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Soil moisture mediates alpine life form and community productivity responses to warming

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Abstract

Climate change is expected to alter primary production and community composition in alpine ecosystems, but the direction and magnitude of change is debated. Warmer, wetter growing seasons may increase productivity; however, in the absence of additional precipitation, increased temperatures may decrease soil moisture, thereby diminishing any positive effect of warming. Since plant species show individual responses to environmental change, responses may depend on community composition and vary across life form or functional groups. We warmed an alpine plant community at Niwot Ridge, Colorado continuously for four years to test whether warming increases or decreases productivity of life form groups and the whole community. We provided supplemental water to a subset of plots to alleviate the drying effect of warming. We measured annual above-ground productivity and soil temperature and moisture, from which we calculated soil degree days and adequate soil moisture days. Using an information-theoretic approach, we observed that positive productivity responses to warming at the community level occur only when warming is combined with supplemental watering; otherwise we observed decreased productivity. Watering also increased community productivity in the absence of warming. Forbs accounted for the majority of the productivity at the site and drove the contingent community response to warming, while cushions drove the generally positive response to watering and graminoids muted the community response. Warming advanced snowmelt and increased soil degree days, while watering increased adequate soil moisture days. Heated and watered plots had more adequate soil moisture days than heated plots. Overall, measured changes in soil temperature and moisture in response to treatments were consistent with expected productivity responses. We found that available soil moisture largely determines the responses of this forb-dominated alpine community to simulated climate warming.

Introduction

Alpine productivity is important to landscape carbon sequestration, mountain sustainability and resilience, and biodiversity (Bowman and Fisk [2001](#), Barni et al. [2007](#), Grêt-Regamey et al. [2008](#)). Effective management decisions to protect important alpine resources and key

species require a clear understanding of how climate change will impact alpine community and ecosystem processes. Climate models project increases in average temperatures of 2–6°C across western North America by 2100, with continued increases in atmospheric greenhouse gas concentrations (Stocker et al. [2013](#)). Models also project a decrease in the snow-to-rain ratio during winter months as a consequence of warmer winter temperatures, while projected changes in total precipitation vary regionally (Stocker et al. [2013](#)). High elevation sites in the Western U.S. have already warmed over the last several decades (Oyler et al. [2015](#)), although local temperature changes can be complex in mountainous terrain (Pepin and Losleben [2002](#), Pepin and Lundquist [2008](#)). The timing of snowmelt is also advancing in many mountainous watersheds (Barnett et al. [2008](#), Clow [2010](#)). Changes in snow accumulation and melt timing may be particularly important in areas where growing season soil moisture is determined by winter snowpack and date of snowmelt (Taylor and Seastedt [1994](#)), such as mountain ecosystems in the Western U.S. (Isard [1986](#), Greenland [1989](#), Walker et al. [1994](#)).

Higher temperatures and changes in snow accumulation and melt will have cascading effects on known drivers of alpine productivity (Billings and Bliss [1959](#), Galen and Stanton [1995](#)). Warmer temperatures may directly affect productivity by enhancing physiological growth processes, or more likely, will affect productivity indirectly by advancing snowmelt, allowing species to initiate growth earlier in the growing season (Shaw et al. [2002](#), Körner [2003](#), Inouye [2008](#), Ernakovich et al. [2014](#)). In many places, moisture from a melting snowpack determines the local distribution and productivity of alpine plants (Billings and Mooney [1968](#), Walker et al. [1994](#), Jonas et al. [2008](#), Engler et al. [2011](#)) and can determine how responsive or resistant a community will be to increased temperatures (Walker et al. [2006](#), Pauli et al. [2012](#)). In addition, increased temperatures that advance snowmelt could also result in drier soils during the growing season if there is no increase in summer rain. This could diminish any positive effect of warming. Although previous studies have experimentally explored these interactions in other systems (Shaw et al. [2002](#), Luo et al. [2008](#), Piper et al. [2013](#), Schaeffer et al. [2013](#), Zhang et al. [2013](#), Xu et al. [2014](#)), the vast majority of alpine ecosystem experiments have assumed temperature to be the sole factor limiting productivity (Zhang and Welker [1996](#), Henry and Molau [1997](#), Yang et al. [2014](#), but see Wipf et al. [2009](#)). Yet, temporal increases in tundra plant abundance and height, generally associated with increasing temperatures, were greatest on wet sites for deciduous shrubs and in the presence of near-surface permafrost for forbs, hinting at potential interactions (Elmendorf et al. [2012a](#)). Further, a meta-analysis revealed differential responses of tundra plants to experimental warming across sites varying in soil moisture (Elmendorf et al. [2012b](#)), with the strongest interaction found for shrubs. For forbs, responses to experimental warming were not consistent and did not differ according to site moisture, while for

graminoids, subgroup responses varied according to site moisture status, with sedges increasing in wet sites, grasses increasing in dry sites, and rushes unresponsive or slightly decreasing in dry sites (Elmendorf et al. [2012b](#)). However, few studies of tundra ecosystems (including those synthesized in Elmendorf et al. [2012b](#)) have advanced snowmelt timing since most researchers use passive open top chambers deployed after snow melts (Henry and Molau [1997](#), Walker et al. [2006](#)). Increased soil moisture stress resulting from higher soil temperature and earlier snowmelt may further modulate plant responses to warming and overall productivity. Controlled warming by watering experiments that include advances in snowmelt timing are required to more definitively determine the interaction between warming and moisture availability.

Finally, given that community productivity is determined by the aggregate individual responses of species to interacting environmental factors (Scott and Billings [1964](#)), productivity changes may also result from shifts in species relative abundances (Klanderud [2008](#), Kullman [2010](#), Elmendorf et al. [2012a](#), Ernakovich et al. [2014](#)). Compensating species level changes may limit community level productivity responses to climate changes, but yield shifts in community structure (Kikvidze et al. [2005](#), Rammig et al. [2009](#)). For example, if increased temperatures produce a decrease in growing season soil moisture, species or life form groups (e.g., graminoids, succulents) that are more phenologically or physiologically buffered from effects of low soil moisture could exhibit temperature responses that differ from those of less buffered groups. This may diminish the strength of any community-wide signal in ecosystems with high diversity in functional responses (Suding et al. [2008](#)). Such interactions might explain results from previous studies in which tundra communities appeared resistant to warming (e.g., Hudson and Henry [2010](#)). Understanding species and/or life form level responses is also critical to predicting changes in alpine ecosystems via changes in plant traits (Cornwell et al. [2008](#), Eskelinen et al. [2012](#)). Further, individual responses that produce shifts in species relative abundance may be as or more important than overall community responses for animals that depend on alpine plants (Dearing [1996](#), Pettoelli et al. [2007](#), Rubidge et al. [2011](#)).

In this study, we used active infrared heaters to advance snowmelt and increase growing season temperatures, and manual watering to offset the drying effect of warming at Niwot Ridge, Colorado. In this region, where 80% of annual precipitation falls as snow, we hypothesized that alpine community above-ground productivity would increase in response to warming only when combined with supplemental water to limit drying, reflecting measured changes in soil temperature and moisture. We also predicted that changes at the life form level would counteract one another, buffering changes in community productivity. By examining life form responses to both warming and watering, we also expected to determine which life forms are responsive to

direct vs. indirect (e.g., soil drying) effects of climate warming, expecting graminoids, in particular, to be least sensitive to warming-induced drying.

Methods

Study site

Our alpine research site is located at Niwot Ridge in the Front Range in the Colorado Rocky Mountains (40° 3' 14.84" N, 105° 35' 37.71" W; 3540 m), on a 15° south-southeast facing slope 400 m above local treeline. The growing season—often defined by mean monthly air temperatures above 0°C—is short and typically lasts from June through September (Greenland [1989](#)). Climate data have been recorded at the nearby Niwot Ridge LTER Saddle weather station (ca. 500 m away; 3528 m asl). From 1981 to 2008, mean annual air temperature was -2.15°C and mean annual precipitation was 966 mm, with approximately 80% of the precipitation falling as snow (Blanken et al. [2009](#)). Snow depth is spatially variable and controlled by topography and westerly winds (Litaor et al. [2008](#)).

Above-ground primary production at Niwot Ridge is similar to that of other alpine environments and ranges from 100 to 300 g·m⁻²·yr⁻¹ depending on the community (Bowman and Fisk [2001](#)). Spatial variation in productivity across communities at Niwot Ridge appears to be greater than temporal variation within a community (Winkler [2013](#)). Vegetation composition in the study site shares similarities with moist and dry meadow community types (May and Webber [1982](#)) and is best described as a herbfield community (*sensu* Bliss et al. [1981](#)).

Experimental design

We established 20 3 m-diameter experimental plots in 2008 as part of the Alpine Treeline Warming Experiment (ATWE; Fig. [1](#)). We assigned five plots to each of four treatments ($n = 20$): control (C), heated (H), watered (W), and heated and watered (HW), stratifying assignments by local elevation and aspect, as well as total plant cover. Plots spanned a ca. 30 m elevation gradient. The mean local slope of plots was 15%, with a range of 8.5–21.5%. Plots were separated by 2–5 m, with no visible effects of treatments outside of plot perimeters.

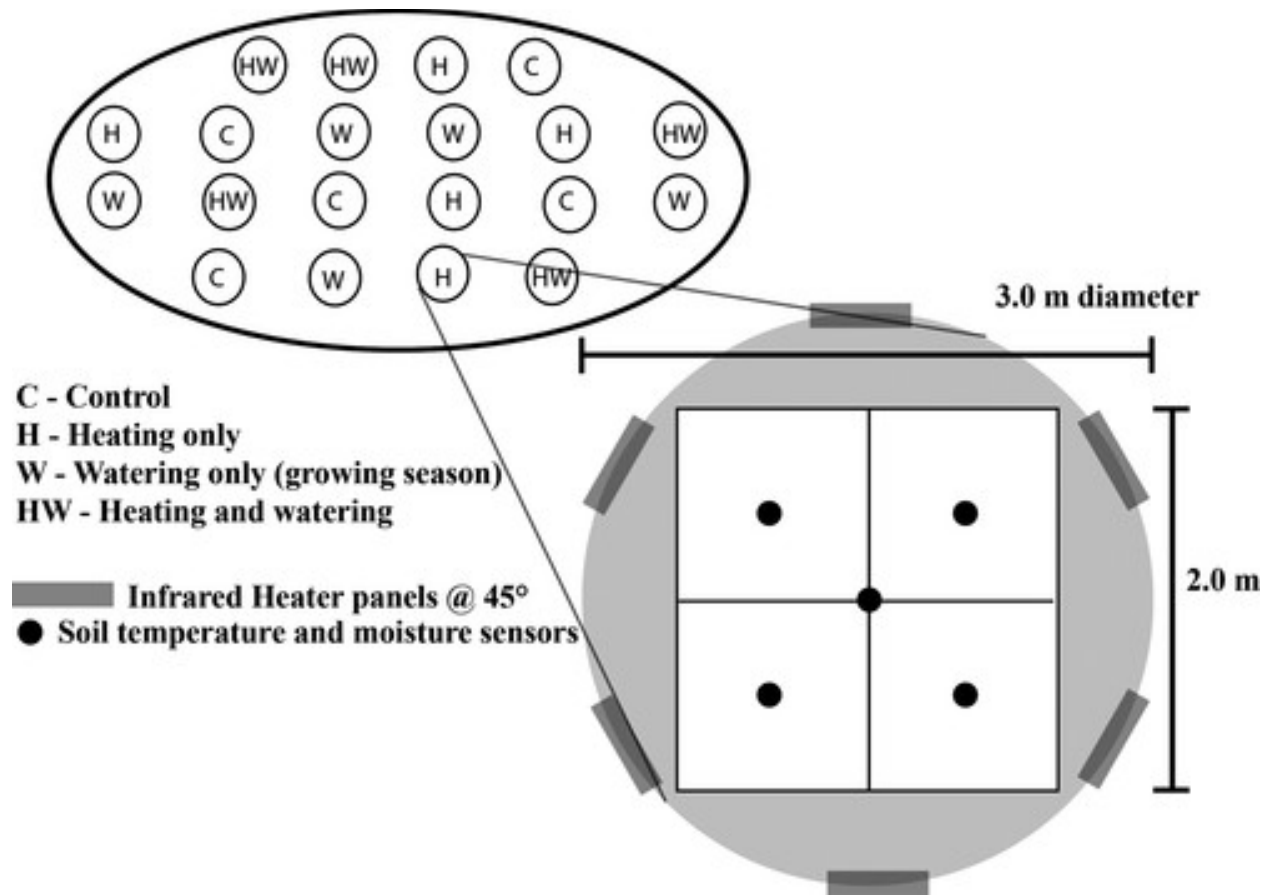


Figure 1

[Open in figure viewer](#) [PowerPoint](#)

Site and plot experimental design. Inset plot represents a heated plot with heater array panels as gray rectangles. Individual quadrats are 1 m² and were surveyed separately. Black circles represent placement of soil temperature and moisture sensors (5–10 cm depth).

[Caption](#)

While most warming experiments have used passive chambers (Elmendorf et al. [2012b](#)), active infrared (IR) heaters have significant methodological advantages, including nighttime warming of plants and soils, maintenance of the natural wind regime, and the ability to modify snowmelt timing, but they do not effectively warm the air (Aronson and McNulty 2009). Six IR heaters (Mor Electric Heating, Comstock Park, MI, USA) were suspended 1.2 m above the ground in hexagonal arrays surrounding heated plots (Kimball et al. [2008](#)). Heaters were turned on in October 2009, and set to deliver 215 W/m² of additional IR with the aim of increasing growing season soil temperatures (infrared radiation influences surfaces and does not directly influence air temperature) by approximately 4–5°C under near-zero wind conditions. Due to hydrological artifacts created by midwinter snowmelt (depressions in the snow refilled by blowing snow), we subsequently adjusted heater output to ca. 42 W/m² in mid-winter (November–February) and to ca. 170 W/m² the rest of the year (March–October) in November 2010. Heaters automatically

turned off at high wind speeds due to low heater efficiency (Kimball et al. [2008](#)). Watering treatments began after snowmelt once the average soil moisture in watered plots dropped to $\sim 0.2 \text{ m}^3/\text{m}^3$ and continued through September. Water addition treatments were achieved manually using garden hose sprayers. We applied 2.5 mm of water weekly to two treatments: HW, to offset soil drying due to heating and W, to examine effects of supplemental growing season moisture on productivity under ambient temperature.

We divided each experimental plot into four 1 m^2 quadrats to assess variation within plots. We recorded soil moisture and temperature every 15 min using a probe (ECTM or 5TM; Decagon Devices, Pullman, WA, USA) at 5–10 cm depth in the center of each quadrat. Soil moisture was recorded as volumetric water content (m^3/m^3), calibrated in the laboratory for dry to saturated conditions. Because snow stabilizes below-ground temperature, we determined the presence of snow on quadrats when days had $\leq 0.5^\circ \text{C}$ diel soil temperature variability (*sensu* Harte and Shaw [1995](#)). Biweekly manual snow surveys were conducted to confirm probe data. Air temperature and wind speed at the site were measured at 2 m height (03101-L; RM Young, Traverse City, MI, USA). Precipitation was measured at a nearby station (NWCC [2014](#)).

Measurements

All environmental variables used in analyses were calculated for each quadrat. We defined the growing season as the time from snowmelt until the end of the snow free period. Soil degree days (growing degree days using soil temperature) were calculated as the sum of mean daily temperatures for days above 0°C between snowmelt and peak aboveground productivity. Adequate soil moisture days were calculated as the total number of days when mean daily $\Theta_v > 0.13 \text{ m}^3/\text{m}^3$. While species differ in their sensitivity to soil moisture, depending on rooting depth and hydraulic traits, 13% volumetric water content corresponded to midday water potentials of about -1.5 MPa for limber pine seedlings growing in our site (Moyes et al. [2013](#)) and also corresponds to decreased daily productivity values in a similar alpine community (Billings and Bliss [1959](#)). For statistical analyses, we divided soil degree days and adequate soil moisture days by the length of the growing season for each quadrat to normalize for variation in growing season length among years.

We conducted vegetation surveys at peak community productivity (determined by weekly inspection of plant phenology in each plot; Negi et al. [1992](#)) during the summer of 2009 (pretreatment) and 2010–2013. 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 cover of all vascular plants

together, and species individually using a 1 m² survey grid divided into 10 cm² units. To determine productivity in experimental plots, we applied regression equations developed using cover estimates and destructive clip harvests in temporary plots. Clip harvests at peak season are a robust method for estimating primary production because all above-ground biomass is produced during the growing season (May and Webber 1982). To relate cover estimates to above-ground productivity, we established temporary 0.25 m² quadrats ($n = 30$) near the experimental plots, within which percent cover of all species was measured as above. Following cover estimation, we harvested all above-ground vascular plant biomass, sorted by species, dried biomass at 60°C for 48 hours, and weighed it. We used linear regressions to convert species level cover to measurements of productivity (Table 1; de Valpine and Harte 2001). We also established seven temporary 1 m² quadrats to test for potential scaling issues and found regressions at the two scales to be comparable (Appendix S1: Table S1). Community and life form level (forb, cushion, graminoid, or succulent) productivity was calculated as the sum of all species-level productivity measurements for species within each group. We included all mat-forming, prostrate forbs and true cushions in the cushion category. Only species whose regressions were significant were used (Table 1). These 20 species accounted for 91% of the cover in the experimental plots.

Table 1. Species list and productivity-cover regressions for species measured in temporary plots (max $n = 37$; actual n varies depending on species presence in plots). Percent values indicate relative contribution of species to life form-level cover and productivity, and life form group to community-level cover and productivity in experimental plots from 2009–2013. Not all species occurred in every plot or every year. All species with a significant ($\alpha = 0.05$) R^2 of at least 0.3 were included in analyses

Species	% Cover	Slope	R^2	n	P	% Productivity
Cushions/Mat-forming forbs	18.27					33.94
<i>Minuartia obtusiloba</i>	10.44	5.76	0.58	26	<0.001	23.65
<i>Silene acaulis</i>	0.88	17.96	0.66	7	0.027	5.74
<i>Sibbaldia procumbens</i>	6.95	1.67	0.91	11	<0.001	4.55

Species	% Cover	Slope	R^2	n	P	% Productivity
Graminoids	11.64					4.05
<i>Carex rupestris</i>	7.34	0.93	0.98	18	<0.001	2.77
<i>Luzula spicata</i>	2.86	0.52	0.83	19	<0.001	0.65
<i>Trisetum spicatum</i>	1.44	1.16	0.35	28	0.001	0.63
Forbs	65.21					58.66
<i>Oreoxis alpina</i>	0.74	1.83	0.95	5	0.004	0.39
<i>Artemisia scopulorum</i>	10.57	1.63	0.94	32	<0.001	7.05
<i>Erigeron simplex</i>	1.14	1.15	0.87	10	<0.001	0.48
<i>Solidago multiradiata</i>	1.38	1.96	0.85	16	<0.001	1.05
<i>Arenaria fendleri</i>	6.03	1.58	0.80	29	<0.001	3.80
<i>Trifolium parryi</i>	7.24	2.10	0.93	25	<0.001	6.16
<i>Lloydia serotina</i>	0.98	1.09	0.80	11	<0.001	0.42

Species	% Cover	Slope	R^2	n	P	% Productivity
<i>Bistorta bistortoides</i>	2.46	1.63	0.95	32	<0.001	1.59
<i>Ranunculus adoneus</i>	1.17	2.52	0.99	3	0.054	1.14
<i>Geum rossii</i>	31.44	2.81	0.95	37	<0.001	35.44
<i>Potentilla diversifolia</i>	2.06	1.37	0.96	24	<0.001	1.14
Succulents	4.86					3.36
<i>Sedum lanceolatum</i>	0.41	2.41	0.58	16	0.001	0.51
<i>Lewisia pygmaea</i>	0.69	0.45	1.00	4	<0.001	0.12
<i>Chionophila jamesii</i>	3.76	1.87	0.82	20	<0.001	2.73

Statistical analyses

We used multi-model comparisons of linear mixed effects models to determine the combination of factors that best predict productivity in our experiment (Aho et al. [2014](#), Barber and Ogle [2014](#), Burnham and Anderson [2014](#)). Our models predicted productivity with heating, watering, and their interaction as main fixed effects, pretreatment (2009) productivity as a covariate to control for preexisting variation across plots, and plot and year as random effects to account for pseudoreplication across quadrats and seasons. We tested for the predictive ability of each main effect by comparing this full model with simpler variants and comparing the change in Akaike Information Criterion corrected for small sample sizes ($\Delta AICc$; Johnson and

Omland [2004](#), Aho et al. [2014](#)). We used ΔAICc to compute Akaike weights (w_i) as a measure of the relative likelihood that a given model is the best of all candidate models. We calculated marginal r^2 to estimate the predictive power of main effects for the best model (*sensu* Nakagawa and Schielzeth [2012](#), Johnson [2014](#)). We used the same approach for each life form group and used slope estimates to identify variation in productivity responses across groups. We used the same approach but with percent cover data in place of productivity to assess the robustness of our findings. Additionally, we compared control plots across years to examine the effects of interannual climate variability on productivity. We also ran full models for each year separately to examine the influence of interannual climate variability on community productivity responses to treatments. Last, we conducted post hoc, one-tailed Wilcoxon tests to confirm that microclimate variables corresponded with expected treatment effects. Models were built using the lme4 package in R (Bates et al. [2013](#), R Core Team [2014](#)).

Results

Community and life form group productivity responses

Community and life form level above-ground productivity were best predicted by the interaction of heating and watering, with pretreatment productivity as a covariate (Table 2, Appendix [S1](#): Tables S2–S5). Main effects in the best models explained 21–53% of the variation in productivity (community $r^2 = 0.32$; forbs $r^2 = 0.39$; cushion $r^2 = 0.53$; succulents $r^2 = 0.21$; graminoids $r^2 = 0.36$). Although there are large standard errors in the estimates of interaction effect sizes, likely due to low statistical power in a variable environment, models with treatments alone or in additive form provided much worse fits to the data (Table 2, Appendix [S1](#): Tables S2–S5).

Table 2. Results of linear mixed effects models predicting community-level, above-ground productivity with heating (H), watering (W), and their interaction as main effects, pretreatment productivity (pre) as a covariate to control for preexisting variation across plots, and plot and year as random effects (Productivity $n = 296$). AICc are Akaike Information Criterion values corrected for small sample sizes. w_i are Akaike weights, which indicate the probability of each model being the best fit relative to others shown

Model	AICc	ΔAICc	k	w_i
H × W + pre	2839.61	0	5	0.93

Model	AICc	Δ AICc	k	w_i
H + W + pre	2845.23	5.62	4	0.06
H × W	2925.05	85.44	4	<0.001
H + W	2931.59	91.98	3	<0.001
W + pre	2849.06	9.45	3	0.008
W	2936.94	97.33	2	<0.001
H + pre	2854.08	14.47	3	<0.001
H	2939.67	100.06	2	<0.001
Pre	2858.15	18.54	1	<0.001
Intercept	3183.42	343.81	1	<0.001

Community level models and slope estimates indicate increases in productivity in response to heating when combined with supplemental water but decreases in productivity with heating alone (Figs 2, 3, Table 3), pointing to co-limitation by both temperature and water. Watering had a larger overall effect on community productivity (Δ AICc = 14.47) than heating (Δ AICc = 9.45; Table 2). Additionally, the effect size of watering on community productivity was nearly three times greater than that of heating (Fig. 2, Table 3); however, the strength of treatment effects and their interaction was not consistent across all life form groups. Forb and succulent productivity

responses to heating were contingent on watering, and the independent effects of the two treatments were balanced. The interaction effect was strongest for forbs, and for both groups, slope estimates suggest that productivity increased with heating only when supplemental water was provided (Fig. 2; Table 3). Conversely, cushion productivity increased with watering and tended to decrease with heating with a weaker negative interaction, indicating an overriding water limitation and negative effect of heating that could not be overcome by the added water (Fig. 2; Table 3). The best graminoid model included an interaction term, and contrary to the other life form groups, productivity tended to increase in response to heating alone (Fig. 2, Appendix S1: Table S5). Nevertheless, forbs accounted for the majority of the biomass produced and drove the community response to heating that was contingent on watering (Table 3), thereby masking the consistently negative response of cushions and positive response of graminoids to heating alone. Cushions appear to have driven the overall positive community response to watering. Statistical results using cover data directly were consistent with those reported for productivity, both at the community level and for individual life forms (Appendix S1: Tables S6–S10).

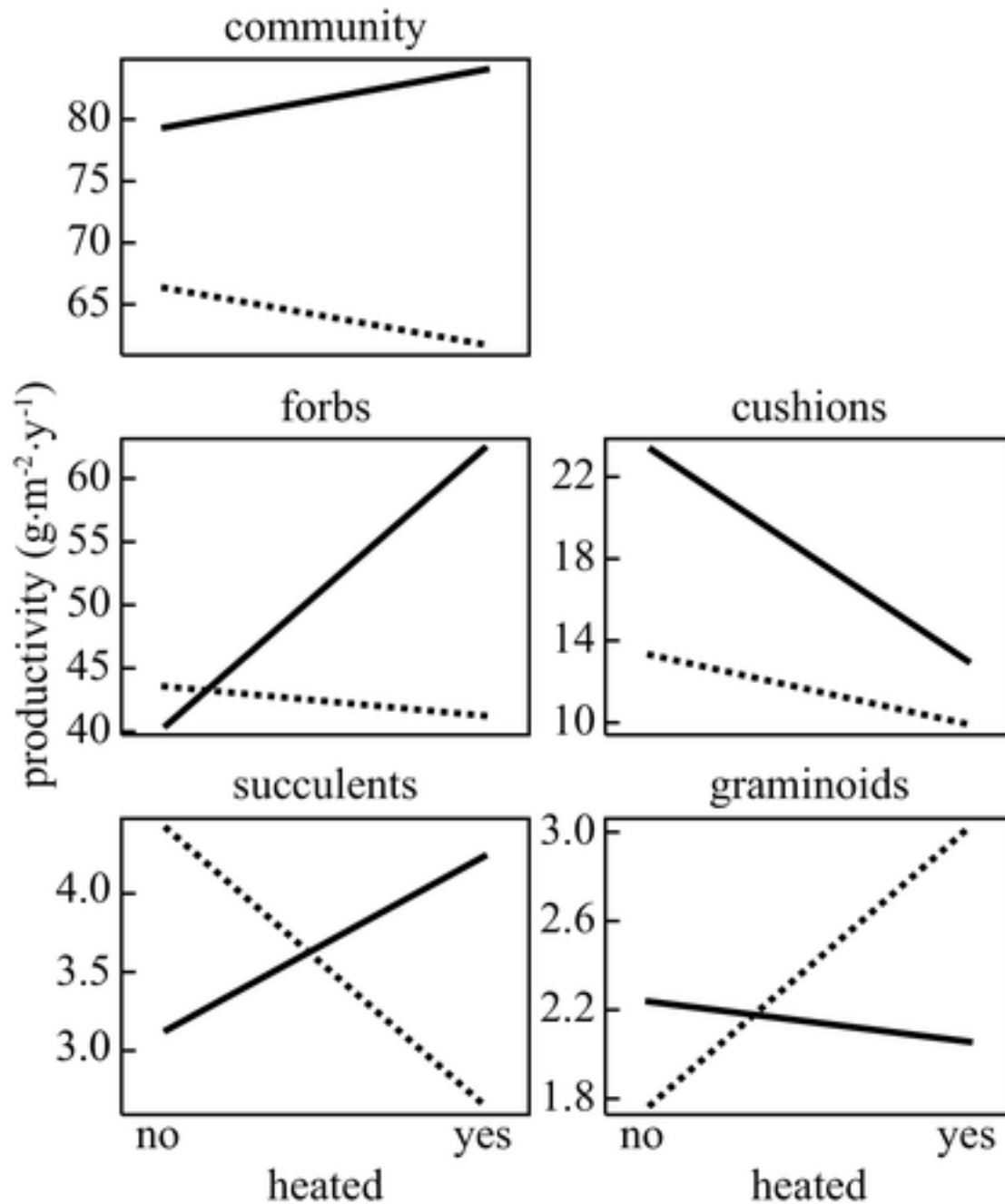


Figure 2

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Interaction plots of community- and life form-level productivity in heated and/or watered treatment groups, with model estimates of productivity on the y-axis ($\text{g}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$) and heating treatment on the x-axis. Model estimates are corrected for random effects and pretreatment productivity. Solid and dashed lines indicate watered and unwatered groups, respectively.

[Caption](#)

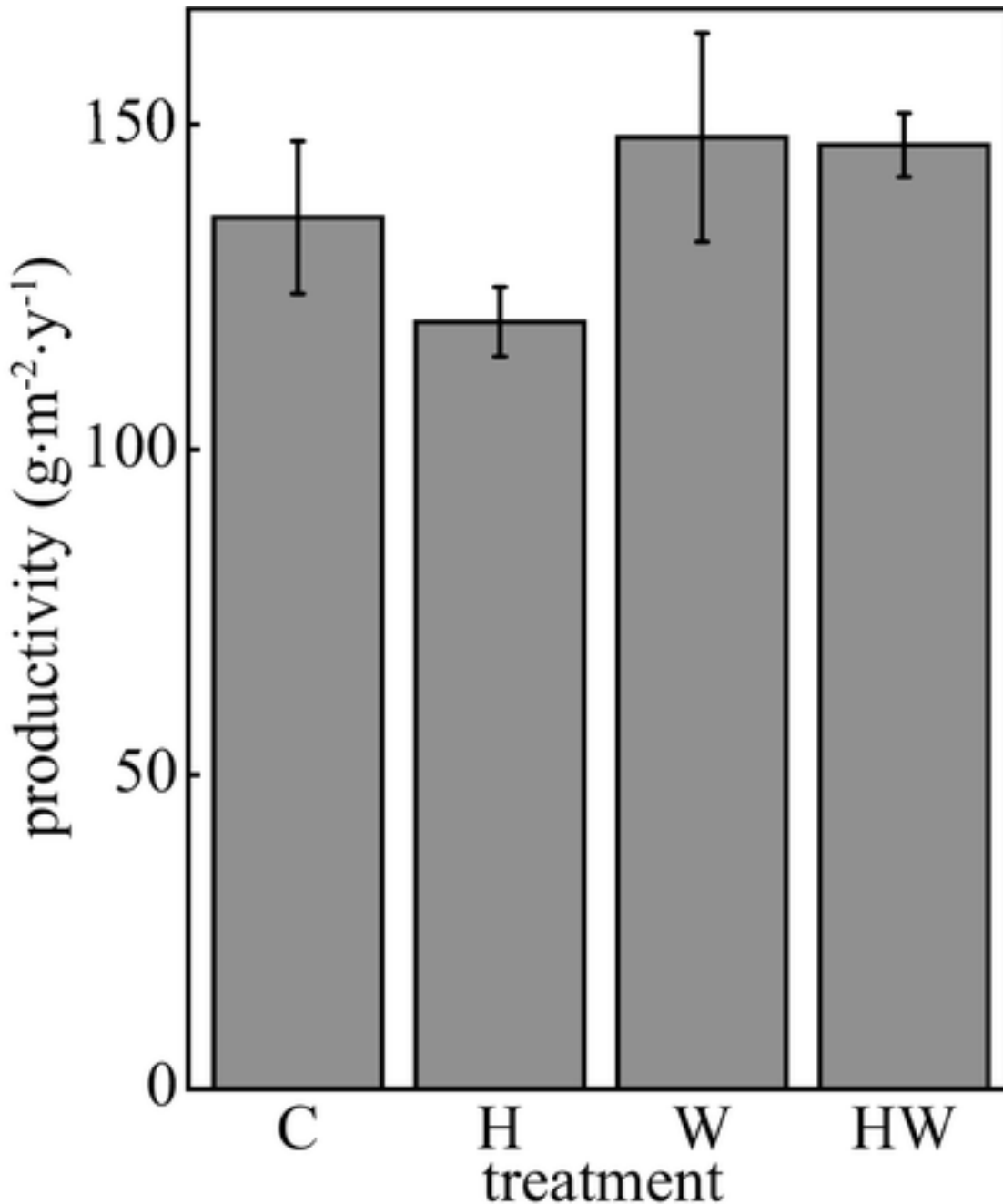


Figure 3

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Observed mean (\pm SEM) community productivity ($\text{g}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$) for 2010–2013 by treatment group. Standard errors were calculated across plot level means ($n = 5$ for each group), which themselves were calculated across years and quadrats.

[Caption](#)

Table 3. Productivity effect sizes (estimates \pm SEM) for heating, watering, and their interaction from linear mixed effects models with plot and year as random effects and controlling for pretreatment productivity. Separate model estimates are presented for the entire community and each life form group across all years of observation

Model	Interaction	Heating	Watering
Community	9.12 ± 15.34	-4.51 ± 10.88	13.1 ± 10.82
Forbs	23.95 ± 13.38	-2.28 ± 9.38	-2.94 ± 9.29
Cushions	-6.92 ± 10.86	-3.35 ± 7.63	10.02 ± 7.64
Succulents	2.84 ± 3.26	-1.74 ± 2.31	-1.27 ± 2.3
Graminoids	-1.41 ± 2.19	1.23 ± 1.55	0.46 ± 1.54

Interannual climate variability had pronounced effects on community productivity (Appendix [S1](#): Fig. S1), and as a result, treatment effects varied among years (Table [4](#)). At the community level, the benefits of watering were most pronounced in 2012 when annual temperatures were highest and precipitation was lowest. Heating effects were most negative in 2011, a year with high spring precipitation and relatively late snowmelt. Last, the productivity response to heating was positive in 2010, the first year of treatment when heaters had the largest effect on timing of snowmelt (Table [4](#), Appendix [S1](#): Table S11). We observed a total of 48 species over the four survey years, but not all species occurred in all plots or years (Appendix [S1](#): Table S12). The mean number of species per 1 m² quadrat was 17.04 ± 0.24 in 2009 before the experiment began and varied from year to year. On average, forbs accounted for 58.7% of the productivity, cushions 33.9%, graminoids 4.1%, and succulents 3.4% (Table [1](#)).

Table 4. Summary of annual climate at Niwot Ridge from 2010–2013 with community productivity effect sizes (estimates ± SEM) for heating, watering, and their interaction from linear mixed effects models with plot as a random effect and controlling for pretreatment productivity. Separate model estimates are presented for each year. Mean annual temperatures (Tmean; °C) and cumulative precipitation (Precip; mm) are reported from a Natural Resource Conservation Service weather station located at Niwot Ridge (<http://www.wcc.nrcs.usda.gov>)

Year	T _{mean} (°C)	Precip (mm)	Interaction	Heating	Watering
2010	2.9	719	14.27 ± 21.28	11.47 ± 15.28	3.22 ± 14.86
2011	2.6	914	13.34 ± 17.71	-18.82 ± 12.75	10.53 ± 12.36
2012	3.8	701	-1.52 ± 17.29	-8.26 ± 12.45	29.17 ± 12.07
2013	2.2	940	14.95 ± 19.97	-4.60 ± 14.35	9.13 ± 13.95

Climate and microclimate responses to manipulations

Community and life form group changes reflect microclimate responses to treatments. Heated plots had greater soil degree days (10.49 ± 0.20 ; $\bar{x} \pm \text{SEM}$) relative to controls (9.98 ± 0.22 ; $W_{146} = 1353$, $P = 0.005$) and watered plots had greater adequate soil moisture days (0.91 ± 0.02) relative to controls (0.88 ± 0.02 ; $W_{150} = 2676$, $P = 0.045$) when controlling for season length. Heated plots that were given supplemental water had greater adequate soil moisture days (0.93 ± 0.01) relative to plots that were only heated (0.91 ± 0.01 ; $W_{594} = 30960$, $P = 0.003$). Heating advanced snowmelt an average of 7.6 ± 0.6 d and heated plots also reached peak productivity 5.4 ± 0.5 d earlier (Appendix [S1](#): Table S11) across the four years of the experiment. Heating did not advance snowmelt the same amount each year due to strong interannual variation in the amount and timing of snowfall, as well as in temperature. The date of snowmelt (for unheated plots) spanned 12–39 d between the earliest and latest date of snowmelt among the plots and varied from 11 May in 2012 to 7 July in 2011, reflecting interannual variation in winter precipitation (Appendix [S1](#): Table S11).

Discussion

Consistent with our hypotheses, our experiment's results suggest that the effects of future, warmer temperatures on alpine productivity are largely contingent upon available growing season soil moisture. Over four years of continuous warming, models predicted that heating and watering interact to affect community productivity and that watering generally increases

productivity. Slope estimates suggest that productivity should decrease with warming alone but increase with warming and additional growing season precipitation, emphasizing the importance of soil moisture to alpine plant responses to climate warming. Models of forb, cushion, and succulent productivity all predicted declines with heating; however models of graminoid productivity predicted increases in the absence of supplemental water. This countervailing graminoid response likely contributed to a more muted community response and highlights the potential for shifts in community composition depending on whether warming is accompanied by additional summer moisture.

Our linear mixed effects model approach allowed us to explore the interactive effects of heating and watering treatments across multiple years and for multiple quadrats within plots. Because we sought to uncover the most parsimonious model form predicting the data, we chose an information theoretic approach over more traditional inference testing (Kenward and Roger [1997](#), Aho et al. [2014](#), Burnham and Anderson [2014](#)). While many effect sizes in the best models had large standard errors, AICc and w_i revealed that heating and watering consistently interacted to jointly affect productivity across all life form groups, as well as for the entire community. Further, we found large positive effects of watering on cushion and community productivity. Therefore, we conclude that growing season moisture will strongly mediate this moist alpine community's responses to warming.

Although most life form groups were consistent with (and indeed, drove) community-level productivity responses, each group's response was distinct. Previous experimental studies that only looked at the effects of increased temperatures showed that graminoids exhibited the largest increase in productivity (Elmendorf et al. [2012b](#)). Our findings of increased graminoid productivity in the absence of watering are consistent and suggest that graminoids may be able to outcompete other life forms in a warmer, drier future, perhaps due to their ability to utilize a longer growing season (Zhang and Welker [1996](#), Arft et al. [1999](#), Klanderud and Totland [2005](#)). In particular, *Carex rupestris* accounts for 68% of the graminoid productivity we measured, is the dominant species in dry meadows at Niwot Ridge, and flowers late in the season when soils are driest (May and Webber [1982](#), Winkler unpublished data). While *C. rupestris* is a relatively shallow-rooted species, it may be able to avoid negative effects of soil drying and/or benefit more strongly from higher temperatures given its relatively conservative gas exchange strategies, a potential indicator of its ability to respond to moisture stress (Bowman et al. [1995](#)). It is possible that *C. rupestris* could replace *Geum rossii*, the dominant forb of Niwot Ridge's alpine, if moist communities become drier. A switch from a forb-dominated community to one dominated by graminoids would likely decelerate nutrient cycling at Niwot Ridge, given that

litter decomposition and productivity would likely decline (Fortunel et al. [2009](#)). Alternatively, graminoids may be less successful than other life form groups in a warmer, wetter future. *Carex rupestris* has been shown to decline sharply when plots became more moist and cooler as a result of increased snow and shorter growing seasons (Scott and Rouse [1995](#)). In our experiment, models predicted much smaller increases in graminoid productivity with supplemental moisture than with heating, suggesting a stronger temperature or growing season limitation for this group. Positive graminoid responses to heating, for example via a longer growing season, may be limited by other species in the community under wetter conditions if competition with more abundant forbs and succulents is enhanced, as suggested by productivity increases in these groups in our experiment.

The best model of cushion productivity indicates a positive effect of watering and negative responses to heating with or without supplemental watering, indicating future climate could negatively affect this life form regardless of changes in growing season precipitation. Cushions, including the mat-forming *Sibbaldia procumbens*, are the dominant life form group in the snow bed communities of Niwot Ridge, and recent evidence has suggested that *S. procumbens*-dominated snow bed communities are highly sensitive to alterations in season length and may decrease productivity in response to future climate conditions (Johnson et al. [2011](#), Spasojevic et al. [2013](#)). Even if additional moisture during the growing season prevents cushions such as *S. procumbens* from experiencing a full seasonal dry-down of soils that is typical of communities at Niwot Ridge (Taylor and Seastedt [1994](#)), warmer temperatures may still drive productivity declines. With our data, we are unable to distinguish whether cushions are more sensitive than other life forms to heating (e.g., exceeding leaf high temperature tolerances; Buchner and Neuner [2003](#)), or if cushion responses were the result of competitive exclusion by other life forms (Kikvidze et al. 2005). Cushion species may also be more sensitive to negative effects of advanced snowmelt, such as increased risk of exposure to suboptimal temperature (Molau [1997](#)) or to earlier soil drying driven by both earlier snowmelt and higher temperature. Some alpine cushion species exhibit strong physiological tolerance to moisture (Terashima et al. [1993](#)) and temperature stress (Kleier and Rundel [2009](#)) but it is possible that our responses are the combined effects of stress and competition with neighboring plants, as well as plants living in between cushion branches (Choler et al. [2001](#)). To distinguish among these potential mechanisms requires additional physiological measurements or removal experiments crossed with climate treatments.

Niwot Ridge receives <25% of total annual precipitation during the growing season (Greenland and Losleben [2001](#)). Mean annual precipitation at Niwot Ridge is similar to that in alpine

“deserts,” including Hawaii's Haleakala and the Chilean Andes (Leuschner and Schulte [1991](#), Rundel [1994](#)). Furthermore, the Chilean Andes have a similar seasonality to Niwot Ridge with most precipitation falling during the winter and relatively little rainfall during the growing season (Cavieres et al. [2006](#)). This is in stark contrast to the European Alps, where average summer precipitation exceeds the total annual precipitation at Niwot Ridge (Beniston [2006](#)), or New Zealand's Southern Alps, where a single rain event can produce more precipitation than Niwot Ridge receives in an entire summer (Henderson and Thompson [1999](#)). Still, precipitation alone does not dictate “dryness” in alpine systems. Instead, climatic water deficits or lack thereof in alpine systems are driven by imbalances between evaporative demand and precipitation (Körner [2003](#)).

Seasonal snowpack depth and the timing of snowmelt at Niwot Ridge largely determine topographic variation in soil moisture, which explains variation in productivity in different plant communities with the earliest melt sites having the highest productivity (Holway and Ward [1965](#), Walker et al. [1993](#), Fisk et al. [1998](#)). However, earlier melt alone may be insufficient to increase productivity in this site if summer precipitation does not subsequently increase to compensate for an earlier summer soil dry down. In this latter scenario of earlier melt and no additional summer rain, early snowmelt alone would simply advance the timing of peak productivity. Summer precipitation can influence alpine productivity both on daily (Billings and Bliss [1959](#), Berdanier and Klein [2011](#)) and seasonal timescales (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 as long as adequate soil moisture for production is maintained, then production continues, but that even a short period of drought has marked effects on productivity. Our results are consistent with these observations: community productivity increases likely occur only in a warmer, wetter future, and decreases should be expected in drier scenarios in spite of the advance in peak productivity driven by earlier snowmelt.

Given the importance of snowmelt timing to initiation of the alpine growing season, the abiotic drivers that plants actually experience during the growing season (e.g., temperature and moisture) should be used to characterize the growing season. Yet, this is often not the case, and instead, abiotic variables are often calculated during a general summer window delineated in months (Bliss [1966](#), Isard [1986](#), Henry and Molau [1997](#), Rammig et al. [2009](#), Elmendorf et al. [2012b](#)), or with daily maximum or minimum temperatures that statistical models select as the most highly correlated with productivity (Kikvidze et al. [2005](#)). These common types of analyses include measurements of abiotic factors after senescence and are not biologically meaningful for explaining peak productivity sampled days or weeks prior. Understanding the

variable responses of alpine plants to climate change requires an understanding of the various biologically meaningful microclimate drivers experienced by plants during the active growing season (Graham et al. [2012](#), Aalto et al. [2013](#), Spasojevic et al. [2013](#)). Thus, we computed microclimate variables directly relevant to plant responses (e.g., considering only temperature observations between snowmelt and peak productivity, and days when moisture levels were above critical values for plant growth; McMaster and Wilhelm [1997](#), Midgley et al. [2002](#)). As expected, heated plots had greater soil degree days and fewer adequate soil moisture days than controls, watered plots had greater adequate soil moisture days than controls, and heated plots that were given supplemental water also had greater adequate soil moisture days than plots that were only heated. It is possible that additional unmeasured effects of heating carried over from prior years or seasons (e.g., through changes in nitrogen availability, date of initial snow accumulation, or below-ground preformed bud development; Blok et al. [2011](#)); however we expect such effects to be second order compared to changes occurring during the growing season.

Interannual variability was a key driver and an important modulator of productivity responses to our treatments. This has been found in previous experiments, both manipulative and observational (Walker et al. [1994](#), Klein et al. [2004](#)). Walker et al. ([1994](#)) found that interannual climate variability explained up to 40% of the observed variation in community biomass produced each year at Niwot Ridge. We also found overall effects of interannual climate variability on alpine productivity, and that interannual differences in treatment effects reflect variation in large-scale abiotic controls (e.g., the timing of snowmelt and summer precipitation) on alpine productivity. For example, in a warm, dry, and early snowmelt year (2012), the benefits of additional summer moisture were strongest, and in a late snowmelt year (2011), the negative effects of heating were strongest.

Contrary to the commonly held expectation that temperature alone limits alpine productivity, available soil moisture largely determines the responses of alpine productivity to warming in our continental, snowmelt-driven site. While alpine sites with consistent summer rain may be more buffered than ours from negative effects of warming, we found that a longer growing season, coupled with more rapid soil drying, results in likely decreases, not increases, in productivity with warming. Our results further suggest that species and life form responses can be distinct and opposite of one another, implying that what may be perceived as community resistance in some instances could actually be community reorganization with potential consequences for ecosystem phenology, nutrient cycling, and biodiversity. Future studies would benefit by considering

changes in productivity at multiple levels of biological organization and under more controlled manipulations so that interactions among climate drivers can be identified.

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