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A multi-level approach to assessing alpine productivity responses to climate change

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A multi-level approach to assessing alpine productivity responses to climate change

A Thesis submitted in partial satisfaction of the requirements
for the degree of Master of Science

in

Environmental Systems

by

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2013

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2013

While mapping the future
is a risky undertaking,
perhaps the only thing riskier
is doing nothing.
AL GORE

Above photo: Hiker at Niwot Ridge, Front Range of the Rocky Mountains, Colorado. Photo taken by Daniel E. Winkler

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Abstract

Future, warmer temperatures are predicted to increase alpine productivity, but few studies have addressed the role of water in constraining such responses. We tested the hypothesis that, in the absence of additional water during the growing season, warming may not increase community-level productivity by warming plots March–November and providing supplemental water during the snow-free growing season in an alpine plant community at Niwot Ridge, Colorado. We measured productivity responses to treatments at three levels of biological organization: community-, life form-, and species-levels in 2010–2012. Heating advanced snowmelt 9.4 ± 0.14 days ($\bar{x}$ ± sd) and subsequently decreased cumulative soil temperatures and increased cumulative soil moisture. Warming alone did not alter community-level productivity during any years of the experiment but warming with watering increased community-level productivity by 20% during the first year of treatments. Forb productivity increased with both warming and watering in all years of the experiment, while cushion productivity only increased with watering treatments after the first year of treatments. Graminoid productivity was insensitive to treatments and year, and while succulent productivity varied idiosyncratically by year and treatment, there were no overriding changes between treatments and controls. Responses at the species-level did not always follow the responses of their respective life form group in all or even a single year of the experiment, nor did they reveal compensatory responses that could fully explain productivity at higher levels of biological organization. For example, when the forb life form group responded to treatments in 2010, *A. fendleri* was the only species to exhibit a response. In 2011, both *A. fendleri* and *G. rossii* responded to

treatments while, in 2012, *G. rossii* was the only species to respond to treatments. In our experiment, warming appears to indirectly increase soil moisture by advancing snowmelt, allowing species to break dormancy earlier and take advantage of early season moisture from a prolonged snowmelt. Our results also suggest that community-level responses mask life form group responses, as well as individual species responses within the community under future climate changes. Further, interannual climate variability strongly influences productivity at all levels of organization and is essential to account for when studying how climate change will influence alpine species, life forms, and communities.

Introduction

Alpine ecosystems account for a mere 3% of terrestrial habitats, have highly adapted species, and often poorly developed, porous soils (Billings 1974; Chapin and Körner 1996; Nagy and Grabherr 2009). These factors coupled with the predominant role of climatic variables in determining productivity of alpine ecosystems suggests that the impacts of climate change on alpine plant communities may be more pronounced than they will be on lower elevation communities (Grabherr et al. 2000; Bowman and Fisk 2001). Alpine ecosystems are also predicted to experience some of the highest levels of warming globally, and to show signs of change before other terrestrial ecosystems as a result of their high sensitivity to perturbation (Beniston et al. 1997; Cannone et al. 2007; McCain and Colwell 2011; but see Rangwala and Miller 2012). Responses of alpine productivity to climate change are important to consider for a range of ecosystem-level processes including energy, carbon, and nutrient fluxes (Bowman and Fisk 2001). Additionally, effective management decisions to protect important water resources, recreational areas, and the key species that maintain ecosystem functioning will not be possible without a clear understanding of alpine ecosystem responses.

Global climate models project increases in average temperatures of 2–6ºC across western North America by 2100 with continued increases in atmospheric greenhouse gas concentrations (IPCC 2007). Clow (2010) recently showed that high elevation sites in the Colorado Rockies experienced an increase in mean winter temperatures of 0.09ºC per decade between 1979 and 2007 and that these increases were substantially greater than those observed for the entire state. Additionally, models project a decrease in winter precipitation falling as snow and increase in winter precipitation falling as rain (IPCC 2007). Higher temperatures and changes in precipitation will have cascading effects on known drivers of alpine productivity including the timing of snowmelt and growing season length (Billings and Bliss 1959; Galen and Stanton 1995). Warmer temperatures may directly affect productivity by way of physiological growth processes of plants or, more likely, will indirectly affect productivity by advancing snowmelt, allowing for species to initiate growth earlier in the growing season (Shaw et al. 2002). These changes may be sufficient to cascade up and increase community-level productivity (Litaor et al. 2008), potentially revealing the combined effects of higher temperatures and increased soil water due to earlier snowmelt. Alternatively, earlier melt and increased temperatures could result in drier soils during the growing season if there is no increase in summer rain, diminishing any benefits from warming. There are already signs that warming may have an impact on high elevation productivity (Zhang and Welker 1996; Arft et al. 1999) due to changes in available nutrient resources, species interactions, and a shortened snow season (Seastedt and Vaccaro 2001; Klanderud and Totland 2005; Cannone et al. 2007).

Responses of alpine productivity to climatic changes will likely be complicated by additional factors that influence alpine productivity including elevation (Choler et al. 2001) and species richness (Nagy et al. 2003; Litaor et al. 2008). Variation in species richness can be found along small elevation gradients (~ 20 meters) as can changes in productivity (Kullman 2010). These factors vary in their importance in determining alpine productivity and it has been shown that community productivity is determined by the aggregate response of many species reacting more or less independently to many interacting environmental factors (Scott and Billings 1964).

Moisture during the growing season largely determines the local distribution and productivity of plants in alpine systems (Tranquillini 1964; Billings and Mooney 1968; Walker et al. 1994; Henry and Molau 1997; Jonas et al. 2008; Litaor et al. 2008) and has been shown to determine how responsive or resistant a community will be to increased temperatures (Walker et al. 2006). Winter precipitation may be critical in areas where seasonal soil moisture is determined by winter snowpack and date of snowmelt (Taylor and Seastedt 1994), such as in seasonally dry high-altitude regions in Western U.S. mountains, where snowmelt provides most of the water supporting summer growth (Isard 1986; Greenland 1989; Walker et al. 1994). It remains unclear how each of these local abiotic and biotic drivers of productivity will interact under various scenarios of change.

Although previous studies have explored the interactive effects of multiple climate changes on ecosystem processes (Shaw et al. 2002; Luo et al. 2008), few have examined alpine environments, where microclimates, topography, and interannual variability in temperatures and precipitation have profound effects on annual productivity (Zhang and Welker 1996; Klein et al. 2007; Jägerbrand et al. 2009; Wipf et al. 2009). A majority of previous tundra warming experiments have looked at arctic regions only (Wookey et al. 1993; Chapin et al. 1995; Molau 2001), and the relative few alpine experiments have focused primarily on temperature as the factor limiting plant productivity (Arft et al. 1999). Based on results from these experiments, warmer temperatures and longer growing seasons are expected to increase overall plant productivity in alpine ecosystems (Kikvidze et al. 2005; Rammig et al. 2009). Yet, increased temperatures may be coupled with a decrease in growing season soil moisture in some regions, resulting in distinct effects at different levels of biological organization, from individual species, to life form groups (e.g., graminoids, succulents), to whole communities. Species or groups sensitive to high temperature or low moisture may increase or decrease their relative contributions to total community productivity but such changes may be undetectable when a higher level of biological organization or even a single, dominant species masks the responses of sensitive species or groups (Gonzalez and Loreau 2009).

Increased soil moisture stress in combination with earlier snowmelt may modulate species-level responses to warming and overall productivity. The aim of our study was to determine whether increased temperatures alter peak alpine aboveground productivity (a proxy for net aboveground primary productivity in this strongly seasonal, herbaceous system) at the community-, life form-, and species-level, and to assess how temperature effects are modulated by growing season soil moisture. We tested three main hypotheses: (1) productivity increases in response to warming only when combined with supplemental water to prevent drying (and decreases with warming alone), (2) the observed treatment responses can be predicted by observed changes in soil temperature and soil moisture, and (3) changes at higher levels of biological organization mask changes at lower levels.

Materials and Methods

Site and experimental design

Our alpine research site is located at Niwot Ridge in the Front Range in the Colorado Rocky Mountains (40º 03’ N, 105º 36’ W; 3,540 m), on a 15º south-southeast facing slope above local treeline. Alpine research has been carried out on Niwot Ridge since the early 1920s and the area became part of the National Science Foundation's Long-Term Ecological Research (LTER) network in 1980 (Bowman 2001). The growing season—defined by mean monthly temperatures above 0ºC—is short, typically June through September (Greenland 1989). Year to year variability in temperature and precipitation has been recorded at the LTER Saddle station, which is the near the experimental site (~500 m) and at approximately the same elevation (3528 m). From 1981 to 2008 the mean annual temperature was −2.15ºC and mean annual precipitation was 966 mm, with approximately 80% of the precipitation falling as snow (Caine 1996; Blanken et al. 2009). Snow depth is spatially variable and controlled by topography and westerly winds at the site (Litaor et al. 2008).

The distribution of alpine vegetation on Niwot Ridge was mapped by Komárková and Webber (1978), described in detail by Komárková (1979), and is representative of vegetation communities found through the southern Rocky Mountains. Based on characteristic species, moisture, snow, and substrate gradients, May and Webber (1982) subsequently identified six unique vegetation communities on Niwot Ridge: dry meadow, dry fellfield, moist shrub tundra, moist meadow, snowbed, and wet meadow. Primary production at Niwot Ridge is similar to that of other alpine sites and ranges between 100 and 300 g m^{-2} yr^{-1}, depending on the community (Bowman and Fisk 2001). However, it is also highly variable within communities; interannual variation in productivity on Niwot Ridge is similar to the range of estimates for alpine sites worldwide, arctic tundra communities, and herbaceous-dominated ecosystems of temperature zones (e.g., arid grasslands; Bowman and Fisk 2001).

Vegetation composition in the study site shares similarities with moist and dry meadow communities described by May and Webber (1982). However, the community is best described as an herbfield where wind is less severe and winter snows are deeper than elsewhere on Niwot Ridge (Bliss 1956; Johnson and Billings 1962; Bliss et al. 1981). The three species that generate the most aboveground biomass consistently throughout the site include the forb *Geum rossii* and the cushions *Minuartia obtusiloba* and *Silene acaulis*. *Carex rupestris* consistently generates the most aboveground biomass of the graminoids. All species found within the site are perennial except for the biennial *Androsace septentrionalis* which was not included in analyses.

We established twenty, 3 m diameter plots (Appendix A: Figure A1) in 2008 as part of the Alpine Treeline Warming Experiment (ATWE). Five replicate plots were assigned to each of four treatments: Control (C), Heated (H), Heated and Watered (HW), and Watered (W). We stratified plot assignments to treatments by local elevation and aspect, as well as total plant cover. The mean local slope of plots was 16% and the minimum and maximum were 8.5 and 21.5%. Six 1,000 W, infrared (IR) heaters (Mor Electric Heating, Comstock Park, MI, USA) were placed 1.2 m above ground on hexagonal arrays surrounding heated plots following the geometry of Kimball et al. (2008).

Heaters were turned on in October 2009, and were set to deliver an estimated 215 W m^{-2} additional IR under near-zero wind conditions in order to increase annual soil temperatures by approximately 2–5°C relative to ambient conditions. Due to hydrological artifacts created by midwinter snowmelt, we subsequently adjusted heater output to ~43 W m^{-2} in mid-winter (Nov–Feb) and to ~170 W m^{-2} the rest of the year (Mar–Oct) in

November 2010. Actual heating varied due to high and variable wind speeds at the site. Heaters automatically turned off when wind speed exceeded 10 m s^{-1} during the winter and 30 m s^{-1} during the summer due to low heater efficiency at high wind speeds (Kimball et al. 2008). Watering treatments began soon after snowmelt, once the average soil moisture in heated plots dropped below that of control plots, and continued through September. We applied 2.5 mm of water weekly to all watered plots (HW and W) to offset soil drying due to heating and to examine effects of supplemental growing season moisture on productivity under ambient temperature.

Climate and soil microclimate

We divided each plot into four 1 m^2 quadrants to account for variation within plots and recorded soil moisture and temperature at 5–10 cm depth every 15 min using one probe (ECTM and 5TM; Decagon, Pullman, WA, USA) placed vertically in the center of each quadrant. Soil moisture was recorded as volumetric water content (Θ, m^3 m^{-3}). We calibrated soil probes in the laboratory to values ranging from dry to saturated using soil collected adjacent to plots and sieved to remove particles >2 mm. Air temperature, relative humidity, and wind speed (HMP45C; Vaisala, Helsinki, Finland; 03101-L; RM Young, Traverse City, MI, USA) were recorded 2 m above ground every 15 min from a meteorological tower located at the center of the site. Snow disappearance is detectable the same day by a large change in soil temperature (Harte et al. 1995). We determined the presence of snow on quadrants when days had < 0.5ºC diel soil temperature variability. Temperature-based snow cover determinations were consistent with bi-weekly manual snow surveys. We calculated the date of snowmelt for each quadrant as the first snow-free day when all subsequent snow cover events lasted less than four continuous days. We calculated soil degree days (SDD_0), analogous to growing degree days, as the sum of mean daily temperatures for all days when the mean daily temperature was > 0ºC, from the date of snowmelt to the date of peak aboveground biomass. Similarly, we calculated soil moisture days (SMD_{25}) as the sum of mean daily volumetric water content (VWC) when the mean daily VWC was > 0.25%. We chose this value since it was the mean VWC of control plots during the experiment.

Productivity

The majority of alpine plant species at Niwot Ridge are perennials that produce aboveground biomass that senesces completely in the late summer or early fall. Although some species (e.g., *Solidago multiradiata*) can overwinter with some green leaves below the snow, the amount of overwinter growth is negligible when compared to biomass produced during the summer growing season (Bowman and Fisk 2001). We conducted vegetation surveys at peak community biomass (determined by weekly visual inspection of plant phenology in each plot). Surveys typically began in late July and were completed in early August following a 5-week gradient in production that paralleled snowmelt timing from the lowest to highest elevation plots at the site. We visually estimated the total cover of vascular plants, solid rock, gravel, lichens, bryophytes, bare ground, fine litter, and woody debris to the nearest 0.25% (with all summing to 100%), and did the same for the top cover of each vascular plant species using a 1 m^2 quadrat divided into 10

cm^2 cells for each quadrant. Species are short in stature (typically less than 10 cm in height), often exhibiting prostrate growth, making top cover a reasonable estimate of aboveground biomass.

We divided all species into one of four life form groups (i.e., forbs, cushions, graminoids, succulents) for analyses in order to evaluate potential compensating increases and decreases in life form groups. Additionally, we selected a subset of species for which to examine compensation within each of the life form groups. We selected two species from each life form group: forbs (*Arenaria fendleri* and *Geum rossii*), cushion/mat-forming species (*Minuartia obtusiloba* and *Sibbaldia procumbens*), graminoids (*Carex rupestris* and *Trisetum spciatum*), and succulents (*Chionophila jamesii* and *Sedum lanceolatum*) based on the amount of biomass produced in control plots across all years of the experiment and occurrence in at least four replicates of each treatment in order to maintain statistical power. *M. obtusiloba*, *S. procumbens*, *C. jamesii*, and *S. lanceolatum* were all the top two producing species in their respective life form groups. *G. rossii* was the top producing forb species and *A. fendleri* was in the top five. *C. rupestris* was the top producing graminoid species and *T. spicatum* was in the top three. All species selected were among the top ten producing species in control plots but their rank changed with year.

To relate cover estimates to aboveground productivity, we established additional 0.25 m^2 quadrats ($n = 27$) near the experimental plots within which percent cover of all species were measured as above. We established an additional 7—1 m^2 quadrats to test for potential scaling issues. Following cover estimation at peak aboveground biomass, we harvested all aboveground vascular plant biomass sorted by species, dried it at 60ºC for

48 hours, and weighed it (Walker et al. 1994). We used linear regressions to convert community- and species-level cover to measurements of productivity (Appendix B: Table B1; de Valpine and Harte 2001). Slope coefficients between cover and aboveground productivity were not significantly different between 0.25 m^2 and 1 m^2 quadrats nor were R^2 values (0.76 and 0.94; Appendix B: Table B2). All species-level regressions were significant at $\alpha < 0.001$ and 6 of the 8 regressions had R^2 values ≥ 0.80. The two remaining regression equations, for *T. spicatum* and *M. obtusiloba*, produced R^2 values of 0.36 and 0.58 and were included in analyses and discussed when necessary. Lastly, we applied conversion equations to all measurements of cover recorded in permanent plots to estimate changes in productivity under the treatments. May and Webber (1982) show clip harvests at peak season is a robust method for estimating primary production.

Analyses

Six of the 80 experimental quadrants were severely disturbed by gophers during the experiment and were not included in analyses. We calculated all statistics using R 2.15.3 (R Core Team 2013). Regression parameters relating cover and aboveground productivity (g m^{-2} yr^{-1}) were calculated using robust standard errors obtained from “sandwich” variance estimates using the sandwich and lmtest packages (Zeileis and Hothorn 2002; Zeileis 2004) to account for the assumptions of homoscedasticity and to allow for a more conservative approach. Aboveground productivity values were log transformed when necessary to meet the test assumptions. We used linear mixed-effects models using the lme function in the nlme package (Pinheiro et al. 2006) to assess heating and watering effects on community-, life form-, and species-level productivity. We also used linear mixed-effects models to assess heating and watering effects on date of snowmelt, SDD_0, and SMD_{25}. This hierarchical approach enabled us to combine the estimation of fixed effects (heating or watering) while allowing for variation in sample sizes (due to gopher disturbance or incomplete environmental data) and multiple levels of nested random effects (repeated measurements of quadrants within plots at a given elevation each year; Zuur et al. 2009).

We used a model building approach following Zuur et al. (2009). Elevation, plot, and quadrant were treated as nested random effects because of repeated measures and to account for spatial autocorrelation between quadrants within the same plot at a given elevation. We used random regression slopes in our models to effectively control for pseudoreplication while accounting for heterogeneity between quadrants within plots. This greatly reduced our risk of making a type I error by allowing for more robust confidence intervals that more accurately fit our data while also potentially reducing our risk of type II errors by lowering residual variance by accounting for between-quadrant variation in slopes (Schielzeth and Forstmeier 2009). The significance of each scale in the random effects nesting (i.e., elevation, plot, and quadrant) was determined by comparing models with and without each level nested using restricted maximum-likelihood. All random effects were significant at $\alpha \leq 0.0001$.

We subsequently built a model for each level tested. We included interactions between heating and watering and year. We tested the relative importance of soil temperature and moisture with SDD_0 and SMD_{25} as additional continuous fixed effects. This enabled us to determine the strength of treatments in predicting productivity and whether or not the treatments were manifest in soil temperature and moisture. We subsequently removed fixed effects and compared models with the Akaike Information Criterion (AIC) using maximum-likelihood to allow for a more conservative comparison of models using unbiased estimators of variance terms (Zuur et al. 2009). We used Wald *F*-tests to assess significance of predictor variables. When treatments and their interactions were significant we used pairwise *t*-tests with a Bonferroni-Holm adjustment to assess differences in productivity between treatments within years. We also used pairwise *t*-tests with a Bonferroni-Holm adjustment to test for pre-treatment differences between plots using productivity data collected in 2009. Additionally, we used diagnostic plots to explore potential violations of assumptions and test model fitting. The same modeling approach was used to assess differences in productivity of community, life form, and species aboveground productivity.

Results

Climate and soil microclimate

Annual climate at Niwot Ridge varied drastically from 2010 to 2012 (Table 1). Mean annual precipitation was 21–23% greater in 2011 compared to 2010 and 2012, and growing season precipitation was lowest in 2011. Mean annual temperature was also lower in 2011 but mean growing season temperature was higher. Date of snowmelt in heated plots was 9.4 ± 0.14 days ($\bar{x}$ ± sd) earlier and heated plots reached peak aboveground biomass 6 ± 0.1 days earlier than non-heated plots throughout the three years of the experiment (Appendix A: Table A1). However, heating did not advance snowmelt the same amount each year and in all plots (Table 2; Fig. 1).

Heating treatments had a limited effect on average soil temperatures (< 2ºC). SDD_0 did not vary predictably with heating and watering treatments but did differ between years (Table 2). Heating affected SDD_0 in 2010, but not in other years ($F_{2,115} = 10.72$, $p = 0.0001$), as did watering ($F_{2,115} = 10.41$, $p = 0.0001$; Table 2; Fig. 1). SDD_0 were 13% lower in heated plots ($p < 0.001$), 16% lower in watered plots ($p < 0.001$), and 7% lower in heated + watered plots ($p = 0.03$) relative to controls in 2010. SDD_0 were 10% higher in watered plots than heated + watered plots ($p < 0.01$). Similarly, heating and watering treatments did not consistently predict SMD_{25} but SMD_{25} did vary by year (Table 2). Heating increased SMD_{25} in 2010 and 2011, but not in 2012 ($F_{2,115} = 3.93$, $p = 0.02$). Watering only increased SMD_{25} in 2011 ($F_{2,115} = 6.82$, $p < 0.01$). Heating more than doubled SMD_{25} in heated plots ($p < 0.01$) and nearly tripled SMD_{25} in heated + watered plots ($p < 0.001$; Fig. 1) in 2010. In 2011, SMD_{25} were 42% greater in heated + watered plots compared to controls ($p < 0.0001$).

Productivity

Plots contained a total of 48 species over the three survey years (Appendix A: Table A2). Not all species occurred in all plots or in all years. The mean number of species in each $1m^2$ quadrant was 17.03 ± 4.30 ($\bar{x}$ ± sd) in 2009, before the experiment began and varied from year to year (Appendix A: Table A3). There was no detectable difference in productivity between plots pre-treatment in 2009 (Appendix A: Fig. A3). Forbs accounted for approximately 63% of the total biomass produced across all years and treatments and represented 28 of 48 species measured (Appendix A: Table A4 and Table A2). Six of the 48 species measured were cushion or mat-forming species which together produced the second largest amount of biomass (23%) across all years and treatments. The ten graminoid and 3 succulent species produced the least amount of biomass (9% and 5%) across all years and treatments (Appendix A: Table A3).

Treatments by themselves did not significantly predict differences in community-level productivity, but year did, with the greatest productivity in 2012 and the least in 2011 (Table 3 and 4; Fig. 2). Productivity was 20% greater in heated + watered plots compared to control plots ($p < 0.01$; Fig. 2) and 18% greater compared to watered in 2010 ($p = 0.01$). Heated plots reached peak aboveground biomass an average of 13 ± 0.3 days earlier than non-heated plots in 2010 (Appendix A: Table A1 and A5; Fig. A2). Heating alone, and in combination with watering, had no effect on productivity in 2012 but watering alone increased productivity by 16% ($p = 0.01$). There was no effect of treatment on community-level productivity in 2011 or on the timing of peak biomass in 2011 or 2012. SDD_0 and SMD_{25} did not successfully predict community-level productivity (Table 2).

Treatment effects and the influence of soil microclimate varied across life form groups (Table 3 and 5). Forbs, cushions, and succulents all responded to heating and watering treatments in some years. Forb productivity decreased by 23% with watering alone in 2010 and decreased by 24% with heating alone in 2011. Overall, forb productivity was greater in heated + watered plots all years of the experiment compared to plots that were only watered. Cushion species productivity increased 41% in watered plots compared to controls and more than doubled in heated + watered plots in 2012 (Fig. 3). There was no treatment, year, or soil microclimate effect on the graminoid life form group throughout the duration of the experiment (Table 2; Fig. 3). Although linear mixed effects models revealed a significant effect of heating on succulent productivity when year was considered (Table 4), no treatment effects were detected in subsequent tests (Fig. 3).

Species-level responses did not always follow that of their entire life form group. Still, species had positive, negative, and no response to the treatments and to soil microclimate variation (Table 3 and 6). Similar to all forbs, *A. fendleri* productivity increased 25% in heated + watered plots compared to heated only plots in 2010 (Fig. 4). In contrast, *G. rossii* did not respond to treatments in the same year. However, both *A. fendleri* and *G. rossii* productivity decreased in heated plots in 2011 and *G. rossii* also decreased in watered plots. Although *A. fendleri* did not respond to treatments in 2012, heating once again decreased *G. rossii* productivity relative to controls. Similar to the entire cushion life form group, *M. obtusiloba* doubled productivity in watered plots compared to heated + watered plots in 2011 and 2012 (Table 6; Fig. 4). Like the graminoid life form group, there was no detectable difference in *C. rupestris* productivity between treatments in any of the years but *T. spicatum* increased productivity by 81% in heated plots in 2010. Conversely to the entire succulent life form group that showed no response to treatments, *S. lanceolatum* in watered plots more than doubled its productivity compared to control and heated plots (Fig. 4).

Discussion

We found that alpine productivity responded to modest heating only when plots were also watered, and then only in some years. Community-level productivity increased in heated + watered plots in 2010; the increase in plots that were only heated was not significant (Figure 2). Thus, it appears that warming effects alone were not sufficient enough to induce changes in community-level productivity. Contrary to what was expected, heated plots were subject to fewer soil degree days (SDD_0) in 2010. This is due to exposure to lower temperatures in spring resulting from earlier snowmelt in combination with reduced exposure to high temperatures later in summer resulting from earlier peak biomass. Additionally, heated plots also experienced a greater number of high soil moisture days (SMD_{25}) in 2010, likely due to the advanced date of snowmelt and slower rate of soil drying earlier in the year, which increased moisture available early in the season for plants cued to timing of snowmelt. This may be an artifact of manipulating plots within a larger landscape, since the seasonal soil dry-down following snowmelt in early melting plots is delayed by water influx from snow continuing to melt upslope (Isard 1986). However, heated only and heated + watered plots both experienced advanced snowmelt relative to control plots but only heated + watered plots achieved observable changes in community-level productivity. It is possible that additional moisture during the growing season coupled with an earlier snowmelt prevents plants from experiencing a seasonal dry-down of soils that is typical of communities at Niwot Ridge (Taylor and Seastedt 1994) and that earlier melt alone is insufficient to increase productivity in this site.

Niwot Ridge and similar high-elevation ecosystems receive < 25% of the total annual precipitation during the growing season (Greenland and Losleben 2001) and previous studies have shown that seasonal snowpack depth along with the timing of snowmelt largely determine topographic variation in soil moisture which explains variation in above- and belowground productivity in different plant communities (Holway and Ward 1965; Walker et al. 1993; Fisk et al. 1998). Our results from 2010 agree that soil moisture and the timing of snowmelt may be determinants in aboveground productivity but also highlight the fact that these two factors alone cannot reliably explain community-level productivity. Growing season length is largely dependent upon the day of snowmelt, as are growing season soil temperatures (SDD_0). Our results from 2010 also show that earlier snowmelt due to heating or due to a shallower seasonal snowpack leads to earlier peak productivity at the community-level, potentially indicating that increased soil moisture stress in combination with earlier snowmelt may in fact modulate overall productivity.

Summer precipitation has been shown to influence alpine productivity both on a daily timescale (Billings and Bliss 1959; Berdanier and Klein 2011) and on a seasonal timescale (Walker et al. 1994). Billings and Bliss (1959) followed daily productivity rates of an alpine community in the Medicine Bow Mountains, Wyoming and found that peak productivity was reached immediately before a seasonal drop in soil moisture and was strongly dependent upon the timing of snowmelt. However, they found that as long as summer rainstorms are consistent (almost daily) and soil moisture for production is maintained then production continues but that even a short period of drought (~7 days without rainfall) has marked effects on productivity. They also suggested that soil and air temperatures are likely not as important for the observed changes in daily productivity since neither of these abiotic variables differ greatly during the growing season. Berdanier and Klein (2011) also showed that soil moisture plays an important role in determining daily alpine productivity, and that an increase in growing season length will only increase production if soil moisture is also increased. Similarly, Walker et al. (1994) showed that none of their communities tested were sensitive to variation in annual thawing degree days (same as our soil degree days) but were strongly linked with seasonal soil moisture and, in some cases, topography. Our findings agree that soil temperatures are likely not as important as soil moisture and that the timing of snowmelt and increased available soil moisture may highlight the importance of topography combined with its role in influencing the timing of snowmelt.

Interannual variability was a key driver and an important modulator of soil microclimate and productivity responses. This has been found in previous experiments, both manipulative and observational (Walker et al. 1994; Seastedt and Vaccaro 2001; Klein et al. 2004). Walker et al. (1994) found that climate variability from year to year explained up to 40% of the observed changes in community biomass produced each year at Niwot Ridge. Our study not only highlights interannual climate variability as an important control on alpine productivity, but also the subsequent effects it has on how treatments are able to influence abiotic controls (e.g., the timing of snowmelt and soil moisture days during the growing season) on alpine productivity.

IPCC (2007) reports that mountain ecosystems will experience not only longer, warmer growing seasons, but also colder winters as a result of a decreased snowpack. This will lead to colder soil temperatures as the insulating affects of a deep, seasonal snowpack is lost. This will likely have profound effects on alpine plants, many of which are dependent on the insulating properties of snow during the winter and spring (Walker et al. 1993), and suggests that some species may be unable to tolerate or take advantage of a longer growing season brought on by advanced snowmelt (Giménez-Benavides et al. 2007; Inouye 2008). Wipf et al. (2009) conducted a winter snow removal experiment in the Swiss Alps and showed that although earlier snowmelt may lead to an earlier start of the seasonal life cycles of some species and an increase in the soil degree days accumulated, annual growth decreases when snowmelt is advanced and species are exposed to early-season frost events. Although we did not make an attempt to assess exposure to early-season frost events and primarily focused on community-level responses, our 2010 results show the opposite and that annual growth increases as snowmelt is advanced. Our heating treatments may provide a more realistic demonstration of how earlier snowmelt will occur under future climate scenarios: as a more gradual melt with increased temperatures while still allowing for interannual variation in winter and spring precipitation to occur, and with fewer frost events experienced by early season species. Furthermore, Walker et al. (1994) found that variation in productivity from year to year is strongly linked to the amount of spring precipitation that typically falls as snow. This coupled with IPCC (2007) projections of changes in precipitation may be important to account for when considering the increases we observed in heated + watered plots. Warmer temperatures advancing snowmelt coupled with an increase in precipitation falling as rain may further influence the changes in alpine productivity we can expect in response to climate change.

There was significant variation between life form groups and species in their responses to treatments and the associated abiotic factors. Some species responded to treatments similar to their respective life form group while others did not. However, none of the selected species pairs showed increases or decreases that would suggest life form productivity was the result of compensatory responses of species; nor did they show equal and opposite responses when there was no response at the life form-level. This may be the result of abundant species driving the responses of their respective life form groups (e.g., *G. rossii* largely determining overall forb responsiveness) while other species within the same life form group responded not as strongly or at all. At the same time, interannual climate variation largely determined the responses of life form groups and species to treatments and did not follow a consistent pattern throughout the experiment. For example, when the forb life form group responded to treatments in 2010, *A. fendleri* was the only species to exhibit a response. In 2011, both *A. fendleri* and *G. rossii* responded to treatments while, in 2012, *G. rossii* was the only species to respond to treatments. It is possible that *G. rossii* responded to treatments in both 2011 and 2012 since they were abnormal years in terms of precipitation. 2011 saw above-average winter precipitation and below-average summer precipitation while, conversely, 2012 saw below-average winter precipitation and above-average summer precipitation. 2010 exhibited average conditions typical of Niwot Ridge and *G. rossii* (the dominant species in the community) did not respond to treatments.

It appears that one dominant species determined the overall life form response for cushions, graminoids, and succulents. *M. obtusiloba* appears to be the cushion species driving the life form group response as there was no detectable response from *S.*

procumbens and *M. obtusiloba* responded to treatments approximately the same way the cushion life form group did (i.e., increasing productivity when watered). Graminoids were the only life form group not to respond to treatments or, even more surprisingly, year. However, *T. spicatum* did respond to heating in 2010 by more than doubling its productivity relative to controls. However, *T. spicatum* generates less than 10% of the overall graminoid productivity in the community. The dominant graminoid species (*C. rupestris*) accounts for approximately 85% of the total graminoid life form productivity but did not respond to any of the treatments or vary by year, maintaining the relatively constant graminoid productivity from year to year and masking the effects of treatments on *T. spicatum*. Succulent productivity did not respond to treatments in 2012 but the succulent species *S. lanceolatum* responded positively to watering treatments by more than doubling its productivity, illustrating the fact that there is presumably variation in the system that is not explained by variation in the two selected species or in microclimate—either treatment driven or year driven. Nonetheless, our results show that overall community responses do mask life form group, as well as individual species responses within the community. At the same time, many species and life form groups were not sensitive to climate manipulations, perhaps because of lagged responses in these largely long-lived perennial species or because of the limited (< 2ºC) average warming.

Approximately 50% or more of alpine plant species are thought to pre-form buds (Theodose et al. 1996; Körner 2003). *Geum rossii* pre-forms leaves and inflorescences which each take a full three years to progress from initiation to emergence, growth, and senescence (Meloche and Diggle 2001). Thus, interannual correlations may not accurately reveal the effects of elevated temperatures and moisture changes on all alpine species. It is possible that environmental conditions from previous years (1—3 years prior to current growth) are partially responsible for any current season's growth and it has been suggested that responses to environmental changes may in fact be delayed for many alpine species (Aydelotte and Diggle 1997). Previous warming experiments in high elevation meadows and tundra have observed little responsiveness of community-level productivity to warming in the first few years of treatments (e.g., Harte et al. 1995; Hobbie and Chapin 1998) but others have observed significant changes after one or two years of warming (e.g., Arft et al. 1999; Klein et al. 2007). Our results suggest that community-level changes can occur even after only one year of warming but, depending on climate variability from year to year, do not fully capture what is occurring at all levels of biological organization.

It is likely that measurements of aboveground productivity by themselves do not fully capture alpine plant responses to treatments and can be better understood by measuring belowground productivity as well. Most of the research on alpine plant productivity has been focused on aboveground biomass with few studies addressing belowground production at anything other than the community level (Scott and Billings 1964; Webber and May 1977; Rehder and Schäfer 1978; Fisk et al. 1998). Even fewer have investigated belowground productivity at the species level (Daubenmire 1941). This is presumably due to the difficulty of extracting entire root structures from individual plants whose root systems are highly overlapping. The majority of alpine plant biomass is located belowground, with up to approximately 85% of it concentrated in the upper 10 cm of soil (Webber and May 1977). Although our results indicate that heating and watering treatments had a small effect on soil temperature, studies such as this one where soil temperature and moisture (measured at 5—10cm depth) are used to assess the impacts of heating and watering treatments on aboveground productivity would be a suitable way to also address belowground responses as well.

The results presented here are short-term responses of an alpine community composed of long-lived, perennial species that varied markedly in their responses to treatments. The biggest restriction on replicating samples within a community is the cost of such an experiment in addition to time constraints in harvesting enough samples from multiple levels. Although it was possible to obtain a highly robust sampling of community-level productivity, it was difficult to replicate species-level samples due to an uneven distribution of species across plots and quadrants. Our species-level responses were only tested on two species from each of the life form groups and, thus, do not capture the full range of variability at the species-level but do successfully highlight a subset of species likely driving life form-level and, when taken together, community-level responses. We further establish that interannual variability has a strong effect on productivity at the community-, life form-, and species-levels and can dictate how effective treatments are in changing abiotic soil variables and altering productivity. Lastly, our results raise significant questions in response to the controls on alpine productivity, the level at which productivity is being measured by the experimentalist, and experimental design in the alpine. Future studies will benefit by addressing these issues and by considering changes in productivity at multiple levels of biological organization.

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Tables

Table 1. Summary table of growing season and annual climate at Niwot Ridge from 2010—2012. Temperatures (Tmin, Tmax, Tmean) and precipitation sums (Precip) are reported from a Natural Resource Conservation Service weather station located at Niwot Ridge (http://www.wcc.nrcs.usda.gov).

	Growing Season				**Annual**	
Year	**Tmin (°C)**	**Tmax (°C)**	**Tmean (°C)**	**Precip (mm)**	**Tmean (°C)**	**Precip (mm)**
2010	-3.4	17.5	10.1	152	2.9	719
2011	9.2	15.5	13.1	89	2.6	914
2012	-0.6	19.7	9.6	211	3.8	701

Table 2. Wald F-test results of linear mixed-effects models for date of snowmelt (Julian day), soil degree days (SDD_0), and soil moisture days (SMD_{25}) as response variables. Elevation, plot, and quadrant were included as random effects in all models.

	Date of snowmelt			**SDD_0**			**SMD_{25}**		
Variable	***df***	**F-value**	***P*-value**	***df***	**F-value**	***P*-value**	***df***	**F-value**	***P*-value**
H	1,16	7.81	**0.01**	1,16	0.06	0.81	1,16	19.54	< **0.001**
W	1,16	0.01	0.91	1,16	0.04	0.84	1,16	3.23	0.09
Year	2,115	1188.29	< **0.0001**	2,115	141.49	< **0.0001**	2,115	11.24	< **0.0001**
H × W	1,16	0.01	0.90	1,16	0.49	0.49	1,16	0.26	0.61
H × Year	2,115	8.63	< **0.001**	2,115	10.92	< **0.0001**	2,115	9.41	< **0.001**
W × Year	2,115	1.15	0.32	2,115	10.17	< **0.001**	2,115	1.56	0.21
H × W × Year	2,115	5.22	< **0.01**	2,115	1.57	0.21	2,115	0.33	0.72

Table 3. Likelihood ratio tests for fixed effect parameters of linear mixed-effects models for productivity at the community, life form, and species levels. Elevation, plot, and quadrant are included as random effects in all models. Significance ($P \leq 0.05$) is assessed as terms are removed from the model and model comparisons are made. Final model Akaike Information Criterion (AIC) values are reported parenthetically for each level.

	H × W × Year				**SDD_0 × SMD_{25}**			
Level (final model AIC)	**ΔAIC**	**df**	***L*-value**	***P*-value**	**ΔAIC**	**df**	***L*-value**	***P*-value**
Community (1590)	31	7	48.86	**< 0.0001**	-4	15	1.81	0.61
Forbs (1548)	22	7	44.40	**< 0.0001**	1	15	2.62	0.45
***Arenaria fendleri* (899)**	10	7	31.90	**< 0.0001**	7	15	11.39	**< 0.01**
***Geum rossii* (1437)**	35	7	56.54	**< 0.0001**	-3	15	2.24	0.52
Cushions (747)	27	7	48.85	**< 0.0001**	-2	15	3.74	0.29
***Minuartia obtusiloba* (1544)**	9	7	30.50	**< 0.01**	6	15	12.25	**< 0.01**
***Sibbaldia procumbens* (548)**	-7	7	15.75	0.15	-1	15	5.63	0.13
Graminoids (436)	-14	7	8.06	0.71	-1	15	4.14	0.25
***Carex rupestris* (315)**	-9	7	11.48	0.41	-5	15	0.20	0.98
***Trisetum spciatum* (300)**	2	7	22.28	**0.02**	0	15	5.87	0.12
Succulents (427)	11	7	32.31	**< 0.0001**	-6	15	0.38	0.95
***Chionophila jamesii* (394)**	7	7	27.81	**< 0.01**	-1	15	4.46	0.22
***Sedum lanceolatum* (264)**	24	7	45.25	**< 0.0001**	5	15	10.22	**< 0.01**

Table 4. Wald F-test results of final linear mixed-effects models for community-level productivity. Elevation, plot, and quadrant are included as random effects in the model.

Variable	***df***	**F-value**	***P*-value**
H	1,16	0.22	0.64
W	1,16	1.08	0.31
Year	2,115	13.87	< **0.0001**
H × W	1,16	0.03	0.87
H × Year	2,115	18.61	< **0.0001**
W × Year	2,115	4.80	**0.01**
H × W × Year	2,115	3.43	**0.04**

Table 5. Wald F-test results of final linear mixed-effects models for life form-level productivity of forbs, cushions, graminoids, and succulents. Elevation, plot, and quadrant are included as random effects in all models.

	Forbs			**Cushions**			**Graminoids**			**Succulents**		
Variable	***df***	***F*-value**	***p*-value**	***df***	***F*-value**	***p*-value**	***df***	***F*-value**	***p*-value**	***df***	***F*-value**	**p-value**
H	1,16	0.94	0.35	1,16	2.48	0.14	1,16	0.05	0.82	1,16	0.08	0.78
W	1,16	0.12	0.74	1,16	1.62	0.22	1,16	0.06	0.80	1,16	0.04	0.84
Year	2,115	14.48	< **0.0001**	2,115	27.95	< **0.0001**	2,109	1.03	0.36	2,114	2.64	0.08
H × W	1,16	6.08	**0.02**	1,16	1.39	0.26	1,16	0.01	0.94	1,16	0.31	0.58
H × Year	2,115	3.76	**0.03**	2,115	3.95	**0.02**	2,109	0.79	0.48	2,114	15.10	< **0.0001**
W × Year	2,115	1.02	0.36	2,115	0.31	0.73	2,109	0.48	0.62	2,114	1.03	0.36
H × W × Year	2,115	3.08	**0.05**	2,115	6.52	< **0.01**	2,109	0.91	0.40	2,114	0.47	0.63

Table 6. Wald F-test results of final linear mixed-effects models for species-level productivity of individual forbs (F), cushions (C), graminoids (G), and succulents (S). Elevation, plot, and quadrant are included as random effects in all models.

	***Arenaria fendleri* (F)**			***Geum rossii* (F)**			***Minuartia obtusiloba* (C)**			***Sibbaldia procumbens* (C)**		
Variable	***df***	***F*-value**	***p*-value**	***df***	***F*-value**	***p*-value**	***df***	***F*-value**	***p*-value**	***df***	***F*-value**	**p-value**
H	1,16	< 0.01	0.98	1,16	0.01	0.93	1,16	3.45	0.82	1,7	0.27	0.62
W	1,16	1.53	0.23	1,16	0.13	0.72	1,16	1.86	0.80	1,7	5.39	**0.05**
Year	2,107	14.91	< **0.0001**	2,113	26.48	< **0.0001**	2,107	19.92	0.36	2,45	0.58	0.56
H × W	1,16	5.28	**0.03**	1,16	6.88	**0.02**	1,16	3.43	0.08	1,7	0.17	0.17
H × Year	2,107	3.27	**0.04**	2,113	1.65	0.20	2,107	4.87	< **0.01**	2,45	0.12	0.12
W × Year	2,107	1.67	0.19	2,113	2.50	0.90	2,107	2.17	0.12	2,45	0.90	0.90
H × W × Year	2,107	2.29	0.11	2,113	2.19	0.12	2,107	1.24	0.29	2,45	0.54	0.54

	***Carex rupestris* (G)**			***Trisetum spicatum* (G)**			***Chionophila jamesii* (S)**			***Sedum lanceolatum* (S)**		
Variable	***df***	***F*-value**	***p*-value**	***df***	***F*-value**	***p*-value**	***df***	***F*-value**	***p*-value**	***df***	***F*-value**	**p-value**
H	1,14	0.07	0.78	1,16	1.45	0.25	1,15	< 0.01	0.98	1,12	0.32	0.58
W	1,14	0.41	0.53	1,16	0.74	0.40	1,15	0.21	0.65	1,12	0.02	0.88
Year	2,67	0.07	0.93	2,71	4.31	**0.02**	2,92	0.20	0.82	2,45	25.40	< **0.0001**
H × W	1,14	0.22	0.64	1,16	1.28	0.27	1,15	1.02	0.33	1,12	7.86	**0.02**
H × Year	2,67	0.85	0.43	2,71	5.44	< **0.01**	2,92	10.38	< **0.01**	2,45	4.47	**0.02**
W × Year	2,67	1.56	0.18	2,71	0.23	0.79	2,92	0.39	0.67	2,45	2.99	0.06
H × W × Year	2,67	2.03	0.14	2,71	0.14	0.86	2,92	1.05	0.35	2,45	1.54	0.22

Figures

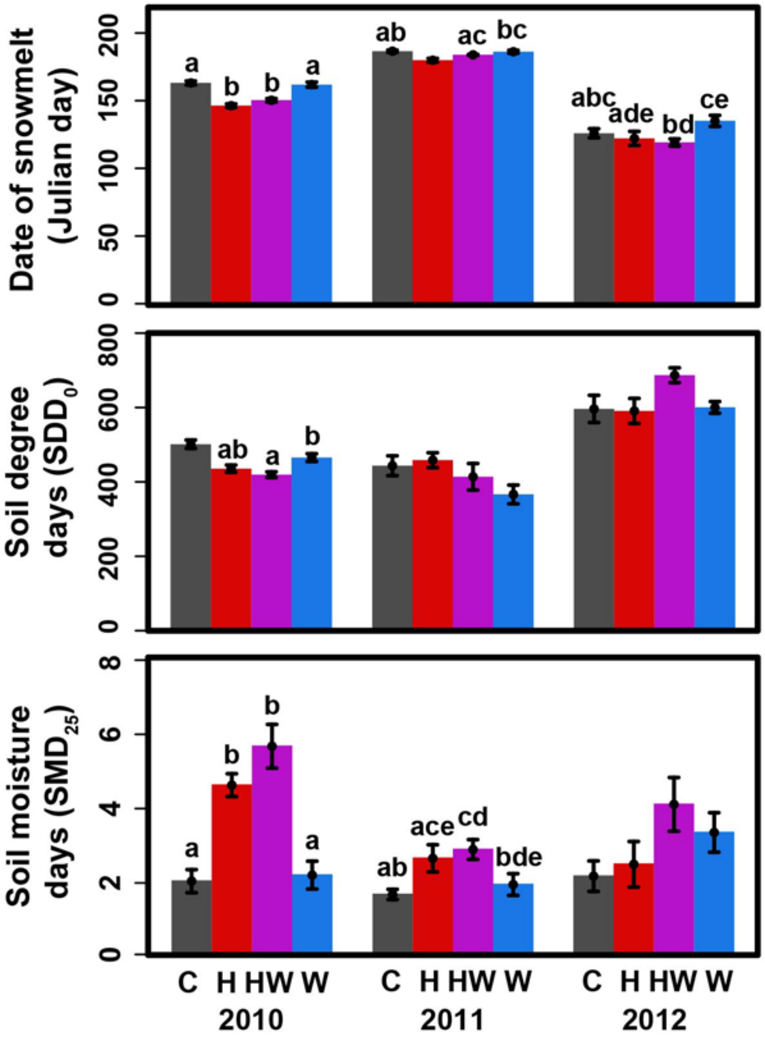

Figure 1. Snowmelt and soil microclimate responses to treatments. Means and standard errors of date of snowmelt (Julian day; top panel), soil degree days (SDD_0; middle panel), and soil moisture days (SMD_{25}; bottom panel) by treatment (C = control; H = heated; HW = heated + watered; W = watered) and year. Different letters above bars indicate statistically significant differences assessed by pairwise *t*-tests within year with Bonferroni-Holm corrected alpha.

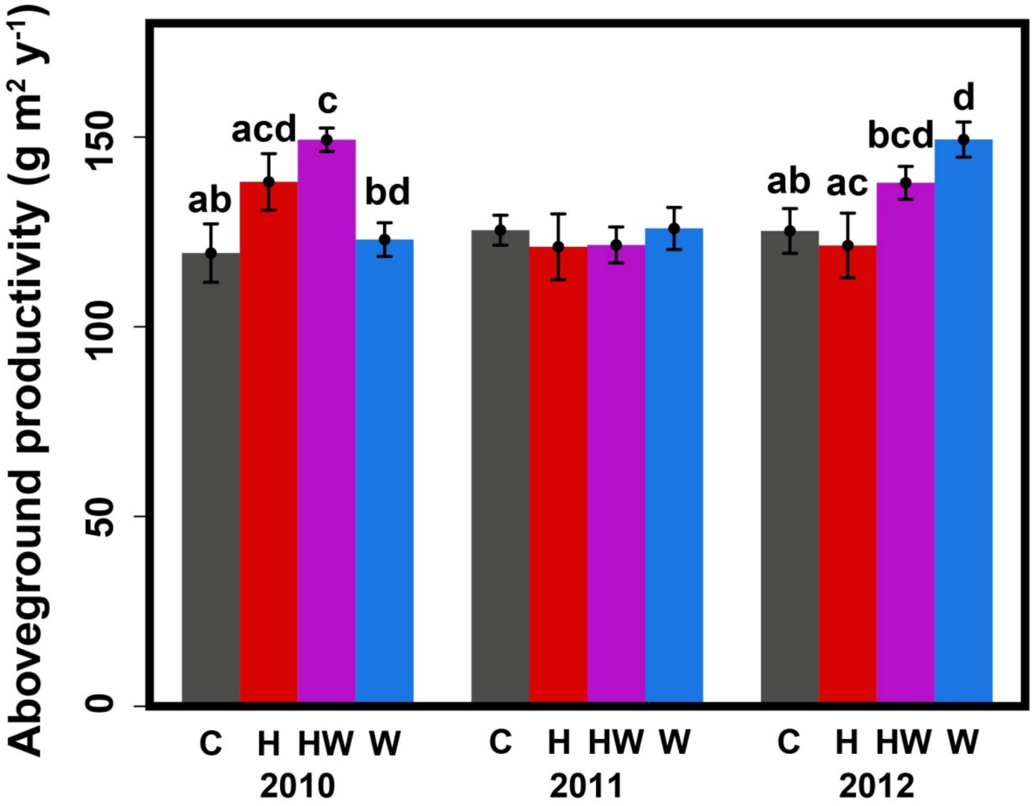

Figure 2. Aboveground productivity responses to treatments at the community-level. Means and standard errors of community-level aboveground productivity by treatment (C = control, H = heated, HW = heated + watered, W = watered) and year. Letters above bars indicate significance assessed by pairwise t-tests within year with Bonferroni-Holm corrected alpha.

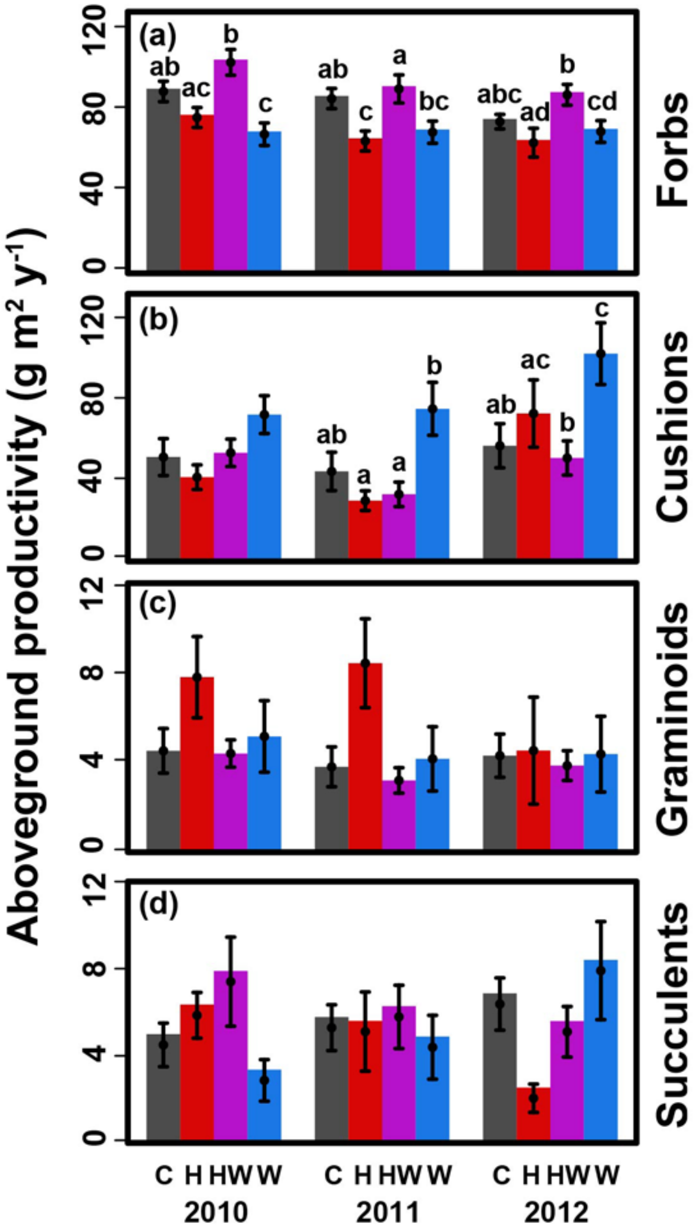

Figure 3. Means and standard errors of aboveground productivity of life-forms, (a) forbs, (b) cushions, (c) graminoids, and (d) succulents by treatment (C = control, H = heated, HW = heated + watered, W = watered) and year. Letters above bars indicate significance assessed by pairwise t-tests within year with Bonferroni-Holm corrected alpha. Note difference in scale of values for each panel.

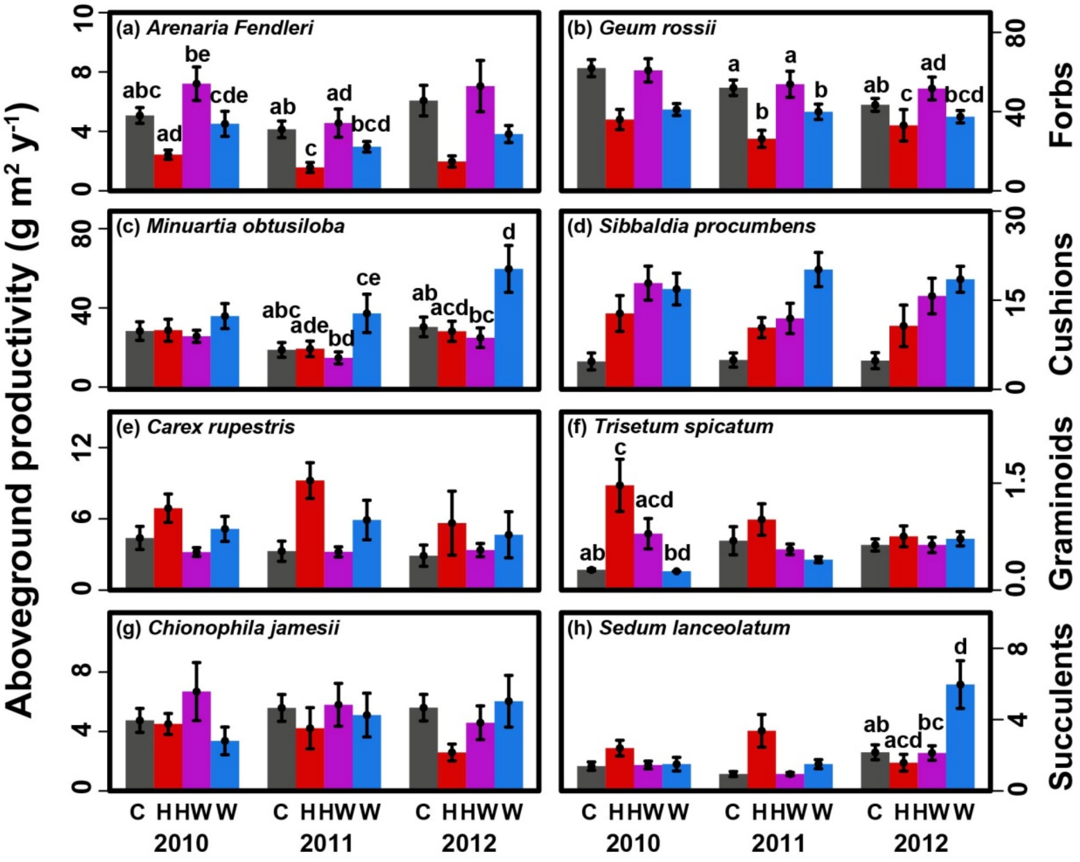

Figure 4. Means and standard errors of aboveground productivity of individual species, (a) *Arenaria fendleri*, (b) *Geum rossii*, (c) *Minuartia obtusiloba*, (d) *Sibbaldia procumbens*, (e) *Carex rupestris*, (f) *Trisetum spicatum*, (g) *Chionophila jamesii*, and (h) *Sedum lanceolatum* by treatment (C = control, H = heated, HW = heated + watered, W = watered) and year. Letters above bars indicate significance assessed by pairwise t-tests within year with Bonferroni-Holm corrected alpha. Note difference in scale of values for each panel.

Appendix A

Table A1. Summary table of the minimums, maximums, and mean with standard errors (± SE) of the dates of snowmelt (DOM) and peak aboveground biomass (DOPB) for each year in the heated and non-heated plots.

Year		**Min DOM**	**Max DOM**	**Mean DOM ± se**	**Min DOPB**	**Max DOPB**	**Mean DOPB ± se**
2010	**Heat**	133	157	150 ± 0.9	195	200	196 ± 0.2
	No Heat	151	174	164 ± 1.2	206	215	209 ± 0.5
2011	**Heat**	174	190	184 ± 0.7	207	234	223 ± 1.5
	No Heat	179	191	188 ± 0.7	209	234	225 ± 1.5
2012	**Heat**	112	144	123 ± 2.4	184	200	190 ± 1.3
	No Heat	112	151	132 ± 2.7	185	200	193 ± 0.7

Table A2. Species list of all species measured in the plots from 2009—2012. Not all species occurred in every plot or every year

Life form	**Family**	**Species**	**Genus**
Cushion/ mat-forming forb	Caryophyllaceae	*Minuartia*	*obtusiloba*
	Caryophyllaceae	*Silene*	*acaulis*
	Fabaceae	*Trifolium*	*dasyphyllum*
	Fabaceae	*Trifolium*	*nanum*
	Polemoniaceae	*Phlox*	*condensata*
	Rosaceae	*Sibbaldia*	*procumbens*
Graminoid	Cyperaceae	*Carex*	*rossii*
	Cyperaceae	*Carex*	*rupestris*
	Juncaceae	*Luzula*	*spicata*
	Poaceae	*Calamagrostis*	*purpurascens*
	Poaceae	*Deschampsia*	*caespitosa*
	Poaceae	*Elymus*	*scribneri*
	Poaceae	*Festuca*	*brachyphylla*
	Poaceae	*Poa*	*alpina*
	Poaceae	*Poa*	*arctica*
	Poaceae	*Trisetum*	*spicatum*
Herbaceous forb	Apiaceae	*Oreoxis*	*alpina*
	Asteraceae	*Antennaria*	*sp.*
	Asteraceae	*Artemisia*	*scopulorum*
	Asteraceae	*Erigeron*	*simplex*
	Asteraceae	*Hymenoxys*	*acaulis*
	Asteraceae	*Hymenoxys*	*grandiflora*
	Asteraceae	*Solidago*	*multiradiata*
	Boraginaceae	*Eritrichium*	*aretrioides*
	Boraginaceae	*Mertensia*	*lanceolata*
	Brassicaceae	*Draba*	*sp.*
	Brassicaceae	*Erysimum*	*capitatum*
	Brassicaceae	*Thlaspi*	*montanum*
	Campanulaceae	*Campanula*	*rotundifolia*
	Caryophyllaceae	*Arenaria*	*fendleri*
	Caryophyllaceae	*Cerastium*	*beeringianum*
	Fabaceae	*Trifolium*	*parryi*
	Liliaceae	*Allium*	*geyeri*
	Liliaceae	*Lloydia*	*serotina*
	Polygonaceae	*Bistorta*	*bistortoides*
	Portulacaceae	*Lewisia*	*pygmaea*
	Primulaceae	*Androsace*	*septentrionalis*
	Ranunculaceae	*Ranunculus*	*adoneus*
	Rosaceae	*Geum*	*rossii*
	Rosaceae	*Potentilla*	*diversifolia*
	Saxifragaceae	*Saxifraga*	*rhomboidea*
	Scrophulariaceae	*Castilleja*	*occidentalis*
	Scrophulariaceae	*Pedicularis*	*scopulorum*
	Selaginellaceae	*Selaginella*	*densa*
Succulent forb	Crassulaceae	*Sedum*	*lanceolatum*
	Primulaceae	*Primula*	*angustifolia*
	Scrophulariaceae	*Chionophila*	*jamesii*

Table A3. Summary table of the minimums, maximums, and mean number of species in a 1 m^2 quadrant from 2009—2012.

Year	Min # of Species	Max # of Species	Mean # of Species
2009	10	28	17.03
2010	10	30	16.85
2011	9	25	16.05
2012	10	27	16.47

Table A4. A summary table of the total productivity produced by each life form group within and across years is provided to highlight the dominant life form groups throughout the time of the experiment. Values are in g, m^{-2} yr^{-1} and summed across all plots each year.

	Year			
Life Form Group	**2010**	**2011**	**2012**	**All Years**
Forbs	301.10	276.550	268.70	846.35
Cushions	106.25	87.650	116.95	310.85
Graminoids	44.40	38.850	42.10	125.35
Succulents	23.60	22.925	22.70	69.225
Total	475.35	425.975	450.45	1351.775

Table A5. Wald F-test results of final linear mixed-effects models for date of peak aboveground biomass. Elevation, plot, and quadrant are included as random effects in the model.

Variable	***df***	**F-value**	***P*-value**
H	1,16	5.22	**0.04**
W	1,16	0.70	0.41
Year	2,115	999.62	< **0.0001**
H × W	1,16	0.99	0.33
H × Year	2,115	27.18	< **0.0001**
W × Year	2,115	3.14	**0.05**
H × W × Year	2,115	0.10	0.91

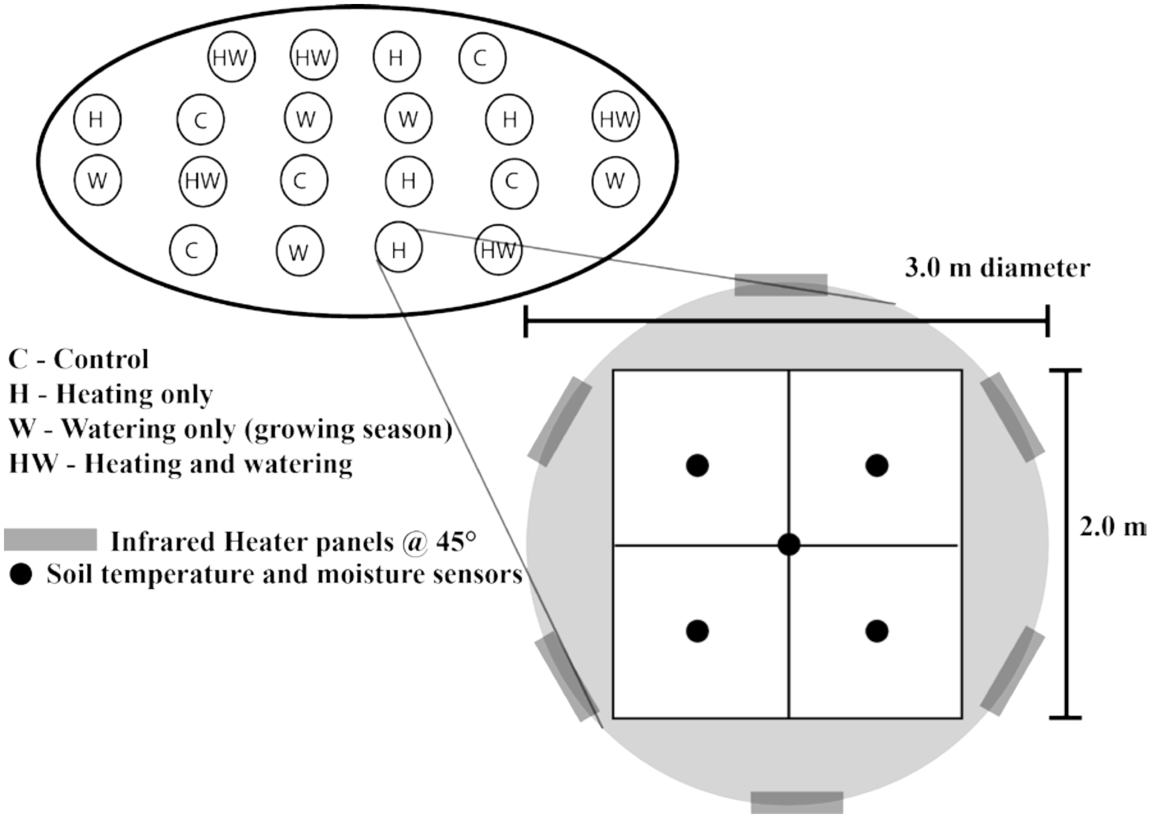

Figure A1. Diagram of site and plot design. Selected plot represents a heated plot with heater array panels as gray rectangles. Quadrant A is the upper right white square and B, C, D are the remaining white squares moving clockwise. Black circles represent soil temperature and moisture sensors.

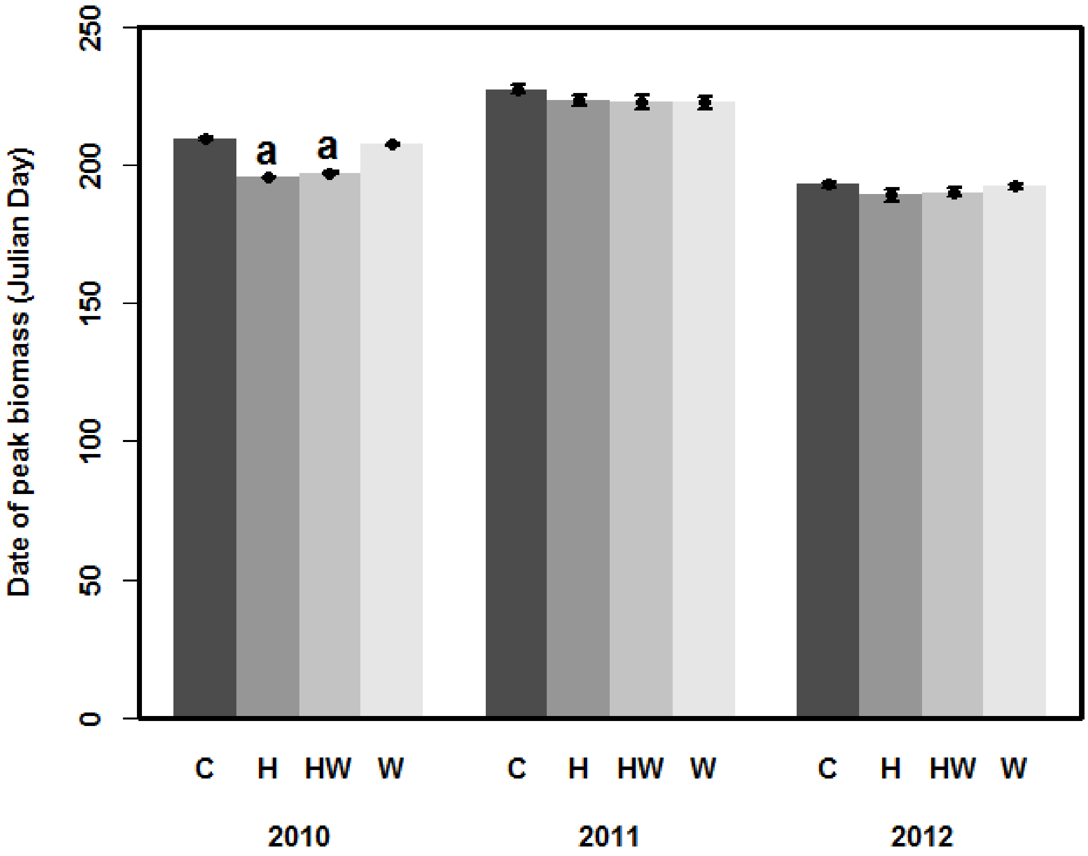

Figure A2. Date of peak biomass responses to treatments. Means and standard errors of date of peak biomass (Julian day) by treatment (C = control; H = heated; HW = heated + watered; W = watered) and year. Letters above bars indicate significance assessed by pairwise *t*-tests conducted on each group of bars per year with Bonferroni-Holm corrected alpha.

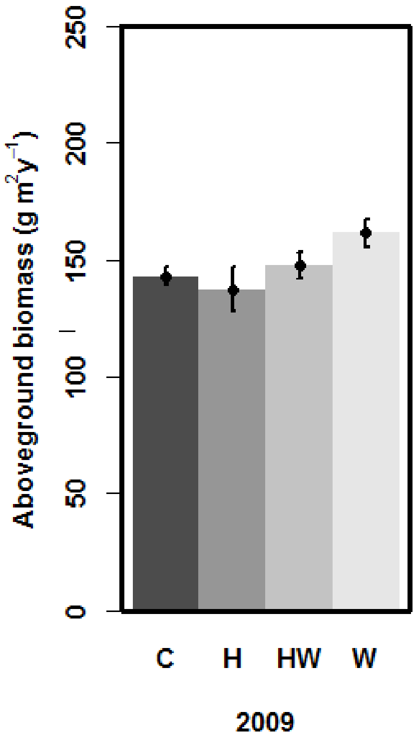

Figure A3. 2009 productivity comparisons of future treatment types. All data was recorded at peak aboveground biomass during the summer of 2009 (pre-treatment). Means and standard errors of peak community-level productivity by future treatment (C = control; H = heated; HW = heated + watered; W = watered). Pairwise *t*-tests conducted on each group of bars with Bonferroni-Holm corrected alpha revealed no detectable difference between plot types.

Appendix B

Table B1. Linear regression statistics for species mass by cover.

Growth Form and Species	***n***	***R^2***	***p*-value**	**slope**	**y-intercept**
Forbs					
Arenaria fendleri	29	0.80	<0.001	1.555	-0.016
Artemisia scopulorum	32	0.94	<0.001	1.628	0.156
Bistorta bistortoides	32	0.96	<0.001	1.543	0.131
Campanula sp.	7	0.94	<0.001	1.624	0.149
Castilleja occidentalis	4	0.35	0.41	1.991	0.505
Erigeron simplex	10	0.82	<0.001	0.873	0.047
Geum rossii	37	0.95	<0.001	2.810	-0.219
Lloydia serotina	11	0.77	<0.001	0.932	0.145
Oreoxis alpina	5	0.95	<0.01	1.794	-0.370
Potentilla diversifolia	24	0.96	<0.001	1.365	0.041
Saxifraga rhomboidea	5	0.63	0.12	0.491	0.414
Solidago spathulata	16	0.85	<0.001	1.892	0.111
Trifolium parryi	25	0.93	<0.001	2.072	0.167
Graminoids					
Carex rossii	4	0.81	0.10	0.996	0.742
Carex rupestris	18	0.98	<0.001	0.925	0.059
Festuca brachyphylla	8	0.04	0.65	0.330	0.231
Luzula spicata	19	0.85	<0.001	0.508	0.132
Trisetum spicatum	28	0.36	<0.001	0.969	0.115
Cushions and mat-forming species					
Minuartia obtusilosa	26	0.58	<0.001	5.614	-0.425
Phlox condensata	4	0.66	0.18	1.544	0.205
Selaginella densa	14	0.21	0.09	3.450	1.396
Silene acaulis	7	0.66	0.02	17.959	-4.748
Sibbaldia procumbens	11	0.90	<0.001	1.627	-0.252
Succulents					
Chionophila jamesii	20	0.82	<0.001	1.841	-0.128
Lewisia pygmaea	4	0.99	<0.001	0.441	0.017
Sedum lanceolatum	16	0.58	<0.001	2.357	0.578

Table B2. Linear regression statistics for plot type mass by cover.

Plot type	***n***	R^2	***p*-value**	**Slope**	**y-intercept**
1 m^2 plots	7	0.94	<0.001	2.084	19.293
0.25 m^2 plots	27	0.76	<0.001	2.290	0.245

Above photo: Silene acaulis *and* Carex rupestris. *Photo taken by Daniel E. Winkler at Niwot Ridge, Front Range of the Rocky Mountains, Colorado.*