and the alpine environment without protection from neighboring species.

For an alpine herb, we predicted that heating would relieve abiotic cold stress and make plant associates less important (*as in* Callaway et al., 2002). Removal of neighbors did lower survivorship, but the addition of heat did not change mortality. Although over the growing season, heating did increase 5-10 cm soil temperatures, according to instantaneous temperature at the soil surface adjacent to plants following removals (**Table 2.1a**), warmed plots were not significantly warmer. Given these plants are relatively long lived, it is possible that treatments

were not strong enough or that the timeframe of exposure (one year) was not long enough to elicit a response.

### *2.4.3 Implications for treeline shifts –*

The combination of warmer and wetter conditions in Rocky Mountain National Park have been associated with spruce and fir migration into the forest-tundra ecotone in the last 150 years (Hessl & Baker, 1997). Understanding the mechanisms that support success in early stages of tree establishment is critically important for projecting the impact of climate change on future tree ranges and potential re-organization of alpine community composition. Biotic associations provided by neighboring species appear to be important for a later-seral conifer, but not as relevant for an early-seral species. In our study, Engelmann spruce demonstrates low invasion potential; all spruce seedlings perished except those that were watered, suggesting a major constraint involves soil drying associated with projected warming. Thus success may depend on the actual realization of future temperature and summer precipitation. Limber pine seedlings are larger, have deeper roots, grow more slowly, and exhibit a higher WUE than Engelmann spruce (Lazarus et al., 2017), which may allow them to better tolerate drying associated with both warming and neighbor removal and provide a physiological advantage for migration into the alpine environment. This species may be able to avoid potential competition by recruiting into vegetation gaps.

This study complements niche models and demography studies, which suggest a reduction in Engelmann spruce's current range in the coming decades (Dobrowski et al., 2015; Kueppers et al., 2017), because it highlights the benefits of biotic association for the leading edge of Engelmann spruce recruitment. This upper edge of its range could be broadened via biotic associations with neighbors which are not limited to but may include shading, which reduces soil drying and needle desiccation, wind buffering and reduction of incoming solar radiation. Even without enhanced precipitation, the alpine will likely become more invasible for limber pine due to its ability to tolerate low moisture conditions. This structural community change will likely have implications for future alpine ecosystem function and biodiversity (Malanson et al., 2007). The result of these shifts could result in ecosystem services more akin to those of a mature forest system such as: greater coupling with the free atmosphere (Germino and Smith, 1999), carbon sequestration and a greater albedo (Jackson et al., 2008) which in turn can impact feedbacks (Bonan et al., 2008) into the climate system.

***Chapter 2 Acknowledgements***

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# 3 Slow alpine tundra vegetation change in the Ruby Mountains of Colorado

*Abstract*

Climate warming is expected to acutely affect high elevation temperature sensitive ecosystems, which have already experienced a greater rate of temperature rise in the last 50 years. We report the response of alpine vegetation to climatic variability and trends for a GLORIA (Global Observation Research Initiative in Alpine Environments) target region in the Ruby Mountains of Colorado. Local climate is changing, evidenced by increasing winter temperatures and earlier snowmelt during the last 40 + years. Consistent with the perennial life histories of plants in this alpine community, we found moderate change in plant community trends over time as well as inter-annual variation, which correlated with climatic variability. Community-wide vegetation cover decreased while species richness increased from 2008 to 2017. The vegetation community composition was organized by aspect and summit but did not change over time. A non-significant trend of increased species with a warmer thermal niche was found on the lowest summit, while colonization by cold-adapted species appears to be occurring on other summits. One short-lived forb and two grasses decreased cover over time. The relatively limited changes that did occur suggest slow trailing edge dynamics since long-lived species changed very little, while increased richness suggests potentially faster transformation on the leading edge, at the highest elevation site. Rising winter temperatures and decreased snow duration will likely cause longer-term changes in vegetation but may take time due to the long-lived nature of these plant communities.

## 3.1 Introduction

The temperature signal associated with anthropogenic climate modification appears to be amplified in high elevation alpine ecosystems (Giorgi et al., 1997; Rangwala and Miller, 2012; MRI 2015). By some estimates these high elevation systems have experienced an approximately 1.2 times faster rise in annual mean temperatures than lower elevation sites, measured by weather stations greater than 500 m above sea level over the period 1961– 2010 (Wang et al., 2014; Wang et al., 2016; *but see* Oyler et al., 2015). Further, spring warming for high-elevation stations in the European Alps has been 3.5 times greater than the corresponding northern hemisphere temperature rise over the last three decades (Marty & Meister, 2012), suggesting alpine tundra communities may be disproportionately impacted by climatic changes (Canone et al., 2007; McCain and Colwell, 2011). These alpine communities can also be sensitive indicators of climate change because of tight phenological coupling to a short snow-free growing season (Korner, 1999; Petralgia et al., 2014; Prevéy et al., 2017) and the greater relative sensitivity of biological and chemical processes occurring in colder temperatures (Kirschbaum, 1995). Conversely, because most alpine plants are long-lived perennials, and are adapted to substantial daily temperature fluctuations during the growing season, they may not respond to short-term oscillations in climate, but rather their response may lag behind longer-term climatic trends (Svenning and Sandel, 2013).

Such lags in the response of species to realized or predicted climatic change has been described by disequilibrium dynamics (Svenning and Sandel, 2013), and occurs when a particular vegetation assemblage or an individual species is out of equilibrium with suitable climatic conditions, creating an extinction debt (Dullinger et al., 2012*a*). This discrepancy can be explained by extinction lags at trailing edges or dispersal and establishment lags at leading edges of species ranges caused by a host of mechanisms including biotic interactions (Alexander et al., 2017). Further, both landscape level and small scale micro-topographic heterogeneity can buffer against loss of climatically suitable habitat and provide refugia for some species (Sherrer and Korner, 2011; Opedal et al., 2015). Despite the potential for disequilibrium, both range expansions (Pauli et al., 2012) and range contractions in mountain systems have been documented (Pauli et al., 2007; Moritz et al., 2008; Lemprecht et al., 2018). Further, there appears to be variability amongst eco-regions including Mediterranean alpine zones and boreal or temperate systems based on differences in moisture regime (Pauli et al., 2012).

Ultimately, changes in plant community assembly can be expected from shifts in individual species abundance or distribution resulting from climate change. Indeed, plant species adapted to warmer climates have either shifted upward in altitude or increased in relative abundance in a process termed thermophilization (Gottfried et al., 2012; Lemprecht et al., 2018), in synch with a global temperature rise of 0.13°C per decade in mountainous areas (IPCC 2013). Although incomplete range filling is common even following post glacial migration (Dullinger et al 2012*b*), climatic changes will likely cause relative shifts in species dominance partly resulting from in-filling from the local species pool. Mountain aspects, which differ in thermal accumulation, have been found to be a strong determinant of vegetation patterns and also the pace of climate-induced changes in plant distributions (Winkler et al., 2016*a*). The impacts of a changing climate may be more pronounced in some vegetation types than others, such as particular life forms (De Valpine and Harte, 2001; Winkler et al., 2016*b*). Finally, changes in community composition can have cascading effects on ecosystem processes such as soil carbon. For example, in an actively heated subalpine site, forbs are being replaced by shrubs (Harte and Shaw, 1995), which has impacted the soil carbon budget (Seleska et al., 2002) and will ultimately impact feedbacks to the climate system (Harte et al., 2015).

In order to track changes in alpine plant communities using a standardized approach, the Global Observation Research Initiative in Alpine Environments (GLORIA) network was established in 2001 (Pauli et al., 2015). This network has already demonstrated changes in richness, vegetation cover, range expansion and thermophilization in alpine plant communities as noted above (Gottfried et al., 2012; Pauli et al., 2012; Winkler et al., 2016*a*; Lemprecht et al., 2018). As part of the larger network, we collected data from four summits over a 10-year period at a GLORIA "target region" in the Ruby Range of the Elk Mountains of Colorado, to assess several questions: 1) Has alpine plant cover or richness changed over time, and are certain aspects or summits driving that change? 2) Is observed variation in cover or richness correlated with inter-annual climate variability or long-term climate trends? 3) Is there a change in community composition over time, driven by particular lifeforms, or species? 4) Has there been a change consistent with a thermophilization effect – an increase in cover or abundance of montane and treeline species and a decrease in alpine and nival (from regions of perpetual snow) species?

## 3.2 Methods

### *3.2.1 Study area –*

In 2007, we established a target "region" which includes four summits at four different elevations in the Ruby Range of the Elk Mountains in Gunnison County, Colorado within the GLORIA project network following the multi-summit approach; *i)* Treasury high (TRH, 4023 m) is located approximately 150 m below the true summit of Treasury Mountain characterized by a mixture of loose rock and cryptobiotic crusts with heterogeneous distribution of alpine flora. *ii)* Ruby mountain (RUB, 3854 m) is characterized by very steep scree slopes on south and east aspects and relatively dense turf-like vegetation. *iii)* Cinnamon mountain (CIN, 3747 m) is characterized by scree slopes on all sides, and *iv)* Treasury low (TRL, 3,566 m) is located on the saddle between Treasury mountain and Cinnamon mountain, just above upper treeline with a small patch of krummholz-form Engelmann spruce approximately 10 m below the east aspect of the summit. The area is mostly loose scree with very sparse vegetation, and the north-facing slope is very steep with outcrops of metamorphic rock.

### *3.2.2 Vegetation data collection and classification –*

Vegetation was sampled according to the GLORIA multi-summit approach (Pauli et al., 2015). Beginning in the growing season of 2008, at each summit a 3 x 3 meter grid was established on aspects facing each cardinal direction 5 m below the summit peak. In each of the four corners of the grid a 1 $m^2$ quadrat was used to visually estimate total vegetation cover of all vascular plant species and a common spike moss, *Selaginella densa* (Rydb). The GLORIA protocol suggests a resampling period of every 5 years. However, to determine whether variation in inter-annual climatic conditions could cause short-term fluctuations in vegetation cover, in the first 5-year period we conducted annual re-surveys to understand the level of inter-annual variability and to more clearly detect long-term trends. This resulted in vegetation surveys in six years over a 10-year period including: 2008, 2009, 2010, 2011, 2012 & 2017. Surveying 4 quadrats for each of 4 aspects, for 4 summits over 6 years provided a total of 384 quadrat-year samples.

To determine if particular lifeforms changed over the course of the survey, species were categorized into one of the following classes: cushion plant (mat-forming, prostrate forbs and true cushions), forb, graminoid, "moss" (the spike moss – *Selaginella densa*), shrub and succulent. To determine the altitudinal rank of a species for the thermophilization (the increase in abundance or cover of species with a warmer, lower elevation thermal niche) analysis, we followed the protocol of Gottfried et al. (2012) and used a standardized flora for Colorado (Ackerfield et al., 2015) to provide an elevation range and habitat description for each species. We modified the altitudinal rank system from Gottfried et al. (2012) (***Supplemental Table 3.1***) to accommodate the available information for species present in the Colorado flora, and assigned ranks 1 – 6 for each species based on both elevation range and habitat description (***Supplemental Table 3.2***). Species with a strictly nival distribution center were assigned to rank level 1, and lower elevation species undifferentiated in distribution from montane to treeline were assigned a rank level 6 (***Supplemental Table 3.1***; Gottfried et al., 2012). A weighted average for all species in each quadrat was then calculated, using assigned ranks, to generate the thermic vegetation indicator *S* using the formula:

$$S = (\Sigma \text{rank}(\text{species}_i) \times \text{cover}(\text{species}_i)) / \Sigma \text{cover}(\text{species}_i)$$

Differences in the thermic vegetation indicator, *S*, between 2008 and all subsequent survey years were used to quantify conversions in the plant community, and termed the thermophilization indicator, *D*, defined by the formula ($D = S_{\text{year } j} - S_{2008}$). Positive differences indicate increased cover (or immigration) of thermic species with a higher altitudinal rank, or the decline or loss of cryophilic species with a lower rank (Gottfried et al., 2012). Negative differences would indicate the reciprocal: increased cover or colonization of cryophilic species with a lower altitudinal rank or the decline or loss of thermic species with a higher rank.

### *3.2.3 Environmental variables –*

To characterize inter-annual climate variation, we used publicly available data from daily observations at a measurement station at the north edge of the Rocky Mountain Biological Laboratory (RMBL), approximately 8-10 km from the summits and 600 m lower in elevation at 2900 m (barr, 2018). We used *i)* total annual snowfall (snow total), *ii)* the date the ground was completely snow free (hereafter termed snowmelt date), and *iii)* monthly average maximum and minimum air temperature measurements for all months each year (2000 – 2018) and just for winter months November through April (1975 – 2018) as measures of inter-annual variability. Summit weather stations and soil temperature loggers in the 3 x 3m plots showed long data gaps due to battery failure, lightning damage and frost heaving, and were not used in this analysis.

### *3.2.4 Data analyses –*

To understand the variability and trend of ambient climatic conditions during a longer-term period while vegetation was establishing, we ran simple linear regressions of maximum and minimum winter temperature, snow total, and snowmelt date against year from 1975 – 2018 (a ~40 year record). To determine whether vegetation cover and richness changed during the survey period, and, whether that change varied by summit or aspect, we used a linear mixed model to predict community-wide vegetation cover with the main effects of year, summit and aspect with the random effect of quadrat nested within plot.

To assess whether change in cover or richness were driven by climate variability, we first ran a correlation analysis to determine which climate variables were correlated (***Supplemental Table 3.3***). To evaluate which climate variables best predicted cover and richness, we compared several models with cover and richness predicted by each individual climate variable and multiplicative models including paired uncorrelated (correlation threshold ≤0.3) climate variables and two-way interactions of: snow total, snowmelt, growing season- (May through August) and winter- (November through April) minimum and maximum temperature using Akaike's Information Criterion (AIC) with the *stats* package in R. To further assess model fit, we calculated Akaike weights (*MuMin* package in R) and $\Delta$ AIC for each model formulation.

To assess changes in community composition we used Nonmetric Multi-dimensional Scaling (NMDS) ordination to visually compare community composition among summits using the metaMDS function within the *vegan* package in R. Relative cover was first calculated by dividing each species cover value by total quadrat cover. For this community dataset, we chose Sorensen (Bray-Curtis) distance, a proportional city-block distance measure capable of handling datasets with multiple zero values (McCune and Grace 2002). Statistical analyses of community

composition predicted by summit, aspect and year were performed in R using a Permutational Multivariate Analysis of Variance (PerManova) with the *adonis* function. Both the ordination and the PerManova are non-parametric and suited to community data, which is often non-normal and contains many zero values (Peterson and McCune 2001, McCune and Grace 2002). PerManova allows partitioning of variance of the distance matrix while preserving the distribution-free qualities of non-parametric tests. The test statistic is calculated directly from the distance matrix, and p-values are obtained using random permutations of the data (Anderson, 2001).

To further evaluate composition changes, and assess whether lifeforms changed over time, we ran a linear mixed model predicting community wide cover by the fixed effects year, lifeform and year*lifeform with a random effect of quadrat nested within plot. We also assessed individual models of richness by time for each summit. To understand whether the proportion of cryophilic species in plots changed over time, or whether thermophilization had occurred, we ran a linear mixed model predicting *S*, the thermic indicator, by year, summit and aspect with a random effect of plot. As a final measure of compositional change amongst individual species, we also analyzed models of individual species with time for species present in all years and present in at least 20 quadrats with a random effect of aspect. Linear mixed models were built using the *lme4* package and all graphics were developed in R (Bates et al., 2015, R Core Team 2016). Significance levels were estimated using Wald $\chi^2$ tests (*car::Anova* in R).

## 3.3 Results

### *3.3.1 Inter-annual variability and trends in climate –*

According to the weather station at RMBL in the Ruby mountains of Colorado, maximum and minimum winter temperatures have increased during a 43-year period between 1975 and 2018 ($r^2 = 0.07$, *slope* = 0.12, *p(t)* = $4.21 \times 10^{-6}$ and $r^2 = 0.04$, *slop*e = 0.08, *p(t)* = 0.0006 respectively, **Figure 3.1c & d**). In addition, snowmelt date decreased weakly ($r^2 = 0.08$, *slope* = –0.3, *p(t)* = 0.06) but total snow accumulation did not change significantly during the same period (**Figure 3.1a & b**).

### *3.3.2 Trends in vegetation cover and richness –*

Vegetation cover declined over the decade of sampling, while richness increased, and both differed summits and aspects (**Table 3.1**, **Figure 3.2**). Ruby and Treasury high had the highest cover while Treasury high had the greatest richness (**Figure 3.2**), and Treasury high had the greatest richness increase over time ($\chi^2$=24.96, $p$ = 0.000001).

Climate variability explained community-wide vegetation cover and richness trends. The AIC model comparisons showed maximum winter temperature was the most predictive variable (**Table 3.2**) for community level vegetation cover and significantly correlated with an overall decline in cover over the time period (**Table 3.3**). The combination of winter maximum and the interaction of winter maximum and minimum temperatures best predicted richness (**Table 3.3**). Winter maximum temperature correlated with an increase in richness.

### *3.3.3 Community changes and organization –*

Community composition did not change over time ($F$ = 1.5, $df$ = 1, $P(f)$ = 0.1), but was organized by summit ($F$ = 31.3, $df$ = 3, $P(f)$ = 0.001) and aspect ($F$ = 14.7, $df$ = 3, $P(f)$ = 0.001; **Figure 3.3**).

Within this alpine vegetation community, lifeform classification predicted vegetation cover, but the interaction of year with lifeform did not (**Table 3.4).** Most lifeforms followed the community wide pattern and decreased in cover over time. Forbs were the most dominant lifeform.

The thermic vegetation indicator, *S,* did not vary over time, but did vary by summit ($\chi^2$ = 14.2, $df$ = 3, $p$ = 0.003) and weakly by aspect (($\chi^2$ = 6.8, $df$ = 3, $p$ = 0.08). Thus, the mean thermophilization indicator, D, exhibited a non-significant negative trend, indicating a shift towards lower thermic indicator values between resurvey years and the baseline year of 2008 (**Figure 3.5**).

We recorded 89 species across the four summits. Twenty-seven of these species were present in all years and in at least 20 quadrats providing sufficient data to perform individual mixed models; of these, three significantly declined in cover over time: one biennial forb, *Androsace septentrionalis* (weakly significant: $\chi^2$ = 3.63, $df$ = 1, $p$ = 0.06), and two grasses *Festuca brachyphylla* ($\chi^2$ = 9.42, $df$ = 1, $p$ = 0.002), and *Trisetum spicatum* ($\chi^2$ = 4.20, $df$ = 1, $p$ = 0.04).

**Table 3.1** Linear mixed effects model parameter estimates for main effects and all two-way interactions for community wide cover and species richness predicted by year, summit and aspect. Wald $\chi^2$ tests and P-values, $P(\chi^2)$, were calculated for fixed effects and the random effect included quad nested within plot. Probabilities <0.05 are given in bold type.

| | *Cover* | | | | | *Richness* | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Coef | SE | $\chi^2$ | df | $P(\chi^2)$ | Coef | SE | $\chi^2$ | df | $P(\chi^2)$ |
| Intercept | 3.12 | 1.58 | | | | -0.13 | 1.37 | | | |
| Year | -0.12 | 0.13 | 9.59 | 1 | **0.002** | 0.06 | 0.07 | 48.64 | 1 | **3.07e-12** |
| Summit | | | 12.05 | 3 | **0.01** | | | 91.68 | 3 | **< 2.2e-16** |
| RUB | 0.52 | 1.51 | | | | 2.61 | 1.47 | | | |
| TRH | 0.57 | 1.36 | | | | 6.79 | 1.46 | | | |
| TRL | -0.90 | 1.69 | | | | -0.11 | 1.46 | | | |
| Aspect | | | 12.91 | 3 | **0.005** | | | 20.24 | 3 | **0.0002** |
| N | -1.47 | 1.15 | | | | 3.97 | 1.46 | | | |
| S | -0.08 | 1.27 | | | | -0.67 | 1.47 | | | |
| W | 1.11 | 1.11 | | | | 2.90 | 1.46 | | | |
| Summit x Year | | | 0.04 | 3 | 1.00 | | | 22.59 | 3 | **4.91e-05** |
| RUB x Year | 0.01 | 0.12 | | | | 0.10 | 0.07 | | | |
| TRH x Year | 0.02 | 0.11 | | | | 0.29 | 0.07 | | | |
| TRL x Year | 0.02 | 0.14 | | | | -0.004 | 0.07 | | | |
| Aspect x Year | | | 1.77 | 3 | 0.62 | | | 1.62 | 3 | 0.66 |
| N x Year | 0.07 | 0.09 | | | | -0.02 | 0.07 | | | |
| S x Year | -0.01 | 0.10 | | | | 0.03 | 0.07 | | | |
| W x Year | -0.03 | 0.09 | | | | 0.07 | 0.07 | | | |

**Table 3.2** Results of linear mixed effects model comparisons predicting community-level vegetation cover and richness by different measures of inter-annual climate variability and all two-way interactions as main effects. Wald $\chi^2$ tests and P-values, $P(\chi^2)$, were calculated for effects of: snow total (*snow*), snowmelt (*melt*), minimum and maximum growing season (*gMin*, *gMax*) and winter (*wMin*, *wMax*) temperatures. All models included a random effect of quad nested within plot. AIC are Akaike Information Criterion values, $w_i$ are Akaike weights, which indicate the probability of each model being the best fit relative to others presented.

| *Cover* | | | | | *Richness* | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Model | AIC | Δ AIC | k | $w_i$ | Model | AIC | Δ AIC | k | $w_i$ |
| wMax | 13548.40 | 0 | 2 | 0.71 | wMax + wMin + wMax*wMin | 1664.17 | 0 | 4 | 0.94 |
| gMax + wMax + gMax*wMax | 13550.57 | 2.17 | 4 | 0.24 | gMax + wMax + gMax*wMax | 1669.64 | 5.473 | 4 | 0.06 |
| wMax + wMin + wMax*wMin | 13553.85 | 5.45 | 4 | 0.05 | wMax | 1682.46 | 18.297 | 2 | <0.001 |
| wMin | 13559.33 | 10.93 | 2 | 0.003 | gMin | 1690.73 | 26.561 | 2 | <0.001 |
| gMin | 13559.43 | 11.03 | 2 | 0.003 | gMax | 1705.12 | 40.951 | 2 | <0.001 |
| gMax | 13561.60 | 13.20 | 2 | <0.001 | wMin | 1706.55 | 42.386 | 2 | <0.001 |
| melt | 13564.04 | 15.64 | 2 | <0.001 | Snow + wMin + Snow*wMin | 1707.86 | 43.697 | 4 | <0.001 |
| gMax + wMin + gMax*wMin | 13564.73 | 16.33 | 4 | <0.001 | gMax + wMin + gMax*wMin | 1711.81 | 47.649 | 4 | <0.001 |
| snow | 13568.45 | 20.05 | 2 | <0.001 | melt | 1712.75 | 48.582 | 2 | <0.001 |
| melt + wMin + Snow*wMin | 13574.47 | 26.07 | 4 | <0.001 | snow | 1718.31 | 54.149 | 2 | <0.001 |
| Snow + wMin + Snow*wMin | 13579.68 | 31.28 | 4 | <0.001 | Snow + gMin + Snow*gMin | 1719.06 | 54.895 | 4 | <0.001 |
| Snow + gMin + Snow*gMin | 13582.55 | 34.15 | 4 | <0.001 | melt + wMin + Snow*wMin | 1723.67 | 59.504 | 4 | <0.001 |

**Table 3.3** Linear mixed effects model parameter estimates for main effects of community wide *i*) cover predicted by winter maximum temperature and *ii*) richness predicted by winter max and minimum temperature with a random effect of quad nested within plot. Wald $\chi^2$ tests and P-values, $P(\chi^2)$ are shown; probabilities <0.05 are given in bold type.

| *Cover* | Coef | SE | X^2 | df | *P(X^2)* |
|---|---|---|---|---|---|
| Intercept | 2.45 | 0.24 | | | |
| Winter Max Temp | -0.20 | 0.05 | 15.49 | 1 | **0.00008** |
| *Richness* | | | | | |
| Intercept | -6.98 | 2.36 | | | |
| Winter Max Temp | 5.06 | 0.89 | 29.18 | 1 | **6.61e-08** |
| Winter Min Temp | -1.24 | 0.23 | 0.69 | 1 | 0.40 |
| wMinTemp x wMaxTemp | 0.49 | 0.09 | 29.20 | 1 | **6.519e-08** |

**Table 3.4** Linear mixed effects model parameter estimates for main effects of community wide cover predicted by year, lifeform and the interaction of lifeform and year, with a random effect of quad nested within plot. Wald $\chi^2$ tests and P-values, $P(\chi^2)$ are shown; probabilities <0.05 are given in bold type.

| | Coef | SE | X^2 | df | *P(X^2)* |
|---|---|---|---|---|---|
| Intercept | 2.82 | 0.45 | | | |
| Year | -0.09 | 0.03 | 8.79 | 1 | **0.003** |
| Lifeform | | | 504.78 | 5 | **< 2e-16** |
| cushion | -1.82 | 1.19 | | | |
| graminoid | -0.15 | 0.76 | | | |
| moss | 4.82 | 1.45 | | | |
| shrub | 6.44 | 1.56 | | | |
| succulent | -2.19 | 2.04 | | | |
| Lifeform x Year | | | 1.07 | 5 | 0.96 |
| cushion x year | 0.07 | 0.10 | | | |
| graminoid x year | 0.01 | 0.06 | | | |
| moss x year | -0.009 | 0.123 | | | |
| shrub x year | 0.07 | 0.13 | | | |
| succulent x year | 0.11 | 0.18 | | | |

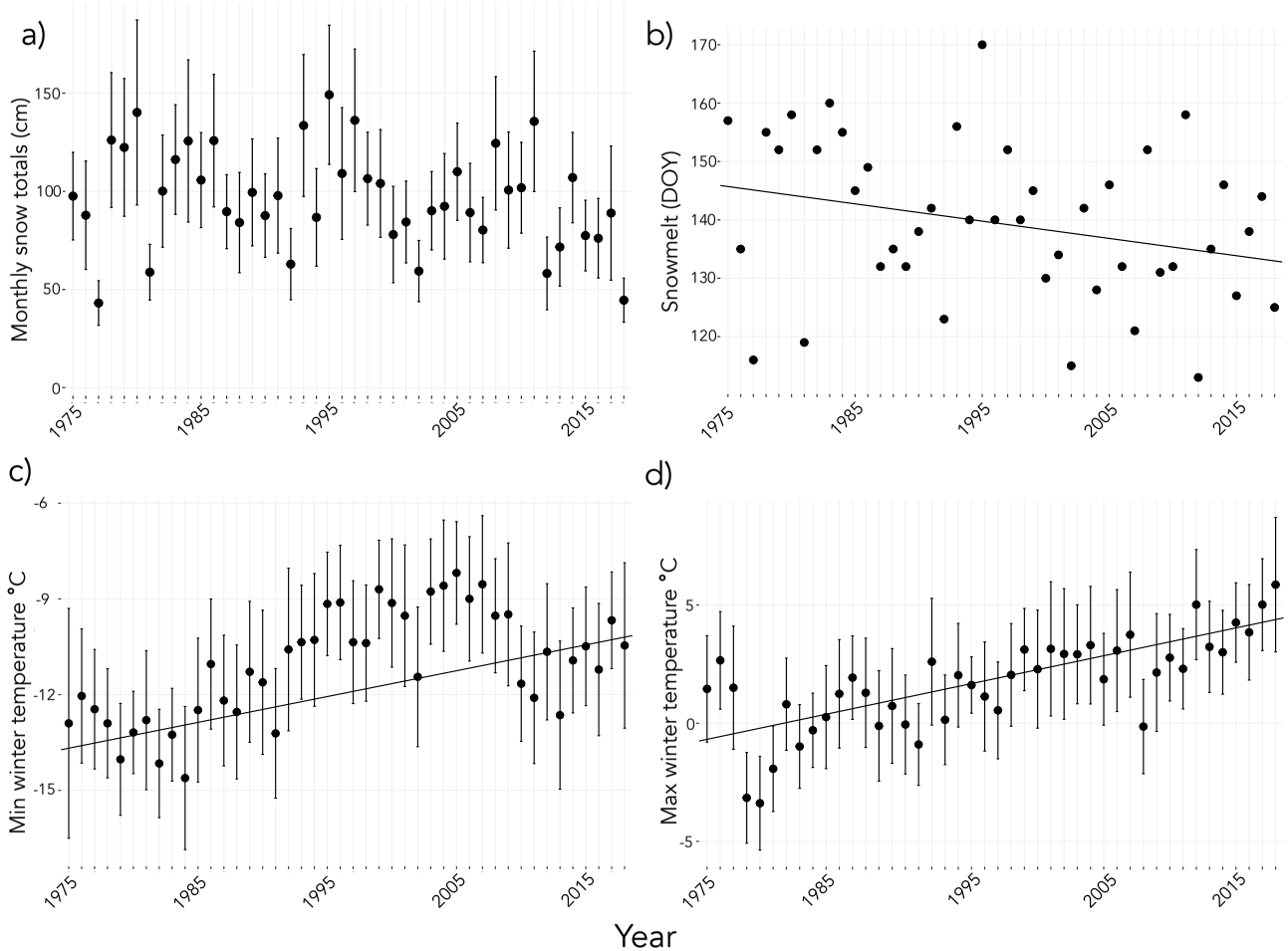


**Figure. 3.1** Interannual variability and trends in climate variables from 1975 to 2018 at a weather station at the Rocky Mountain Biological Laboratory (RMBL) for *a)* monthly snow totals *b)* snowmelt (day of year), *c)* minimum- and *d)* maximum- winter temperature (November – April).

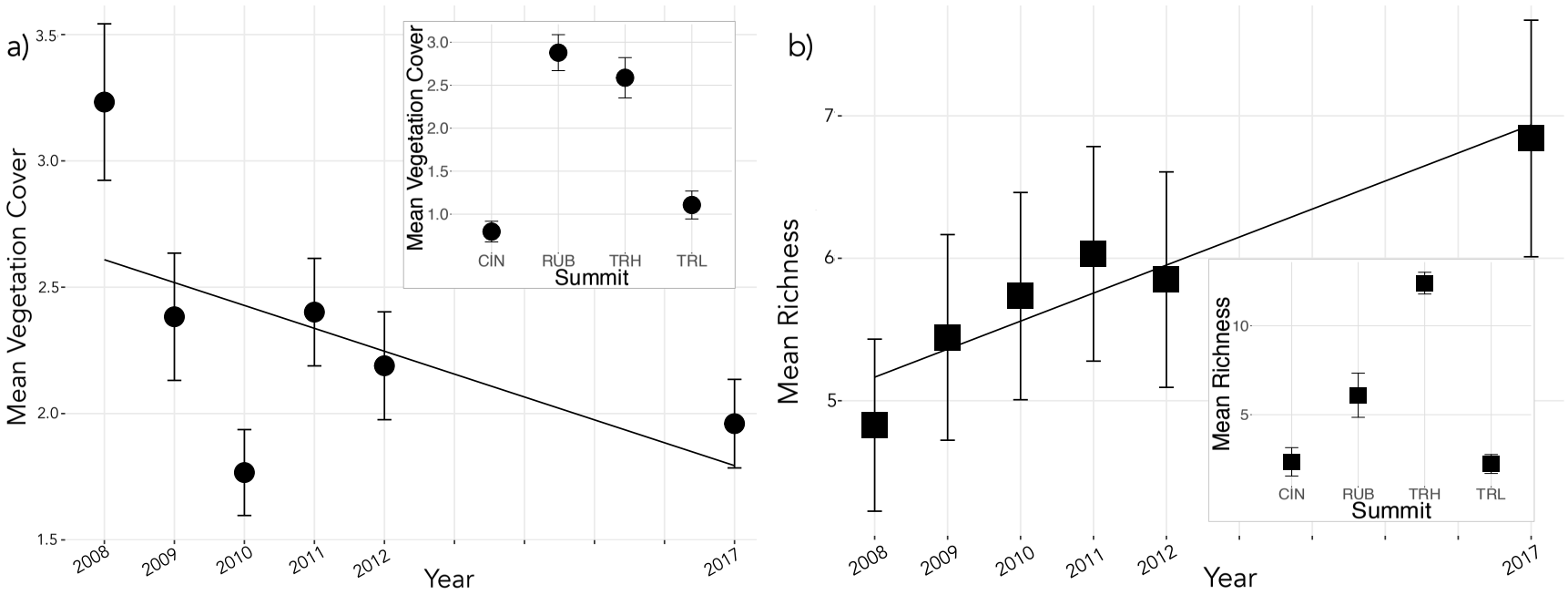


**Figure 3.2** Alpine community level vegetation *a)* percent cover and *b)* richness over the decade of survey. Insets depict average summit differences in richness and cover over the decade of sampling respectively.

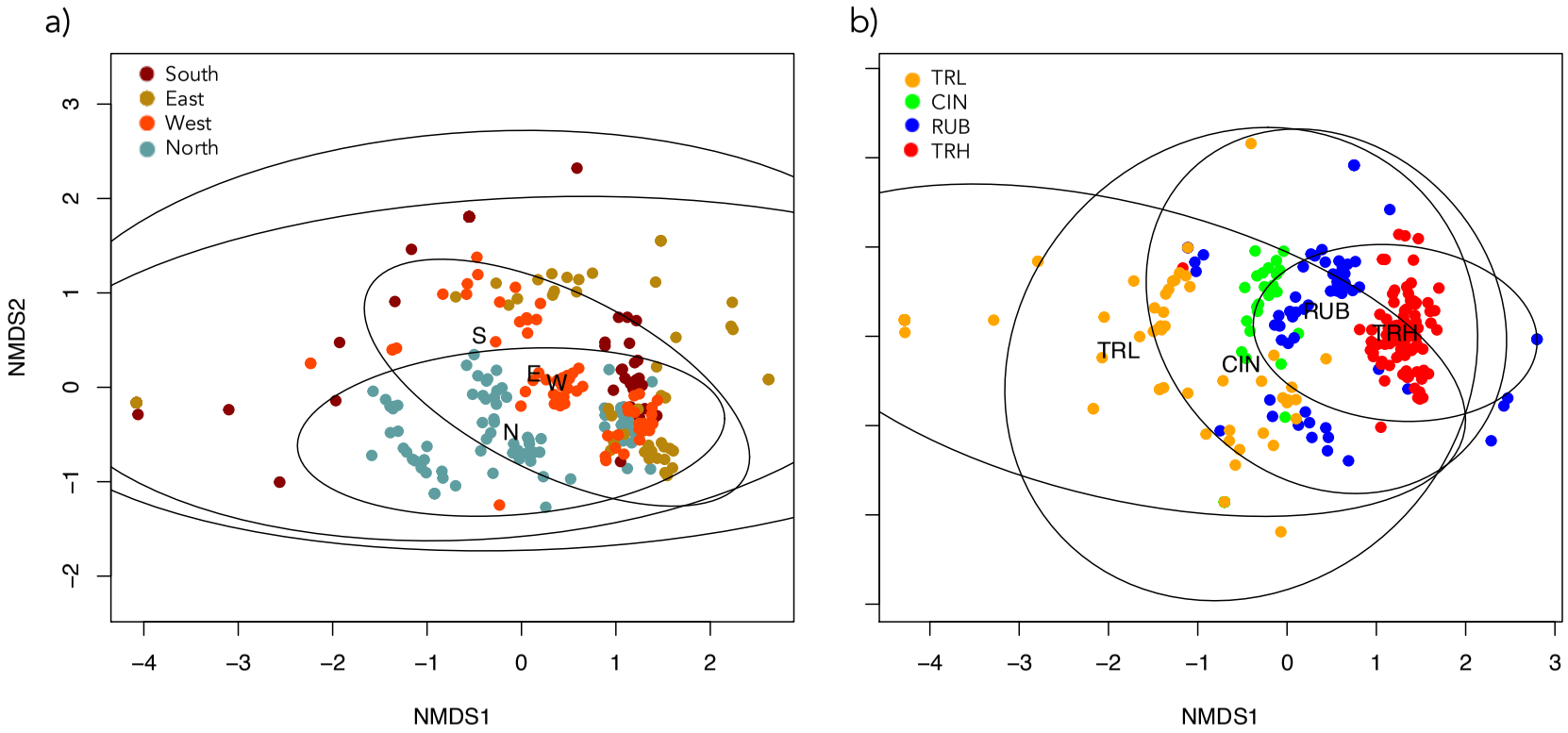


**Figure 3.3** In this NMDS ordination, each point represents a quadrat, and ellipses represent the variability of quadrats within a summit. Summits and aspects with similar community composition are represented as points that are in close proximity, while points that are farther apart represent communities that are less similar. This alpine plant community is organized by summit and aspect primarily ($P = 0.0001$, for each organizing factor).

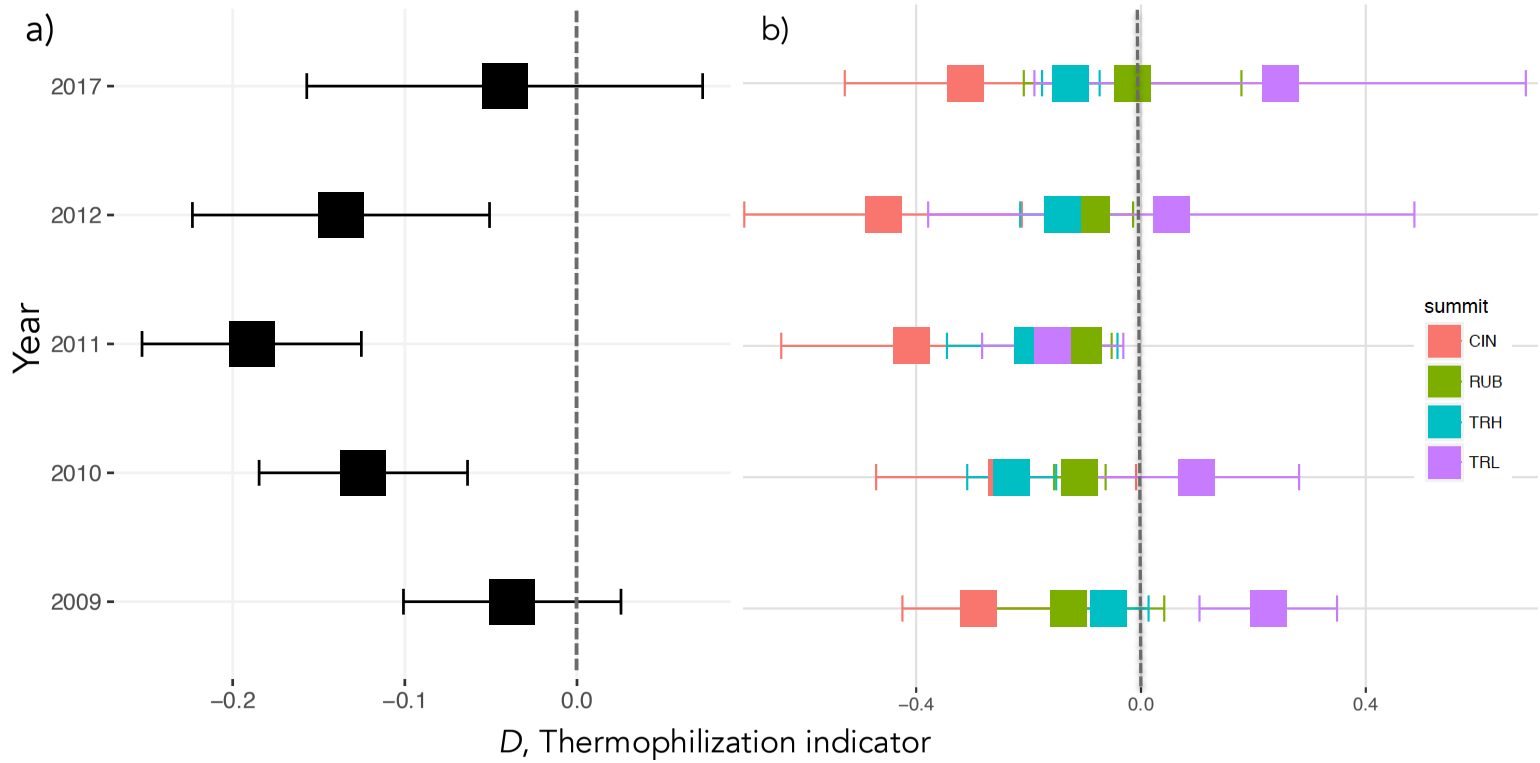


**Figure 3.4** Thermophilization indicator, *D*, or difference in the thermic index, *S*, *a)* across all summits by year and *b)* by summit over the time period of the survey.

## 3.4 Discussion

### *3.4.1 Vegetation patterns with climate and over time –*

Over the course of the decade of observations, community wide vegetation cover decreased while species richness increased, and maximum winter temperatures increased. Observed losses in plant cover could be a product of higher total snow accumulation in the baseline year, 2008 (**Figure 3.1**), causing higher cover in the baseline year, however since higher cover best correlated with cooler maximum winter temperatures, this alternate hypothesis is unlikely. Using a large number of digital herbarium records (2,468) for angiosperm taxa throughout North America, mean maximum temperature was the best predictor of phenology, out of 25 climate parameters assessed (Park and Mazer, 2018). Another GLORIA site in the Alps on Mt Schrankogel also documented a community level decrease in cover and increased richness (Lemprecht et al., 2018) in keeping with our findings here for the Ruby Mts. Further, resurveys of historical plots on 26 summits in the Alps and Australia in 1992 found an increase in richness (Grabher et al., 1994), and several other GLORIA studies have also found a trend of increased species richness, though not always site-wide increases. Studies have found richness increases only on the lowest summit (Michelsen et al., 2011), differences amongst regions (Pauli et al., 2012), or at the upper elevation edge (Pauli et al., 2007) suggesting expansion at the leading edge for alpine pioneers. At our site, an increase in species richness could be a product of improved sampling efforts from greater knowledge of the community over time, or considered with lower it cover could suggest colonization events occurring and thus more, smaller (and younger) individuals comprising cover estimates.

### *3.4.2 Thermophilization not in the direction expected –*

The thermophilization analysis provides a few clues to the drivers of species shifts. Instead of a positive thermophilization indicator, as would be expected if lower-elevation species were colonizing (or increasing cover, Gottfried et al., 2012) we found consistently negative differences (*D*) between the baseline and subsequent sampling years at three of the four summits. Despite a lack of "thermophilization" our results could nonetheless be a product of climate change. Cinnamon mountain (CIN) had a particularly negative thermophilization index, but with scree slopes on all sides it could be gaining cryophilic plants, simply adding plants where none existed before, or existing cryophilic plants may be increasing cover (**Figure 3.4b**). Cryophilic species colonizing higher, colder slopes thus may still be reflective of higher elevation locations becoming more suitable for plant life in a warming climate (Pauli et al., 2007). Further, it is likely that more than one process is occurring. On the lowest elevation summit, Treasury low (TRL), thermophilization may be occurring demonstrated by a positive thermophilization indicator and an increase of warmer ranked species (or cover, **Figure 3.4b**). Such conversion was also found at the lowest, least rugged summit at a GLORIA target region in the Alps (Lemprecht et al., 2018), and is consistent with an expansion of species ranges upslope (Pauli et al., 2012), and also consistent with dispersal limitations at the leading edge of species ranges (Alexander et al., 2017).

### *3.4.3 Aspect as an organizing factor –*

I show that the composition of the alpine plant communities on four summits at our site in the Ruby Range of Colorado is organized by summit and aspect (**Figure 3.3**). Mountain aspect was

correlated with temperature sums for 123 summits in 32 regions in the GLORIA network across Europe (Winkler et al., 2016*a*), with higher temperature sums in east and south facing aspects. Further, species colonization in temperate GLORIA regions was positively related to temperature with greater colonization on east and south aspects. At our site in CO, some aspects were entirely missing plants, primarily due to loose, rocky outcroppings with poor or no organic soil formation. Further, we found higher cover on west aspects instead of east and south. Many factors, including solar input, predominant wind direction, substrate, biotic associations and microsite conditions (Sherrer and Korner, 2011) will determine the final product of community assembly. With increasing global temperatures it is possible on alpine summits with predominantly facilitative species interactions, the more thermally exposed aspects will be the first to experience enhanced thermal stress gradient, which may shift species interactions from predominantly facilitative to competitive as cold temperature limitations are relieved (Callaway et al. 2002; Winkler et al., 2016*a*).

### *3.4.4 Slow to change or persistence –*

During the decade of record, this alpine plant community experienced relatively little change. We did not find changes in community composition or in particular lifeforms over time. Long-lived perennial species, some of which have a lifespan of 50-300 years (Morris and Doak, 1998) may not respond in the short term (i.e. 10-year timeframe). This could be a product of disequilibrium dynamics (Svenning and Sandel, 2013), remnant populations (Erikkson 2000) persisting in the midst of a changing climate, or that the pace of climate change is actually slow. Even though steep climatic gradients exist within small spatial scales in the alpine (Loarie et al., 2009), range filling following the last glacial period is not complete (Dullinger et al., 2012*b*). A resistant response in longer lived species is consistent with findings at an actively warmed study in the alpine tundra that found little change in flowering phenology for cushion and succulent species as compared with more responsive forbs and graminoids (Jabis et al., 2018 *in review*), and is also consistent with the un-watered response of biomass in the same experiment (Winkler et al., 2016*b*). The decline in cover in the present study was driven by the most dominant group, forbs, also consistent with a decline in cover for heated but not watered plots in the alpine on Niwot ridge, CO (Winkler et al., 2016*b*) suggesting a potential interactive water limitation.

We did find three individual species lowered cover over time; two perennial grasses and one annual to short lived perennial, *Androsace septentrionalis*. Reduced cover in this relatively short-lived montane species is consistent with findings in a warming meadow in the subalpine (Panetta et al., 2018) which demonstrated climate change reduced population size and purged seed banks. It is also consistent with species with shorter lifespans responding more strongly to climate (Moritz et al., 2008).

### *3.4.5 Conclusions –*

Climate change appears to be occurring, evidenced by increasing winter temperatures and earlier snowmelt date during the last 40 + years in the Ruby mountains of CO. Rising temperature (**Table 3.1c & d**) and decreased snow duration (**Table 3.1b**) will likely have an impact on future composition, performance and persistence of plant species in alpine and nival communities. Consistent with the largely perennial composition of this alpine community, however, we found moderate change over time with simultaneous variation in inter–annual climatic conditions. The relatively limited changes that did occur suggest slow trailing edge dynamics since long–lived

species changed very little; while increased richness suggests potentially faster transformation on the leading edge, at the highest elevation site. That plant communities are organized by aspect is not novel, however consistency with other alpine sites in Europe suggests future work, with more time points, should assess whether thermophilization is more likely to occur on warmer southern and eastern aspects and if northern and western aspects are refugia for cryophilic species. This study has achieved a preliminary assessment of a single GLORIA site, however moving forward, it has also demonstrated an approach that can be used to analyze a larger set of exiting GLORIA sites across the western US, which is in keeping with the original and stated GLORIA network goals.

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# CONCLUSION

The aim of this dissertation was to understand how climate change might alter assembly of plant communities in the alpine environment with implications for local extinction and ecosystem processes. I examined three main topics: flowering phenology, species interactions, and range shifts using both an actively warmed experiment and long-term observations.

In the first chapter, I examined alpine plant flowering response to an actively heated environment over a four-year period. Consistent with organization of communities on a snowmelt and depth gradient, flowering phenology advanced concurrent with advance in snowmelt rather than in response to warmer temperatures. Due to very tight coupling of alpine species to a short growing season, constrained on either end by growth limiting cold events (killing frosts), community wide flowering duration was conserved. Early season species responded most strongly to snowmelt and also capitalized on warmer temperatures to extend senescence. Forbs and graminoids capitalized on a longer season by expanding duration while cushion plants and succulent flowering duration was unchanged. Shifts in plant flowering phenology are important because of the importance of synchrony in the plant-pollinator mutualism, the role of flowering in plant reproduction and persistence, and potential links between flowering and growth phenology on ecosystem processes such as carbon cycling, which will feedback into the atmosphere.

In the second chapter I examined the role of alpine neighbors in recruitment of treeline conifers into the alpine ecosystem. I found that seedlings of a shade and moisture tolerant conifer, *Picea engelmanii*, appear to require the facilitation of neighbors in short term (3-week) survival while soil moisture is limiting in the longer term. Further, higher instantaneous water use efficiency than would be expected in *Picea engelmanii* suggests stomatal closure and high relative water stress as compared with seedlings of *Pinus flexilis* and a native alpine herb *Chionophylla jamesii*. For seedlings of a sun loving and drought tolerant conifer, *P. flexilis*, neighbors were unimportant to survival but did enhance photosynthetic efficiency. Contrary to the stress gradient hypothesis, at the low elevation edge of a stress gradient for an obligate alpine herb, *C. jamesii*, neighbors facilitated survival to one year following removals.

The objective of the final chapter was to record shifts in vegetation cover, richness, colonization or disappearance of species on four mountain summits occurring along an elevation gradient, and to decipher the role of inter-annual variability and climate trends in any conversion. Over the course of one decade, community wide vegetation cover declined while richness increased across all summits. During a 40 year period while vegetation was establishing, at a local weather station (approximately 8 km away and 600 m lower in elevation), snowmelt occurred earlier while winter minimum and maximum temperatures increased. Community-level vegetation cover varied by aspect and summit with western aspects and the highest summit exhibiting greatest cover. Similarly, the greatest richness was found on the two tallest summits and western aspects. Community level composition did not change but also varied by aspect and summit. A non-significant thermophilization effect (or an increase in warm-adapted species cover or richness) occurred on the lowest summit while colonization (or increased cover) of cryophilic species may

be occurring on other summits. Changes in particular lifeforms were consistent with the overall community level pattern, while one short-lived herb and two grasses declined over time. Overall this study showed slow change in plant community patterns with concurrent slow change in climatic conditions, which does not provide evidence for disequilibrium dynamics but also does not refute them.

This dissertation contributed to a broader understanding of three processes, phenology, species interactions, and range dynamics, all occurring within alpine plant communities in the context of climate change. While the overall response of alpine tundra communities, comprised of primarily long lived species, has been generally slow, certain life-forms appear to respond more readily: relatively shorter-lived graminoids and forbs, consistent with an expectation of disequilibrium dynamics and extinction lags in longer-lived species. While it is expected that global treeline will shift upward in elevation, for western US forests, this may depend on species interactions and trends in precipitation as well as temperature. Over time it is likely that continued changes in climate would produce new and potentially novel assemblages of species, particularly if new lifeforms including trees do colonize. We can certainly expect changes in dominance patterns and perhaps local extinctions, which could alter forage for alpine endemics like pika, may exhibit differences in albedo, and will likely provide alternate feedbacks to the climate system.

# A: Supplementary information for Chapter 1

**Supplemental Table 1.1** Mean and standard error of the date of *first* and *last* flower, and flowering *duration*.

| ***Treatment*** | ***First*** | ***+/- se*** | ***Last*** | ***+/- se*** | ***Duration*** | ***+/- se*** |
|---|---|---|---|---|---|---|
| Control | 196.75 | 0.68 | 216.67 | 0.79 | 20.17 | 0.50 |
| Heat | 188.99 | 0.64 | 210.04 | 0.72 | 21.12 | 0.34 |
| H + W | 190.78 | 0.67 | 211.37 | 0.73 | 20.70 | 0.47 |
| Water | 196.43 | 0.70 | 216.07 | 0.72 | 19.98 | 0.45 |

**Supplemental Table 1.2** Linear mixed effects model parameter estimates for main effects and all two-way interactions for the *categorical* model (1). Wald $\chi^2$ tests and P-values, $P(\chi^2)$, were calculated for effects of treatment, year, lifeform and their interactions. For effects with only two levels, the coefficient for the level not shown is the same magnitude but opposite sign as the coefficient shown. Random effects included: plot, quad nested within plot, and species. Probabilities <0.05 are given in bold type.

| | *First flower* | | | | | *Last flower* | | | | | *Duration of flowering* | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Coef | SE | X^2 | df | *P(X^2)* | Coef | SE | X^2 | df | *P(X^2)* | Coef | SE | X^2 | df | *P(X^2)* |
| Intercept | 168.21 | 4.01 | | | | 178.11 | 7.79 | | | | 16.11 | 2.18 | | | |
| H | -7.67 | 1.22 | 48.23 | 1 | **3.79E-12** | -7.04 | 1.28 | 48.37 | 1 | **3.53E-12** | 0.66 | 1.07 | 0.00 | 1 | 0.98 |
| W | -1.77 | 1.22 | 0.02 | 1 | 0.90 | 0.17 | 1.30 | 0.18 | 1 | 0.67 | 1.39 | 1.10 | 0.45 | 1 | 0.50 |
| H x W | 1.44 | 1.55 | 0.86 | 1 | 0.35 | 1.87 | 1.57 | 1.40 | 1 | 0.24 | 0.37 | 1.06 | 0.12 | 1 | 0.73 |
| Pre-phenol | 0.12 | 0.02 | 56.07 | 1 | **6.99E-14** | 0.14 | 0.03 | 19.56 | 1 | **9.73E-06** | 0.11 | 0.02 | 28.72 | 1 | **8.35E-08** |
| Year | | | 13543.84 | 3 | **< 2.2e-16** | | | 6229.73 | 3 | **< 2.2e-16** | | | 175.39 | 3 | **< 2.2e-16** |
| 2011 | 19.88 | 0.66 | | | | 19.02 | 0.82 | | | | -1.32 | 0.97 | | | |
| 2012 | -21.86 | 0.65 | | | | -16.92 | 0.80 | | | | 4.51 | 0.95 | | | |
| 2013 | 4.12 | 0.67 | | | | 5.65 | 0.83 | | | | 1.18 | 0.98 | | | |
| Lifeform | | | 3.55 | 3 | 0.31 | | | 2.46 | 3 | 0.48 | | | 0.40 | 3 | 0.94 |
| cushions | 1.01 | 5.29 | | | | 3.70 | 7.27 | | | | 2.83 | 4.17 | | | |
| graminoids | 6.97 | 5.30 | | | | 9.48 | 7.28 | | | | 2.67 | 4.17 | | | |
| succulents | 6.82 | 5.33 | | | | 7.48 | 7.31 | | | | 0.30 | 4.24 | | | |
| Lifeform x H | | | 11.31 | 3 | **0.01** | | | 6.65 | 3 | 0.08 | | | 9.97 | 3 | **0.02** |
| cushions x H | 1.68 | 0.81 | | | | -1.76 | 0.99 | | | | -3.67 | 1.16 | | | |
| graminoids x H | 0.50 | 0.80 | | | | -0.09 | 0.98 | | | | -0.50 | 1.18 | | | |
| succulents x H | 2.47 | 0.82 | | | | 1.48 | 1.01 | | | | -0.75 | 1.19 | | | |
| Lifeform x W | | | 0.37 | 3 | 0.95 | | | 0.52 | 3 | 0.91 | | | 0.64 | 3 | 0.89 |
| cushions x W | 0.10 | 0.81 | | | | 0.42 | 0.99 | | | | 0.68 | 1.17 | | | |
| graminoids x W | 0.12 | 0.82 | | | | -0.01 | 1.01 | | | | -0.41 | 1.21 | | | |
| succulents x W | -0.42 | 0.82 | | | | -0.49 | 1.01 | | | | -0.26 | 1.19 | | | |
| Year x Heat | | | 68.64 | 3 | **8.36E-15** | | | 13.31 | 3 | **4.02E-03** | | | 8.29 | 3 | **0.040** |
| 2011 x H | 4.71 | 0.77 | | | | 2.91 | 0.95 | | | | -1.65 | 1.13 | | | |
| 2012 x H | -1.35 | 0.76 | | | | 0.08 | 0.93 | | | | 1.56 | 1.11 | | | |
| 2013 x H | 0.33 | 0.78 | | | | 0.06 | 0.96 | | | | -0.28 | 1.14 | | | |
| Year x Water | | | 5.63 | 3 | 1.31E-01 | | | 2.33 | 3 | 0.506648 | | | 3.37 | 3 | 0.33842 |
| 2011 x W | 1.09 | 0.77 | | | | -1.21 | 0.95 | | | | -1.62 | 1.13 | | | |
| 2012 x W | 1.79 | 0.76 | | | | -0.61 | 0.93 | | | | -1.85 | 1.11 | | | |
| 2013 x W | 1.04 | 0.78 | | | | -1.27 | 0.96 | | | | -1.46 | 1.14 | | | |

**Supplemental table 1.3** Linear mixed effects model parameter estimates for main effects and all two-way interactions for the *continuous* model (2). Wald $\chi^2$ tests and P-values, $P(\chi^2)$, were calculated for effects of lifeform, meltdate, mean soil temperature (*MeanTemp*), adequate soil moisture (*AdqMoist*), and their interactions. Random effects included: plot, quad nested within plot, and species. Probabilities <0.05 are given in bold type.

| | *First flower* | | | | | *Last flower* | | | | | *Duration of flowering* | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Coef | SE | X^2 | df | *P(X^2)* | Coef | SE | X^2 | df | *P(X^2)* | Coef | SE | X^2 | df | *P(X^2)* |
| Intercept | 187.77 | 1.93 | | | | 207.90 | 3.33 | | | | 20.44 | 1.99 | | | |
| Lifeform | | | 2.08 | 3 | 0.56 | | | 1.06 | 3 | 0.79 | | | 0.62 | 3 | 0.89 |
| cushions | 0.18 | 4.07 | | | | 1.47 | 7.11 | | | | 1.74 | 4.29 | | | |
| graminoids | 3.58 | 4.06 | | | | 5.66 | 7.11 | | | | 1.14 | 4.27 | | | |
| succulents | 5.48 | 4.07 | | | | 5.72 | 7.11 | | | | -2.15 | 4.28 | | | |
| Meltdate | 16.19 | 0.32 | 3104.83 | 1 | **< 2.2e-16** | 15.13 | 0.36 | 1987.32 | 1 | **< 2.2e-16** | -2.90 | 0.50 | 39.14 | 1 | **3.944E-10** |
| MeanTemp | 6.28 | 0.30 | 629.32 | 1 | **< 2.2e-16** | 3.98 | 0.36 | 99.49 | 1 | **< 2.2e-16** | 0.37 | 0.37 | 1.90 | 1 | 0.17 |
| AdqMoist | 3.30 | 0.21 | 589.62 | 1 | **< 2.2e-16** | 3.96 | 0.23 | 502.52 | 1 | **< 2.2e-16** | -0.14 | 0.33 | 0.04 | 1 | 0.83 |
| Lifeform x Meltdate | | | 29.69 | 3 | **1.60E-06** | | | 100.22 | 3 | **< 2.2e-16** | | | 30.67 | 3 | **9.98E-07** |
| cushions x Meltdate | -0.08 | 0.69 | | | | 1.52 | 0.70 | | | | 3.42 | 1.06 | | | |
| graminoids x Meltdate | -2.84 | 0.54 | | | | -5.44 | 0.64 | | | | -2.29 | 1.07 | | | |
| succulents x Meltdate | -1.41 | 0.57 | | | | 1.26 | 0.67 | | | | 3.75 | 1.07 | | | |
| Lifeform x MeanTemp | | | 4.87 | 3 | 0.18 | | | 27.60 | 3 | **4.41E-06** | | | 18.53 | 3 | **3.42E-04** |
| cushions x MeanTemp | 0.06 | 0.55 | | | | -1.16 | 0.68 | | | | -2.01 | 0.74 | | | |
| graminoids x MeanTemp | 1.31 | 0.60 | | | | 2.44 | 0.72 | | | | 1.10 | 0.81 | | | |
| succulents x MeanTemp | 0.29 | 0.59 | | | | -1.93 | 0.68 | | | | -2.25 | 0.78 | | | |
| Lifeform x AdqMoist | | | 45.42 | 3 | **7.53E-10** | | | 27.58 | 3 | **4.44E-06** | | | 2.53 | 3 | 0.47 |
| cushions x AdqMoist | 2.15 | 0.44 | | | | 1.39 | 0.42 | | | | -0.38 | 0.64 | | | |
| graminoids x AdqMoist | -0.97 | 0.36 | | | | -0.93 | 0.43 | | | | 0.82 | 0.68 | | | |
| succulents x AdqMoist | -0.89 | 0.38 | | | | -1.11 | 0.47 | | | | -0.32 | 0.67 | | | |
| Meltdate x AdqMoist | -3.05 | 0.12 | 668.61 | 1 | **< 2.2e-16** | -2.33 | 0.20 | 140.39 | 1 | **< 2.2e-16** | -0.33 | 0.25 | 1.72 | 1 | 0.19 |
| Meltdate x MeanTemp | 1.53 | 0.10 | 221.47 | 1 | **< 2.2e-16** | 2.15 | 0.11 | 416.67 | 1 | **< 2.2e-16** | -0.62 | 0.26 | 5.62 | 1 | **0.02** |
| AdqMoist x MeanTemp | 2.43 | 0.16 | 226.29 | 1 | **< 2.2e-16** | 2.09 | 0.22 | 88.63 | 1 | **< 2.2e-16** | -0.24 | 0.30 | 0.63 | 1 | 0.43 |

**Supplemental table 1.4** Marginal (fixed factors only) and conditional (all factors) $R^2$ values for the two models presented in Tables 3 & 4 computed using the method of Nakagawa and Schielzeth (2013).

| | *First* | | *Last* | | *Duration* | |
|---|---|---|---|---|---|---|
| Model | $R_M^2$ | $R_C^2$ | $R_M^2$ | $R_C^2$ | $R_M^2$ | $R_C^2$ |
| Categorical (Table 3) | 0.72 | 0.90 | 0.52 | 0.84 | 0.08 | 0.38 |
| Continuous (Table 4) | 0.81 | 0.93 | 0.53 | 0.88 | 0.07 | 0.41 |

**Supplemental table 1.5** Marginal (fixed factors only) and conditional (all factors) $R^2$ values for the two models presented in Tables 5 & 6 computed using the method of Nakagawa and Schielzeth (2013).

| | *First* | | *Last* | | *Duration* | |
|---|---|---|---|---|---|---|
| Model | $R_M^2$ | $R_C^2$ | $R_M^2$ | $R_C^2$ | $R_M^2$ | $R_C^2$ |
| Categorical (Table 5) | 0.84 | 0.89 | 0.66 | 0.83 | 0.08 | 0.36 |
| Continuous (Table 6) | 0.89 | 0.93 | 0.75 | 0.88 | 0.05 | 0.39 |

**Supplemental table 1.6** The 39 species recorded in plots at our site, the number of plots (of 20 possible) in which they were present, and their lifeform and phenological functional group (*PhenFG*). Species which do not have lifeform or phenological functional group listed were not included in the community-level analysis; species highlighted in bold were also included in Figure 1.

| **Code** | **Genus** | **Species** | **# Plots** | **Lifeform** | **PhenFG** |
|---|---|---|---|---|---|
| *ALGE* | *Allium* | *geyeri* | *2* | - | - |
| *ANSE* | *Androsace* | *septentrionalis* | *7* | forb | early |
| **ARFE** | ***Arenaria*** | ***fendleri*** | **20** | forb | middle |
| **ARSC** | ***Artemisia*** | ***scopulorum*** | **20** | forb | middle |
| **BIBI** | ***Bistorta*** | ***bistortoides*** | **20** | forb | middle |
| **CAMP** | ***Campanula*** | ***spp.*** | **12** | forb | late |
| **CAOC** | ***Castilleja*** | ***occidentalis*** | **16** | forb | middle |
| **CARU** | ***Carex*** | ***rupestris*** | **17** | graminoid | early |
| *CEBE* | *Cerastium* | *beeringianum* | *5* | - | - |
| **CHJA** | ***Chionophila*** | ***jamesii*** | **20** | succulent | middle |
| *ERAR* | *Eritrichium* | *aretioides* | *9* | forb | early |
| **ERSI** | ***Erigeron*** | ***simplex*** | **20** | forb | middle |
| **FEBR** | ***Festuca*** | ***brachyphylla*** | **17** | graminoid | late |
| **GERO** | ***Geum*** | ***rossii*** | **20** | forb | early |
| *HYAC* | *Hymenoxys* | *acaulis* | *2* | - | - |
| **HYGR** | ***Hymenoxys*** | ***grandiflora*** | **12** | forb | middle |
| **LEPY** | ***Lewisia*** | ***pygmaea*** | **20** | succulent | middle |
| **LLSE** | ***Lloydia*** | ***serotina*** | **16** | forb | early |

| | | | | | |
|---|---|---|---|---|---|
| **LUSP** | ***Luzula*** | ***spicata*** | **20** | graminoid | middle |
| *MELA* | *Mertensia* | *lanceolata* | *6* | - | - |
| **MIOB** | ***Minuartia*** | ***obtusiloba*** | **20** | cushion | middle |
| *MISP* | *Minuartia* | *spp.* | *15* | - | - |
| **ORAL** | ***Oreoxis*** | ***alpina*** | **8** | forb | early |
| *PESC* | *Pedicularis* | *scopulorum* | *2* | forb | late |
| **PHCO** | ***Phlox*** | ***condensata*** | **11** | forb | middle |
| *POAL* | *Poa* | *alpina* | *4* | graminoid | late |
| **POAR** | ***Poa*** | ***arctica*** | **10** | graminoid | middle |
| **PODI** | ***Potentilla*** | ***diversifolia*** | **17** | forb | middle |
| **PRAN** | ***Primula*** | ***angustifolia*** | **8** | forb | early |
| *RAAD* | *Ranunculus* | *adoneus* | *6* | forb | early |
| **SARH** | ***Saxifraga*** | ***rhomboidea*** | **16** | forb | middle |
| **SELA** | ***Sedum*** | ***lanceolatum*** | **16** | succulent | late |
| **SIAC** | ***Silene*** | ***acaulis*** | **14** | cushion | middle |
| **SIPR** | ***Sibbaldia*** | ***procumbens*** | **13** | cushion | early |
| **SOMU** | ***Solidago*** | ***multiradiata*** | **20** | forb | late |
| **THMO** | ***Thlaspi*** | ***montanum*** | **8** | forb | early |
| *TRDA* | *Trifolium* | *dasyphyllum* | *4* | - | - |
| **TRPA** | ***Trifolium*** | ***parryi*** | **19** | forb | middle |
| **TRSP** | ***Trisetum*** | ***spicatum*** | **20** | graminoid | late |

**Supplemental table 1.7** Linear mixed effects model parameter estimates for main effects and all two-way interactions for the *categorical* model (1). Wald $\chi^2$ tests and P-values, $P(\chi^2)$, were calculated for effects of treatment, year, phenological functional group and their interactions. For effects with only two levels, the coefficient for the level not shown is the same magnitude but opposite sign as the coefficient shown. Random effects included: plot, quad nested within plot, and species. Probabilities <0.05 are given in bold type.

| | *First flower* | | | | | *Last flower* | | | | | *Duration of flowering* | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Coef | SE | X^2 | df | *P(X^2)* | Coef | SE | X^2 | df | *P(X^2)* | Coef | SE | X^2 | df | *P(X^2)* |
| Intercept | 161.24 | 3.40 | | | | 171.53 | 7.55 | | | | 15.91 | 2.64 | | | |
| Heat | -6.86 | 1.22 | 51.24 | 1 | **8.17E-13** | -6.27 | 1.36 | 45.87 | 1 | **1.27E-11** | 0.65 | 1.15 | 0.00 | 1 | 0.97 |
| Water | -1.92 | 1.23 | 0.02 | 1 | 0.90 | 0.21 | 1.38 | 0.12 | 1 | 0.73 | 1.69 | 1.20 | 0.30 | 1 | 0.58 |
| Heat x Water | 1.45 | 1.50 | 0.93 | 1 | 0.34 | 1.81 | 1.62 | 1.26 | 1 | 0.26 | 0.27 | 1.09 | 0.06 | 1 | 0.80 |
| Pre-phenology | 0.12 | 0.02 | 62.30 | 1 | **2.96E-15** | 0.14 | 0.03 | 20.36 | 1 | **6.40E-06** | 0.11 | 0.02 | 30.19 | 1 | **3.92E-08** |
| Year | | | 13496.83 | 3 | **< 2.2e-16** | | | 6229.50 | 3 | **< 2.2e-16** | | | 175.75 | 3 | **< 2.2e-16** |
| 2011 | 19.88 | 0.66 | | | | 2.92 | 0.95 | | | | -1.36 | 0.97 | | | |
| 2012 | -21.84 | 0.65 | | | | 0.13 | 0.94 | | | | 4.42 | 0.95 | | | |
| 2013 | 4.08 | 0.67 | | | | 0.08 | 0.96 | | | | 1.16 | 0.98 | | | |
| PhenFG | | | 52.57 | 2 | **3.84E-12** | | | 20.12 | 2 | **4.29E-05** | | | 0.72 | 2 | 0.70 |
| middle | 10.15 | 2.13 | | | | 11.36 | 3.91 | | | | 1.12 | 3.09 | | | |
| late | 23.95 | 3.58 | | | | 28.55 | 6.44 | | | | 5.27 | 5.18 | | | |
| PhenFG x Heat | | | 0.31 | 2 | 0.85 | | | 3.18 | 2 | 0.20 | | | 1.79 | 2 | 0.41 |
| middle x h | -0.10 | 0.60 | | | | -1.24 | 0.74 | | | | -1.15 | 0.88 | | | |
| late x h | -0.74 | 1.32 | | | | -1.74 | 1.63 | | | | -1.17 | 1.93 | | | |
| PhenFG x Water | | | 0.75 | 2 | 0.69 | | | 0.15 | 2 | 0.93 | | | 1.10 | 2 | 0.58 |
| middle x w | 0.14 | 0.61 | | | | -0.16 | 0.75 | | | | -0.42 | 0.88 | | | |
| late x w | 1.21 | 1.40 | | | | 0.42 | 1.72 | | | | -2.14 | 2.07 | | | |
| Year x Heat | | | 67.80 | 3 | **1.26E-14** | | | 13.14 | 3 | **0.004** | | | 8.63 | 3 | **0.035** |
| 2011 x h | 4.68 | 0.78 | | | | 2.92 | 0.95 | | | | -1.61 | 1.13 | | | |
| 2012 x h | -1.40 | 0.76 | | | | 0.13 | 0.94 | | | | 1.66 | 1.11 | | | |
| 2013 x h | 0.40 | 0.78 | | | | 0.08 | 0.96 | | | | -0.32 | 1.14 | | | |
| Year x Water | | | 5.28 | 3 | 0.15 | | | 2.23 | 3 | 0.53 | | | 3.05 | 3 | 0.38 |
| 2011 x w | 1.10 | 0.78 | | | | -1.16 | 0.95 | | | | -1.58 | 1.13 | | | |
| 2012 x w | 1.73 | 0.76 | | | | -0.63 | 0.94 | | | | -1.76 | 1.11 | | | |
| 2013 x w | 0.99 | 0.78 | | | | -1.26 | 0.96 | | | | -1.35 | 1.14 | | | |

**Supplemental table 1.8** Linear mixed effects model parameter estimates for main effects and all two-way interactions for the *continuous* model (2). Wald $\chi^2$ tests and P-values, $P(\chi^2)$, were calculated for effects of phenological functional group, meltdate, mean soil temperature (*MeanTemp*), adequate soil moisture (*AdqMoist*), and their interactions. Random effects included: plot, quad nested within plot, and species. Probabilities <0.05 are given in bold type.

| | *First flower* | | | | | *Last flower* | | | | | *Duration of flowering* | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Coef | SE | X^2 | df | *P(X^2)* | Coef | SE | X^2 | df | *P(X^2)* | Coef | SE | X^2 | df | *P(X^2)* |
| Intercept | 183.64 | 1.28 | | | | 203.52 | 2.57 | | | | 20.35 | 2.66 | | | |
| PhenFG | | | 62.67 | 2 | **2.46E-14** | | | 29.26 | 2 | **4.43E-07** | | | 0.11 | 2 | 0.94 |
| middle | 5.55 | 1.48 | | | | 6.88 | 3.13 | | | | -0.08 | 3.30 | | | |
| late | 19.62 | 2.15 | | | | 25.77 | 4.38 | | | | 1.46 | 4.60 | | | |
| Meltdate | 16.66 | 0.48 | 2889.47 | 1 | **< 2.2e-16** | 12.84 | 0.51 | 2028.15 | 1 | **< 2.2e-16** | -2.43 | 0.76 | 39.16 | 1 | **3.91E-10** |
| MeanTemp | 6.24 | 0.37 | 754.04 | 1 | **< 2.2e-16** | 7.59 | 0.44 | 134.52 | 1 | **< 2.2e-16** | 0.53 | 0.56 | 1.51 | 1 | 0.22 |
| AdqMoist | 5.15 | 0.40 | 613.55 | 1 | **< 2.2e-16** | 6.66 | 0.37 | 568.41 | 1 | **< 2.2e-16** | 1.12 | 0.48 | 0.11 | 1 | 0.74 |
| PhenFG x Meltdate | | | 16.74 | 2 | **0.0002** | | | 60.45 | 2 | **7.49E-14** | | | 0.40 | 2 | 0.82 |
| middle x Meltdate | -1.87 | 0.54 | | | | 2.24 | 0.55 | | | | 0.35 | 0.88 | | | |
| late x Meltdate | -0.19 | 0.79 | | | | 6.38 | 0.82 | | | | -0.34 | 1.39 | | | |
| PhenFG x MeanTemp | | | 12.62 | 2 | **0.0018** | | | 134.84 | 2 | **< 2.2e-16** | | | 5.11 | 2 | 0.08 |
| middle x MeanTemp | 1.21 | 0.44 | | | | -4.41 | 0.51 | | | | -1.06 | 0.63 | | | |
| late x MeanTemp | -1.07 | 0.96 | | | | -10.49 | 1.01 | | | | 0.66 | 1.06 | | | |
| PhenFG x AdqMoist | | | 98.56 | 2 | **< 2.2e-16** | | | 112.87 | 2 | **< 2.2e-16** | | | 11.81 | 2 | **0.003** |
| middle x AdqMoist | -1.57 | 0.41 | | | | -2.67 | 0.40 | | | | -1.83 | 0.54 | | | |
| late x AdqMoist | -4.66 | 0.52 | | | | -5.50 | 0.52 | | | | -0.88 | 0.87 | | | |
| Meltdate x AdqMoist | -3.57 | 0.13 | 741.80 | 1 | **< 2.2e-16** | -3.74 | 0.20 | 340.65 | 1 | **< 2.2e-16** | -0.42 | 0.26 | 2.66 | 1 | 0.10 |
| Meltdate x MeanTemp | 1.41 | 0.11 | 151.05 | 1 | **< 2.2e-16** | 2.05 | 0.11 | 365.41 | 1 | **< 2.2e-16** | -0.53 | 0.26 | 4.00 | 1 | **0.05** |
| AdqMoist x MeanTemp | 3.19 | 0.18 | 310.99 | 1 | **< 2.2e-16** | 3.70 | 0.23 | 265.73 | 1 | **< 2.2e-16** | -0.18 | 0.31 | 0.36 | 1 | 0.55 |

**Supplemental table 1.9** Linear mixed effects model parameter estimates of main effects and all two-way interactions for the 15 species analyzed individually, using the categorical model. Wald $\chi^2$ tests and P-values, $P(\chi^2)$, were calculated for effects of treatment, year, lifeform and their interactions. For effects with only two levels, the coefficient for the level not shown is the same magnitude but opposite sign as the coefficient shown. A random effect of plot was included.

| | *First flower* | | | | | *Last flower* | | | | | *Duration of flowering* | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Coef | SE | X^2 | df | *P(X^2)* | Coef | SE | X^2 | df | *P(X^2)* | Coef | SE | X^2 | df | *P(X^2)* |
| GERO | | | | | | | | | | | | | | | |
| Intercept | 162.15 | 6.64 | | | | 141.36 | 18.65 | | | | 25.56 | 2.68 | | | |
| Heat | -5.68 | 1.45 | 34.26 | 1 | **4.83E-09** | -11.75 | 2.54 | 11.59 | 1 | **0.0007** | -6.43 | 2.34 | 0.01 | 1 | 0.93 |
| Water | 0.86 | 1.48 | 0.20 | 1 | 0.66 | -5.62 | 2.60 | 0.02 | 1 | 0.89 | -6.88 | 2.44 | 0.00 | 1 | 0.97 |
| Heat x Water | -0.79 | 2.08 | 0.14 | 1 | 0.71 | 11.56 | 3.68 | 9.86 | 1 | **0.002** | 13.22 | 3.42 | 14.89 | 1 | **0.0001** |
| Pre-phenology | 0.10 | 0.04 | 8.78 | 1 | **0.003** | 0.32 | 0.08 | 14.85 | 1 | **0.0001** | 0.16 | 0.06 | 8.22 | 1 | **0.004** |
| Year | | | 4149.22 | 3 | **< 2.2e-16** | | | 1220.95 | 3 | **< 2.2e-16** | | | 18.88 | 3 | **0.0003** |
| 2011 | 25.44 | 0.70 | | | | 26.09 | 1.25 | | | | 1.07 | 1.32 | | | |
| 2012 | -18.79 | 0.70 | | | | -15.66 | 1.25 | | | | 3.17 | 1.32 | | | |
| 2013 | 8.05 | 0.71 | | | | 13.26 | 1.27 | | | | 5.36 | 1.34 | | | |
| CARU | | | | | | | | | | | | | | | |
| Intercept | 154.71 | 10.16 | | | | 224.75 | 19.63 | | | | 17.32 | 4.22 | | | |
| Heat | -7.71 | 2.62 | 10.36 | 1 | **0.001** | -3.59 | 2.63 | 3.24 | 1 | 0.07 | 4.03 | 4.23 | 0.64 | 1 | 0.42 |
| Water | -3.01 | 2.71 | 0.49 | 1 | 0.49 | -0.55 | 2.70 | 0.05 | 1 | 0.83 | 1.47 | 4.55 | 0.01 | 1 | 0.93 |
| Heat x Water | 3.36 | 3.83 | 0.77 | 1 | 0.38 | 0.28 | 3.84 | 0.01 | 1 | 0.94 | -3.43 | 6.40 | 0.29 | 1 | 0.59 |
| Pre-phenology | 0.18 | 0.05 | 11.54 | 1 | **0.001** | -0.06 | 0.09 | 0.43 | 1 | 0.51 | 0.19 | 0.09 | 4.07 | 1 | **0.04** |
| Year | | | 1031.32 | 3 | **< 2.2e-16** | | | 543.50 | 3 | **< 2e-16** | | | 267.70 | 3 | **< 2e-16** |
| 2011 | 24.50 | 1.37 | | | | 22.92 | 1.42 | | | | -1.78 | 1.87 | | | |
| 2012 | -21.66 | 1.28 | | | | -4.99 | 1.33 | | | | 16.62 | 1.73 | | | |
| 2013 | 2.57 | 1.23 | | | | -9.45 | 1.28 | | | | -12.54 | 1.68 | | | |
| LLSE | | | | | | | | | | | | | | | |
| Intercept | 150.13 | 13.31 | | | | 203.28 | 19.03 | | | | 13.86 | 1.92 | | | |
| Heat | -7.52 | 1.67 | 23.17 | 1 | **1.48E-06** | -2.49 | 2.59 | 1.61 | 1 | 0.20 | 6.76 | 1.38 | 15.69 | 1 | **0.0001** |
| Water | -2.16 | 2.02 | 0.04 | 1 | 0.84 | 1.55 | 2.86 | 0.75 | 1 | 0.39 | 6.04 | 1.99 | 1.30 | 1 | 0.25 |
| Heat x Water | 4.16 | 2.80 | 2.21 | 1 | 0.14 | 0.14 | 3.81 | 0.00 | 1 | 0.97 | -7.55 | 2.60 | 8.46 | 1 | **0.004** |
| Pre-phenology | 0.19 | 0.07 | 7.80 | 1 | **0.005** | -0.01 | 0.09 | 0.02 | 1 | 0.90 | -0.01 | 0.06 | 0.05 | 1 | 0.83 |
| Year | | | 1974.93 | 3 | **< 2.2e-16** | | | 1389.07 | 3 | **<2e-16** | | | 30.30 | 3 | **1.19E-06** |
| 2011 | 27.89 | 1.16 | | | | 19.00 | 1.25 | | | | -8.62 | 1.59 | | | |
| 2012 | -23.30 | 1.03 | | | | -26.05 | 1.10 | | | | -2.44 | 1.41 | | | |

| | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 2013 | 5.34 | 1.06 | | | | 1.34 | 1.13 | | | | -3.58 | 1.44 | | | |
| SIPR | | | | | | | | | | | | | | | |
| Intercept | 160.55 | 16.25 | | | | 278.50 | 49.39 | | | | 23.12 | 3.90 | | | |
| Heat | -5.11 | 1.23 | 17.98 | 1 | **2.23E-05** | -2.02 | 1.47 | 8.11 | 1 | **0.004** | 2.76 | 1.85 | 1.95 | 1 | 0.16 |
| Water | -1.56 | 1.34 | 1.08 | 1 | 0.30 | 0.39 | 1.43 | 0.21 | 1 | 0.65 | 1.36 | 1.86 | 0.25 | 1 | 0.62 |
| Heat x Water | 1.19 | 1.89 | 0.40 | 1 | 0.53 | -2.33 | 2.31 | 1.02 | 1 | 0.31 | -1.34 | 2.47 | 0.29 | 1 | 0.59 |
| Pre-phenology | 0.12 | 0.08 | 1.86 | 1 | 0.17 | -0.32 | 0.22 | 2.09 | 1 | 0.15 | 0.05 | 0.12 | 0.14 | 1 | 0.71 |
| Year | | | 2011.43 | 3 | **< 2.2e-16** | | | 746.46 | 3 | **< 2.2e-16** | | | 85.23 | 3 | **<2e-16** |
| 2011 | 28.40 | 1.05 | | | | 14.28 | 1.49 | | | | -14.38 | 1.68 | | | |
| 2012 | -18.69 | 1.04 | | | | -26.44 | 1.48 | | | | -7.86 | 1.67 | | | |
| 2013 | 7.98 | 1.03 | | | | -3.73 | 1.47 | | | | -11.71 | 1.65 | | | |
| PODI | | | | | | | | | | | | | | | |
| Intercept | 159.28 | 12.14 | | | | 182.40 | 31.41 | | | | 15.56 | 2.33 | | | |
| Heat | -5.79 | 2.36 | 4.70 | 1 | **0.03** | -4.07 | 2.23 | 3.07 | 1 | 0.08 | 1.74 | 2.00 | 0.37 | 1 | 0.54 |
| Water | 0.14 | 2.35 | 1.21 | 1 | 0.27 | -0.47 | 2.30 | 0.14 | 1 | 0.71 | -2.32 | 2.05 | 3.69 | 1 | 0.05 |
| Heat x Water | 4.50 | 3.61 | 1.55 | 1 | 0.21 | 2.61 | 3.52 | 0.55 | 1 | 0.46 | -1.99 | 3.17 | 0.39 | 1 | 0.53 |
| Pre-phenology | 0.17 | 0.06 | 7.69 | 1 | **0.01** | 0.12 | 0.14 | 0.73 | 1 | 0.39 | 0.09 | 0.05 | 2.76 | 1 | 0.10 |
| Year | | | 1349.80 | 3 | **< 2.2e-16** | | | 933.75 | 3 | **< 2e-16** | | | 24.24 | 3 | **2.22E-05** |
| 2011 | 20.65 | 1.20 | | | | 23.47 | 1.54 | | | | 2.76 | 1.85 | | | |
| 2012 | -23.04 | 1.22 | | | | -21.52 | 1.56 | | | | 1.52 | 1.87 | | | |
| 2013 | 3.51 | 1.27 | | | | 12.41 | 1.63 | | | | 9.02 | 1.95 | | | |
| LEPY | | | | | | | | | | | | | | | |
| Intercept | 150.76 | 10.81 | | | | 194.99 | 14.43 | | | | 13.79 | 2.32 | | | |
| Heat | -6.04 | 1.87 | 5.48 | 1 | **0.02** | -2.16 | 1.62 | 6.42 | 1 | **0.01** | 4.75 | 2.16 | 0.44 | 1 | 0.51 |
| Water | -2.68 | 1.96 | 0.17 | 1 | 0.68 | 2.00 | 1.74 | 1.18 | 1 | 0.28 | 5.20 | 2.29 | 0.43 | 1 | 0.51 |
| Heat x Water | 5.87 | 2.65 | 4.90 | 1 | **0.03** | -1.34 | 2.30 | 0.34 | 1 | 0.56 | -7.69 | 3.10 | 6.14 | 1 | **0.01** |
| Pre-phenology | 0.19 | 0.06 | 11.41 | 1 | **0.001** | 0.03 | 0.07 | 0.23 | 1 | 0.63 | 0.03 | 0.06 | 0.26 | 1 | 0.61 |
| Year | | | 1346.79 | 3 | **< 2.2e-16** | | | 2477.97 | 3 | **< 2e-16** | | | 21.11 | 3 | **9.97E-05** |
| 2011 | 24.69 | 1.14 | | | | 21.52 | 0.88 | | | | -2.72 | 1.15 | | | |
| 2012 | -16.80 | 1.14 | | | | -22.11 | 0.88 | | | | -4.77 | 1.14 | | | |
| 2013 | 3.21 | 1.13 | | | | 2.24 | 0.88 | | | | -0.71 | 1.14 | | | |
| ARSC | | | | | | | | | | | | | | | |
| Intercept | 175.00 | 11.24 | | | | 210.28 | 12.09 | | | | 15.16 | 2.07 | | | |
| Heat | -8.95 | 2.47 | 19.75 | 1 | **8.82E-06** | -6.48 | 2.26 | 11.36 | 1 | **0.001** | 2.76 | 2.23 | 3.07 | 1 | 0.08 |
| Water | -1.41 | 2.47 | 0.02 | 1 | 0.89 | -1.28 | 2.27 | 0.01 | 1 | 0.92 | 0.11 | 2.26 | 0.01 | 1 | 0.93 |

| | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Heat x Water | 2.31 | 3.45 | 0.45 | 1 | 0.50 | 2.21 | 3.19 | 0.48 | 1 | 0.49 | 0.05 | 3.15 | 0.0003 | 1 | 0.99 |
| Pre-phenology | 0.10 | 0.06 | 3.18 | 1 | 0.07 | 0.00 | 0.06 | 0.00 | 1 | 0.98 | 0.00 | 0.06 | 0.0001 | 1 | 0.99 |
| Year | | | 1723.73 | 3 | **< 2.2e-16** | | | 1669.37 | 3 | **< 2.2e-16** | | | 322.85 | 3 | **< 2e-16** |
| 2011 | 23.37 | 1.33 | | | | 20.67 | 0.82 | | | | -2.40 | 1.40 | | | |
| 2012 | -30.84 | 1.32 | | | | -12.17 | 0.81 | | | | 19.46 | 1.39 | | | |
| 2013 | 4.75 | 1.50 | | | | 3.52 | 0.92 | | | | -1.08 | 1.58 | | | |
| MIOB | | | | | | | | | | | | | | | |
| Intercept | 155.59 | 9.96 | | | | 135.74 | 40.46 | | | | 26.80 | 3.43 | | | |
| Heat | -6.04 | 3.19 | 3.56 | 1 | 0.06 | -5.57 | 2.76 | 23.41 | 1 | **1.31E-06** | -0.96 | 3.26 | 5.82 | 1 | **0.02** |
| Water | -0.72 | 3.11 | 0.21 | 1 | 0.65 | 4.20 | 2.63 | 0.19 | 1 | 0.66 | 4.77 | 3.09 | 0.14 | 1 | 0.71 |
| Heat x Water | 3.59 | 4.46 | 0.65 | 1 | 0.42 | -7.24 | 3.87 | 3.50 | 1 | 0.06 | -8.52 | 4.51 | 3.57 | 1 | 0.06 |
| Pre-phenology | 0.18 | 0.05 | 14.14 | 1 | 0.0002 | 0.39 | 0.18 | 4.82 | 1 | **0.03** | 0.21 | 0.08 | 6.89 | 1 | **0.01** |
| Year | | | 1253.98 | 3 | **< 2.2e-16** | | | 740.77 | 3 | **< 2.2e-16** | | | 18.16 | 3 | **0.0004** |
| 2011 | 20.09 | 1.16 | | | | 16.95 | 1.46 | | | | -3.38 | 1.70 | | | |
| 2012 | -20.85 | 1.17 | | | | -21.45 | 1.47 | | | | -1.06 | 1.71 | | | |
| 2013 | 2.87 | 1.15 | | | | 6.71 | 1.45 | | | | 3.64 | 1.70 | | | |
| ERSI | | | | | | | | | | | | | | | |
| Intercept | 163.33 | 16.46 | | | | 255.68 | 28.81 | | | | 13.34 | 1.73 | | | |
| Heat | -5.51 | 2.44 | 4.14 | 1 | **0.04** | -7.33 | 3.16 | 7.82 | 1 | **0.005** | -1.79 | 1.48 | 5.53 | 1 | **0.02** |
| Water | 1.65 | 3.93 | 4.08 | 1 | **0.04** | 3.75 | 5.04 | 1.15 | 1 | 0.28 | 0.92 | 2.69 | 4.21 | 1 | **0.04** |
| Heat x Water | 4.76 | 4.75 | 1.00 | 1 | 0.32 | -0.93 | 6.09 | 0.02 | 1 | 0.88 | -6.77 | 3.27 | 4.28 | 1 | **0.04** |
| Pre-phenology | 0.16 | 0.08 | 3.68 | 1 | 0.06 | -0.23 | 0.13 | 2.90 | 1 | 0.09 | -0.01 | 0.05 | 0.01 | 1 | 0.92 |
| Year | | | 882.89 | 3 | **< 2e-16** | | | 1037.68 | 3 | **< 2.2e-16** | 3.16 | 1.72 | 11.32 | 3 | **0.01** |
| 2011 | 24.05 | 1.67 | | | | 28.00 | 1.61 | | | | 3.12 | 1.64 | | | |
| 2012 | -22.35 | 1.60 | | | | -19.42 | 1.54 | | | | 6.03 | 1.80 | | | |
| 2013 | 6.30 | 1.76 | | | | 12.34 | 1.69 | | | | | | | | |
| SIAC | | | | | | | | | | | | | | | |
| Intercept | 181.30 | 70.41 | | | | 114.03 | 63.47 | | | | 12.35 | 5.20 | | | |
| Heat | -11.24 | 4.64 | 6.70 | 1 | **0.01** | -17.02 | 4.77 | 12.00 | 1 | **0.001** | -11.41 | 5.80 | 1.44 | 1 | 0.23 |
| Water | -3.84 | 3.02 | 0.83 | 1 | 0.36 | -3.71 | 3.45 | 0.00 | 1 | 0.98 | 1.00 | 3.94 | 1.06 | 1 | 0.30 |
| Heat x Water | 5.45 | 4.95 | 1.21 | 1 | 0.27 | 11.26 | 6.03 | 3.49 | 1 | 0.06 | 10.66 | 6.83 | 2.4350 | 1 | 0.12 |
| Pre-phenology | 0.09 | 0.35 | 0.07 | 1 | 0.79 | 0.49 | 0.29 | 2.85 | 1 | 0.09 | 0.60 | 0.28 | 4.5314 | 1 | **0.03** |
| Year | | | 590.07 | 3 | **< 2.2e-16** | | | 118.35 | 3 | **< 2.2e-16** | | | 9.54 | 3 | **0.02** |
| 2011 | 22.30 | 1.69 | | | | 12.91 | 3.51 | | | | -9.81 | 3.58 | | | |
| 2012 | -20.20 | 1.66 | | | | -26.27 | 3.48 | | | | -6.79 | 3.63 | | | |
| 2013 | 5.17 | 1.89 | | | | -4.05 | 3.94 | | | | -9.52 | 4.03 | | | |

| | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| BIBI | | | | | | | | | | | | | | | |
| Intercept | 181.43 | 8.53 | | | | 182.44 | 20.71 | | | | 15.04 | 2.43 | | | |
| Heat | -7.41 | 1.92 | 32.27 | 1 | **1.34E-08** | -6.07 | 1.66 | 32.05 | 1 | **1.50E-08** | 0.50 | 2.53 | 0.17 | 1 | 0.68 |
| Water | 0.42 | 1.90 | 0.12 | 1 | 0.73 | 0.43 | 1.63 | 0.02 | 1 | 0.88 | -1.10 | 2.48 | 0.27 | 1 | 0.60 |
| Heat x Water | 0.08 | 2.56 | 0.00 | 1 | 0.98 | -0.48 | 2.21 | 0.05 | 1 | 0.83 | 0.39 | 3.41 | 0.01 | 1 | 0.91 |
| Pre-phenology | 0.09 | 0.04 | 4.23 | 1 | **0.04** | 0.14 | 0.09 | 2.26 | 1 | 0.13 | 0.05 | 0.05 | 1.16 | 1 | 0.28 |
| Year | | | 1004.56 | 3 | **< 2.2e-16** | | | 658.00 | 3 | **< 2.2e-16** | | | 130.06 | 3 | **<2e-16** |
| 2011 | 17.33 | 1.24 | | | | 15.11 | 1.15 | | | | -3.05 | 1.37 | | | |
| 2012 | -19.27 | 1.21 | | | | -9.39 | 1.13 | | | | 8.93 | 1.34 | | | |
| 2013 | 4.44 | 1.41 | | | | 15.12 | 1.31 | | | | 10.10 | 1.56 | | | |
| CHJA | | | | | | | | | | | | | | | |
| Intercept | 188.87 | 9.43 | | | | 224.55 | 50.04 | | | | 15.00 | 1.98 | | | |
| Heat | -2.02 | 1.88 | 5.70 | 1 | **0.02** | -3.12 | 1.75 | 12.83 | 1 | **0.0003** | -0.58 | 1.92 | 0.37 | 1 | 0.55 |
| Water | 0.63 | 2.02 | 0.35 | 1 | 0.55 | 1.33 | 1.93 | 0.04 | 1 | 0.84 | 1.26 | 2.13 | 0.45 | 1 | 0.50 |
| Heat x Water | -2.61 | 2.72 | 0.92 | 1 | 0.34 | -2.59 | 2.42 | 1.15 | 1 | 0.28 | -0.55 | 2.78 | 0.04 | 1 | 0.84 |
| Pre-phenology | 0.03 | 0.05 | 0.47 | 1 | 0.49 | -0.06 | 0.23 | 0.07 | 1 | 0.79 | 0.04 | 0.06 | 0.50 | 1 | 0.48 |
| Year | | | 2034.75 | 3 | **< 2e-16** | | | 1284.34 | 3 | **< 2.2e-16** | | | 46.74 | 3 | **3.94E-10** |
| 2011 | 22.81 | 0.85 | | | | 22.80 | 1.17 | | | | -0.07 | 1.23 | | | |
| 2012 | -15.15 | 0.85 | | | | -16.72 | 1.16 | | | | -1.61 | 1.22 | | | |
| 2013 | 6.39 | 0.84 | | | | 12.46 | 1.14 | | | | 5.97 | 1.20 | | | |
| LUSP | | | | | | | | | | | | | | | |
| Intercept | 195.73 | 48.53 | | | | 205.87 | 38.30 | | | | 18.94 | 3.31 | | | |
| Heat | -6.32 | 1.80 | 21.62 | 1 | **3.33E-06** | -4.71 | 2.31 | 7.10 | 1 | **0.008** | 3.41 | 2.75 | 0.82 | 1 | 0.37 |
| Water | -1.37 | 1.72 | 0.07 | 1 | 0.79 | 0.39 | 2.14 | 0.61 | 1 | 0.43 | 2.16 | 2.52 | 0.12 | 1 | 0.72 |
| Heat x Water | 1.93 | 2.34 | 0.68 | 1 | 0.41 | 1.44 | 2.94 | 0.24 | 1 | 0.63 | -3.03 | 3.50 | 0.75 | 1 | 0.39 |
| Pre-phenology | -0.01 | 0.22 | 0.003 | 1 | 0.96 | 0.04 | 0.17 | 0.05 | 1 | 0.83 | 0.00 | 0.43 | 0.0001 | 1 | 0.99 |
| Year | | | 602.12 | 3 | **< 2.2e-16** | | | 260.01 | 3 | **< 2.2e-16** | | | 21.90 | 3 | **6.83E-05** |
| 2011 | 22.14 | 1.19 | | | | 14.52 | 1.52 | | | | -5.09 | 2.15 | | | |
| 2012 | -7.15 | 1.26 | | | | -10.24 | 1.61 | | | | 0.18 | 2.27 | | | |
| 2013 | 6.84 | 1.29 | | | | -4.50 | 1.64 | | | | -9.35 | 2.34 | | | |
| ARFE | | | | | | | | | | | | | | | |
| Intercept | 201.11 | 17.40 | | | | 229.61 | 42.02 | | | | 31.22 | 2.83 | | | |
| Heat | -3.94 | 2.57 | 3.85 | 1 | **0.05** | -9.63 | 2.00 | 31.02 | 1 | **2.56E-08** | -5.65 | 2.45 | 6.70 | 1 | **0.01** |
| Water | -1.67 | 2.78 | 0.63 | 1 | 0.43 | 0.28 | 2.25 | 1.19 | 1 | 0.27 | 2.23 | 2.66 | 3.15 | 1 | 0.08 |
| Heat x Water | 0.26 | 3.91 | 0.00 | 1 | 0.95 | 2.81 | 3.14 | 0.80 | 1 | 0.37 | 1.87 | 3.66 | 0.26 | 1 | 0.61 |

| | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Pre-phenology | -0.01 | 0.08 | 0.005 | 1 | 0.94 | 0.01 | 0.19 | 0.00 | 1 | 0.96 | 0.04 | 0.09 | 0.1705 | 1 | 0.68 |
| Year | | | 649.53 | 3 | **< 2e-16** | | | 342.48 | 3 | **< 2.2e-16** | | | 6.71 | 3 | 0.08 |
| 2011 | 19.76 | 1.77 | | | | 16.45 | 2.15 | | | | -3.36 | 2.54 | | | |
| 2012 | -24.84 | 1.73 | | | | -22.24 | 2.10 | | | | 2.60 | 2.49 | | | |
| 2013 | 1.77 | 1.75 | | | | 3.92 | 2.12 | | | | 2.09 | 2.51 | | | |
| TRSP | | | | | | | | | | | | | | | |
| Intercept | 185.45 | 17.24 | | | | 318.56 | 77.49 | | | | 24.82 | 3.12 | | | |
| Heat | -7.60 | 1.79 | 22.43 | 1 | **2.19E-06** | -5.71 | 1.86 | 16.88 | 1 | **3.98E-05** | -0.86 | 2.05 | 0.34 | 1 | 0.56 |
| Water | -0.35 | 1.93 | 0.15 | 1 | 0.70 | -0.17 | 2.15 | 0.19 | 1 | 0.67 | -1.84 | 2.28 | 1.45 | 1 | 0.23 |
| Heat x Water | 1.99 | 2.87 | 0.48 | 1 | 0.49 | -1.05 | 3.08 | 0.12 | 1 | 0.73 | -0.31 | 3.30 | 0.01 | 1 | 0.93 |
| Pre-phenology | 0.12 | 0.08 | 2.210 | 1 | 0.14 | -0.39 | 0.34 | 1.32 | 1 | 0.25 | 0.02 | 0.10 | 0.0400 | 1 | 0.84 |
| Year | | | 454.54 | 3 | **< 2.2e-16** | | | 165.76 | 3 | **< 2.2e-16** | | | 52.24 | 3 | **2.66E-11** |
| 2011 | 19.17 | 2.84 | | | | 8.45 | 2.99 | | | | -15.28 | 3.25 | | | |
| 2012 | -22.99 | 1.98 | | | | -14.02 | 2.09 | | | | 4.42 | 2.32 | | | |
| 2013 | 5.61 | 2.00 | | | | 6.01 | 2.10 | | | | -4.02 | 2.34 | | | |

# B: Supplementary information for Chapter 3

**Supplemental Table 3.1.** Descriptions of altitudinal ranking designations used for assigned species rank levels 1-6 of the thermophilization analysis.

| Rank | Distribution | Altitudinal range (m) |
|---|---|---|
| 1 | nival distribution center | 3200 - 4200 + |
| 2 | alpine to nival species that do not descend to the treeline; | 3200 - any |
| 3 | alpine centered species which do not descend to the montane belt | 3000 - >3500 |
| 4 | alpine centered species that descend to the montane belt | 2700 - >3000 |
| 5 | centered in treeline ecotone or indifferently distributed from the montane to alpine | 2400 - 3000 |
| 6 | montane-centered or indifferently distributed from the montane to treeline | any - 2500 |

**Supplemental Table 3.2.** All species recorded at four summits during vegetation surveys with their associated habitat type and altitudinal distribution (*from* Ackerfield, 2015), lifeform classification, and assigned altitudinal rank for the thermophilization analysis.

| Species | Lifeform | Alt Rank | Habitat Type | Elev Range |
|---|---|---|---|---|
| *Abies lasiocarpa* | conifer | 6 | mountains and subalpine forests | 2300-3800 |
| *Agoserus glauca* | forb | 4 | open rocky places, along streams and in mts: sagebrush, pinyon-juniper, oak, open meadows | 1700-4200 |
| *Androsace septentrionalis* | forb | 4 | open slopes, meadows, roadsides, forests, alpine | 1500-4300 |
| *Anemone multifida* | forb | 4 | alpine, apen spruce fir or pine forests | 1900-4300 |
| *Angelica grayii* | forb | 3 | mountian meadows & alpine slopes | 3000-4200 |
| *Antennaria media* | forb | 2 | rocky alpine slopes | 3000-4300 |
| *Antennaria parvifolia* | forb | 4 | open meadows and rocky slopes | 1400-3000 |
| *Antennaria pulcherrima* | forb | 5 | wet meadows, streambanks, willow- thickets | 2200-2900 |
| *Antennaria rosea* | forb | 4 | open meadows, rocky slopes, wooded forests | 1500-3700 |
| *Antennaria umbrinella* | forb | 4 | rocky slopes, dry meadows, open forests | 2200-4000 |
| *Aquilegia coerulea* | forb | 5 | meadows, along streams, forests, alpine | 1600-4200 |
| *Arabis drummondii* | forb | 4 | rocky slopes, open forests, meadows, alpine | 2100-4000 |
| *Arabis lemmonii* | forb | 1 | alpine, scree slopes, fellfields | 3600-4300 |
| *Arenaria congesta* | forb | 4 | meadows & open slopes in sandy, rocky soil | 2000-3900 |
| *Arnica longifolia* | forb | 4 | well drained soil around seeps, springs, along cliffs and river banks | 2800-3600 |
| *Arnica mollis* | forb | 4 | subalpine meadows, rocky slopes, moist places in the mountians | 2200-4100 |
| *Artemisia scopulorum* | forb | 1 | open, rocly places & meadows in the alpine | 3000-4300 |
| *Besseya alpina* | forb | 2 | rocky ridges and alpine in scree | 2900-4400 |
| *Calamagrostis canadensis* | graminoid | 5 | moist meadows, along streams & moist areas | 1500-3800 |
| *Calamagrostis montanensis* | graminoid | 4 | dry ridgetops and alpine | 2400-4000 |
| *Calamagrostis purpurascens* | graminoid | 4 | forests, rocky slopes, alpine ridges | 2200-4000 |
| *Campanula parryi* | forb | 4 | moist meadows, along creeks and streams | 1900-4200 |
| *Campanula uniflora* | forb | 1 | dry alpine meadows and scree slopes | 3500-4300 |

| Species | Lifeform | Alt Rank | Habitat Type | Elev Range |
|---|---|---|---|---|
| *Carex arapahoensis* | graminoid | 1 | meadows & alpine slopes | 3100-4300 |
| *Carex elynoides* | graminoid | 2 | alpine and meadows | 2700-4300 |
| *Carex heteroneura var. chalciolepis* | graminoid | 2 | streams, pond margins, meadows, alpine | 2700-4000 |
| *Carex nardina var. hepburnii* | graminoid | 1 | alpine ridges and scree slopes | 3300-4300 |
| *Carex nelsonii* | graminoid | 2 | lake margins, melting snowbanks, moist meadows, alpine | 2600-4200 |
| *Carex pelocarpa* | graminoid | 2 | along streams, in meadows, talus slopes | 2700-3700 |
| *Carex perglobosa* | graminoid | 1 | alpine | 3300-4200 |
| *Carex phaeocephala* | graminoid | 2 | alpine, meadows, open slopes | 2500-4000 |
| *Carex rupestris* | graminoid | 2 | dry slopes and in the alpine | 2500-4000 |
| *Castilleja occidentalis* | forb | 2 | alpine and mountian meadows | 3000-4300 |
| *Cerastium beeringianum* | forb | 4 | subalpine spruce-fir & alpine | 2900-4300 |
| *Chaenactis douglasii var. alpina* | forb | 2 | alpine scree slopes or in rocky places; occasionally subalpine | 2800-4200 |
| *Chamerion angustifolium* | forb | 4 | forests, meadows, along streams | 1600-3900 |
| *Chamerion latifolium* | forb | 4 | along streams and creeks, gravelly soil | 2200-4000 |
| *Chionophylla jamesii* | forb | 1 | alpine | 3300-4300 |
| *Cirsium eatonii* | forb | 4 | rocky open slopes at high elevations | 2800-3900 |
| *Claytonia megarhiza* | forb | 1 | rock crevices in alpine | 3300-4300 |
| *Crepis nana* | forb | 2 | uncommon scree and talus slopes in the alpine | 3000-4300 |
| *Cymopterus longilobus* | forb | 4 | rocky soil | 1800-3400 |
| *Dasiphora fruticosa* | forb | 4 | meadows, along streams, forests | 2200-4200 |
| *Descaurainia incana* | forb | 5 | forests, meadows, along streams | 1600-3500 |
| *Deschampsia caespitosa* | graminoid | 4 | moist meadows, moist alpine, along lakes, wetlands | 1500-4300 |
| *Draba aurea* | forb | 4 | alpine meadows, forests | 2400-4200 |
| *Draba crassa* | forb | 1 | alpine and scree slopes | 3200-4300 |
| *Draba crassifolia* | forb | 4 | alpine and subalpine spruce-fir forests and meadows | 2700-4200 |

| Species | Lifeform | Alt Rank | Habitat Type | Elev Range |
|---|---|---|---|---|
| *Draba lonchocarpa* | forb | 1 | uncommon alpine | 3200-4300 |
| *Draba spectabilis* | forb | 4 | forests , meadows, alpine | 2400-4000 |
| *Draba streptocarpa* | forb | 4 | alpine and forests | 2200-4300 |
| *Dryas octopetala* | forb | 1 | alpine | 3200-4300 |
| *Elymus scribneri* | graminoid | 1 | alpine and high subalpine meadows | 3000-4200 |
| *Elymus trachycaulus* | graminoid | 6 | roadsides, dry slopes, meadows, grasslands, forests | 1300-3800 |
| *Epilobium anagallidifolium* | forb | 4 | along streams, lakes, moist meadows & other places | 2500-4200 |
| *Ericameria discoidea* | forb | 2 | rocky alpine and subalpine slopes & dry meadows | 2600-4300 |
| *Erigeron grandiflorus* | forb | 1 | alpine and subalpine meadows | 2800-4300 |
| *Erigeron peregrinus* | forb | 4 | mountain meadows, streams, forest openings | 2400-4400 |
| *Erigeron pinnatisectus* | forb | 2 | rocky subalpine and alpine meadows | 2700-4200 |
| *Erigeron simplex* | forb | 1 | alpine and subalpine meadows | 2800-4300 |
| *Eriogonum coloradense* | forb | 4 | grasslands, sagebrush meadows, talus slopes, alpine ridges | 2700-3900 |
| *Eriogonum umbellatum* | forb | 6 | dry slopes, sagebrush flats, meadows, forests | 1600-3100 |
| *Erysimum capitatum* | forb | 4 | plains, foothills, mt meadows, alpine | 1000-4200 |
| *Festuca brachyphylla* | graminoid | 1 | alpine, meadows, on ridges | 2800-4300 |
| *Festuca thurberi* | graminoid | 5 | dry slopes, meadows, forest openings | 1900-3800 |
| *Gentiana prostrata* | forb | 1 | moist alpine | 3200-4300 |
| *Gentianodes algida* | forb | 2 | moist subalpine & alpine meadows | 3000-4300 |
| *Geum rossii* | forb | 2 | apine and subalpine | 2400-4400 |
| *Heterotheca pumila* | forb | 2 | common in mountians | 3000-4000 |
| *Hieracium gracile* | forb | 4 | subalpine and alpine forests and meadows | 2800-4000 |
| *Ivesia gordonii* | forb | 3 | alpine and dry slopes | 2200-3900 |
| *Juncus drummondii* | graminoid | 3 | moist meadows, lakes and stream shores, alpine | 2600-4200 |
| *Juniperus communis* | conifer | 6 | aspen and spruce-fir forests | 1600-3900 |
| *Kobresia myosuroides* | graminoid | 2 | alpine and meadows | 2800-4000 |
| *Kobresia simpliciuscula* | graminoid | 2 | moist alpine and fens | 2800-4000 |

| Species | Lifeform | Alt Rank | Habitat Type | Elev Range |
|---|---|---|---|---|
| *Ligusticum porteri* | forb | 4 | meadows, open gravely slopes, aspen, coniferous woods | 2200-3700 |
| *Lloydia serotina* | forb | 1 | alpine and high meadows | 3000-4300 |
| *Lupinus argenteus* | forb | 5 | dry, open or moist mountian, forest openings | 1400-3200 |
| *Luzula spicata* | graminoid | 2 | alpine and moist meadows | 2900-4400 |
| *Mertensia lanceolata var. viridis* | forb | 2 | common in alpine (occasional lower elev) | 2500-4300 |
| *Minuartia macrantha* | cushion | 2 | alpine and spruce-fir forests | 2700-4500 |
| *Minuartia obtusiloba* | cushion | 2 | alpine and occasional spruce-fir forests | 3000-4300 |
| *Minuartia rubella* | cushion | 3 | alpine on rocky ridges and spruce-fir forests | 2900-4300 |
| *Noccaea fendleri* | forb | 4 | rocky slopes, alpine, forest openings | 1500-4400 |
| *Oxyria digyna* | forb | 3 | rocky alpine and meadows | 2500-4400 |
| *Packera werneriifolia* | forb | 3 | subalpine and alpine meadows, forest openings, dry & rocky slopes | 1900-4300 |
| *Papaver kluanense* | forb | 1 | rare dry alpine meadows & scree slopes | 3500-4300 |
| *Pedicularis bracteosa* | forb | 4 | Moist spruce fir forests, moist meadows, along streams | 2400-3800 |
| *Pedicularis groenlandica* | forb | 4 | moist meadows, marshes, along streams and creeks | 2300-4000 |
| *Pedicularis parryi* | forb | 4 | alpine and mountian meadows & dry places | 2600-4000 |
| *Pedicularis racemosa* | forb | 5 | spruce-fir forests & moist meadows | 2200-4000 |
| *Pedicularis scopulorum* | forb | 1 | bogs, marshes, meadows, alpine | 3000-4200 |
| *Penstemon harbourii* | forb | 1 | alpine scree or talus slopes. Endemic | 3200-4200 |
| *Penstemon whippleanus* | forb | 4 | mountian forests, meadows, alpine | 2400-4200 |
| *Phacelia hastata* | forb | 4 | meadows and dry slopes | 1600-3400 |
| *Phacelia sericea* | forb | 4 | meadows, open slopes & in alpine | 1900-4200 |
| *Picea engelmannii* | conifer | 6 | subalpine forests | 2200-3650 |
| *Poa alpina* | graminoid | 2 | mountian meadows & alpine | 2500-4300 |
| *Poa arctica* | graminoid | 2 | alpine and subalpine meadows & scree slopes | 2900-4300 |
| *Poa glauca* | graminoid | 1 | alpine/ mountain meadows | 2900-4300 |
| *Polemonium viscosum* | forb | 2 | high meadows, alpine, talus or scree slopes | 2900-4400 |

| Species | Lifeform | Alt Rank | Habitat Type | Elev Range |
|---|---|---|---|---|
| *Polygonum bistortoides* | forb | 3 | moist meadows and marshes, aspen forests, alpine | 2100-4300 |
| *Potentilla diversifolia* | forb | 3 | meadows and alpine | 2600-4300 |
| *Potentilla gracilis var. flabelliformis* | forb | 4 | meadows, forests, alpine | 1500-3500 |
| *Potentilla nivea* | forb | 3 | alpine and subalpine meadows | 2900-4300 |
| *Potentilla pulcherrima* | forb | 3 | meadows, along creeks, on open slopes, alpine | 2100-4000 |
| *Potentilla rubricaulis* | forb | 2 | alpine and subalpine meadows | 2900-4300 |
| *Potentilla subjuga* | forb | 2 | meadows and alpine | 2700-4200 |
| *Pseudocymopterus montanus* | forb | 4 | wooded slopes and in meadows | 1800-4300 |
| *Rhodiola integrifolia* | succulent | 2 | streams, wet meadows, alpine rock crevices | 2700-4300 |
| *Ribes montigenum* | forb | 3 | subalpine & alpine slopes and spruce forests | 2500-4000 |
| *Sagina saginoides* | forb | 2 | streams, moist areas, alpine | 2500-4200 |
| *Salix arctica* | shrub | 1 | alpine | 3300-4200 |
| *Salix brachycarpa* | shrub | 2 | streams, dry slopes, forests, meadows, alpine | 2100-4200 |
| *Salix glauca* | shrub | 3 | streams, forests, alpine | 2200-4200 |
| *Salix reticulata* | shrub | 1 | alpine | 3200-4200 |
| *Saxifraga bronchialis* | forb | 4 | rocky outcrops, spruce-fir forests, alpine | 2000-4200 |
| *Saxifraga caespitosa ssp. delicatula* | forb | 1 | rocky alpine, talus & scree slopes | 3300-4300 |
| *Saxifraga cernua* | forb | 1 | rocky alpine, talus & scree slopes and alpine creeks | 3200-4300 |
| *Saxifraga chrysantha* | forb | 1 | alpine meadows and scree slopes | 3500-4400 |
| *Saxifraga flagellaris* | forb | 1 | alpine meadows and scree slopes | 3500-4300 |
| *Saxifraga flagellaris ssp. crandallii* | forb | 1 | alpine meadows and scree slopes | 3500-4300 |
| *Saxifraga rhomboidea* | forb | 5 | foothills to alpine | 1500-4300 |
| *Sedum lanceolatum* | succulent | 3 | rocky soil & dry slopes | 1600-4300 |
| *Selaginella densa* | moss | 3 | dry grasslands, rocky forests, rocky slopes & outcrops, alpine ridges, boulder fields | 1200-4000 |

| Species | Lifeform | Alt Rank | Habitat Type | Elev Range |
|---|---|---|---|---|
| *Senecio amplectens* | forb | 2 | mountain meadows & alpine | 2500-4400 |
| *Senecio amplectens var. amplectans* | forb | 2 | mountain meadows & alpine | 2500-4400 |
| *Senecio crassulus* | forb | 2 | mountain meadows, subalpine & alpine slopes, open forests | 2500-4300 |
| *Senecio fremontii* | forb | 2 | rocky soil of alpine and subalpine slopes | 2800-4200 |
| *Senecio soldanella* | forb | 1 | rocky alpine & scree slopes | 3400-4300 |
| *Silene acaulis* | cushion | 1 | alpine | 3200-4300 |
| *Silene kingii* | cushion | 1 | alpine | 3200-4300 |
| *Smelowskia calycina* | forb | 2 | alpine and subalpine slopes | 3100-4300 |
| *Solidago multiradiata* | forb | 3 | rocky soil of mountain meadows, forest, alpine | 1900-4000 |
| *Taraxacum officinale* | forb | 6 | common and widespread, variety disturbed habitats | 1000-3200 |
| *Tetraneuris grandiflora* | forb | 1 | widespread alpine | 3000-4300 |
| *Tonestus pygmaeus* | forb | 1 | rocky soil of the alpine | 3000-4300 |
| *Trifolium dasyphyllum* | forb | 2 | subalpine, alpine meadows | 2900-4300 |
| *Trifolium nanum* | forb | 1 | alpine | 3200-4400 |
| *Trisetum spicatum* | graminoid | 3 | streams, forests, meadows, alpine | 2100-4300 |
| *Zigadenus elegans* | forb | 3 | meadows, dry to moist slopes, forests, alpine | 1900-4000 |

**Supplemental Table 3.3.** Correlation analysis for six climate variables used to determine which variables to include in linear mixed model regressions to predict cover and richness on all four summits. Variables include: growing season maximum and minimum temperature °C (*gMaxTemp*, *gMinTemp*), snow total (*SnowTotal*), day of year snow was off ground (*Snowmelt*), winter maximum and minimum temperature °C (*wMinTemp, wMaxTemp*), and year. Correlations highlighted in bold indicate the correlations less than a threshold of 0.3 that were used in an Akaike Information Criterion model comparisons.

| | Year | gMaxTemp | gMinTemp | SnowTotal | Snowmelt | wMinTemp | wMaxTemp |
|---|---|---|---|---|---|---|---|
| Year | 1 | **-0.18** | -0.63 | -0.51 | -0.09 | **-0.10** | 0.79 |
| gMaxTemp | **-0.18** | 1 | 0.35 | -0.41 | -0.39 | **0.26** | **0.10** |
| gMinTemp | -0.63 | 0.35 | 1 | **-0.04** | -0.39 | 0.41 | -0.36 |
| SnowTotal | -0.51 | -0.41 | **-0.04** | 1 | 0.84 | **0.08** | -0.75 |
| Snowmelt | **-0.09** | -0.39 | -0.39 | 0.84 | 1 | **-0.06** | -0.57 |
| wMinTemp | **-0.10** | **0.26** | 0.41 | **0.08** | **-0.06** | 1 | **-0.12** |
| wMaxTemp | 0.79 | **0.10** | -0.36 | -0.75 | -0.57 | **-0.12** | 1 |

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